COMMUNITY DYNAMICS AND DEMOGRAPHY OF SMALL MAMMAL POPULATIONS IN NATURAL GRASSLANDS AND REHABILITATED ASH DAMS

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ABSTRACT

While small mammal communities in various rehabilitated ecosystems have been well studied, no data are available for rehabilitated sites in the heavily transformed grasslands of South Africa. Small mammal community characteristics and successional trends on fly-ash disposal sites (ash dams), and in adjacent natural grasslands (control grids), at Hendrina Power Station (Mpumalanga) were therefore examined, and the success of current rehabilitation strategies at restoring sustainable small mammal populations was evaluated.

Population sizes and biomass of small mammals on the ash dams and controls were similar and varied significantly on a seasonal basis, being highest in autumn and winter and lowest in summer. Such seasonal variation in population sizes is atypical of small rodents in the summer rainfall zone of southern Africa and apparently reflected localized immigration and emigration, both on a seasonal basis and also following a veld fire during 1998, as well as the effects of weather and resource availability on trapability in the wet summer months. Small mammal communities on all grids were dominated by *Rhabdomys pumilio*, numbers of which increased progressively with increasing rehabilitation age to peak at nine years. *Mastomys coucha* occurred in significantly higher numbers on the slopes of the ash dams, particularly those adjacent to agricultural fields and disturbed or undisturbed grasslands. Population sizes of this species, and thus community composition on the ash dam slopes, were apparently influenced by the ecological status of adjoining areas, perhaps reflecting recolonization opportunities and rates. Conversely, *Tatera brantsii* occurred in highest numbers on the plateaux grids surrounded by rehabilitated areas, and was absent from the controls, suggesting that numbers of this species, and the composition of the plateaux communities, was not markedly influenced by recolonization from adjacent unrehabiliated areas.

Successional tendencies on the ash dam grids were characterized by changes in equitability, local extinctions of less common (more stenoeious) species and species replacements. Diversity and equitability increased with rehabilitation age between four to seven years post-rehabilitation (when these parameters were significantly higher than on the control grids), and then declined

dramatically to levels observed on the control grids. This decline reflected increased dominance of the communities by *R. pumilio* (especially on the slopes) and *T. brantsii* (on the plateaux). Small mammal species diversity and equitability generally increased with an increase in the diversity, equitability and richness of plant communities on the ash dam grids. Stepwise regression and ordination analyses, however, suggested that certain edaphic factors were the best predictors of small mammal community structure and dispersion.

Given the general resemblance in small mammal community attributes and demography on the ash dams and controls, and similar successional tendencies evident in these areas, I conclude that current rehabilitation actions have been successful at restoring reasonably diverse small mammal communities over the short term. These communities do not, however, appear to be sustainable over the medium-long term, necessitating further management actions and changes to current rehabilitation strategies.

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INTRODUCTION

Small mammals are important components of terrestrial ecosystems,- by virtue of their diversity, role as regulators of energy / nutrient transfers between producers, consumers and decomposers (Golley, Ryskowski & Sokur 1975; Hayward & Phillipson 1982); and their often dramatic effects on the structure and dynamics of plant communities (Dean & Milton 1991; Hulme 1996; Olff & Ritchie 1998). Their high fecundity and short generation times allow them to respond rapidly to fluctuating environments and for these reasons they are ideal candidates for study when monitoring recovery of disturbed ecosystems (Bourlière 1975).

The autecology of small mammal species in natural grasslands of southern Africa (Meester, Lloyd & Rowe-Rowe 1979; Perrin 1980; Willan 1992), and ecological succession following veld fires (Willan 1984; Bigalke & Willan 1985), have been well-studied, but no detailed study of small mammal community characteristics following the rehabilitation of ash disposal areas has yet been done. Such areas are associated with coal-fired power stations located mainly in the eastern grasslands of South Africa. Given that the grassland biome has been transformed by anthropogenic activities, ESKOM (Electricity Supply Commisson of South Africa) has instituted rehabilitation programmes on ash dams to minimize the ecological impacts of these power stations. This study documents the structure and ecological succession of small mammals on ash dams at Hendrina Power Station, and assesses if current rehabilitation strategies have been successful at restoring sustainable small mammal communities.

1.1 Biology of small mammals

Small mammals comprise about one-third of the 4500 living species of mammals and natural populations of small mammals are to be found almost worldwide. The term "small mammal" refers to mammal species whose adult body mass ranges from less than 2 grams to about 5 kilograms, and includes the mammalian orders Insectivora, Rodentia, Lagomorpha, Carnivora (in part), and Chiroptera (Bourlière 1975; Hayward & Phillipson 1982). The majority of terrestrial mammals fit this definition (Bourlière 1975).

Being small has several ecological and evolutionary advantages for a mammal:

- Small body size is generally correlated with a high reproductive potential, rapid population turnover rates and faster evolutionary time scales (Willan 1992).
- It provides easy access to a number of food resources that are sparsely exploited by other animals and thereby enables small mammals to take full advantage of certain micro-habitats (Bourlière 1975).
- Small size enables populations to split into a number of local demes, each well-adapted to particular local conditions (Bourlière 1975).
- Small size facilitates relatively easy concealment from predators, particularly since most species are nocturnal or crepuscular in habits (Bourlière 1975).

Being small, however, also has disadvantages, including:

- Owing to the relationship between body size / volume and surface area, small mammals have a high mass-specific metabolic rate, and thus have high energy requirements.
- This high energy expenditure requires a high daily food intake, which in return requires moving around more often and over longer distances. This in turn also increases the energy cost associated with locomotion (Bourlière 1975).

Small mammals have definite food preferences and their feeding habits vary from primarily

granivorous to generalized omnivorous (Fleming 1975; Golley *et al.* 1975; Kerley 1992; Willan 1992). Omnivorous species have the advantage of being able to shift their feeding habits to take advantage of seasonally-abundant food resources. Many small mammals, particularly rodents, are generalists and opportunists that adapt easily to changing environmental conditions (Leirs 1994). They occupy almost every kind of terrestrial environment, but many species are micro-habitat specific which facilitates species coexistence (Kerley, Knight & Erasmus 1990; Willan 1992). Many species are highly territorial in stable environments, or communal in harsher environments (Willan 1992) and their life-history strategies may vary geographically and temporally (Perrin 1980).

In temperate or unstable areas, certain physical factors are often limiting to populations, which leads to the production of large litters (r-selection) in order to take full advantage of available resources which may prevail for a short time, while in tropical or more stable habitats resources are almost always available and competitive interactions predominate leading to K-selection. The concepts of r- and K-selection relate to changes in population density and the potential rate of increase in relation to resource availability and stability. r-Strategists are characterized by large litter sizes, small body masses and a short life span, and highly variable population sizes, while K-strategists show the opposite trend with more stable populations in which competition is high and numbers are close to carrying capacity of the habitat. According to Pianka (1970), r-Strategists have a pronounced ability to colonize unoccupied and ephemeral habitats owing to their high reproductive potential and euryoecious nature (Perrin 1980).

Periodic population irruptions of some small mammal species may occur, especially in opportunistic rodents such as *Mastomys*, *Mus*, *Tatera* and *Rattus* (Willan 1992; Leirs 1994; Christensen 1996). These population increases can be the result of excessive food availability, good rains in the late wet season or a decline in predation during droughts (Willan 1992). Population explosions are usually followed by a crash in numbers because of the depletion of food, (Coetzee 1975; Willan 1992), and sometimes also a dramatic

reduction in reproductive activity and a breakdown in social structure that influences litter size, size of the young born and the survival rate of the young (Coetzee 1975).

Owing to their opportunistic and generalized life styles, many small mammal species are well adapted for exploiting man-made environments and disturbed ecosystems (Coetzee 1975; Willan 1992; Leirs 1994), with the result that some are considered pest species. Most other vertebrates cannot survive in such areas. As a result, interspecific competition, except with man, is almost absent for such r-selected small mammals (Leirs 1994). *Mastomys* is one such major pest in Africa and causes considerable damage to crops such as maize, wheat and other cereals in parts of tropical east Africa (Bourlière 1975; Leirs 1994). It also acts as a vector for several human pathogens, which it transmits from natural reservoir species such as *Tatera*, to man (Leirs 1994).The gerbil, *Tatera brantsii*, is one of the commonest mammals on the highveld of South Africa and is the endemic reservoir of bubonic plague in this country (De Moor 1969; Leirs 1994).

1.2 Ecological correlates of community structure

Numerous habitat features influence the dispersal and occurrence of small mammals. Of these, vegetation structure and cover are the most important (Els & Kerley 1996). Most small mammals are dependant on plant cover for protection from predators and climatic extremes (Willan 1992). Numerous studies have shown that diurnal species prefer habitats with dense vegetation cover, which provides cover and protection from predators. These habitats often also support a higher diversity of small mammal species (Gust & Schmidly 1986; Happold & Happold 1990; Willan 1992; Oguge 1995; Els & Kerley 1996; Monadjem 1997; Monadjem & Perrin 1998).

In desert habitats, small mammal diversity has been reported to initially increase with an increase in plant cover. This increase in diversity occurred as plant cover increased to around 60%, whereafter it decreased (Abramsky 1988; Kerley 1992). The initial increase

in small mammal diversity with increasing plant cover may be the result of greater resource availability correlated with an increase in micro-habitat heterogeneity. Abramsky (1988) showed that the establishment of shrubs in a desert habitat creates more niches, so that the coexistence of many small mammal species becomes possible. Predation is greatest in open areas and thus predation promotes coexistence between fast foragers that specialize in avoiding predators, and species with anti-predation adaptations. In these areas species with and without anti-predator adaptations may coexist, resulting in high small mammal diversity. The subsequent sudden decline in diversity observed by Abramsky may have been the result of disturbance, a limited distribution of resources or the exclusion of species by a few competitive dominant individuals (Kerley 1992).

Plant cover may also influence the micro- and macro-climate of a habitat, which in return may play a role in determining species distributions and population sizes (Bond, Ferguson & Forsyth 1980). Certain habitat features frequently interact with each other in determining community composition and dispersion. Numerous studies have reported an increase in small mammal numbers after good rainfall (Whitford 1976; Nel 1978; Bronner, Rautenbach & Meester 1988; Monadjem & Perrin 1997), in response to an increase in the availability of food and vegetation cover. An increase in food supply may also result in an extension of the breeding season, an increase in reproductive intensity and an increase in the growth rate and body weight of small mammal species (Rowe-Rowe & Meester 1982; Rowe-Rowe 1995; Monadjem & Perrin 1997). Furthermore, these habitat features may vary seasonally, and population sizes of small mammals may thus also show seasonal variations. This has been well documented for many habitats in Africa.

Studies done in areas varying from sub-humid grasslands to temperate forests have shown similar seasonal trends, with an increase in population size during the wet season and a decline during the dry season. These fluctuations are associated with rainfall (Happold & Happold 1989;1990;1991;1992; Wirminghaus & Perrin 1993; Oguge 1995; Monadjem 1997). At the beginning of the wet season, rain initiates the growth of grass, which

increases the available plant biomass, cover, height and abundance of food. This results in elevated high small mammal numbers as a result of the recruitment of young, and immigration of adults. The subsequent decline in numbers during the dry season can be attributed to dying-back of the grass sward, a reduction in cover and a lack of food and other resources, with an increase in mortality, dispersal to other more suitable habitats and the cessation of reproduction (Happold & Happold 1989; 1990; 1991; 1992).

A study by Gliwicz (1985) in a dry African savanna, however, showed a different pattern: numbers of small mammals were highest in the middle of the dry season, and declined in the rainy season. Possible explanations for this could be low trapability because of the presence of plentiful food in the study area, bait becoming unattractive to the animals, or because of dispersal of small mammals into surrounding areas rich in food (Gliwicz 1985).

Rainfall is thus apparently the most important habitat feature determining the time of breeding in many rodents, but is clearly not the only factor. Some studies have shown that a secondary plant compound, 6-methoxybenzoxazolinone (6MBOA), can act as a short-term cue stimulating reproduction by signaling an increase in food availability (White & Bernard 1999). 6MBOA is present in young green growing shoots, especially those of grasses and sedges. This compound has been shown to have stimulatory effects on the reproduction of several African species, such as *Gerbillus hardwoodii* and *Mastomys coucha* (Leirs 1994), but species such as *Tatera leucogaster* reacted negatively towards this compound. This plant compound (6MBOA) also does not play a major role in the stimulation of reproduction in *Saccostomus campestris*. The absence of an effect of 6MBOA on certain species may be related to their omnivorous behavior (White & Bernard 1999).

Fluctuations in small mammal numbers may also reflect seasonal migrations of small mammals, which disperse temporarily and gather in refugia where they will stay until conditions in surrounding habitats are suitable for reproduction. This trend is particularly

evident in burned grasslands. When conditions in burned grassland improve, small mammals disperse from unburnt areas into these areas (Gliwicz 1985; Happold & Happold 1989; Rowe-Rowe 1995).

1.3 The role of small mammals in terrestrial ecosystems

Ecologically, small mammals are important components of terrestrial ecosystems. Their most numerous representatives, the rodents, are major vertebrate pests and have been well studied all over the world (Bourlière 1975). By virtue of their small size, high reproductive potential, fast generation times and rapid response to environmental conditions, they are ideal models for use in ecological studies (Bourlière 1975; Hayward & Phillipson 1982; Hingten 1984).

According to Batzli (1975), small mammals may impact on all components of any ecosystems, in particular on the soil, vegetation and predator guilds (Hayward & Phillipson 1982). The impacts small mammals may have on temperate ecosystems (forests, grasslands and cultivated fields) can be grouped into five categories:

- energy- and nutrient cycling, in particular between the producer and decomposer components in an ecosystem
- the destruction or alteration of vegetation communities
- spatial movement of materials (nutrients)
- alteration of soil characteristics and plant community attributes and
- impact on consumers and predators (Golley *et al*. 1975).

One of the most important roles they appear to play is that of seed or seedling predators, pollinators and seed-dispersal agents. According to a study done by Kerley (1992) in the semi-arid Karoo, South Africa, small mammals are important components of arid- and semi-arid systems, playing a role as both predators and dispersers of seeds. In some

cases, the predation of seed can be an important regulatory factor for some plant species (Hayward & Phillipson 1982).

Little information is available on the population dynamics of tropical small mammals and their functional role in their ecosystems (Fleming 1975). Furthermore, their activities as economic pests and/or reservoirs for infectious diseases can render them of direct concern to man and his welfare (Fleming 1975). Korn (1987) showed that small mammals in a subtropical savanna ecosystem may consume as much energy as other, often larger mammal species, and that they are important for ecosystem functioning in terms of recycling and movement of nutrients and micro-organisms. His results were, however, based on allometric scaling of metabolic parameters, and must be regarded as equivocal since this technique is replete with controversy.

The movement of nutrients and minerals from deeper layers of soil profiles to the surface influences and enriches the soil chemistry in grassland ecosystems. Through the destruction and consumption of foliage by small mammals, the transfer of energy and nutrients from vegetation to the decomposers is accelerated. In this way small mammals can act as an analog to fire in reducing organic material to a more easily decomposed form. Small mammals also play an important role in the decomposition of organic materials so that essential nutrients can be released and used for primary production, which is why the greatest impact of small mammals will be in grassland ecosystems where the decomposition of the annual primary production is one of the key ecosystem processes (Golley *et al.* 1975).

Many small mammals are granivorous and their foraging activities can influence the species composition, abundance, distribution, form and reproduction of plant species as well as the number of progeny (Golley *et al.* 1975). The digging of burrows by certain gerbil species can also influence ecosystems by altering the habitat and opening patches of land denuded of dominant grasses, which in turn opens up areas where seedlings can

germinate (Korn & Korn 1989; MacMahon, Parmenter, Johnson & Crisafulli 1989).

Digging of burrows by small mammals may also enhance the movement, storage and drainage of water and nutrients in the soil, and thereby improve the growth conditions of plants (Golley *et al.* 1975). In southern African highveld grasslands, drainage effects can be pronounced, amounting to over 2500 l of water per burrow within three hours (Eloff 1953). Burrowing also leads to a mixing of soil profiles, and studies done by Kucheruk (1963) have shown that burrowing activity increases the calcium and magnesium content of the soil, and also alters the pH (Golley *et al.* 1975; Hayward & Phillipson 1982). Groves & Keller (1983) furthermore found that small mammals may redistribute radio-active materials during their burrowing activities. They can thus serve as a vector for transportation of radio-nuclides from contaminated areas.

