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CHAPTER 9

MODEL AND CONCLUDING REMARKS

9.1. INTRODUCTION

The need to formulate general rules in complex systems in ecology often result in the construction of qualitative, mathematical or graphical models. According to Price (1984) a model should represent a simplified view of the system being modeled, and yet capture the essence of the system such that the model has explanatory and predictive power. According to Begon *et al.* (1995) there are four reasons for constructing a model.

i) Models bring together in terms of a few parameters, the important, shared properties of unique examples.

ii) Models force us to try to extract the essentials from complex systems. If each example can be expressed in a common language, then their properties relative to one another will be more apparent.

iii) Models can provide a standard of idealized behaviour against which reality can be judged and measured.

iv) Models can shed light on the real world.

These four reasons for constructing models are also criteria by which any model should be judged. A model will only be useful if it performs one or more of these four functions (Begon *et al.* 1995).

After a series of life tables has been developed, covering a wide range of conditions, it is likely that one or two key variables will be revealed that are mainly responsible for population changes. According to Price (1984) the basis for understanding the population dynamics of any organism lies in the identification of these key factors.

According to Dempster (1991) the largest single cause of changes in the distribution and abundance of insects in Britain over the past 50-100 years is loss of habitat resulting from changing land use. Humans tend to create a patchy landscape of numerous ecosystem types ranging from crop monocultures to botanical gardens (Odum, 1993). Environmental resource patches are patches of vegetation left behind despite environmental change and these are important refugia for many insects (Samways, 1994). In a patchy landscape, patch size is an important factor in determining what species of animals are able to survive. A patchy landscape would not necessarily result in a decrease of diversity because there are a host of rare species, which are able to adapt to new conditions in these habitat patches. These edge species can adapt to changed conditions and become abundant in the absence of dominant species. According to Samways (1994) the disturbed landscape, if not too severe to cause deterministic extinction, will set in motion a chain of events that may lead to at least increased extinction risks. For insects, with their small size and generally high susceptibility to adverse environmental influences, it is the fragmentation of the population and decrease in abundance in the population, making it vulnerable to further disturbances, that is significant. Farmers control most of the land which act as matrix for nature reserves and provides good insect habitat and potential corridors (Moore, 1991). Pastoralism is not new and grazing both by domestic cattle and indigenous megaherbivores has continued side by side for centuries. Many grassland insect species have adapted and diversified under these conditions. It is, however, major disturbances such as ploughing and heavy overgrazing that leads to declining population levels and a loss of insect populations (Samways, 1994).

An ecosystem is composed of many individuals interacting among themselves and with their physical environment. Preservation of varying and overlapping ecosystems is necessary because insect species and other biota are an intrinsic part of it (Samways, 1994). Dung beetle assemblages are important for the successful functioning of any grazing ecosystem. Continued adverse environmental disturbances caused by farming activities such as overgrazing have placed stress on dung beetle assemblages on farms. These disturbances have influenced the dung beetle assemblages on farms in such a way that their ecological role in the grazing ecosystem has been affected. It is therefore important to determine the key variables responsible for these changes, species influenced and to construct a simple model to describe the most important factors influencing dung beetle assemblages and to shed some light on changes in these assemblages. This will enable us to make predictions and recommendations to farmers and managers of nature reserves.

