Chapter 1
INTRODUCTION

1.1. Influence of farming and agricultural practices on grassland ecosystems in southern Africa.

Natural grasslands occur where rainfall is intermediate between that of deserts and forests. Large grassland areas occupy the interior of the north American and Eurasian continents and extensive natural grasslands are also located in southern South America, central and southern Africa, and Australia (Odum, 1993). Large herbivores, mostly mammals, are a characteristic feature of grasslands (Odum, 1993). In the past a great diversity of wild herbivore populations used to dominate the South African landscape and the grazers and browsers occurring here maintained a balance in the variety of herbs and woody plants (Downing, 1978). According to Owen-Smith (1989) African savannas have an evolutionary history of high levels of grazing and browsing ungulate herbivory, capable of significantly modifying vegetation structure and composition. During the latter part of the 19th century the wild herbivore populations were replaced as dominants by cattle and sheep. Odum (1993) states that, because grasslands are adapted to heavy energy flow along the grazing food chain, the switch from native grazers to domestic grazers is ecologically sound, but that humans, however, have had a history of misuse of grassland resources by allowing overgrazing and overploughing. The carrying capacity (in biomass kg/ha) of a grassland ecosystem is much higher for wild ungulates (52,5-80,00) than for cattle, sheep and goats (40,7-53,5) (Opperman, 1980). The grassland ecosystems in South Africa can therefore support fewer cattle, sheep and goats than wild herbivores, yet more of these animals are kept in smaller areas than wild herbivores resulting in degradation of the veld. The ratio of domestic grazers to browsers is also higher than for indigenous grazers and browsers and this results in encroachment of woody plants (Trollope, 1975). Teague & Smit (1992) also found that the replacement of grazing herbivores by domestic livestock, mainly cattle, has placed a great deal of pressure on grazing resources and is one of the main reasons for large increases in woody biomass. Preferred grasses are also reduced by cattle and sheep and continuous grazing and overstocking can ultimately reduce even unpalatable grasses to such an extent that inferior forbs become common (Downing, 1978). According to Opperman (1980) the problem with grazing ecosystems in South Africa is that in many cases they are artificial and have to stabilise on different levels needing high energy inputs for maximum productivity. The recycling of minerals has decreased drastically due to total utilisation practices by farmers and mineral supplementation costs farmers millions annually (Opperman, 1980). Due to wrong management practices microclimatic conditions have changed resulting in slow recovery of veld (Opperman, 1980). Danckwerts & Stuart-Hill (1988) attribute the slower rate of recovery on grazed than on ungrazed veld to the effect grazing has on seedling establishment and tuft regeneration from a limited number of secondary tillers. The botanical diversity of old grasslands is also often reduced by replacing the lands with grass leys or by treating them with selective herbicides and fertilizers, resulting in a habitat that does not contain some of the basic requirements essential for many species (Goudie, 1990). Grazing also damages soil structure through trampling and compaction. Heavily grazed lands have a lower infiltration capacity than ungrazed lands and the removal of vegetation cover and associated litter also changes infiltration capacity (Goudie, 1990). According to Skinner (1981) semi-arid grassveld is particularly susceptible to drought. Opperman (1980) states that 64% of South Africa's natural grazing receives less than 500mm rain per year and is therefore susceptible to drought. Replacement of wild herbivores with cattle, goats and sheep therefore places further stress on an already stressed ecosystem. According to Eckholm (1985) 12 million hectares world-wide deteriorate each year to a point where they are agriculturally worthless, 40 percent are rainfed croplands that lose topsoil and nutrient stocks and the rest are rangelands, which, through over-grazing, suffer erosion and a shift in vegetation from nutritious grasses to weeds. This results in many grasslands becoming human-made deserts, thus stressing the importance of ecological indicators in the early detection of overgrazing. Were these lands to continue to support agriculture, their output could be worth at least $20 billion a year (Eckholm, 1985).