Another important role small mammals play in terrestrial ecosystems is to link primary producers and secondary consumers (Golley *et al.* 1975; Hayward & Phillipson 1982). The success and survival of many terrestrial and avian predators depends on the abundance of small mammals because these mammals represent a basic component in many natural terrestrial food chains (Parker 1989). This also makes small mammals a buffer to predation of other consumers (Golley *et al.* 1975). An increase in predation on certain small mammal species results in a reduction of the impact of these species on the ecosystem. The role of small mammals as secondary consumers has not, however, been well studied. Some small mammals, like shrews, are insectivores and can have a direct impact on their prey populations, and they can also destroy insects which are predators or parasites of other phytophagous invertebrates (Hayward & Phillipson 1982).

Small mammals may also have a dramatic direct impact as consumers on the structure and dynamics of vegetation, while the nature of the vegetation in turn determines the distribution of small mammals through the food and cover it provides (Delany 1964). They can alter plant species composition and plant communities through their feeding on green

leaves and shoots, or indirectly via burrowing, which impacts on substrate characteristics and thus has an effect on plants. The destruction of leaves may reduce photosynthesis, while the destruction of bark and roots may cause stunting or death of shrubs and trees. Seedlings are also preferred to older plants because of their nutritional value, and seedling predation may result in the disappearance of certain plant species (Golley *et al.* 1975; Hayward & Phillipson 1982; Korn & Korn 1989; Huntly & Reichman 1994).

A study by Hulme (1996) in a grassland area showed that rodents had the greatest trophic influence of all consumers on plant performance, and reduced plant biomass by 50%. The activity of other herbivores, such as molluscs, reduced plant numbers but the plants appeared more able to compensate for any biomass lost through grazing. By comparison, arthropods played only a minor role in determining either plant biomass or survival (Hulme 1996). Selective feeding on vegetation by small mammals can also promote the occurrence of specific plants so that certain plant species are associated with certain rodent colonies. This positively influences the abundance of plants that are avoided or which benefit from disturbance, which in return may lead to an increase in plant species diversity (Hayward & Phillipson 1982; Huntley & Reichman 1994).

The primary role of small mammals within an ecosystem is that of regulators of nutrient and energy flows between the producers, other consumers and decomposers owing to their rapid response time, their variety of feeding habits and the role they play in the decomposition of organic material. However, their impacts appear to be habitat-specific, and the functional role that small mammals may play in the maintenance and regulation of ecosystem dynamics is dependant on physical habitat factors, the structure and composition of plant communities, and also on the eco-physiological nature of the small mammals concerned (Hayward & Phillipson 1982).

1.4 Small mammal ecological research in South Africa

Earlier research in the grassveld biome of South Africa concentrated on autecological studies of selected rodent species, such as *Rhabdomys pumilio* (Brooks 1974), *Otomys irroratus* (Davis 1973), *Tatera brantsii* (De Moor 1969) and *Mastomys natalensis* (de Wit 1972; Coetzee 1975) as well as on community structure and succession of small mammals (Rowe-Rowe 1995). Little work has, however, been done on functional aspects, except for a study done by Korn & Korn (1989), which concentrated on the effect of gerbils on primary production and plant species composition in a savanna area near Nylsvley in the savanna biome. They reported that the digging activity of gerbils causes a reduction in climax grasses, as well as in root biomass, and resulted in a significant increase in plant species diversity and equitability. They also found that the activities of gerbils destroyed perennial plants, especially grasses, but annual plants such as dicotyledonous herbs were favoured. This study was, however, methodologically flawed since the study area was also inhabited by many large herbivores, which more than likely also impacted on the vegetation. Furthermore, Korn & Korn (1987) relied only on *a posteriori* analyses of vegetation characteristics since they had no data on the vegetation on the study sites prior to disturbance by *Tatera brantsii*. Their use of nearby "undisturbed" sites as controls was not justified since vegetation characteristics can be highly variable even within a localized habitat owing to edaphic fluctuations. Consequently, their findings that *T. brantsii* have such a dramatic effect on vegetation communities must be treated with caution.

Other studies done on the ecological role and preferences of small mammal communities in South Africa include the following:

- the habitat preferences (Monadjem 1997), distributional patterns and conservation status of small mammals (Monadjem 1998) and the effects of supplemental food on the habitat selection by *M. natalensis* (Monadjem & Perrin 1998) in the grasslands of Swaziland

- the semi-arid Karoo has also received a lot of attention the past few years and work done includes studies such as the trophic status (Kerley 1992) and ecological correlates (Kerley 1992) of small mammal community structure, and the effect of small mammals as granivores on the vegetation in the Karoo (Kerley 1990; Kerley, Knight & Erasmus 1990; Kerley & Whitford 1994) .
- Rowe-Rowe & Meester (1982) concentrated on the population dynamics and reproduction of small mammals in the highest mountain range in South Africa, the Drakensberg of Natal.
- Els & Kerley (1996) conducted a study in the Groendal Wilderness Area, Eastern Cape and found that in order to maintain a diversity of small mammal communities, management should ensure a mosaic of diverse vegetation communities.
- a study by Bond, Ferguson & Forsyth (1980) in the southern Cape mountains showed that small mammal distribution and diversity were controlled by certain habitat factors and an understanding of small mammal distribution can be of value in conservation management of mountain ecosystems.

1.5 Successional tendencies of small mammal populations

1.5.1 General tendencies and hypotheses

Succession refers to the changes observed in an ecological community following a particular event that changes the habitat and opens up a relatively large ecological space for recolonization and re-establishment (Connel & Slater 1977). Clements (1916) proposed that ecological succession is a process of vegetation change through a number of intermediate stages until an equilibrium is attained among the extant species and the environment. This succession theory predicted that a habitat deprived of its original structure and appearance (by fire or any other natural force) is rapidly colonized by a variety of plant and animal species. These species modify certain environmental features so as to ultimately make the ecological milieu less suitable for themselves, and allow other

species to become established. These new species then replace residual species and there is a progressive change in the species composition of the community (Krebs 1985; MacMahon *et al.* 1989).

Connel & Slater (1977) proposed that the process of ecological succession can be incorporated into three models:

- a facilitation model, which suggests that early pioneer species improve and prepare the environment in such a matter so that other species can later establish themselves in this area (Connel & Slater 1977);
- a tolerance model, which suggests that a predictable sequence is produced by the existing species which have developed different strategies for exploiting resources. The establishment of later species is determined by their tolerance to a changing environment with low levels of resources (Connel & Slater 1977);
- an inhibition model, which suggests that existing species prevent the establishment of other competitive species and will continue to regulate succession and exclude later colonists until the former die or are damaged, releasing resources (Connel & Slater 1977).

Successional patterns are seen as complex systems with spatial and temporal variation, historical effects and stochastic dispersal of species. Interactions with herbivores, predators and pathogens are of critical importance to the course of succession (Connel & Slater 1977). Ecological succession of small mammal communities is dependant on successional tendencies of plant populations and is characterized by changes in density, species composition, species richness, diversity, biomass, niche breath and/or equitability (Connel & Slater 1977; Fox 1982; Parker 1989; Kirkland 1990; Ferreira & van Aarde 1996).

Small mammal activities can play a role in succession via differential pressure on plant species associated with early successional stages. In this way they may assist in the recovery of disturbed habitats and promote a series of secondary successions that lead

to open areas (Hayward & Phillipson 1982). Small mammals will then leave the succession when the local physical conditions are no longer in their optimal range (Fox 1982; Oguge 1995). Replacement sequences in succession may result in coexistence between certain species, (increased species richness) and can determine the composition and structure of small mammal communities.

Early successional species may alter the plant succession in such a way that habitat changes which could favor later successional species are delayed. These actions prolong mammalian succession and exclude subsequent colonists, (Fox 1982), which is concordant with the inhibition model proposed by Connel & Slater (1977). A study on the Mount St. Helens Volcano (MacMahon *et al.* 1989) showed that disturbance reduces or eliminates resident populations, while species that colonize this area join residents and together they alter the biotic environment. This action may influence the establishment of future migrants as well as the survival of the offspring of both residents and migrants.

Cook (1959), however, postulated that succession is characterized by changes in abundance of species, rather than species replacement, and is determined by certain external factors with species playing no role in modifying the habitat. This is concordant with the habitat accommodation model which states that animal or plant species enter the succession when physical conditions meet their requirements, and then leave the succession as soon as the conditions are no longer suitable (Fox 1982).

1.5.2 Fire

Fire is a natural and integral ecological force in many terrestrial environments (Christian 1977; Fox 1982), and it has a dramatic effect on small mammal populations owing to its effect on the vegetation (Beck & Vogl 1972; Cheeseman & Delany 1979; Ojeda 1989; Fa & Sanchez-Cordero 1993). These effects include a decrease in abundance owing to reduced vegetational cover (Fa & Sanchez-Cordero 1993), a decrease in species diversity

and biomass, and sometimes a sustained dominance of species (like *Tatera brantsii*) which are favoured by post-burn conditions (Kern 1981). The removal of vegetation by fire promotes the abundance of certain species with ecomorphological traits enabling them to exploit more open areas (Ojeda 1989; Fa & Sanchez-Cordero 1993).

The response of small mammals to fire, or a post-burn area varies inter-specifically and is part of a response continuum (Fox 1982). This response is not so much a direct response to fire as a reaction to the fire-altered habitat since mortality during veld fires is generally low (Beck & Vogl 1972; Willan 1992). This results in species replacement that may facilitate coexistence, which in turn increases species richness and determines species composition and community structure (Fox 1982). Fire can also create new habitats into which certain species can immigrate, and may also cause under-utilized habitats to be occupied by fugitive species which are replaced by later mammal species (Fox 1982). The removal of litter by fire probably increases the availability of food, primarily seeds. After fire, seeds on the soil surface are more readily available and many seeds that are not destroyed by fire and remain viable, with the result that granivores are favoured in the initial stages of fire-induced succession (Kaufman, Kaufman & Finck 1988).

1.6 Rehabilitation ecology of small mammal communities

1.6.1 General

Man has played an important role in modifying or transforming virtually every ecosystem in southern Africa. South Africa, especially the Mpumalanga province, is by far the most industrialized of any other country in Africa, with its electrical generating capacity being 60% of that of the whole continent (MacDonald 1991). The grassland biome, where most of the country's industrialized activities are concentrated, has been heavily transformed with estimates ranging from 25% to 65% of the area being degraded (MacDonald 1991; Wessels, Reyers & Van Rensburg 2000). Rehabilitating areas transformed by mining,

cultivation or any other form of habitat modification is thus a major component of environmental planning and protection. The Convention of Biological Diversity, ratified by the South African Government in 1995, demands the rehabilitation of degraded areas so that sustainable biological diversity is restored, to resemble a system (or similar ones) in the same area prior to development. In South Africa the law requires that the rehabilitation of any environment disturbed by industries, especially after accepting the strictures of the Convention of Biological Diversity in 1995. However, the environmental legislation act (Act No. 107 1998) is vague on what rehabilitation entails, and only states that when any disturbance cannot altogether be avoided , it must be minimised and remedied (Section 2, subsection (4:i-viii).

What is ecological rehabilitation? According to Barnard's (1995) interpretation of prevailing legislation in South Africa, rehabilitation can be defined as restoring a land changed through exploitation and disturbance to a "proper" condition that satisfies the demands of sustainability. The economic value of a rehabilitated area must be equal to that of the resource that was or will be destroyed during development. The emphasis, therefore, lies more on the economic value of a rehabilitated area rather than on ecological sustainability. The rapid rise of ecological rehabilitation practices is forcing renewed consideration of what good rehabilitation entails. Good rehabilitation requires an expanded view that includes historical, social, cultural, political, aesthetic, and moral aspects (Higgs 1997).

The definition of good rehabilitation will vary from site to site and will be rooted by ecological fidelity. Ecological fidelity is the avowed goal of rehabilitation and the quest is to restore, as far as possible, the ecological system(s) which once existed on a specific site (Higgs 1997). Ecological fidelity incorporates three principals:

- structural/compositional replication, whereby a restored ecosystem must strongly resemble the structure and composition of the so-called natural ecosystem. Here time is an important element and succession can take as little as a few years to

many decades.

- functional success, which is related to the restoring/establishment of basic ecological processes, such as basic energy/nutrient cycles and depends on the presence of diverse biotic components and their interactions. These processes must operate normally according to the attributes of the specific ecosystem and depends on management and human practices.
- persistence, which is an issue of growing importance. For rehabilitation to be successful, the resulting ecosystem must be resilient enough to survive short-term unfavourable environmental conditions, such as droughts and fires (Higgs 1997).

The sustainability and durability of industrial ecosystems depends largely on the diversity and adaptability of animal and plant populations (Inouye 1995). To determine reliable estimates of population parameters and ecological stability, comprehensive data are needed on the diversity and community structure(s) of sites at various stages of rehabilitation (Inouye 1995). Animals such as pollinators, herbivores, predators and detritivores play an important role in ecosystem functioning, and as indicators of ecosystem stability (McKenzie, Hyatt & MacDonald 1993). The long-term sustainability of rehabilitated sites will depend to a large extent on the organic content of the topsoil layer and therefore the role played by soil organisms (such as ants and small mammals) on the organic content of the top layer, and the factors affecting these animals, are also important.

1.6.2 Successional trends of small mammals in rehabilitated landscapes

Studies done on reclaimed strip-mined areas in Texas (Gust & Schmidly 1986) showed that species differ in their ability to altered habitats, especially when an area is disturbed, and rehabilitation results in plant communities very different from the original vegetation. This may also lead to a change in the structure and composition of small mammals. A study by Kirkland (1990) on the changes of a small mammal community after clear-cutting

of temperate forests in North America showed a significant pattern of increase in abundance, species diversity and species richness after clear-cutting. Certain habitat features such as slope, aspect, vegetation type and climatic conditions can also influence the physical and biotic environmental conditions in disturbed areas, since successional trends tend to be habitat-specific.

Published information on successional tendencies of small mammals in rehabilitated ecosystems has been well documented in other parts of the world but in South Africa it is restricted to coastal dune forests of KwaZulu-Natal, which were mined by Richards Bay Minerals (Ferreira & van Aarde 1996). In this study, successional changes in the small mammal community composition could be explained by species-specific habitat preferences, movernent from unmined areas and competition between species. If the abundance of a resource does not selectively favour one species over another, interspecific competition lead to exclusion or coexistence and not to species replacement, as in the case when a resource selectively favour one species. Species specific immigration, emigration, birth and death rate influenced the colonization of a habitat and the extinction of a species occurring there (Ferreira & van Aarde 1996).

1.7 Motivation for this study

ESKOM (Electricity Supply Commission of South Africa) operates 9 coal-fired power stations in the grassland biome region of South Africa. The coal used by these stations is of a very low quality and has a 20-36% ash content. During 1998, 87.2×10^6 tons of coal were used, and $20\text{-}22 \times 10^6$ tons of ash was produced (M. Michael, *pers. com.*[1]). Nine thousand seven hundred and fifty tons of ash was used for the production of other products, such as cement, 1.175×10^6 tons of ash were exported, whereas the remaining $\pm 20 \times 10^6$ tons was deposited on ash dams (PFA - lagoons - 'Pulverised Fuel Ash' -

[1]M. Michael, 3 Technology Service International, Private Bag 40175, Cleveland, 2022, South Africa.

lagoons). The effective rehabilitation of these ash disposal areas is very important for ESKOM (Electricity Supply Commission of South Africa), to minimize the impact of coal-fired power stations on the environment, especially since 65% of the grassland biome has already been radically transformed by anthropogenic activities (MacDonald 1991; Wessels *et al.* 2000).

The above review of the role of small mammals in terrestrial ecosystems indicates that they may play an important role in the rehabilitation of disturbed areas. The enormous population build-up of rodents in rehabilitated sites, as recorded during this study, could seriously reduce biomass by up to 47% (Bronner, Wright, Van Hamburg, Morgenthal & Michael 1999), by selective feeding on certain grass species and thus influence rehabilitation success. On the other hand, rodents could also have a positive effect in a rehabilitated ecosystem by increasing species richness and biomass of dicotyledonous plants (Korn & Korn 1989). The rate of success of rehabilitation, and the factors involved in effective, sustainable rehabilitation, depend ultimately on the sustainability of the plant and animal communities in these areas, and small mammals can clearly exert a casual influence in this regard.

Ecological stability is enhanced by species and habitat diversity, and herbivore/plant interactions. Thus, it may be necessary to find one or more indicator species and measure fluctuations in their abundance (Inouye 1995). Small mammal community characteristics are ideal as indicators for evaluating sustainable rehabilitation success. This study documents the structure and ecological succession of small mammals on ash dams at a power station, and assesses if current rehabilitation strategies have been successful at restoring sustainable communities.