9.2 Factors influencing the success of dung beetle assemblages in a grazing ecosystem

Ecosystems are complex, gradually changing over time and subject to many abiotic and biotic influences. Change in an ecosystem is one of the most obvious attributes, particularly in vegetational attributes, but also in the kinds of animals that reside in the ecosystem. Usher & Jefferson (1991) consider the process of ecological succession the single most important factor causing change in an arthropod community. Ecological succession is usually predictable and directional so that a pattern of change can be observed (Price, 1984). The dung beetle assemblages at Sandveld nature reserve and on the neighbouring farms are subject to many natural changes over time. These changes can be both allogenic (external) and autogenic (internal) (Fig. 9.1). Odum (1993) proposed a general systems model of succession where the internal or autogenic inputs and the periodic external allogenic inputs both affect the progress of a system developing toward climax. The autogenic forces tend to drive the system toward equilibrium, while strong allogenic inputs tend to disrupt progress toward equilibrium and set back the succession to a younger stage (Odum 1993). Begon, *et al.* (1995) distinguishes between successions that occur as a result of biological processes that modify conditions and resources (autogenic successions) and successions occurring as a result of external forces (allogenic successions). Natural allogenic changes are periodic and dung beetle assemblages can continue to exist without severe changes to the assemblage. Many insect populations show quick recovery from naturally adverse conditions, but it is when conditions are severe and prolonged that populations begin to fragment (Samways, 1994). Situations created by human impacts such as overgrazing is often severe and prolonged.

There are many variables to consider when looking at the success of a dung beetle assemblage in an ecosystem (Fig. 9.1):

Allogenic factors

The allogenic variables influencing dung beetle assemblages in an ecosystem are: the human impact, season and habitat.

***Human impact:**

According to Goudie (1990) humankind has possibly had a greater influence on vegetation than on any of the other components of the environment. Through inducing vegetation change, whole landscapes have been transformed. Human induced changes such as overgrazing, trampling of vegetation and fragmentation of habitats transform the microhabitat (Fig. 9.1). These microhabitat changes can have severe effects on the dung beetle assemblages. Degradation of vegetational ground cover will influence the cover for dung beetles and trampling will affect the breeding space in the soil. Fragmentation will isolate dung beetle assemblages increasing the chances for extinction.

***Season:**

Seasonal variables, which have the greatest influence on dung beetle assemblages, are temperature and rainfall. Increased temperatures and higher rainfall will be favourable for dung beetle assemblages. There is, however an upper threshold, with too high temperatures and rainfall having a negative effect on the dung beetle assemblages. The study area is an unpredictable habitat with wet and dry seasons of varying length, and downpours alternating with extended periods of drought (Chapter 2). Dung beetles in the study area seemed to be adapted to arid conditions and high temperatures. Temperature seemed to be a key factor in the distribution of dung beetle assemblages, while rainfall was less important (Chapter 4). Dung beetle assemblages were able to survive adverse seasonal periods of low temperatures, high temperatures and drought, because these periods were periodic and assemblages recovered quickly afterwards.

Seasonal changes have an indirect influence on the dung beetle assemblages by causing changes in the habitat (Fig. 9.1). Changes in temperature and rainfall will cause changes in the vegetational ground cover. These, in turn, will influence the composition of the dung beetle assemblage (Fig. 9.1). Seasonal changes influences the dung beetle assemblages directly with temperature, rainfall and length of day influencing the succession, diel, aggregation and dung preferences of dung beetles (Fig. 9.1).