Insects are severely influenced by the misuse of land. According to Samways (1994) several thousands of species extinctions can be expected world-wide by the year 2000 as a result of habitat loss and modification A disturbance can be seen as an event which disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment (White & Pickett, 1985). Reduction in species and genetic diversity resulting from human activities will influence the future adaptability of species in both natural ecosystems and agroecosystems (Odum, 1983). Fences do not limit insects, but they are limited by the habitat. Insects are able to adapt to small environmental changes, but it is the major disturbances such as ploughing, heavy grazing, fertilising plots and recreational pressure that contribute to declining population levels and eventual loss of the local insect populations (Fry & Lonsdale, 1991). Insects can survive in the most intensively farmed landscapes and a major aim of conservationists is to enhance, perpetuate and improve this survival (Collins & Thomas, 1990).

1.2. The dung beetle assemblage

Dung beetles are essential for the correct functioning of any grazing ecosystem. Dung serves as food for adult dung beetles and their immature stages. The two main types of food resource used by dung beetles are large herbivore dung and omnivore dung (Hanski & Cambefort, 1991a), while relatively few dung beetles are attracted to carnivore dung (Hanski, 1987a). Some species feed within the dung mass, while others feed on buried dung. Three distinct groups of dung beetles are recognised according to their habits of food manipulation. Telecoprids form dung into balls and remove the ball from the dung pat, paracoprids bury the dung underneath the dung pat and endocoprids feed on the dung and complete their life-cycle inside the dung pat. The size and dung burial behaviour of dung beetles are important determinants of their capacity to compete for dung and Doube (1990) used these determinants to further divide groups of species with similar habits into separate functional groups. The large telocoprid dung beetles represent FG I, the small telocoprid dung beetles FG II, the fast burying paracoprid dung beetles FG III, the large slow burying paracoprid dung beetles FG IV, the small slow burying paracoprid dung beetles FG V, the kleptocoprid dung beetles FG VI and the endocoprid dung beetles are represented by FG VII.

There are three basic "niche dimensions" for dung beetles, namely space, food and time (Christiansen & Fenchel, 1977). Giller & Doube (1994) found that different dung beetle species differ in their behavioural responses to environmental conditions. Some species show a high degree of habitat specificity, while others are much more widespread. Certain dung beetle species will quickly adapt to a new environment and become dominant, while those with low dispersal ability and adaptability will not be able to survive in a changing environment. Species may be represented in small local populations, but be well distributed on a local scale, because their environmental tolerance allows them to colonise all the dung pats in a particular area despite environmental differences. Species found with greatest frequency in dung pats are those with a greater ecological capacity, not those with the highest abundance (Lobo, 1993). According to Hanski & Cambefort (1991a) the large African tunneling beetles have low rates of dispersal compared to the many smaller species. This may result in communities where the large tunneling beetles are excluded in changed environments, while smaller paracoprids and endocoprids become dominant because of better dispersal abilities. Competition for dung appears to play a major role in structuring communities dominated by FG I and FG II (Giller & Doube, 1989). Competition is, however, not a limiting factor in other communities where dung is not limiting and FG V and FG VI are major elements. As the community structure changes with a changing environment the ability of the dung beetle community to remove dung efficiently will also change. According to Doube (1990) the potential of dung beetles to remove dung varies markedly between functional groups.

Succession in coprophages is a typical example of heterotropic succession (Koskela & Hanski, 1977). The energy sources available to the animals are largest at the beginning and decrease continually. Flight activity of dung beetles begins at different times depending on the species. This results in a succession pattern of species colonising the dung depending on the time the dung is deposited and also on the habitat in which the dung is dropped

(Fincher *et al.*, 1971). Environmental changes seem to play an important role in the succession of dung beetles. Valiela (1974) found that during succession, neither food limitation nor predation appeared to be limiting to dung beetles, but that local alterations in the environment and in the dung itself, however, may influence the succession in a dung pat. According to Koskela & Hanski (1977) the variation in the early successional stages among dung beetles is mainly due to macrohabitat differences.

The quality of dung might also have a significant influence on dung beetle assemblages. Edwards (1991) found that dung quality can produce a 100-fold change in the reproductive rate of dung beetles. This indicates that it is potentially a major variable in the population dynamics of species. With the changes in the environment caused by farming it was important for dung beetles to adapt to a new dung type. In many areas of Africa, many herds of game animals have been exterminated by man, but many species of dung beetles are still abundant because they have adapted to the dung of introduced animals (Bornemissza, 1960).