The specific aims of this study were to:

- document and compare small mammal communities in rehabilitated ash disposal areas and natural grassland in terms of community structure and population

dynamics of the dominant species

- document successional trends of rehabilitated communities and the most important abiotic and biotic factors which impinge thereon
- evaluate how effective has rehabilitation been by restoring viable and functional populations, relative to the adjacent natural (unrehabilitated) areas
- examine ecological correlates of community structure and development in the highly-specific rehabilitated ecosystem.

CHAPTER 2

STUDY SITES AND GENERAL METHODOLOGY

2.1 Study sites

This study was conducted at Hendrina Power Station in the Mpumalanga Province (26°03'S; 29°35'E), located in the grassland biome of South Africa (Rutherford & Westfall 1986). According to Acocks (1988), the vegetation of this area is part of the eastern variation of the Bankenveld (veldtype # 61) and plant species occurring here include *Tristachya leucothrix*, *Eragrostis racemosa*, *Heteropogon contortus*, *Trachypogon spicatus*, *Digitaria tricholaenoides*, *Themeda triandra*, *Brachiaria serrata*, *Elionurus muticus* and others. The recent vegetation map of southern Africa by Bredenkamp & van Rooyen (1996) classifies the vegetation of this area as part of the Moist Sandy Highveld Grassland. Average annual rainfall in this region is highest in summer (November-January) and varies from 500 -700mm, and lowest in winter (May-July), usually below 62.5 mm. Mean daily temperatures vary from 20.1-22.5°C in summer and from 7.5 -10.0°C in winter. This area is thus characterized by warm, wet summers and cool, dry winters (Figure 2.1 & Figure 2.2).

The study site consists of a series of four ash disposal dams (Figure 2.3). Ash dam A is situated closest to the power station, while ash dams B - D were built to the south of ash dam A. The construction of ash dam B was never finished because the stock piles collapsed. Ash dam D is situated separately from the others and was still in construction during the study. The construction of the fifth ash dam (ash dam E) was started late in 1997. The ash dams are bordered by a number of land uses. The northern boundary of

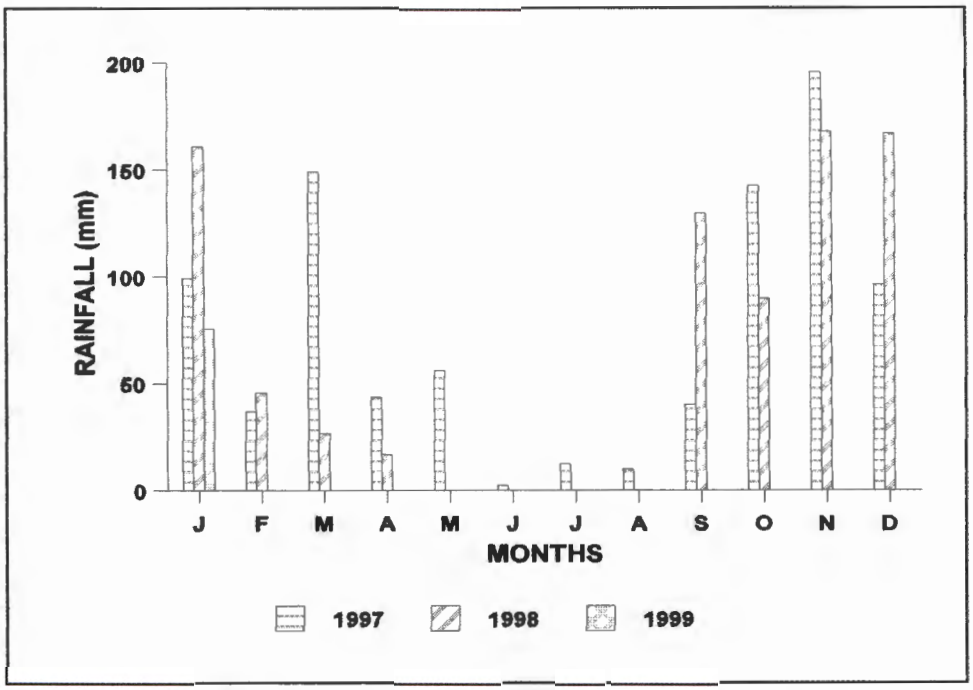


FIGURE 2.1: Mean monthly rainfall during the study period at Hendrina Power Station.

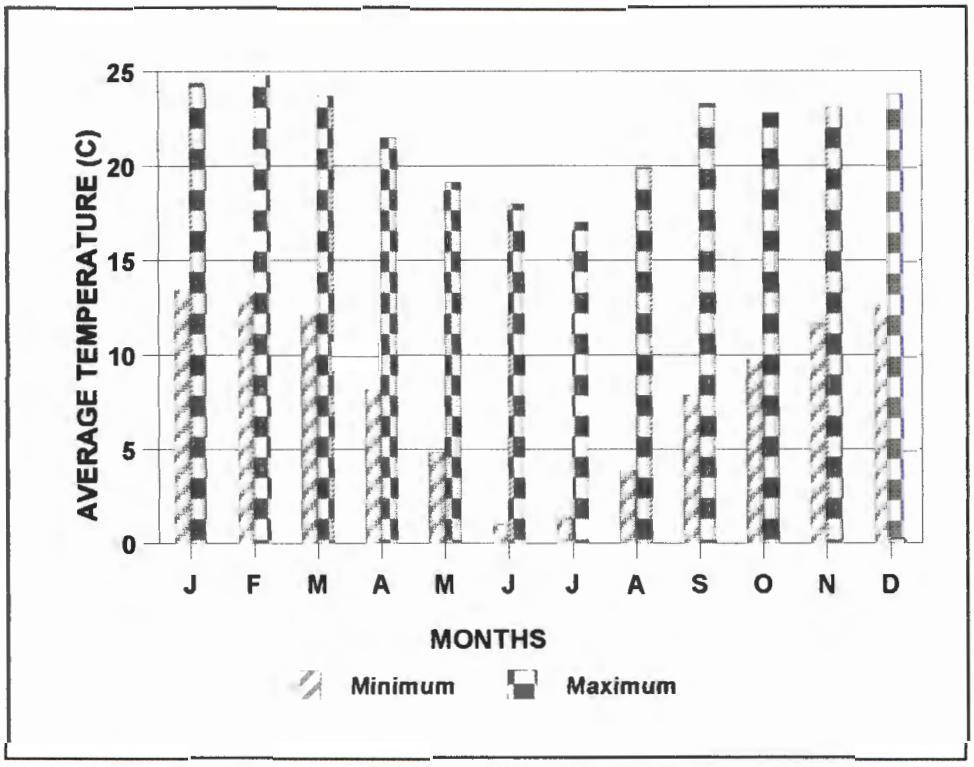


FIGURE 2.2: Average monthly minimum and maximum temperatures at Hendrina Power Station.

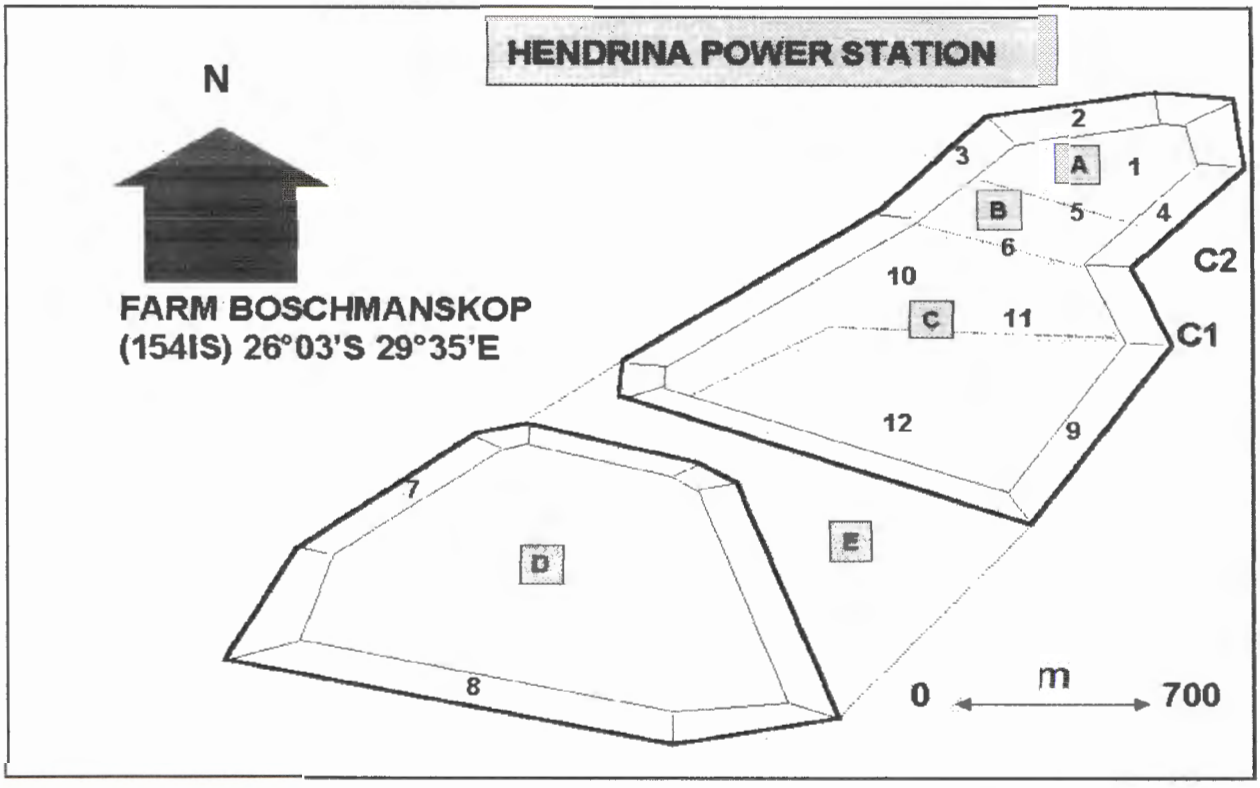


FIGURE 2.3: A map of the ash dams (A-E) at Hendrina Power Station showing the location of the survey grids 1-12 and of the control grids (C1 & C2).

the area adjoins the power station, while the north-west boundary adjoins of a railway line and a coal-loading area. The south-western, southern, and parts of the eastern side of the area are bordered by maize fields. The north-eastern border of the ash disposal areas consists of open cast coal mines and severely disturbed and reclaimed areas due to these mining activities.

2.2 Rehabilitation history

The surface of ash dams A, B, C and D cover an area of approximately 215 ha. The plateaux of ash dam A was revegetated in the early 1980's with *Cortaderia* sp and *Pennisetum clandestinum* (Table 2.1). The *Cortaderia* sp. were removed during 1995 and a 50mm layer of topsoil was added. The soil that was used was possibly a soil form with a plinthic horizon because the soil layer consists of numerous iron and manganese oxide concretions. Revegetation of ash dam C was undertaken at the beginning of the 1990 growing season and a 10cm layer of topsoil, 250kg/ha superphosphate and 200kg/ha of 4:3:4 (30) zinc fertilizer were added. An area of 15 ha was planted with a seed mixture of 16 species of grasses (Table 2.1). The slopes of ash dams A and C were rehabilitated during 1992 and 1994 and 10cm soil layer and a seed mixture of 13 species were added (Table 2.1). *Pennisetum clandestinum* and *Cynodon dactylon* were also planted for erosion control and to stabilize the slopes. The slopes of ash dam D were similar rehabilitated as the rehabilitation of 1992, but the topsoil was from a previous maize field (Table 2.1).

2.3 Survey areas

Ten homogeneous grids were established on the ash dams (Table 2.2). Two control grids (C1 and C2) were also established in a adjacent natural grassland (Figure 2.3). On the ash dams, homogeneous areas were selected to reduce variation in the data and yet also to circumscribe certain factors, such as rehabilitation age, topography, aspect and

ecological status of neighboring areas, which might impact on rehabilitation success. Grids on the ash dams represented both plateaux (Grids 1,10,11 and 12) and slopes (Grids 2,3,4,7,8 and 9). Grids 7and 8 are part of ash dam D, which is still in use and only the middle and bottom parts of these grids are revegetated. Grids 5 and 6 were only used during one pilot study in 1996; further use of these grids were prevented by their small size which precluded the use of the standardized trapping format employed.

TABLE 2.1: Seed mixtures applied on ash dams at Hendrina Power Station

(a) Ashdam A: 1995	(b) Ashdam C: 1990-1991	(c) Slopes (A&C): 1992-1994	(d) Slopes (D): 1992
Pennisetum clandestinum	*Cenchrus ciliaris*	*Chloris gayana*	*Chloris gayana*
Cortaderia sp.	*Chloris gayana*	*Chloris virgata*	*Eragrostis teff*
	Chloris virgata	*Cynodon dactylon*	*Eragrostis curvula*
	Cynodon dactylon	*Digitaria eriantha*	*Eragrostis lehmanniana*
	Digitaria eriantha	*Enneapogon cenchroides*	*Enneapogon cenchroides*
	Enneapogon cenchroides	*Eragrostis chloromelas*	*Eragrostis echinochloidea*
	Eragrostis chloromelas	*Eragrostis curvula*	*Themeda triandra*
	Eragrostis curvula	*Eragrostis echinochloidea*	*Digitaria eriantha*
	Eragrostis echinoclodea	*Eragrostis lehmanniana*	*Cynodon dactylon*
	Eragrostis lehmanniana	*Eragrostis teff*	*Pogonarthria squarrosa*
	Eragrostis teff	*Hyparrhenia hirta*	*Panicum maximum*
	Fingerhutia africana	*Themeda triandra*	*Pennisetum clandestinum*
	Heteropogon contortus	*Pennisetum clandestinum*	
	Hyparrhenia hirta	*Cynodon dactylon*	
	Panicum maximum		
	Themeda triandra		

TABLE 2.2: Layout of grids at Hendrina ash disposal sites to show the date of rehabilitation, topography, aspect and status of adjoining areas. Adjoining area codes are as follow: 0 = rehabilitated land; 1 = rehabilitated and agricultural land; 2 = rehabilitated and disturbed grassland; 3 = rehabilitated and natural grassland; 4 = natural grassland.

Grid	Burnt	Rehabilitation date	Topography	Seed mixtures	Aspect	Adjoining area
C1	Winter 1998	/	FLAT	/	/	4
C2	Winter 1998	/	FLAT	/	/	4
1	Winter 1998	1995	FLAT	a	/	0
2	Winter 1998	1994	SLOPE	c	N	2
3	Winter 1998	1994	SLOPE	c	N	1
4	-	1994	SLOPE	c	E	3
7	-	1992	SLOPE	d	W	1
8	-	1992	SLOPE	d	S	2
9	-	1992	SLOPE	c	E	1
10	-	1991	FLAT	b	/	0
11	-	1992	FLAT	b	/	0
12	-	1990	FLAT	b	/	0

2.4 Vegetation

The vegetation of the study area was classified into three communities, two sub-communities and six variants by Morgenthal (1999), as shown in Table 2.3.

TABLE 2.3: The grouping of the grids at Hendrina Power Station into treatment categories according to the vegetation occurring there (See the text for an explanation of treatment numbers and codes).

GRID	COMMUNITY	SUB-COMMUNITY	VARIANT	TREATMENTS	
1	2	2.1	2.1.3		1
10	2	2.1	2.1.1	2.1	2
11	2	2.1	2.1.1		
12	2	2.1	2.1.1	2.2	
2	2	2.1	2.1.2	3.1	3
3	2	2.1	2.1.2		
4	2	2.1	2.1.2	3.2	
9	2	2.1	2.1.2	3.3	
7 (Top transect)	3	/	/	4.1	4
7 (Middle transect)	2	2.2	2.2.3	4.2	
7 (Bottom transect)	2	2.1	2.1.2	4.3	
8 (Top transect)	3	/	/	5.1	5
8 (Middle transect)	2	2.2	2.2.3	5.2	
8 (Bottom transect)	2	2.1	2.1.2	5.3	
Controls	1	/	/	/	/

Community 1: *Brachiaria* serrata-Setaria *sphacelata* var. *torta*

This community represents the adjacent unrehabilitated grasslands (C1 and C2) which is probably an indication of the type of vegetation that occurred on the area where the ash dams were built. Grass species representing this community are *Brachiaria serrata*, *Setaria sphacelata* var. *torta*, *Tristachya leucothrix*, *Elionurus muticus* and *Heteropogon*

contortus. This area is also characterized by a variety of forbs which include species like *Veronia oligocephala*, *Hermannia transvaalensis*, *Acrotome hispida* and *Pentanisia angustifolia*. During this study there was no indication that this area was utilized for grazing but veld fires occasionally occurred in this area.