***Habitat:**

Both seasonal and human impacts have a great influence on the habitat (Fig. 9.1). It appears that drought is a normal phenomena in the study area (Chapter 2). According to Skinner (1981) semi-arid grassveld is particularly susceptible to drought. Seasonal impacts on the habitat are periodic and the habitat is able to recover after periods of drought. It is the human impact, however, that has the greatest influence on the condition of the veld. Danckwerts & Stuart-Hill (1988) found a slower rate of recovery on grazed than on ungrazed veld and attribute this to the ill-effect grazing had on seedling establishment and tuft regeneration from a limited number of secondary tillers. Veld condition is primarily related to its ecological status such as succession stage, species composition and cover density (Nel, 1991). The veld in the disturbed habitat on the farm Rietvlei in the study area is still in a pioneer stage, while the veld in the nature reserve is in subclimax (Table 2.1, Chapter 2). The basal cover and relative veld condition is also much lower on the farm than in the nature reserve (Table 2.1, Chapter 2). Without human impact plants will be able to survive periodic adverse seasonal impacts. Combined seasonal and human impacts, however, can be detrimental to plant cover. Excessive trampling when conditions are dry will reduce the size of soil aggregates and plant litter to a point where they are subject to aeolian deflational processes and heavy grazing can kill plants or lead to a marked reduction in their level of photosynthesis (Goudie, 1990). A change in vegetation caused by heavy grazing and the soil caused by trampling will influence the composition of the dung beetle assemblage in this habitat by determining the size and competitive ability of the dominant species (Fig. 9.1). This in turn will influence processes in the dung beetle assemblage such as succession in the dung, diel flight during a 24-hour period, interspecific and intraspecific aggregation of species and individuals and the dung preferences of the dung beetles (Fig. 9.1). These processes will in turn influence the recycling of dung in a habitat. The size and competitive ability of the dominant species will determine the rate and amount of dung removed. The success of the dung beetle assemblage will ultimately determine the success of the habitat by improving the recycling of nutrients (Fig. 9.1). Dung decomposition has been widely associated with inprovement in soil fertility (Petersen, *et al.*, 1956; Dickinson *et al.*, 1981; Omaliko, 1984; Herrick & Lal, 1996; Lovell & Jarvis, 1996). Herrick & Lal (1996) found that processes associated with dung decomposition play a role in reducing surface compaction by increasing the volume of soil macropores and that these changes appear to be tied to macroinvertebrate activity. According to Lovell & Jarvis (1996) the substantial amounts of nutrients that are contained in cattle dung can potentially be recycled back to the soil in an available form. Fast breakdown and mixing of dung with the soil increases the size and the activity of the soil microbial biomass, whereas slow breakdown and release of nutrients from dung pats does not (Lovell & Jarvis, 1996). Fast breakdown of dung by dung beetles will therefore release nutrients back into the soil, improving the plant growth, before it is lost. In a system where recycling of dung is ineffective undegraded dung will accumulate in the environment, with little nutrients being released back into the soil. 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 volatilization, which then cannot be incorporated into the soil.

Autogenic factors:

Dung beetles do not divide resources along one resource dimension at one time but, like the populations of most animals and plants, populations of dung beetles are affected by several dimensions simultaneously (Hanski & Cambefort, 1991a). There are many biological and behavioral differences between co-occurring species within a dung beetle assemblage, which influences the interactions within the assemblage and which may facilitate co-existence. There are differences in the type of dung used and how it is used;

succession in the dung differs in terms of the age of dung colonized by different species and functional groups; there are differences in diel activity of different species during a 24-hour period and habitat selection at small and large spatial scales differ. All these processes are interrelated and a change along one resource dimension might result in changes in the others (Fig. 9.1). These processes are also influenced by outside factors such as the season (Fig. 9.1). The season also influences the composition of dung beetle assemblages and subsequently succession, diel, aggregation and dung preference. The habitat and the human impact, by influencing the habitat, will also influence these activities (Fig. 9.1).

***Succession:**

Both the season and the habitat in which the dung was dropped had a strong influence on the succession of dung beetles in the dung (Fig. 9.1). Maximum species richness, biomass and number of individuals of dung beetles were reached earlier in summer. Dung beetles also stayed in the dung for longer periods during the colder seasons (Chapter 6). By influencing the habitat the human impact also influenced the succession of dung beetles. The maximum species richness, biomass and number of individuals were reached earlier in the natural habitats (Chapter 6). Species generally colonized fresher dung in the natural grassveld habitat and stayed in the dung for shorter periods than in the disturbed grassveld habitats (Chapter 6). The rate of change in succession was also more rapid in the natural habitats (Chapter 6). The habitat determines the size and competitive ability of the dominant species and this will in turn influence the succession. Larger dung beetles belonging to FG I and II were more abundant in the natural grassveld habitat and this resulted in earlier colonisation of dung by other species to ensure a part of the resource. The abundance of larger dung beetles in the natural habitat will also result in a larger amount of dung buried within a shorter time (Fig. 9.1).