1.3. Influence of habitat on dung beetle assemblages

In South Africa there are 780 species of dung beetles plus approximately 60 species of dung dwelling Aphodiinae (Doube, 1991) currently known. There is considerable specialisation, particularly amongst African dung beetles, along a variety of environmental niche axes (Hanski & Cambefort, 1991a). There are several factors influencing the presence or absence of dung beetle species in an area. Of all the factors the habitat structure seems to be the most important. According to Mohr (1943) the environment in which dung is dropped has a profound effect on the composition of its dung fauna. More specifically, it would seem that vegetational ground cover and soil type have the most important effect on habitat preference of dung beetles (Hallfter & Matthews, 1966; Fincher *et al.*, 1970; Howden & Nealis, 1975; Hanski & Koskela, 1977; Nealis, 1977; Doube, 1983; Janzen, 1983; Davis *et al.*, 1988). Davis *et al.* (1988) found that 32 of the 46 species and species complexes he studied showed significant associations with either vegetative cover, soil type or both. In this context, Doube (1991) found that the relative abundance of species changed across vegetational boundaries, where, in Mkuzi Game Reserve, many species showed a preference for either grassveld or bushveld. Here there was no important variation in habitat parameters other than vegetation cover. Thus overall, the habitat affects the microclimatic conditions of the dung, which in turn influences the dung beetle community colonising the dung. Jameson (1989) compared diversity of coprophagous Scarabaeidae in grazed and ungrazed Sandhills Prairie in Western Nebraska. She found that key elements of microclimate (wind, sun, soil, plant cover, humidity and precipitation) influenced the quality, availability and malleability of the dung as a nutritional resource for dung-feeding scarabs. Doube (1983) found that some species are characterised by preferences for habitat of particular light intensities. Natural dispersal of these species will occur through connecting corridors of bushveld. This may pose problems for dispersal. Changes in the environment might have an influence on certain species. The biomass of large telocoprids is greater in regions of grassveld within a bush-grass mosaic than in areas of extensive grassveld, which may be related to the dung and microhabitat requirements of breeding beetles. *Kheper nigroaeneus* uses many types of dung, which it buries in soft soil. This species is abundant in Mkuzi Game Reserve, but scarce in the surrounding pastoral regions, irrespective of soil type (Doube, 1991).

The environmental change created by man in his destruction of grasslands also affects the dung beetles through changes in the species and numbers of food-producing vertebrate animals (Fincher, *et al.*, 1970). It is thus clear from observations by several authors that habitat seems to be one of the most important factors influencing the structuring in dung beetle assemblages. It can therefore be assumed that the influence of man by changing the habitat through farming and agriculture will also have an important influence on dung beetle assemblages.