Community 2: *Eragrostis curvula-Cynodon dactylon*

This community represent all the rehabilitated study sites on the ash dams and includes grasses like *Eragrostis curvula* and *Cynodon dactylon* and forb species such as *Cyperus esculentus* and *Chamaecrista biensis*. Two sub-communities and six variants were recognized in this community, based on phyto-sociological analysis.

Sub-community 2.1: *Hyparrhenia hirta-Eragrostis curvula*

The two dominant grass species in this sub-community are *Hyparrhenia hirta* and *Eragrostis curvula*. This sub-community includes rehabilitated areas that are older than one year. Three variants occur in this sub-community.

Variant 2.1.1: *Chamaecrista biensis*

This variant represents the plateaux of ash dam C (Figure 2.3) and includes the older rehabilitated sites. The dominant species occurring here are the grasses *Eragrostis curvula*, *Hyparrhenis hirta* and *Cynodon dactylon* and the forb *Chamaecrista biensis*.

Variant 2.1.2: *Lespedeza cuneata-Hyparrhenia hirta*

Most of the slopes of the ash dams rehabilitated during 1992 and 1994 are associated with this variant. Dominant grasses here include *Hyparrhenia hirta*, *Eragrostis curvula* and *Pennisetum clandestinum*. The shrub *Lespedeza cuneata* occurring in this variant is of great interest. It is an exotic species which can be used for the rehabilitation of disturbed areas in a warm climate.

Variant 2.1.3: *Lepidium bonariensis-Eragrostis trichophora*

This variant is characterized by the forb species *Lepidium bonariense*, *Acanthospermum glabratum*, *Hypochaeris radicata* and *Verbena bonariensis* and the dominant occurrence of *Pennisetum clandestinum*. The habitat of this variant is very similar to that of the *Chamaecrista biensis* variant. The *Chamaecrista biensis* variant habitat was revegetated with a seed mixture whereas this habitat was planted with *Pennisetum clandestinum* and *Cortaderia* sp. during the 1980's.

Sub-community 2.2: *Amaranthus hybridus-Cyperus esculentus*

This sub-community is represented by annual forb species such as, *Amaranthus hybridus* and *Chenopodium album* and can be described as a purely ruderal vegetation area dominated by the species, *Cyperus esculentus* and *Tagetes minuta*. This sub-community can also be subdivided into three variants.

Variant 2.2.1: *Portulaca oleracea-Bidens formosa*

Dominant species on this variant include the annual forbs *Tagetes minuta* and *Bidens formosa* and it represents areas where domestic refuse were dumped on already rehabilitated areas on ash dam C. This variant occurs as small mosaics in the *Chamaecrista biensis* Variant.

Variant 2.2.2: *Panicum maximum-Digitaria eriantha*

This variant occupies a small area along a drainage line on the north-eastern slope of ash dam A (Figure 2.3) and is characterized by species like *Panicum maximum*, *Pennisetum clandestinum*, *Digitaria erriantha* and the sedge *Cyperus esculentus*.

Variant 2.2.3: *Eragrostis tef-Enneapogon cenchroides*

This variant represents newly rehabilitated areas which are less than one year old. Two of the most important species occurring here are the annual pioneer grass species, *Enneapogon cenchroides* and *Eragrostis tef* and another annual grass species occurring

here is *Eleusine coracana* subspecies and the crop *Zea mays*.

Community 3: *Spergularia media*

This community is found on the unrehabilitated areas of ash dam D (Figure 2.3) and includes the top parts of grids 7 and 8 where no small mammal sampling was done. Only two species are evident here, the perennial forb *Spergularia media* and the annual forb *Chenopodium album*. This community will eventually be destroyed during the rehabilitation process and will be replaced by other species found in the seed mixtures or topsoil that will be used.

2.5 Small mammal populations

2.5.1 Census methods

Small mammals were sampled on permanent (135 x 60 m) grids, consisting of 5 rows, spaced 15 m apart, with 10 trap stations per row. For each sampling session at each grid, 50 Sherman live traps were set for three consecutive days/nights. Each trap was baited with a peanut butter\oats\garlic polony\sunflower oil mixture and equipped with a piece of cotton wool to reduce cold-induced mortalities. Each trap station was assigned a unique number to ensure that movements of animals within and between grids could be monitored. Traps were checked at dawn and rebaited 48 hrs after initial setting. Sampling was done seasonally and began in May 1997 and ended in January 1999 (Table 2.4).

2.5.2 Handling of animals

Captured animals were identified, anaesthetized and given an individual mark (indicating both the grid number and individual animal number), using either the 1-2-4-7 toe-clipping system (Bronner 1986), or a fur clipping and/or dye method. Upon every capture each small mammal was weighed, sexed and reproductive condition was noted. For males,

external criteria were used to assess reproductive condition. Males were recorded as scrotal (testis enlarged; breeding) and non-scrotal (testis small and/or abdominal). For females, morphological criteria were used to assess reproductive condition. Females were recorded as non-perforated (smooth vaginal closure membrane present), perforated (vaginal membrane rough and scaly) and pregnant or lactating (McCravy & Rose 1992). Once these data were recorded, the animal was released at the point of capture.

TABLE 2.4: The dates and duration of census trapping on the grids during the study period at Hendrina Power station.

MONTH	DATE	SEASON	TRAP-NIGHTS
May 1997	16/5 - 21/5	Autumn	1740
July 1997	15/7 - 20/7	Winter	1740
September 1997	30/9 - 5/10	Spring	1740
December 1997	2/12 - 7/12	Summer	1740
January 1998	28/1 - 2/2	Late summer	1740
May 1998	9/5 - 8/5	Autumn	1740
July 1998	29/7 - 3/8	Winter	1740
September 1998	22/9 - 27/9	Spring	1740
December 1998	1/12 - 6/12	Summer	1740
January 1999	23/ 1- 28/1	Late summer	1740

2.6 Data analysis

Population sizes were estimated using the Minimum Number Alive (MNA) method. This method is less subject to distortions caused by fluctuations in sample size than other statistically based methods (Bronner & Meester 1987). Numerous statistical methods for estimating population sizes were also employed, but proved to be highly variable and unreliable (Chapter 3). Shannon diversity ($\log_e$) and equitability indices were calculated using the MVSP software package and other statistical tests were conducted with STATISTICA 5.1.

Parametric analysis of variance (ANOVA) and multiple regression analysis were used when data were normally distributed and satisfied the criterion of homoscedasticity. When data did not satisfy the criteria of normality and significant deviations from parametric assumptions were detected, non-parametric tests (Kruskal-Wallis ANOVA, Mann-Whitney U-tests) were used. Repeated Measures ANOVA for time-related analyses were used where three or more replicates per survey for each population parameter were available. Tuckey's Honestly-Significant-Difference tests were used for post-hoc comparisons when significant between-groups differences were indicated by parametric analysis of variance. All values illustrated in graphs are mean ± 1 standard deviation. For all tests the 95% level ($p<0.05$) was regarded as statistically significant.

Multivariate ordination techniques were used to investigate the possible small mammal-plant interactions in various survey areas. According to Ter Braak (1986), ordination is the collective term for multivariate techniques that arrange sites along axes on the basis of data on species composition. In an ordination more taxa can be included independently of the biology of a species and the distribution of many species and their relationship to environmental parameters can simultaneously be assessed (Kremen 1992). The result of an ordination in two dimensions (two axes) is a diagram in which sites are represented by points in a two-dimensional space. The aim of the ordination is then to arrange the points in such a matter, that the points which are close together, correspond with sites that are similar in species composition (Ter Braak 1986).

Multivariate analysis was performed using the multivariate statistical package, CANOCO. A Detrended Correspondence Analysis (DCA), which is an indirect gradient analysis, was applied to determine the possible relationship between small mammal species and various plant species on the ash dam and control grids. The eigenvalues associated with each axis is the proportion of variation in sample or species dispersion explained by that axis (Gauch 1982). A DCA was chosen over other available ordination techniques because: (1) this algorithm removes several artifacts such as the arch effect and compression of

gradients at ends; (2) it ordinates sites and species simultaneously within the same ordination space by reciprocal averaging; and (3) it requires no *a priori* assumptions about directions of environmental gradients or weighting of species or sites (Gauch 1982; Knox & Peet 1989; Kremen 1992). DCA is an indirect gradient analysis and the analysis is performed on the distribution of species abundance values alone. Therefore, in the absence of other information, this technique is a good preliminary technique for assessing the ability of faunal and floral distributional data to indicate a particular environmental pattern.

To provide further information on the relationship between small mammal species and other edaphic parameters, a Canonical Correspondence Analysis (CCA) was used. This is an indirect gradient analysis technique and according to Whittaker (1978) such an analysis is used to study the distribution of species along easily measured, recognizable environmental gradients. The significance of a particular edaphic variable can be assessed with a Monte Carlo test of the axis associated with that variable, using the axis' eigenvalue as the test statistic ($p<0.05$) (Ter Braak & Prentice 1988). This technique simultaneously displays the plot and species data along axes of a multi-dimensional space, and is a product of the variability of the environmental - and species data (Kent & Coker 1992). This ordination technique was used during this study due to the long gradients and heterogeneity in the composition of the small mammal community. The aim of a CCA ordination is therefore to detect the main pattern in the relations between the species and the environment and the resulting diagram expresses the patterns of variation in floristic composition and also demonstrates the principal relationship between the species and each of the environmental variables (Kent & Coker 1992).

CHAPTER 3

RESULTS AND DISCUSSION

3.1 Composition of the small mammal fauna

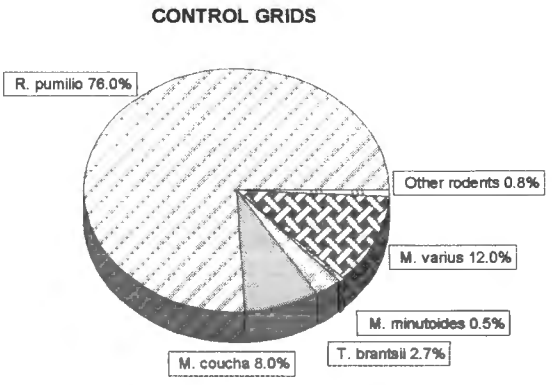
Distribution records included in a national mammal conservation database (Gelderblom, Bronner, Lombard & Taylor 1995), showed that the potential small mammal fauna at Hendrina Power Station comprises 27 species, representing 6 orders. Of these, 20 have been recorded in the study area to date (Appendix 3.1), but only 9 species were captured on the ash dam study grids. A comparison of both the potential and recorded faunas in the study areas with the small mammal communities recorded sub-climax grasslands in similar vegetation types on the highveld (de Wit 1972; Davis 1973) suggests that small mammal diversity has not yet been severely impacted by local industrial activities or agricultural land transformations.

The recorded faunas of both the ash dam grids and the control grids were dominated by rodents, which accounted for more than 85% of the species and individuals captured during all the seasons (Figure 3.1). Three r-selected rodent species predominated in both habitat types, namely *Rhabdomys pumilio*, *Mastomys coucha* and *Tatera brantsii*.

Rhabdomys pumilio (Sparrman, 1784)

The dominant small mammal, both on the ash dams and controls, was the striped mouse *R. pumilio*. This is a small, diurnal and highly adaptable rodent with a mean body mass

(a)



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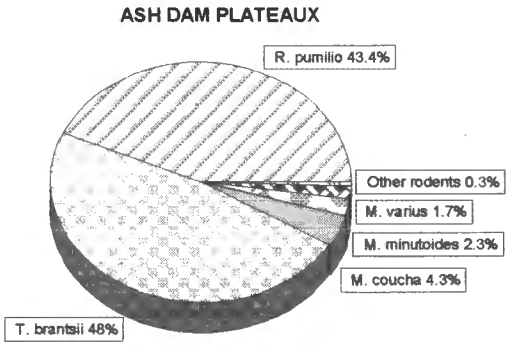


(c)

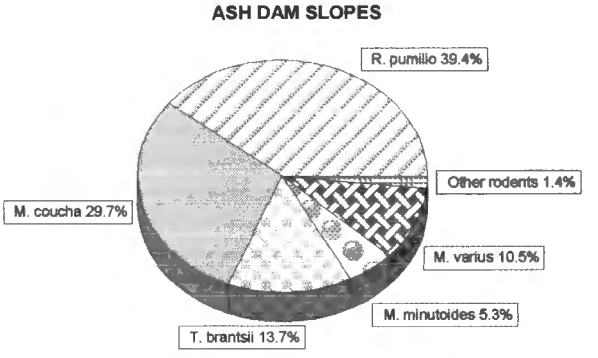


FIGURE 3.1: Small mammal community composition (% of individuals individuals plotted per taxon / group) on control grids (a), ash dam plateaux (b) and ash dam slopes (c), during the two year study period (data for all surveys pooled).

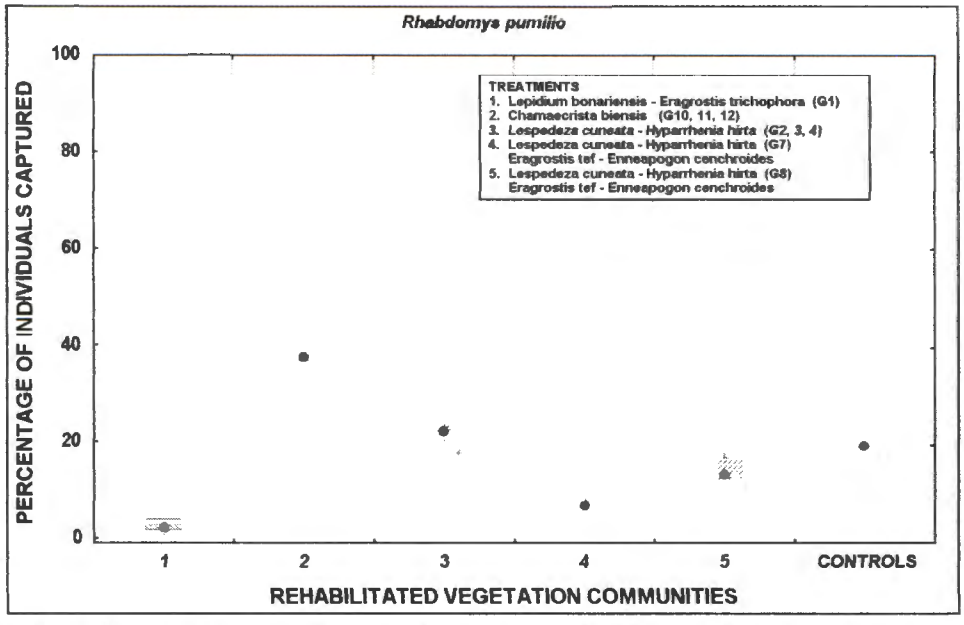


FIGURE 3.2: Percentage of *R. pumilio* individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes indicate ±1se).

of 40-70g. It is easily recognizable because of the presence of the four dark longitudinal stripes along its back. This species is mainly granivorous, but also feeds on green plant materials as well as insects (David & Jarvis 1985). *Rhabdomys pumilio* occurs through most of South Africa, except in the northeastern parts of the country, and is essentially a grassland species present in a diverse area of habitats supporting adequate grass cover. The abundance of this species in relation to the rehabilitation treatments and vegetation communities identified previously (Table 2.3, Section 2.4) is shown in Figure 3.2. *R. pumilio* was especially predominant on the grids associated with the *Lespedeza cuneata-Hyparrhenia hirta* variant, the *Chamaecrista biensis* variant and the controls (Figure 3.2), but these differences were not statistically significant ($H_{5,120}$=8.48; p>0.05). The low numbers in the *Lepidium bonariensis - Eragrostis trichophora* variant (Grid 1) may have been due to the low vegetation cover of this variant (Morgenthal 1999), since *R. pumilio* is a favoured prey item of many diurnal raptors.

Mastomys coucha (A. Smith, 1836)

The multi-mammate mouse, *M. coucha*, is closely related to the Natal multi-mammate mouse, *M. natalensis*, but these species differ in diploid chromosome number (2n=32 vs. 2n=36, respectively; Gordon & Watson 1986). This species ranges from the Eastern Cape northwards through the Free State into Mpumalanga (De Graaff 1981), has 12 pairs of mammae and weighs from 56-70g (Skinner & Smithers 1990).