***Diel activity:**

Although many species had specific flight times, because of specific physiological adaptations, there were minor changes influenced by season and habitat. Activity periods for the community as a whole were shorter during autumn and spring and also occurred later in the morning and earlier in the afternoon during these seasons (Chapter 5). The habitat influenced the diel activity of larger dung beetle species, whose activity periods were longer in the natural habitats, while smaller species had longer diel flight activity in the disturbed habitats (Chapter 5). Dung degradation would therefore be more effective throughout a 24-our hour period in the natural habitat.

***Aggregation:**

The habitat had a very important influence on the aggregation of dung beetle species. In the natural grassveld habitat the larger superior competitors showed a lower level of intraspecific aggregation, while in the disturbed grassveld habitat these competitors were more aggregated intraspcifically and there was also stronger interspecific aggregation (Chapter 8). In the natural grassveld habitat aggregation decreased with increasing size and in the disturbed grassveld habitat increased with increasing size (Chapter 8).

***Dung preferences:**

Although dung beetles showed preferences for certain dung types this did not reflect association with a particular habitat. Dung beetles seem to be very adaptable and will colonize the most favourable dung type when it is available (Chapter 7).

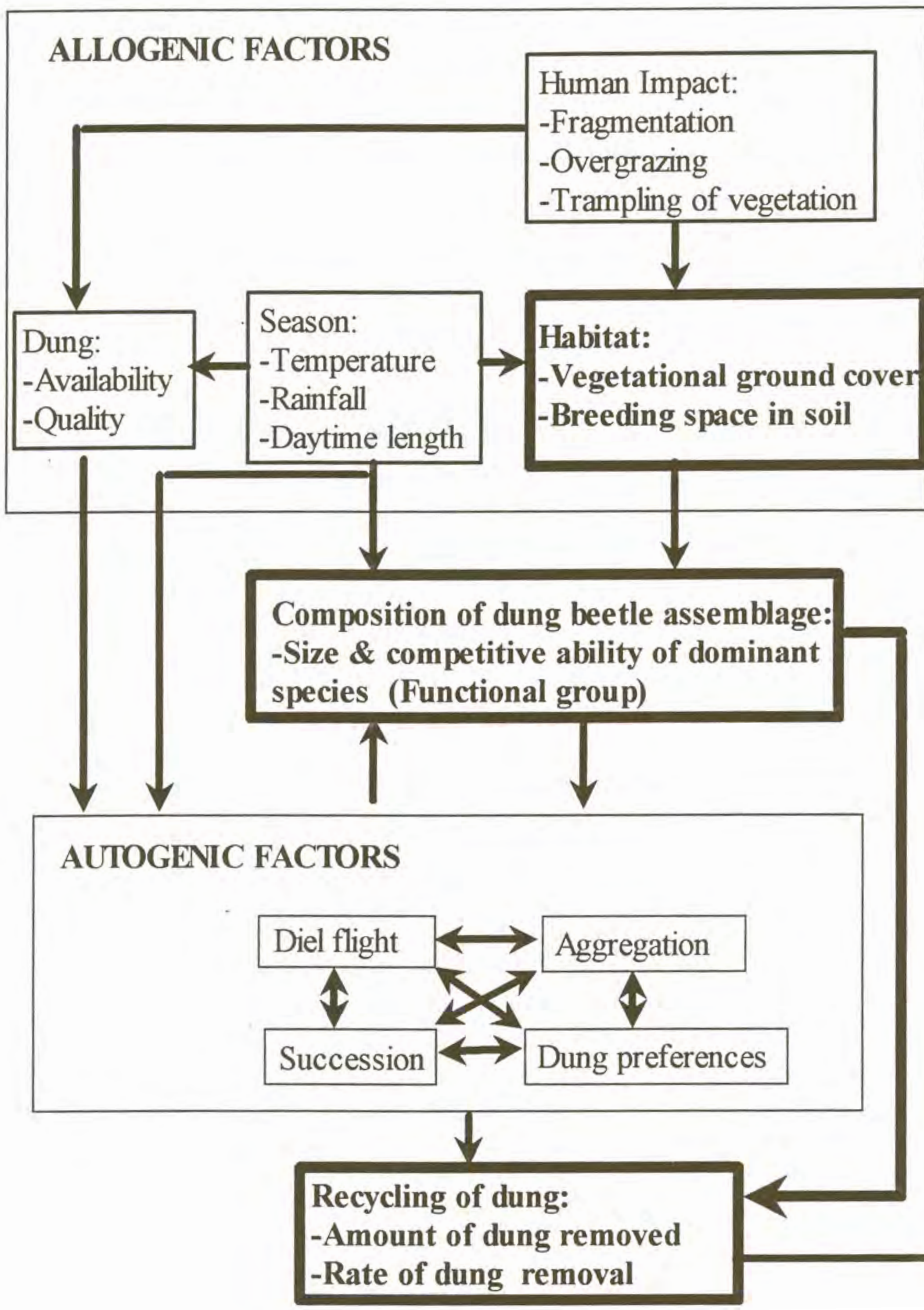

Fig. 9.1: Autogenic and allogenic factors influencing the success of a dung beetle assemblage in a grazing ecosystem

9.3. The importance of size in a dung beetle assemblage

The key factors in these dung beetle assemblages seem to be the habitat and size of the dominant species within this habitat. The size and competitive ability of the dominant species influences the succession, diel activity and aggregation in a dung beetle assemblage. This in turn will influence the rate of dung decomposition in a habitat. Human