1.4. Importance of dung beetles in a grazing ecosystem

Dung beetles evolved together with large grazers and browsers, exploiting an important niche within the grasslands. An indispensable condition for the correct functioning of all pasture ecosystems is that the dung be rapidly utilised and transformed (Galante *et. al.*, 1991). Dung beetles play a very important role in grazing ecosystems. They form a part of a lengthy food-chain which starts with the assimilation of energy from the sun in plants used by grazing animals. The viability of every pasture ecosystem is based on the normal functioning of its nutrient cycle. Different components, including the grazing animal, play a role to keep the system running productively (Bornemissza, 1960). The malfunction or disappearance of any of the components in the grazing ecosystem or the invasion of external elements in the system could lead to serious repercussions. A sign of a grazing ecosystem functioning improperly is accumulation of dung. This happens in the absence of a viable dung beetle population or when the existing dung beetle population cannot cope with the large amounts of dung. According to Waterhouse (1974) dung deposited on the soil can eventually cause serious damage because it deteriorates the pastureland by preventing plant growth. It also causes the loss of nitrogen by, which then cannot be incorporated into the soil and other nutrients are tied up in the deposits for several months or years and are unavailable for plant growth (Fincher, 1981). The substantial amounts of nutrients that are contained in cattle dung can potentially be recycled back to the soil in an available form. Fincher (1981) states that the accumulation of dung in a pasture takes many hectares of pasture out of production by smothering the herbage under each deposit and by creating areas of rank growth around each deposit that is not normally grazed by cattle. According to Bornemissza (1960) undegraded cattle dung from five cows would decrease the effective area of pasture by one acre over a period of a year. Jones & Ratcliff (1983) found that dung pats were a source of patchiness in pastures and that the proportion of a pasture where grazing is reduced due to deposition of dung pats is much greater than the area of pasture physically covered by dung pats. Furthermore, reduced grazing on areas affected by dung increases grazing pressure on the remaining area. Shifting patterns of grazing pressure, following the deposition of dung pats, have the potential to affect botanical composition on the micro scale and, consequently, at the paddock level (Jones & Ratcliff, 1983). There is an impression that this problem can be overcome successfully under conditions of intensive grassland management, *i.e.* where high rates of fertiliser N are applied and the rate of stocking is high, but Castle & MacDaid (1972) found that the level of fertiliser N applied to the grazing sward had no direct effect on the rate of breakdown of dung. This problem can, however, be solved when there is a dung beetle assemblage able to successfully break down the dung. According to Gillard (1967) 80% of the nitrogen content is lost when cattle dung remains on the surface until it is dry, but when adequate numbers of dung beetles are present and bury the dung the nitrogen loss is reduced to 5-15%. According to Jenkinson (1988) soil microbial biomass plays a key role in nutrient transformations in soil and largely controls the rate at which C, N and other nutrients cycle through the agricultural ecosystem. Addition of mineral nutrients alone may not have marked effects on soil microbial biomass, whereas incorporation of mobile organic materials from dung may cause changes by providing readily-available energy sources and substrates for metabolism (Lovell & Jarvis, 1996). Lovell & Jarvis (1996) found that complete mixing of finely-chopped dung with soil had a major impact on both the size and activity of the soil microbial biomass, whereas the slow breakdown and release of nutrients from dung pats did not. By breaking down the dung, dung beetles therefore play a key role in increased size and activity of soil microbial biomass and ultimately in the increased rate of C, N and other nutrient cycling.

In addition to playing a key role in nutrient cycling dung beetles also act as biological control agents for nematode parasites of cattle and sheep (Miller, 1961; Fincher, 1973; Bergstrom *et al.*, 1976; Gormally, 1993) and dung breeding flies (Hughes *et al.*, 1978; Moon *et al.*, 1980; Ridsdill-Smith, 1981; Fay & Doube, 1983; Walker & Doube, 1984; Ridsdill-Smith & Hayles, 1987; Doube *et al.*, 1988; Fay *et al.*, 1990; Kirk, 1992; Peitzmeier *et al.*, 1992; Davis, 1994). Communities rich in dung beetles that are able to degrade cattle dung efficiently are therefore of great economic importance.

1.5. Research plan and hypothesis

In view of the important role that dung beetles play in grazing ecosystems the main aim of this study was to determine whether disturbance in a habitat caused by human activities, such as farming, has an effect on the dung beetle assemblages in these habitats. Behavioural factors such as succession, diel flight activity, aggregation and dung preferences influence the success of certain dung beetle species in an assemblage. Seasonal affects are also important to the behaviour of dung beetle species. All these factors were taken into account in the different natural and disturbed habitats.
The following hypotheses were tested:

i) Will natural veld support a different assemblage of dung beetles to disturbed farms? The changes in habitat caused by farming will possibly have an effect on the dung beetle assemblage. Domestic cattle exert constant forces in a limited area, thus possibly degrading potential habitat for dung burying beetles.

ii) Will there be a difference in the assemblage of dung beetles between different habitats in natural veld (grassveld and bushveld)? Different species are adapted to different environments resulting in some species being more successful in certain habitats than others, consequently affecting the community structure.

iii) Will decomposition of dung differ in the different habitats? The most important factor influencing the decomposition of dung is probably the dung insects colonising it and disturbing it by their feeding activity. The influence which disturbance of a habitat has on dung beetle assemblages will therefore also affect the decomposition of dung in this habitat.

iv) Will some habitats be more easily disturbed than others?

This study will enable us to identify certain key factors influencing dung beetle assemblages. Changes in a dung beetle community, which may act as an early indication of habitat degradation, might also be identified. This will enable us to make predictions and recommendations on veld management.