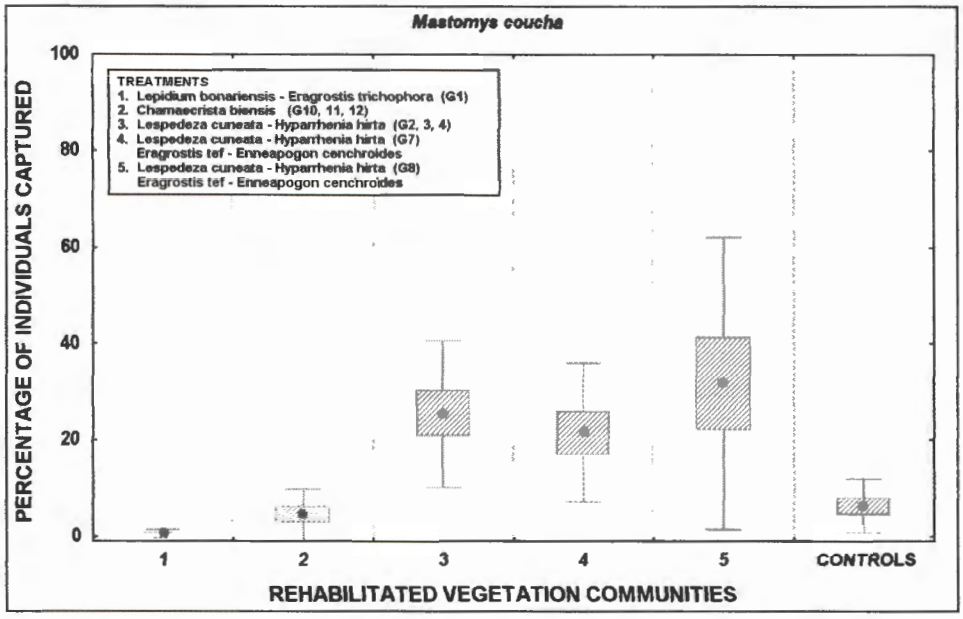


FIGURE 3.3: Percentage of *M. coucha* individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes ±1se).

The multi-mammate mouse, and its cryptic counterpart *M. natalensis*, are extremely adaptable and are therefore found in a wide variety of habitats. They are common in cultivated areas and around human habitations (Coetzee 1975; Meester *et al.* 1979). Being pioneer species, they are commonly found in areas recovering from disturbance, and tend to dominate small mammal communities until other more specialized species become established (Meester *et al.* 1979). Both species are somewhat dependent on water and Coetzee (1980) commented that food water content and relative humidity may influence

their distribution. They are nocturnal animals that eat mainly seeds, but grass stems, rhizomes and insects can also form part of their diet (Coetzee 1975).

During this study, *M. coucha* was captured mainly on the rehabilitated slope grids of the ash dams, associated mainly with the *Lespedeza cuneata-Hyparrhenia hirta* variant, as well as the *Eragrostis tef-Enneapogon cenchroides* variant on grids 7 and 8 (Figure 3.3). These differences in the occurrence of *M. coucha* in the different vegetation variants on the ash dam grids were significant ($H_{4,100}$=33.85; p<0.001).

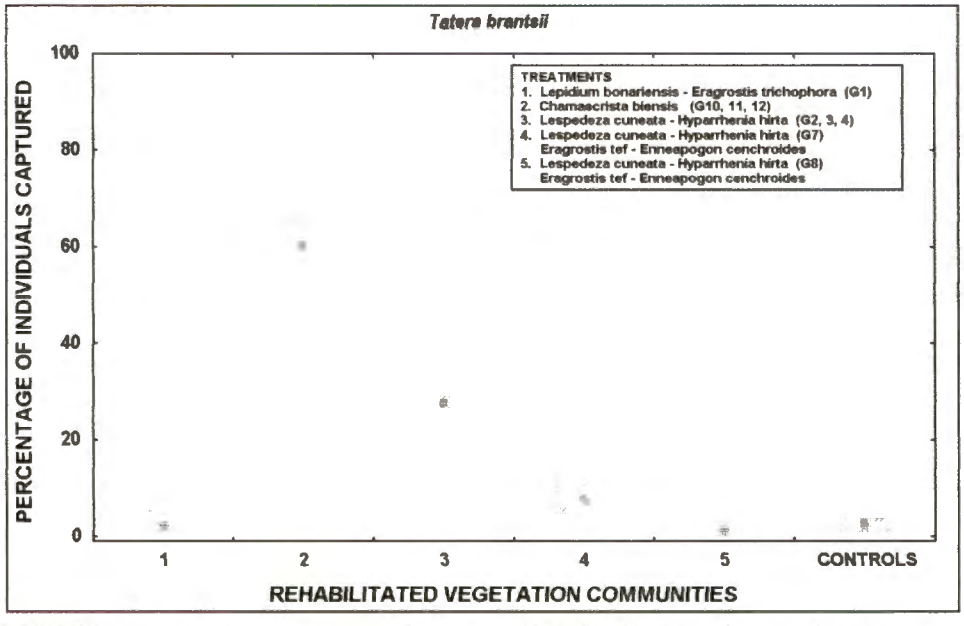


FIGURE 3.4: Percentage of *T. brantsii* individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes ±1se).

Tatera brantsii (A. Smith, 1836)

The Highveld gerbil, *Tatera brantsii,* is one of the most common small mammals on the highveld of South Africa, and also occurs in subtropical and wooded grassland. It is omnivorous with a diet consisting of seeds, grass, leaves and stems and insects (such as

termites) on a seasonal basis. It is a nocturnal species which may have a significant effect on vegetation communities bordering its warrens, through its selective feeding and the constructions of burrows (Korn & Korn 1989; Bronner *et al.* 1999). Figure 3.1 shows that this was the second most abundant species on the ash dams, especially on the plateaux of older rehabilitated grids. Most individuals were captured in the *Chamaecrista biensis* variant and treatment 3 (Figure 3.4). These differences in the occurrence of this species in the different vegetation variants on the ash dam grids were significant ($H_{4,100}$=27.83; $p<0.001$), indicating a clear preference by this species for these vegetation types.

Only 10 individuals were ever caught on the controls, shortly after a veld fire and were therefore considered migrants. The absence of this species from the control grids may be attributed to two factors:

- vegetation differences, since the control grids are characterized by high floristic diversity and crown cover (Morgenthal 1999), whereas *T. brantsii* prefers open areas in the initial stages of plant succession (Kern 1981).
- differences in substrate friability. The soils of the control grids are heavy and rocky, which may deter these burrowers which prefer deep, loose substrates such as the ash dams.

Mus minutoides (A. Smith, 1836)

The pygmy mouse, *Mus minutoides*, ranks among the world's smallest mammals and occurs throughout South Africa. This species occurs in many different types of vegetation and is nocturnal and feed on grass seeds and insects (Skinner & Smithers 1990). During this study it was caught throughout the study area, but in lower numbers on the control grids and Grid 1. It was especially associated with the *Lespedeza cuneata-Hyparrhenia hirta* and *Eragrostis tef - Enneapogon cenchroides* variant (Figure 3.5). These differences in the occurrence of this species in the different vegetation variants on the ash dam grids were highly significant ($H_{4,100}$=14.95; $p<0.01$). Where this species occurs it can also be

considered a pioneer species (De Graaff 1981) and an increase in numbers of this species coincided with an increase in the numbers of the multi-mammate mouse, which may act as a predation shield for the pygmy mouse (De Graaff 1981). This phenomenon was also evident during this study ($r=0.383$; $p<0.001$).

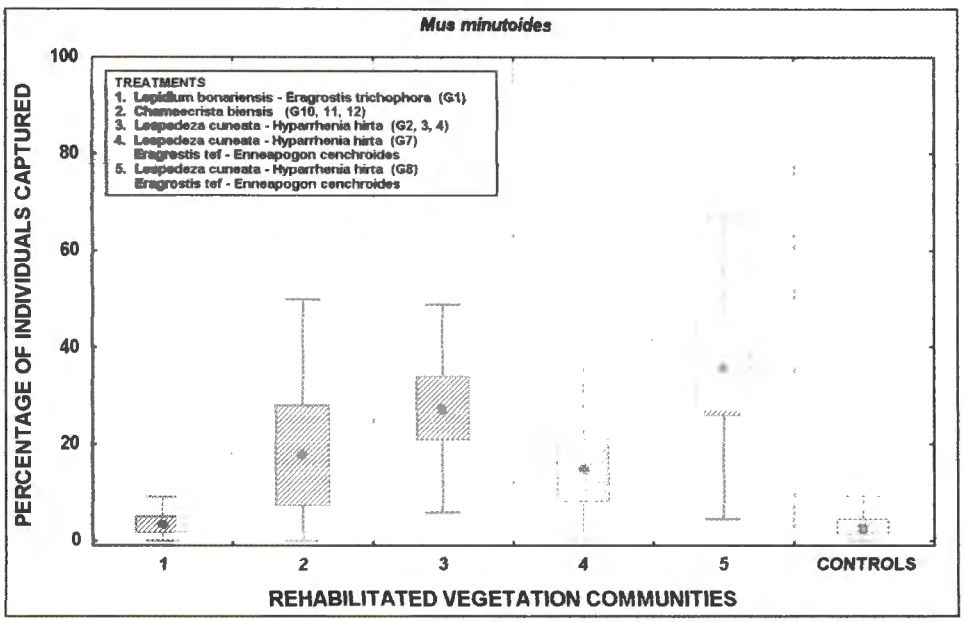


FIGURE 3.5: Percentage of *M. minutoides* individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes ±1se).

Myosorex varius (Smuts, 1832)

The forest shrew, *M. varius*, is the most widely distributed shrew in South Africa and occurs in habitats ranging from primary forest and montane grassland to areas associated with permanent water on the highveld. It is predominantly nocturnal and an opportunistic feeder, consuming a variety of invertebrates (Skinner & Smithers 1990). Where this species occurs it can be considered as a pioneer species which can survive fire better than species such as *R. pumilio* (Meester *et al.* 1979).

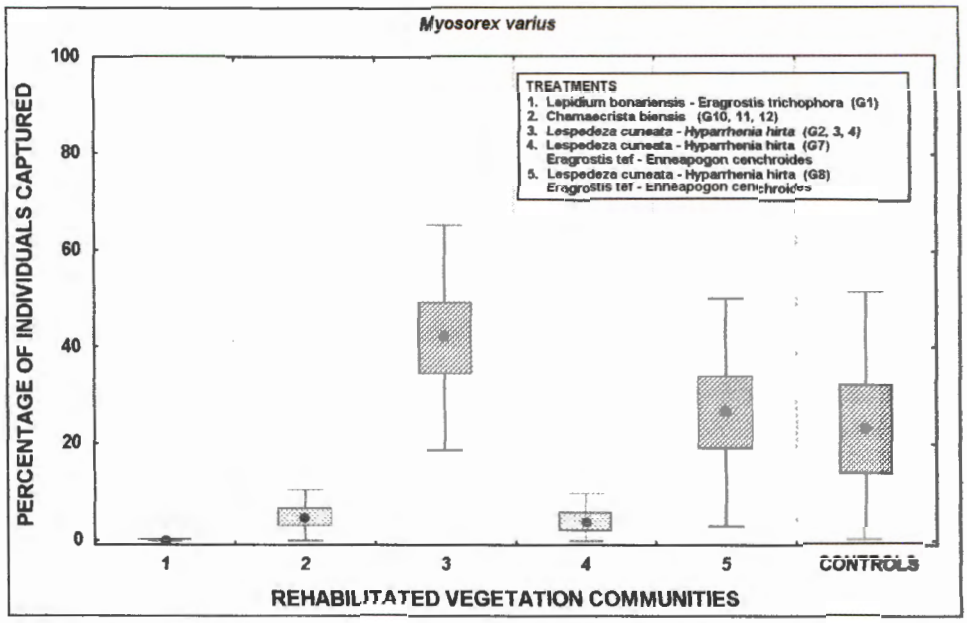


FIGURE 3.6: Percentage of *M. varius* individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes ±1se).

This species was also the only insectivore recorded on the ash dams during the study period. It was not captured on grid 1 and occurred in only low numbers in the *Chamaecrista biensis* variant on the plateaux of ash dam C (Figure 3.6). This species was especially associated with the *Lespedeza cuneata-Hyparrhenia hirta* and *Eragrostis tef - Enneapogon cenchroides* variant on the slope sites of ash dam A, C and D (Figure 3.6). These differences in the occurrence of this species in the different vegetation variants on the ash dam grids were significant ($H_{4,100}$=23.43; $p<0.001$).

Other rodents

Other rodents captured on the study grids during the study period included the Vlei rat, (*Otomys irroratus*), Chestnut climbing mouse (*Dendromys mystacalis*), House mouse (*Mus musculus*) and the House rat (*Rattus rattus*). These were rare species caught in relatively small numbers on all the grids, except on Grid 1 where none of these taxa were recorded

(Figure 3.7).

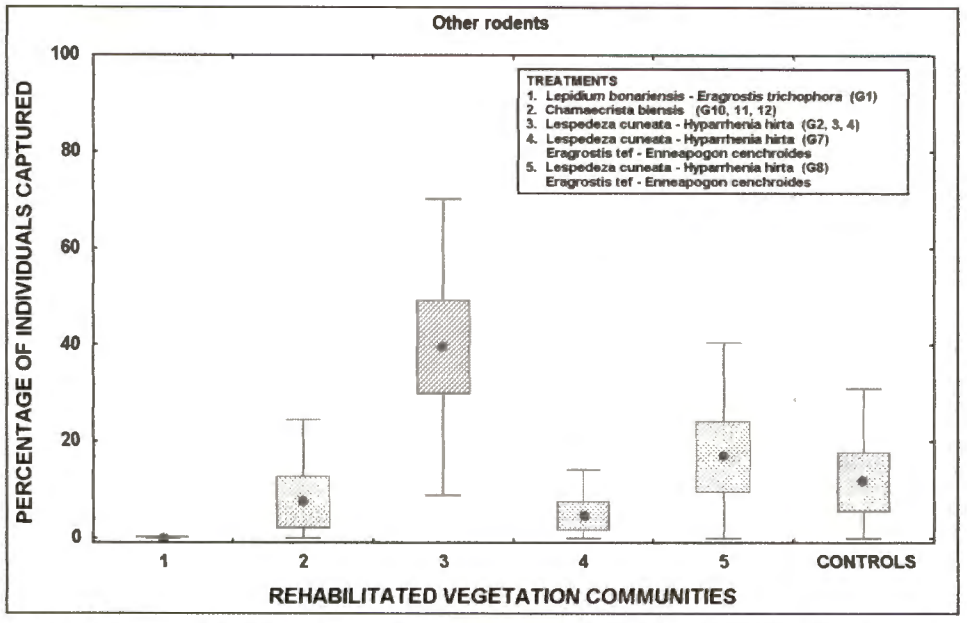


FIGURE 3.7: Percentage of other rodent individuals captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; boxes ±1se)

Fox & Fox (1984) found that *M. musculus* is an opportunistic species and the first small mammal colonist in a disturbed area in Australia, whereas during this study only two individuals were captured (on grids 7 & 8). In South Africa, Skinner & Smithers (1990) reported that *Mus musculus* and *Rattus rattus* are confined to areas around human habitations and that these species seldom move far into natural veld. During this study these species were caught near to a kraal and buildings, which supports this finding.

The vlei rat is a specialized herbivore and is particularly associated with marsh and swamps but is also found in grasslands (Skinner & Smithers 1990). During this study, *Otomys irroratus* was recorded only sporadically on the ash dams, and was caught only in summer and spring. These animals may move over greater distances in summer as part

of their seasonal migration (Rautenbach 1982; Bronner 1986).

Figure 3.8 presents a summary of small mammal community structure at Hendrina Power Station and shows that vegetation variant 3 (*Lespedeza cuneata - Hyparrhenia hirta*), represented by grids 2, 3, 4 & 9, supported the greatest species richness. Conversely vegetation variant 1 (*Lepidium bonariensis - Eragrostis trichophora*), represented by grid 1, was characterized by the lowest species richness. Analysis of patterns of species richness in relation to rehabilitation treatments are considered further in Section 3.6.3. The relationship of the number of small mammal species with different vegetation types is discussed further in Section 3.6.5.