impact on a habitat such as overgrazing and trampling influences the composition of the dung beetle assemblage in this habitat. Here size of dung beetles played an important role because the change in habitat, caused by human impact, affected the larger better competitors more severely, while the smaller less effective competitors did not seem to be affected by human impact on a habitat (Chapter 3). According to Begon, *et al.* 1995) individual size is perhaps the most apparent aspect of an organism's life-history. Large size may increase an organism's competitive ability and large organisms are also better able to maintain a constancy of body function in the face of environmental variation because their smaller surface-to-volume ratio makes them less 'exposed' to the environment. Larger size, however, can increase some risks. Larger individuals require more energy for maintenance, growth and reproduction, and may therefore be more prone to a shortage of resources (Begon, *et al.*, 1995). Larger dung beetles need more breeding space in the soil and also better vegetation for cover. Larger dung beetles will therefore be more prone to disturbances in the habitat than smaller dung beetles. The larger dung beetles belonging to functional groups I, II and III, which are the better competitors in an assemblage, can therefore be considered as the key species. It is these species which will be affected first by a disturbance in a habitat. These species can therefore be used as early indicators of disturbance. Dufrêne & Legendre (1997) found that when local consequences of habitat fragmentation needs to be determined and this information cannot be obtained by bird or botanical studies, studies on invertebrates will be the best alternative.

A simple size index is proposed to determine the influence of a disturbance in the habitat on ecological role of the dung beetle assemblage as a whole in this habitat:

Size index = B/N

Where B is the total biomass of a dung beetle assemblage in a habitat and N is the total number of individuals in this habitat.

When applying this index to the dung beetle assemblages at Sandveld Nature Reserve and the neighbouring farms we find that the value for the size index is much higher for dung beetle assemblages in the natural grassveld habitat than in the disturbed grassveld habitat (Fig. 9.2). In both the bushveld habitats the value for the size index is low (Fig. 9.2). The size index reflects the degree of dominance in biomass in a habitat and therefore the abundance of larger species in the habitat. This is related to the ecological role, the recycling of dung, of dung beetles in an ecosystem. Merritt & Anderson (1977) found that biomass per dung pat was more important than the number species or individuals per pat in influencing the rate of dung degradation. Larger dung beetles will remove more dung at a faster rate than small dung beetles. The higher the size index the nearer the dung beetle assemblage would be to its full ecological potential in a specific habitat. The recycling of dung will, therefore, be more effective in the natural grassveld habitat than in the disturbed grassveld habitat and also more effective in the natural grassveld habitat than in the bushveld habitats. Because of a difference in vegetation in the bushveld habitats the dung beetle assemblage differ from the dung beetle assemblage in the grassveld habitat. Because of tree cover, which may influence searching success the larger dung beetle species are much less abundant in the bushveld habitats. To determine the effect of habitat disturbance on dung beetle assemblages this model is more applicable to grassveld habitats where larger dung beetle species are abundant. Disturbance of a habitat results in a decrease of the size index and a dung beetle assemblage moving away from its full ecological potential (Fig. 9.2).

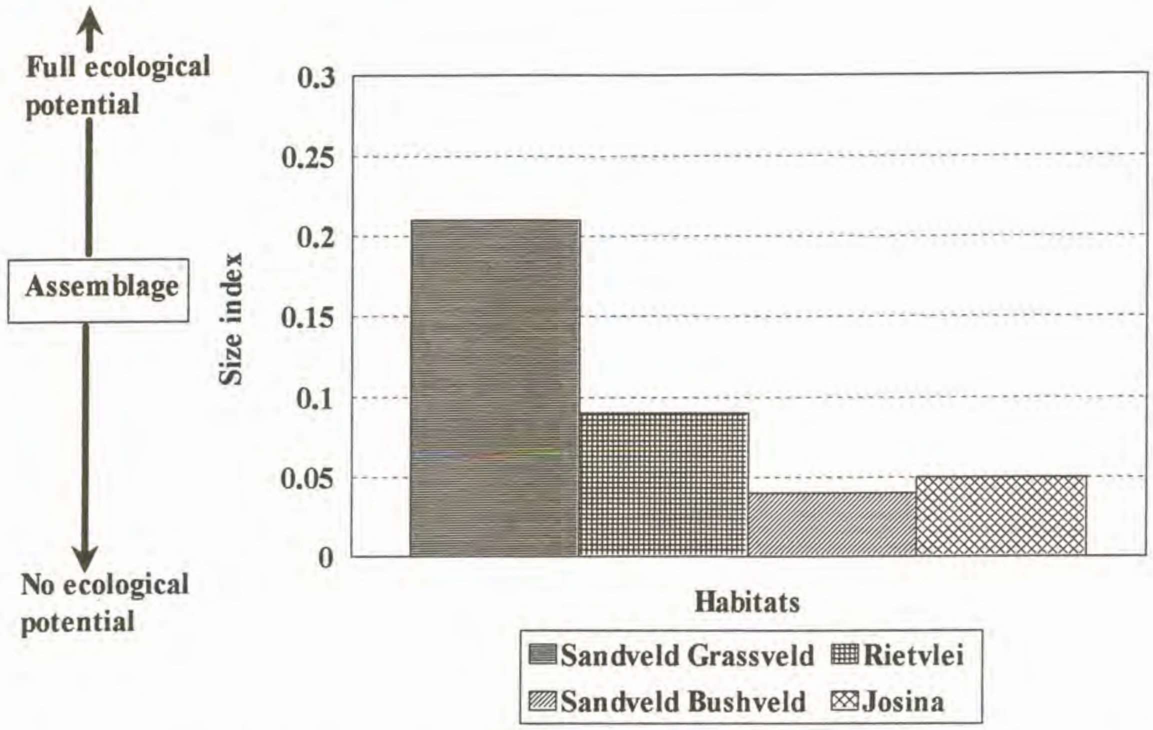

Fig. 9.2: Size index, indicating the ecological role of dung beetle assemblages in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld Bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