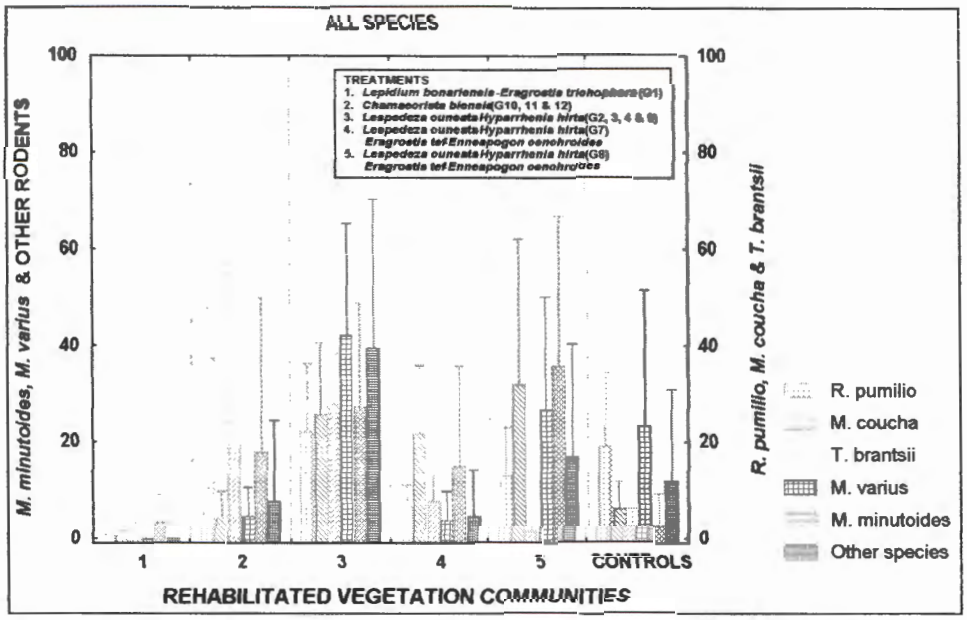


FIGURE 3.8: Percentage of all species captured in different vegetation variants (Table 2.3) within the rehabilitated areas, and on the controls, during all seasons (Bars indicate ±1sd; columns ±1se).

3.2 Trapping success

One commonly-used index of population size is trapping success, defined as the percentage of occupied traps among the total number of traps that were set during a particular capture session (Leirs 1994).

Survey trapping over a period of 17400 trap-nights resulted in 2576 captures involving 2070 small mammals, representing 9 species. An average trap-success of 14.8±7.3% was recorded, while the overall recapture rate was relatively low (27.3±8.9%; Table 3.1). The mean trap success recorded during this study was considerably higher than the mean trap success (2.4%) recorded by Els & Kerley (1996) in the Groendal Wilderness area, Eastern Cape and nearly equal to the mean trap success (11.6%) recorded in the southern parts of the Kalahari (Kerley, Knight, Erasmus 1990). The relevance of such variability is, however, equivocal since trapability and population sizes vary seasonally and spatially in relation to habitat characteristics and resource availability, and are also affected by the trapping regime employed (Flowerdew 1976).

Trapping success varied markedly on a seasonal basis and was highest in autumn and winter 1997, and again in autumn 1998. A significant decrease ($F_{3,6}$= 7.43; $p<0.05$) in trapping success was evident in the spring and summer seasons of both 1997 and 1998/9. Recapture rates, however, tended to increase progressively throughout the study, with a peak in the summer of 1998/9, but this increase was not significant (Table 3.1; Figure 3.9).

The marked seasonal fluctuations in trapping success imply that either trapability or movement patterns changed seasonally, or that there was a marked reduction in population size towards the end of the study period (Figure 3.9). Seasonal fluctuations in trap success similar to those found in this study were also recorded in studies done in Malawi (Happold & Happold 1989; 1990; 1991). This can be related to rainfall, which in turn influences food availability and cover for protection from predators (Section 1.2).

TABLE 3.1: Summary of trapping results for surveys of small mammal populations at Hendrina Power Station.

SURVEY	TRAP NIGHTS	CAPTURES	% TRAP SUCCESS	RECAPTURE RATE	NO. OF INDIVIDUALS	NO. OF SPECIES
Autumn 1997 (May)	1740	440	25.3	14.1	378	8
Winter 1997 (July)	1740	469	27.0	20.7	373	6
Spring 1997 (Sept)	1740	283	16.3	20.9	235	7
Summer 1997 (Dec)	1740	136	7.8	29.5	105	5
Summer 1998 (Jan)	1740	143	8.2	26.1	115	6
Autumn 1998 (May)	1740	402	23.1	17.5	342	6
Winter 1998 (July)	1740	223	12.8	31.2	170	7
Spring 1998 (Sept)	1740	208	12.0	33.3	156	6
Summer 1998 (Dec)	1740	145	8.3	34.3	108	5
Summer 1999 (Jan)	1740	127	7.3	45.5	88	7
TOTAL/ MEAN±SD	**17400**	**2576**	**14.8±7.3**	**27.3±8.9**	**2070**	**9**

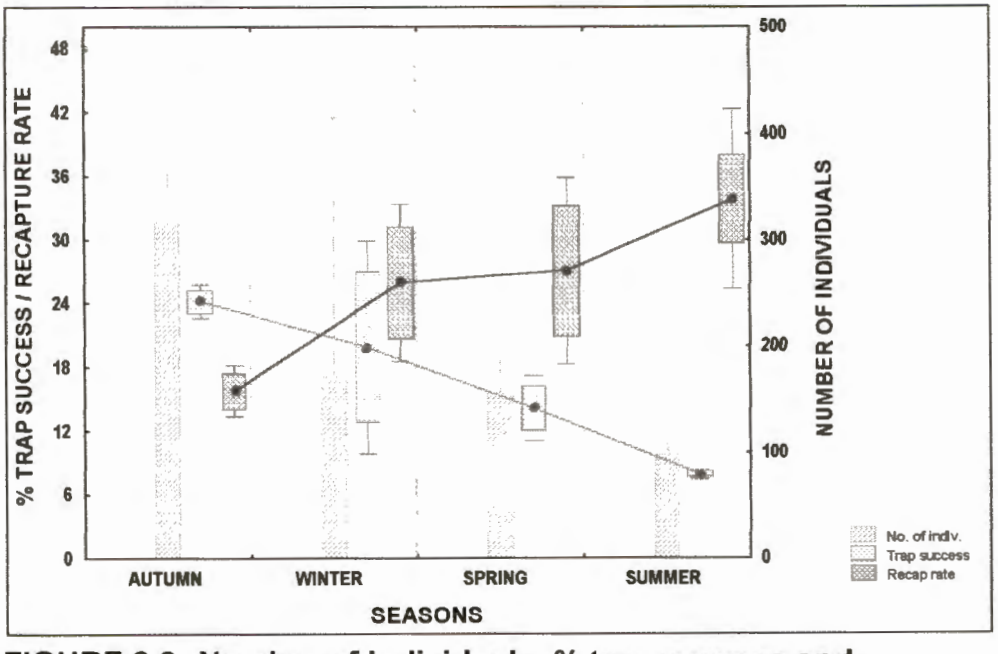


FIGURE 3.9: Number of individuals, % trap success and recapture rates per season during the study period 1997- 1999, for the control and ash dam grids combined (Bars indicate ±1sd; boxes ±1se).

3.3 Catchability & trapability

3.3.1 Catchability

Direct counting of small mammals in a given area is seldom possible and one has to resort to a variety of techniques and methods to obtain a reasonably accurate estimate of population numbers (Leirs 1994). One way to estimate the size of a population is to capture and mark individuals from the population, release them, and then re-sample the population to ascertain which fraction of individuals carry marks (Southern 1973; Krebs 1989). This capture-mark-recapture (CMR) technique can also be used to provide information on birth and mortality rates, and movement patterns.

Enumeration methods, while based on solid data (rather than on statistical estimates), do not provide confidence limits for population estimates, and invariably under-estimate population sizes (Leirs 1994). Statistical methods for estimating population sizes with confidence limits require a set of very restrictive assumptions about the properties of the population being studied (Krebs 1989). Such assumptions are seldom satisfied in living populations, and all of these methods assume that the catchability of individuals is equal. Earlier studies have, however, shown that equal catchability is rare during CMR studies (Krebs 1989). It is thus important to test this assumption during any study of small mammal community dynamics.

According to Smith (1968), the probability of capturing an animal is a function of three separate probabilities:

- the probability of encountering a trap;
- the efficiency of the traps;
- the animal's response to the trap(s);

The probability of encountering a trap depends largely on trap spacing. If traps are placed

too far apart, some animals may be missed between capture points, and thus never encounter a trap. According to Smith, Gardner, Gentry, Kaufman & O' Farrell (1975), a trap spacing of 15m (as used in this study) is a good compromise for most small mammals. Approximate average distances moved by each species during this study mostly exceeded 15m (Section 3.4.1), so it is unlikely that this trap-spacing could have significantly biased results. In any event, biases that may have been introduced were probably standardized (since the same traps and trapping configuration were used on all sampling occasions), and can therefore be ignored.

Animal's responses to traps may vary in relation to age, sex and other demographic factors as well as spatio-temporally (Smith *et al.* 1975; Flowerdew 1976). When Cormack's Method 2 test was applied to CMR results for this study, the variation in catchability of each of the three dominant species was so large that the formulae to calculate significance could not be solved, indicating a strong violation of assumption of the test (Krebs 1989). It is thus clear that in the studied population catchability was not equal for all individuals. This presented serious drawbacks for the interpretation of the population size estimates obtained using CMR procedures. Similar computational problems were reported by Leirs (1994).

Owing to the unequal catchability of individuals in this study, the mean number of captures per individual within and between species was used to determine the influence of certain factors on trapability. This approach follows Bronner (1986) and Leirs (1994).

3.3.2 Trapability

Differential trapability is one of the greatest sources of bias in census studies, and results from differences in behavior when encountering a trap. Certain species are more curious than others and will be caught more easily, while species that are xenophobic avoid traps (Smith *et al.* 1975). This may lead to the overestimation of the number of trap-prone small

mammal species, while the number of trap-shy species will be underestimated (Fleming 1975). When considering behavioral response to traps, factors such as age, sex and reproductive condition must be considered, since these may influence trapability rates within species (Smith *et al.* 1975). Older animals, which often rank higher in the social order, may be caught more often than younger individuals due to differential learning and differences in activity and movement patterns. Trapability may also vary between sexes, with breeding males moving over larger areas than non-breeding males in search of mates, leading to higher trapability rates during the breeding season; whereas breeding females may be restricted to the vicinity of the nests and the young (Smith *et al.* 1975).

Activity patterns of most vertebrates are also affected by changes in weather, and small mammals are generally more active on warm, cloudy nights accompanied by rain (Gentry, Golley & McGinnis 1966; Smith *et al.* 1975). Weather can thus affect the activity and trapability of small mammals. According to Gentry *et al.* (1966), habitat characteristics have a greater influence on captures than changes in weather, and effects of weather are difficult to isolate due to interactions between factors such as, rainfall, temperature, moonlight, seasons, etc.

3.3.2.1 Differences in trapability between species

Trapability rates, expressed as the mean number of captures per individual (Bronner 1986), differed among species on a seasonal basis. There was a significant difference in trapability between species in autumn (May) and winter (July) 1997, autumn (May) 1998, spring (September) 1998 and late summer (January 1999; Table 3.2). During autumn and winter, *R. pumilio* and *M. coucha* were significantly more trapable than the other species. This is a phenomenon that has been documented by numerous studies (Skinner & Smithers 1990), and points to the trap-prone nature of these species. In spring and summer of 1998, *T. brantsii* and *M. varius* also showed elevated trapability relative to the other species (Table 3.2).

TABLE 3.2: Trapability rates for 9 small mammal species (mean ± 1sd captures per individual, all grids combined). NC = not captured; N/A = sample sizes insufficient for statistical comparisons; NSD = no significant difference. Statistical comparisons using Kruskal-Wallis Analysis of Variance (H statistic) due to non-parametric distribution of variables. (* = p<0.05; ** = p<0.01; *** = p<0.001). Sample sizes are given in parentheses.

SPECIES	MAY 1997	JULY 1997	SEPT 1997	DEC 1997	JAN 1998	MAY 1998	JULY 1998	SEPT 1998	DEC 1998	JAN 1999	KW ANOVA
Rhabdomys pumilio	1.28 ± 0.5 (229)	1.31 ± 0.5 (200)	1.27 ± 0.5 (112)	1.32 ± 0.5 (56)	1.26 ±0.5 (77)	1.18 ±0.4 (183)	1.27 ±0.5 (44)	1.31 ±0.6 (42)	1.48 ±0.7 (27)	1.55 ±0.8 (31)	$H_{1.100}$= 17.26 *
Mastomys coucha	1.25 ±0.5 (49)	1.49 ±0.6 (47)	1.30 ± 0.6 (43)	1.40 ±0.5 (10)	NC	1.33 ±0.5 (43)	1.44 ±0.6 (57)	1.47 ±0.6 (58)	1.38 ±0.7 (32)	1.5 ± 0.5 (60	NSD
Tatera brantsii	1.00 ±0.0 (39)	1.10 ± 0.6 (68)	1.08 ±0.3 (50)	1.29 ±0.6 (24)	1.32 ±0.5 (19)	1.06 ±0.2 (67)	1.17 ±0.4 (60)	1.13 ±0.4 (48)	1.23 ±0.5 (40)	1.27 ±0.5 (43)	$H_{8.458}$= 24.6 **
Mus minutoides	1.00 ±0.0 (12)	1.11 ±0.3 (9)	1.17 ±0.4 (6)	1.25 ±0.7 (8)	1.00 ±0.0 (1)	1.00 ±0.0 (22)	1.00 ±0.0 (2)	1.5 ±0.7 (2)	1.13 ±0.4 (8)	1.00 ±0.0 (1)	NSD
Otomys irroratus	1.00 ±0.0 (1)	1.00 ±0.0 (2)	1.00 ±0.0 (2)	NC	1.00 ±0.0 (1)	1.00 ±0.0 (2)	1.00 ±0.0 (3)	NC	NC	NC	N/A
Dendromus mystacalis	1.00 ±0.0 (1)	NC	NC	NC	NC	NC	1.00 ±0.0 (1)	1.00 ±0.0 (10	NC	NC	N/A
Mus musculus	NC	NC	NC	NC	2.00 ±0.0 (1)	NC	NC	NC	NC	1.33 ±0.6 (3)	N/A
Rattus rattus	1.00 ±0.0 (1)	NC	1.00 ±0.0 (1)	NC	NC	NC	NC	NC	NC	1.00 ±0.0 (1)	N/A
Myosorex varius	1.02 ±0.2 (42)	1.13 ± 0.3 (45)	1.05 ±0.2 (20)	1.00 ±0.0 (8)	1.27 ±0.6 (15)	1.11 ±0.3 (28)	1.14 ±0.4 (7)	1.13 ±0.4 (8)	1.00 ±0.0 (3)	2.2 ±0.8 (5)	$H_{8.181}$= 33.15 ***
KW ANOVA	$H_{4.371}$= 19.98 ***	$H_{4.369}$= 21.07 ***	NSD	NSD	NSD	$H_{4.343}$= 17.04 **	NSD	$H_{4.158}$= 11.14 *	NSD	$H_{4.86}$= 10.32 *	

However, if this was the case, trap success and the number of individuals captured (MNA) would also be expected to increase in summer, instead of decreasing as observed. This again suggests that resources were so abundant that animals were not inclined to enter traps.

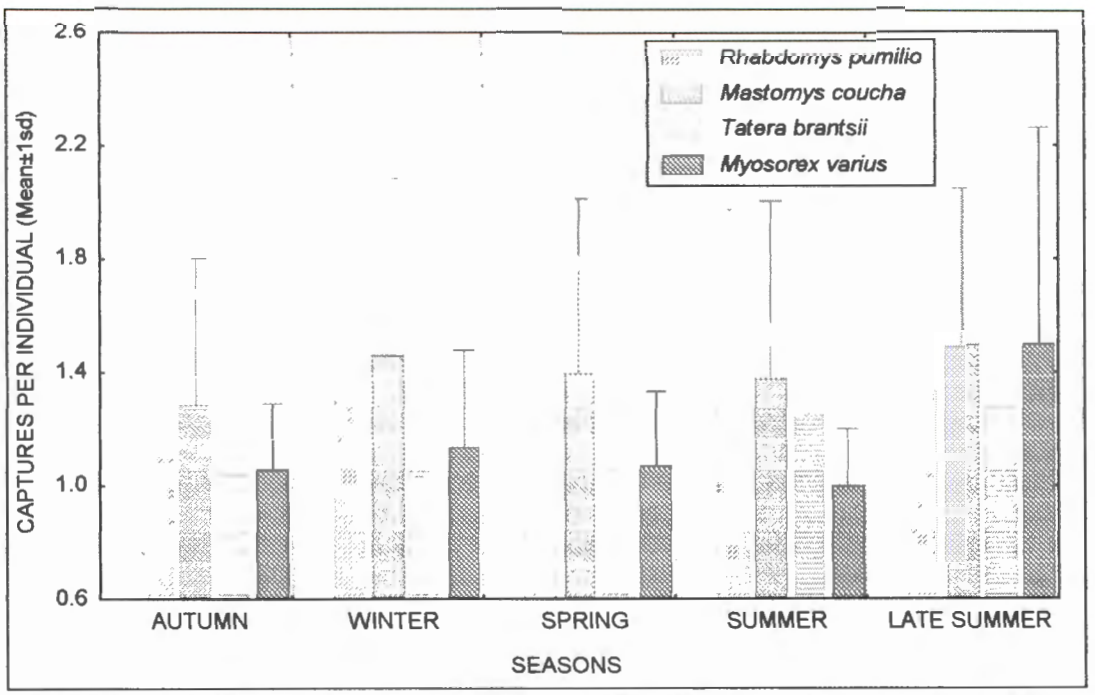


FIGURE 3.10: Seasonal trapability rates for the four dominant small mammal species at Hendrina Power Station throughout the survey period 1997-1999 (Data for seasons pooled; bars indicate ±1sd).