Seasonal changes can also cause slight disturbances in a habitat. The size index for dung beetle assemblages changed with seasonal changes throughout the year (Fig. 9.3). There were peaks in the index from October to November and from January to February (Fig. 9.3). There was a drop in the index during December, when the temperatures became too high. It also dropped from March to July and was low during the cold, dry winter months (Fig. 9.3). Seasonal disturbances caused a decrease in the size index. During times of adverse seasonal impacts such as too high or too low temperatures and periods of drought there was very little difference between the size index for the natural grassveld habitat and the disturbed grassveld habitat (Fig. 9.3). As seasonal conditions improved there was an increase in the size index in both habitats but there was a marked difference in size index with the size index being much higher in the natural habitat (Fig. 9.3). Dung beetle assemblages in a habitat experience natural seasonal disturbances, but because these disturbances are periodic they are able to recover quickly when seasonal conditions change. A combination of human and natural impacts, however, might influence the dung beetle assemblage in such a way that they recover more slowly when seasonal conditions change and a stage might be reached where the human disturbances influence the assemblage in such a way that it could no longer recover. At this stage larger species will be replaced by smaller generalist species which are better able to cope with adverse conditions and the assemblage will near a stage where it no longer has ecological potential in the habitat. This will have an effect on the recycling of dung because the dung beetle assemblage is no longer able to fulfill its ecological role successfully resulting in dung left undegraded in the ecosystem. This will place further stress on the habitat because nutrients are not recycled effectively and pastures are fouled by undegraded dung.