3.3.2.2 Differences in trapability within the three dominant species

When considering differential trapability, the influence of several inter-related factors such as sex, age and reproductive condition must be borne in mind (Smith *et al.* 1975). These factors may influence the behavioral response of animals to traps, so that some are trap-shy, while others are capture-prone (Smith *et al.* 1975; Flowerdew 1976).

According to Tanaka (1956; in Smith *et al.* 1975), trap-proneness is indicated when the recapture rate exceeds the initial capture rate. During this study, the initial capture rate exceeded recapture rates for each of the three dominant species (*R. pumilio* 1.27±0.52 vs. 1.15±0.35; *M. coucha* 1.39±0.59 vs. 1.18±0.38; *T. brantsii* 1.14±0.38 vs. 1.08±0.28), indicating that none were particularly trap-prone. This was also evident for all species during each season on both the control and ash dam grids (Table 3.3).

TABLE 3.3: Mean capture- and recapture rates during each season on the control and ash dam grids for all species combined.

	ASH DAM GRIDS		CONTROL GRIDS	
SEASONS	CAPTURE RATE	RECAPTURE RATE	CAPTURE RATE	RECAPTURE RATE
AUTUMN	1.16 ± 0.40	1.10 ± 0.30	1.20 ± 0.45	1.11 ± 0.31
WINTER	1.26 ± 0.49	1.10 ± 0.30	1.30 ± 0.58	1.25 ± 0.44
SPRING	1.27 ±0.52	1.16 ± 0.37	1.11 ± 0.36	1.14 ± 0.38
SUMMER	1.31 ±0.56	1.19 ± 0.40	1.29 ± 0.57	1.25 ± 0.46
ALL SEASONS	1.24 ± 0.49	1.14 ± 0.35	1.22 ± 0.49	1.17 ± 0.38

3.3.2.2.1 Differences in trapability according to sex

Rhabdomys pumilio

Table 3.4 compares mean trapability for males and females of the striped mouse, *R. pumilio,* based on a total capture of 1001 (538 males and 463 females) individuals. Regardless of whether surveys were treated separately or pooled, there were no significant differences in trapability between males and females. There were also no significant differences between the survey periods in either males or females, but trapability tended to increase towards the end of the study period in December 1998 and January 1999 in both sexes. Mean trapability for males was generally lower than females during May 1997 and January 1999, when females were more trapable than males. Sex-related differences in trapability were thus negligible for this species.

TABLE 3.4: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for *R. pumilio* during the different surveys for all grids combined. Most *R. pumilio* individuals were only captured once and therefore the trapability data deviated from normality (K-s d=0.465 p<0.01; Shapiro-Wilk W=0.544 p<0.000) and were characterized by kurtosis (2.26 ± 0.15) and skewedness (1.77 ± 0.08). Non-parametric statistical analyses were therefore used.

	MALES		FEMALES		MANN-WHITNEY	
SURVEYS	**n**	**Mean ± sd**	**n**	**Mean ± sd**	**U**	**p**
May 1997	120	1.22 ± 0.47	109	1.24 ± 0.47	6367	0.729
July 1997	105	1.32 ± 0.55	95	1.28 ± 0.54	4784	0.619
Sept 1997	69	1.32 ± 0.56	43	1.19 ± 0.39	1339	0.387
December 1997	22	1.36 ± 0.49	34	1.29 ± 0.58	334	0.502
January 1998	41	1.29 ± 0.46	36	1.22 ± 0.54	657	0.827
May 1998	101	1.23 ± 0.49	82	1.21 ± 0.33	3811	0.354
July 1998	27	1.41 ± 0.57	17	1.06 ± 0.24	157	0.083
Sept 1998	25	1.36 ± 0.57	17	1.24 ± 0.56	184	0.473
December 1998	12	1.50 ± 0.80	15	1.47 ± 0.64	88	0.922
January 1999	16	1.44 ± 0.63	15	1.67 ± 0.90	108	0.635
All surveys	538	1.29 ± 0.52	463	1.24 ± 0.50	117 957	0.148
KW ANOVA	nsd		nsd			

Mastomys coucha

A total of 344 (173 males and 171 females) individuals were captured during this study. The trapability of males and females is compared in Table 3.5. There were no statistically-significant differences between the mean trapability of the sexes or between the surveys, regardless of whether data for the different surveys were analyzed separately or pooled. The same trend was evident in a study on *M. natalensis* by Bronner (1986), whereas Leirs (1994) found that male *M. natalensis* were significantly more trapable than females.

TABLE 3.5: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for *M. coucha* during the different surveys. Data for all grids combined. Most individuals of *M. coucha* were captured only once and therefore the data deviated from normality (K-s d=0.413 p<0.01; Shapiro-Wilk W=0.629 p<0.000) and were characterized by kurtosis (0.62 ± 0.26) and skewedness (1.28 ± 0.13). Non-parametric statistical analyses were therefore used.

	MALES		FEMALES		MANN-WHITNEY	
SURVEYS	**n**	**Mean ± sd**	**n**	**Mean ± sd**	**U**	**p**
May 1997	20	1.35 ± 0.67	29	1.17 ± 0.38	262	0.576
July 1997	23	1.43 ± 0.66	24	1.54 ± 0.59	242	0.469
Sept 1997	22	1.32 ± 0.65	21	1.29 ± 0.56	231	1.00
December 1997	5	1.40 ± 0.55	5	1.40 ± 0.55	13	1.00
January 1998	-	-	-	-	-	-
May 1998	24	1.38 ± 0.50	19	1.26 ± 0.56	195	0.420
July 1998	31	1.48 ± 0.68	26	1.39 ± 0.57	379	0.70
Sept 1998	31	1.58 ± 0.72	27	1.33 ± 0.48	351	0.293
December 1998	16	1.31 ± 0.60	15	1.47 ± 0.74	109	0.649
January 1999	1	2.00 ± 0.00	5	1.40 ± 0.59	-	-
All surveys	173	1.43 ± 0.64	171	1.35 ± 0.55	14 055	0.425
KW ANOVA		*nsd*		*nsd*		

No individuals of this species were caught during the January 1998 survey period and only a few individuals were caught during January 1999. Possible explanations for this could be:

- the bait used in traps become unattractive with plentiful food around;
- in the rainy season the ash dams may have been less attractive to this species because of the abundance of food and shelter in adjoining natural (i.e. unrehabilitated) areas. Dispersal is often elevated under such conditions (Gliwicz 1985). At Hendrina Power Station this phenomenon may be pronounced since

adjoining unrehabilitated areas are burned (accidentally or deliberately) almost every winter, and the vegetation is only restored during the subsequent spring and summer. Under such a regime it is likely that the ash dams, which are to a large extent protected from veld fires by management practices, may serve as refugia for small mammals in the dry winter and early spring months when vegetation on adjacent natural areas has been destroyed; and that dispersal from the ash dams into adjoining areas is high in summer when vegetation on the latter has recovered. Although probable, I have no data to substantiate this hypothesis since the configuration of trapping grids used would not have detected any such dispersal.

Tatera brantsii

During this study 458 individuals (174 males and 284 females) were captured. Trapability did not vary significantly between males and females within any survey, or among survey periods (Table 3.6). However, trapability tended to be higher during the summer survey periods for both sexes, a trend evident also in the other two dominant species.

3.3.2.2.2 Differences in trapability according to reproductive status

Rhabdomys pumilio

Pregnant or lactating females were caught in the traps from September to May during the study period, with the highest mean trapability occurring during May 1997 and January 1999. While pregnant or lactating females tended to be more trapable than non-breeding individuals across all surveys, the trapability of females did not differ significantly in relation to reproductive status during any survey (Table 3.7a). The trapability of non-reproductive females varied significantly among surveys, being lower from September 1997 to July 1998, but no such statistical trend was evident for pregnant and lactating females.

TABLE 3.6: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for *T. brantsii* during the different surveys. Data for all grids combined. Most of the individuals of *T. brantsii* were only captured once and therefore the data deviated from normality (K-s d=0.516 p<0.01; Shapiro-Wilk W=0.404 p<0.001) and were characterized by kurtosis (6.78 ± 0.23) and skewedness (2.68 ± 0.11). Non-parametric statistical analyses were therefore used.

	MALES		FEMALES		MANN-WHITNEY	
SURVEYS	**n**	**Mean ± sd**	**n**	**Mean ± sd**	**U**	**p**
May 1997	8	1.00 ± 0.0	31	1.00 ± 0.0	-	-
July 1997	28	1.11 ± 0.32	40	1.1 ± 0.30	556	0.960
Sept 1997	13	1.08 ± 0.28	37	1.08 ± 0.28	240	0.980
December 1997	9	1.22 ± 0.44	15	1.33 ± 0.62	64	0.811
January 1998	3	1.33 ± 0.58	16	1.31 ± 0.48	24	0.955
May 1998	26	1.04 ± 0.20	41	1.07 ± 0.26	515	0.811
July 1998	22	1.23 ± 0.43	38	1.13 ± 0.34	378	0.539
Sept 1998	19	1.05 ± 0.23	29	1.17 ± 0.47	252	0.613
December 1998	23	1.17 ± 0.39	17	1.29 ± 0.59	182	0.702
January 1999	23	1.26 ± 0.54	20	1.25 ± 0.55	227	0.932
All surveys	174	1.138 ± 0.36	284	1.141 ± 0.39	24 602	0.939
KW ANOVA		nsd		nsd		

Males showed similar trends in trapability as females (Table 3.7 b). Some males were able to breed throughout the year, a result reported also by David & Jarvis (1985). However, when data for all surveys were pooled, reproductively-active males were significantly more trapable than non-reproductive males (Table 3.7 b). This could be due to increased activity and movement of reproductive males associated with a search for mates during the breeding season (Golley *et al.* 1975). The highest number of non-breeding individuals was captured towards the end of the trapping period (January 1999), reflecting recruitment associated with summer breeding (Section 3.7.2).

TABLE 3.7: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for breeding and non-breeding females (a) and males (b) of *R. pumilio* throughout the study period.

(a) FEMALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
SURVEYS	n	Mean ± sd	n	mean ± sd	U	p
May 1997	80	1.21 ± 0.44	5	1.80 ± 0.84	114	0.106
July 1997	75	1.33 ± 0.58	-	-	-	-
Sept 1997	27	1.19 ± 0.40	9	1.22 ± 0.44	117	0.869
December 1997	8	1.13 ± 0.35	23	1.39 ± 0.66	75	0.430
January 1998	15	1.13 ± 0.52	21	1.29 ± 0.56	133	0.422
May 1998	76	1.11 ± 0.31	6	1.33 ± 0.52	176	0.354
July 1998	16	1.06 ± 0.25	1	1.00 ± 0.0	-	-
Sept 1998	16	1.25 ± 0.58	1	1.00 ± 0.0	-	-
December 1998	10	1.50 ± 0.53	5	1.40 ± 0.89	20	0.540
January 1999	6	1.83 ± 0.98	9	1.56 ± 0.88	23	0.596
All surveys	329	1.22 ± 0.48	80	1.38 ± 0.64	11 816	0.156
KW ANOVA	$H_{8,254}$ = 18.56; p<0.05		nsd			

(b) MALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
SURVEYS	n	Mean ± sd	n	Mean ± sd	U	p
May 1997	75	1.20 ± 0.49	16	1.31 ± 0.48	516	0.381
July 1997	86	1.31 ± 0.54	1	3.00 ± 0.0	-	-
Sept 1997	18	1.28 ± 0.46	45	1.38 ± 0.61	384	0.749
December 1997	4	1.25 ± 0.50	17	1.41 ± 0.51	29	0.622
January 1998	6	1.00 ± 0.0	35	1.34 ± 0.48	69	0.184
May 1998	86	1.24 ± 0.48	9	1.22 ± 0.67	353	0.666
July 1998	26	1.42 ± 0.58	1	1.00 ± 0.0	-	-
Sept 1998	10	1.20 ± 0.42	15	1.47 ± 0.64	59	0.375
December 1998	3	1.00± 0.0	8	1.75 ± 0.89	6	0.221
January 1999	2	1.50 ± 0.71	14	1.43 ± 0.65	13	0.812
All surveys	316	1.26 ± 0.50	161	1.40 ± 0.59	22 620	0.048
KW ANOVA	nsd		nsd			

Mastomys coucha

For females, sample sizes were generally too small within survey periods for meaningful statistical analysis, except in July and September 1998. Non-breeding individuals appeared to be more trapable than breeding individuals in the first year of the study, whereas trapability of breeding individuals tended to be higher in the last three surveys. However, no significant differences were evident among surveys within either group (Table 3.8a). For males, again the sample sizes were generally too small for any meaningful statistical analysis. Non-breeding individuals, however, tended to be more trapable than breeding individuals during the last three surveys. Again, no significant differences were evident within either group (Table 3.8b).

Tatera brantsii

There were no statistically significant differences in mean trapability of either males or females in relation to reproductive status within any survey (Table 3.9 a & b). Reproductive females were, however, significantly more trapable during the wet, warm spring and summer months (from September to January), whereas the trapability of non-reproductive females remained relatively high throughout the study period (Table 3.9 a). Trapability of breeding females was significantly lower in autumn (May) and winter (July). This cannot be attributed to seasonal differences in movement patterns, since the average distance moved between recaptures did not vary significantly among seasons, and tended to be higher in autumn and winter (Section 3.4.2). This low trapability rate could therefore reflect the reduced activity during the cold winter months when food is limited and foraging may be less economical in terms of satisfying energetic demands.

Non-breeding males however, were only captured during May, July and September of each year, whereas breeding males were generally more trapable throughout the survey period. No significant differences in trapability were however evident between these two groups (Table 3.9b).

TABLE 3.8: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for breeding and non-breeding females (a) and males (b) of *M. coucha* throughout the study period.

(a) FEMALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
SURVEYS	n	Mean ± sd	n	Mean ± sd	U	p
May 1997	26	1.15 ± 0.37	1	1.00 ± 0.0	-	-
July 1997	19	1.47 ± 0.61	1	1.00 ± 0.0	-	-
Sept 1997	19	1.32 ± 0.58	1	1.00 ± 0.0	-	-
December 1997	4	1.50 ± 0.58	1	1.00 ± 0.0	-	-
January 1998	-	-	-	-	-	-
May 1998	19	1.26 ± 0.56	-	-	-	-
July 1998	23	1.43 ± 0.59	3	1.00 ± 0.0	21	0.279
Sept 1998	20	1.35 ± 0.49	5	1.4 ± 0.55	48	0.865
December 1998	13	1.38 ± 0.77	2	2.0 ± 0.0	-	-
January 1999	2	1.00 ± 0.0	3	1.67 ± 0.58	-	-
All surveys	145	1.33 ± 0.55	17	1.35 ± 0.49	1173	0.743
KW ANOVA	nsd		nsd			

(b) MALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
SURVEYS	n	Mean ± sd	n	Mean ± sd	U	p
May 1997	17	1.35 ± 0.70	-	1.5 ± 0.70	-	-
July 1997	19	1.42 ± 0.61	-	-	-	-
Sept 1997	7	1.29 ± 0.49	14	1.21 ± 0.58	43	0.654
December 1997	-	-	3	1.33 ± 0.58	-	-
January 1998	-	-	-	-	-	-
May 1998	24	1.38 ± 0.49	-	-	-	-
July 1998	30	1.5 ± 0.68	-	-	-	-
Sept 1998	21	1.71 ± 0.78	8	1.38 ± 0.52	66	0.367
December 1998	4	1.75 ± 0.96	13	1.15 ±0.38	16	0.258
January 1999	-	-	-	-	-	-
All surveys	123	1.47 ±0.66	41	1.24 ± 0.49	2180	0.131
KW ANOVA	nsd		nsd			

TABLE 3.9: Mean trapability (mean number of captures per individual), sample sizes (n) and standard deviations (sd) for breeding and non-breeding females (a) and males (b) of *T. brantsii* throughout the study period.