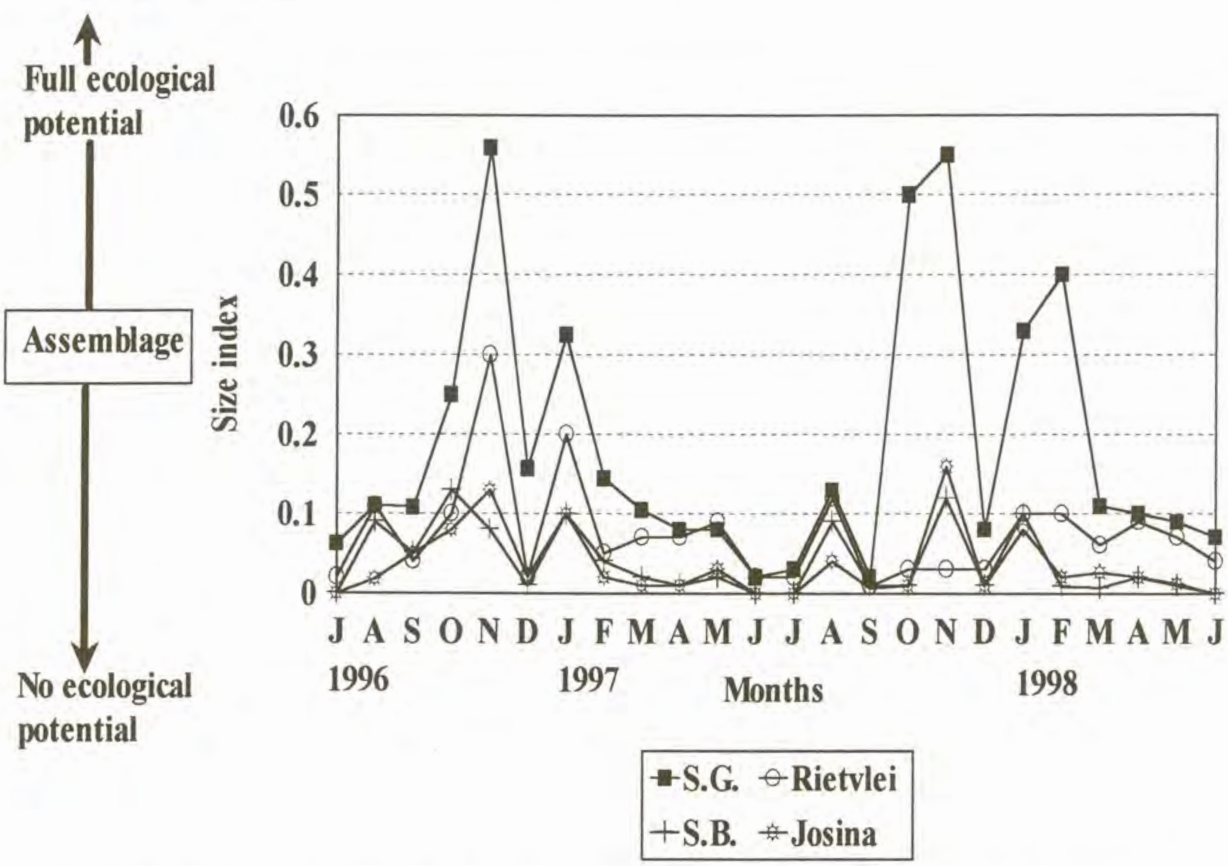

Fig. 9.3: Seasonal change in size index of dung beetle assemblages in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld Bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

9.4. Conclusion

The focus of this study was the dung beetle assemblages in a particular habitat and their ecological role in an ecosystem. The important shared parameters in this system was the human impact, season and habitat as external factors and succession, diel activity, aggregation and dung preferences in dung beetle assemblages as internal factors. All these parameters are interrelated with a change in one resulting in a change in another. These parameters cannot be separated from one another but two key variables could be extracted. These key variables are the influence of habitat and the size of the dominant species in this habitat. These two key variables represent the essentials of the system and by looking at them predictions can be made as to in which direction the dung beetle assemblage in a habitat will move. This will then enable us to make predictions about the condition of the habitat.

Conservation of insects cannot be separated from the conservation of the other biota of the habitats in which those insects live. Conservation action should focus on the conservation of whole ecosystems and this includes insects, because insects play an important role in any ecosystem. Dung beetles are an intrinsic part of any grazing ecosystem, especially open grassveld systems. Traditional pasture improvement strategies for reducing compaction are frequently not practicable because of financial, equipment, and topographic limitations (Herrick & Lal, 1995). When managing natural resources there are two issues of concern: productivity and sustainability. In the management of ecosystems in nature reserves as well as on farms maintaining dung beetle population, which are able to fulfill their ecological role successfully, can provide a cheap and effective alternative for improvement of pastures in a way that will increase productivity as well as sustainability. In looking at the ecological role of dung beetles, diversity alone is not an effective indication of success of a dung beetle assemblage in an ecosystem. The key indicator species are the larger dung beetles. A drop in numbers of these species might act as an early warning. Continued and severe impacts on the habitat might eventually result in the total disappearance of these species consequently leading to impoverished pastures. Improving the habitat will automatically improve the success of the key species. This will improve the recycling of dung and subsequently the quality of the grazing. By limiting disturbances in the habitat with better management practices such as rotation grazing and putting less pressure on the veld during times of periodic natural disturbances such as droughts, the quality of the ecosystem will automatically improve. Resting the veld for as long as possible after a drought is very important and farmers should weigh the costs of supplementary feeding for their livestock after a drought versus their long-term losses associated with reduced veld condition as a result of injudicious grazing. It is important to consider the conservation of habitats rather than species. Not only ecosystems in nature reserves should be focussed on, but also ecosystems on farms. Better communication with farmers is therefore a prerequisite for conservation of dung beetles. By the conservation of whole ecosystems farmers will also benefit by improvement of their grazing pastures, soil fertility, less accumulation of dung and fouling of pastures and less insect pests breeding in dung. By these actions ecological corridors, acting as shelter for dung beetle assemblages, will be created. Connecting these corridors to nature reserves will ensure the future well being of grazing ecosystems in both nature reserves and on farms.