(a) FEMALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
	n	Mean ± sd	n	Mean ± sd	U	p
May 1997	19	1.00 ± 0.0	12	1.00 ± 0.0	114	1.00
July 1997	24	1.13 ± 0.34	16	1.06 ± 0.25	180	0.740
Sept 1997	9	1.00 ± 0.0	25	1.12 ± 0.33	99	0.598
December 1997	3	1.00 ± 0.0	9	1.56 ± 0.73	8	0.267
January 1998	3	1.67 ± 0.58	13	1.23 ± 0.44	11	0.253
May 1998	37	1.08 ± 0.28	4	1.00 ± 0.0	68	0.792
July 1998	30	1.17 ± 0.38	8	1.00 ± 0.0	100	0.474
Sept 1998	25	1.16 ± 0.47	4	1.50 ± 0.58	32	0.255
December 1998	15	1.27 ± 0.59	-	-	-	-
January 1999	17	1.24 ± 0.56	-	-	-	-
All surveys	182	1.14 ± 0.39	95	1.17 ± 0.40	8337	0.626
KW ANOVA	nsd		$H_{5\ df} = 19.04$; $p<0.05$			

(b) MALES	NON-BREEDING		BREEDING		MANN-WHITNEY	
	n	Mean ± sd	n	Mean ± sd	U	p
May 1997	1	1.00 ± 0.0	7	1.00 ± 0.0	-	-
July 1997	4	1.00 ± 0.0	24	1.13 ± 0.34	42	0.694
Sept 1997	2	1.00 ± 0.0	10	1.10 ± 0.32	9	0.830
December 1997	-	-	7	1.29 ± 0.49	-	-
January 1998	-	-	-	-	-	-
May 1998	10	1.00 ± 0.0	16	1.06 ± 0.25	75	0.792
July 1998	6	1.00 ± 0.0	16	1.31 ± 0.48	33	0.269
Sept 1998	5	1.00 ± 0.0	14	1.07 ± 0.27	33	0.817
December 1998	-	-	21	1.19 ± 0.40	17	0.663
January 1999	-	-	23	1.26 ± 0.54	-	-
All surveys	32	1.00 ± 0.0	140	1.17 ± 0.40	1872	0.148
KW ANOVA	nsd		nsd			

3.3.2.2.3 Differences in trapability among survey areas

Rhabdomys pumilio

Trapability of *R. pumilio* was significantly higher ($H_{1,1001}$=5.03; p<0.05) on the ash dam grids than on the control grids (Figure 3.11). This was due to the fact that female individuals were significantly more trapable on the ash dam grids than on the control grids ($H_{1,463}$=4.01; p<0.05). The trapability of males, however, did not vary significantly between the two areas (Figure 3.11). The higher overall trapability on the ash dam grids could reflect the less heterogenous habitats of the rehabilitated areas (Morgenthal 1999), with lower resource availability, and /or greater movement by this species on the ash dam grids ($H_{1,257}$=4.29; p<0.05; Section 3.4).

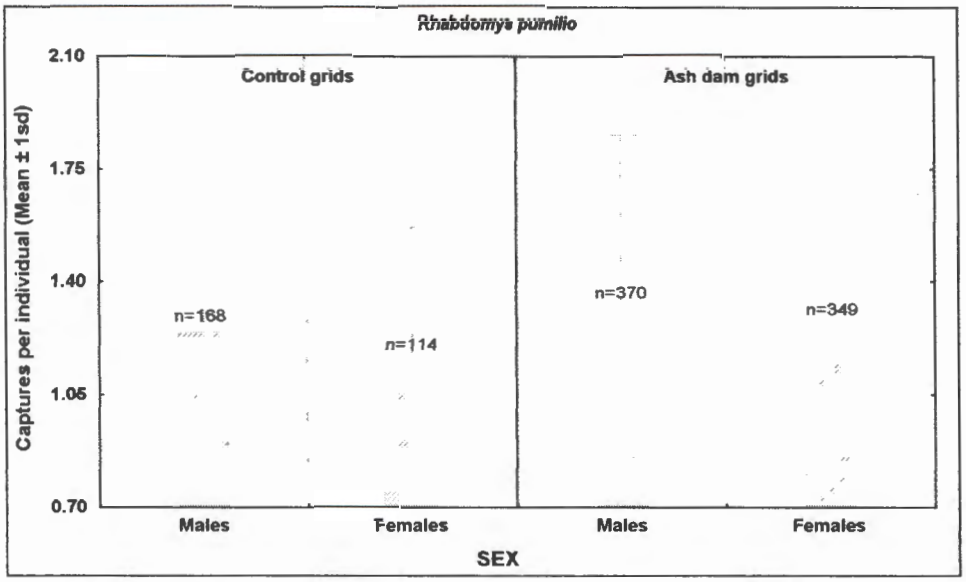


FIGURE 3.11: Trapability rates for male and female *R. pumilio* on the control and ash dam grids at Hendrina Power Station. (Data for all surveys combined; bars indicate ±1sd).

Mastomys coucha

Of the 344 individuals captured during the study period, only 30 were caught on the two control grids. No significant differences in trapability were evident between the control- and ash dam grids over all surveys. Male *M. coucha* were slightly more trapable than females on the ash dam grids, but this difference was not significant. Conversely, on the control grids females were slightly more trapable than males (Figure 3.12). Trapability was significant higher during July 1998 on the ash dam grids ($H_{1,57}$=4.46; $p<0.05$). This cannot be attributed to seasonal differences in movement patterns, which were negligible (Section 3.4.1). This, however, could reflect higher activity to satisfy energetic demands in cold dry months when food is limited.

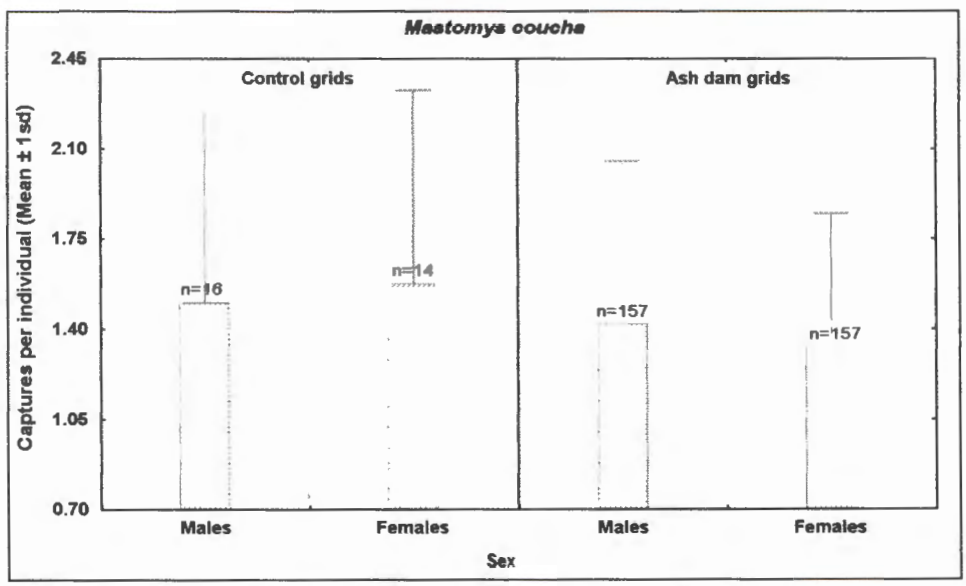


FIGURE 3.12: Trapability rates for male and female *M. coucha* on the control and ash dam grids at Hendrina Power Station. (Data for all surveys combined; bars indicate ±1sd).

Tatera brantsii

This Highveld gerbil was first captured on the control grids in July 1998. Only 10

individuals were ever caught in this area, and no significant differences in trapability of the sexes were evident. However, sample sizes were low so this result must be considered equivocal. Animals caught on the control grids were considered temporary migrants or vagrants, since their appearance on the controls followed veld fires which created a niche suitable for them.

Trapability did not differ significantly between males and females on the ash dam grids, and was lower than trapability on the control grids (Figure 3.13). Differences in trapability between the control- and ash dam grids were not, however, significant.

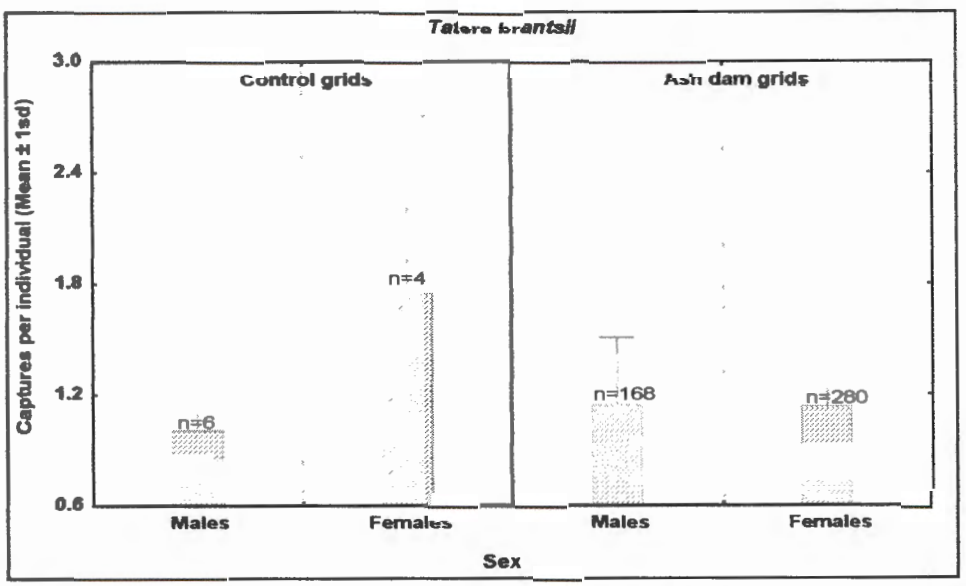


FIGURE 3.13: Trapability rates for male and female *T. brantsii* on the control and ash dam grids at Hendrina Power Station. (Data for all surveys combined; bars indicate ±1sd).

3.4 Movement patterns

Small mammals are confined by morphological and ecophysiological constraints to a relatively small area of the total available environment. These constraints are determined

to a large extent by the spatial distribution of resources such as food, mates, cover, etc. Within this area, the distribution and movement of small mammals may be further restricted by factors such as social organization and status (Delany & Happold 1979). Movement patterns within this particular living space involve the "home range" concept. A "home range" is an area used by individuals to obtain essential resources, and is thus the area covered during vital activities such as food gathering, mating and caring for young. It excludes areas covered by migratory movements (Brooks 1974).

An animal's home range is, therefore, a reflection of its response to the environment and is a fundamental mirror of its ecology. Trapping has generally been shown to restrict or otherwise interfere with the normal movement pattern of rodents, and seldom reveals the true extent of their home ranges (Hoffman 1999). The probability of capture is not constant in time, or throughout an animal's range, but varies in response to the spatial dispersion of resources.

3.4.1 Differences in movement patterns between species

Movement patterns can be elucidated by examining the distances between successive captures within each trapping session (Brant 1962), an approach followed here. Owing to low recapture rates, data for control and ash dam grids were combined for each species. During this study, most individuals moved only short distances between successive captures, with the result that the distance moved between recaptures deviated significantly from normality for all of the dominant mammal species. These data could not, therefore, be analyzed by parametric methods, thereby preventing the simultaneous statistical comparison of both seasonal effects and possible differences between the ash dam and control grids.

Figure 3.14 shows that most of the individuals of *R. pumilio* moved only short distances (0-40 meters) between recaptures. The data, therefore, deviated from normality and were

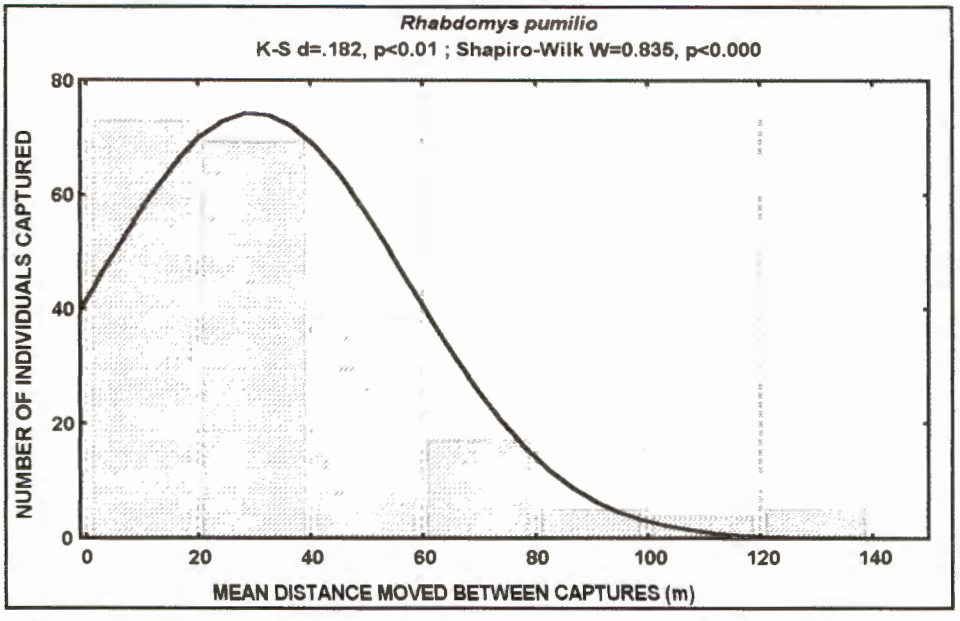


FIGURE 3.14: Histogram of the mean distances between recaptures for *R. pumilio*, based on all data (control and ash dam grids combined). A curve showing the normal expected frequency is superimposed.

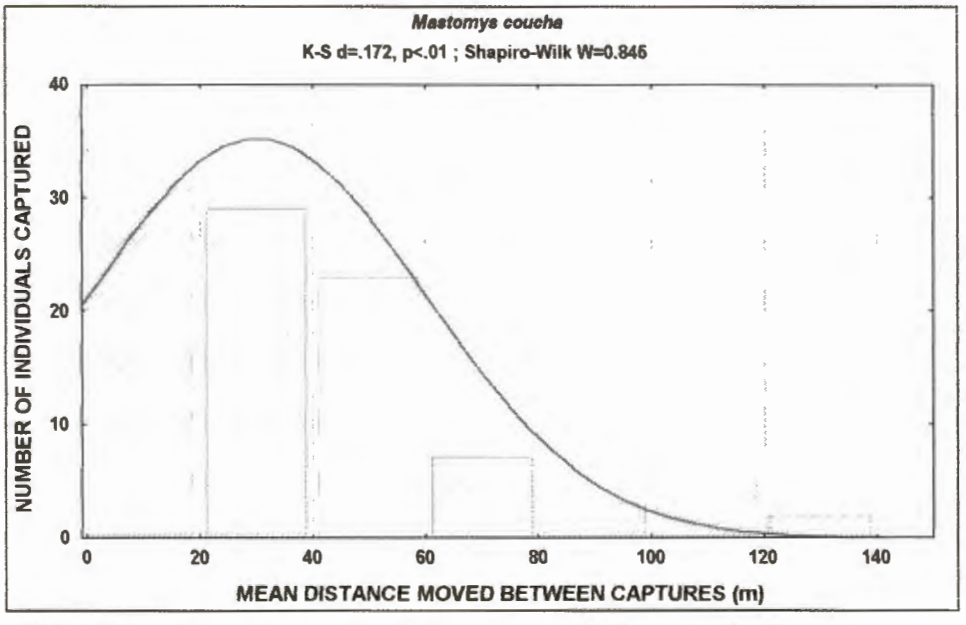


FIGURE 3.15: Histogram of the mean distances between recaptures for *M. coucha*, based on all data (control and ash dam grids combined). A curve showing the normal expected frequency is superimposed.

characterized by marked leptokurtosis (2.74 ± 0.303) and moderate negative skewedness (1.54 ± 0.15). The same pattern was evident for *M. coucha*, with most individuals moving only short distances (0-40 meters) between recaptures throughout the study period. Only a few individuals (n=5) moved over distances greater than 100 meters between recaptures (Figure 3.15). Recapture data for this species also deviated from normality and were characterized by moderate leptokurtosis (1.202 ± 0.149) and negative skewedness (1.249 ± 0.211).

Most *T. brantsii* individuals moved over distances of 30 meters or less between recaptures, but five were recorded to move distances greater than 100 meters (Figure 3.16). Unlike the other two dominant rodent species, the distribution of distances between captures was characterized by both platykurtosis (1.39 ±0.578) and skewedness (1.491 ± 0.293). This indicates a more even dispersion of distances between recaptures than in *R. pumilio* and *M. coucha*.

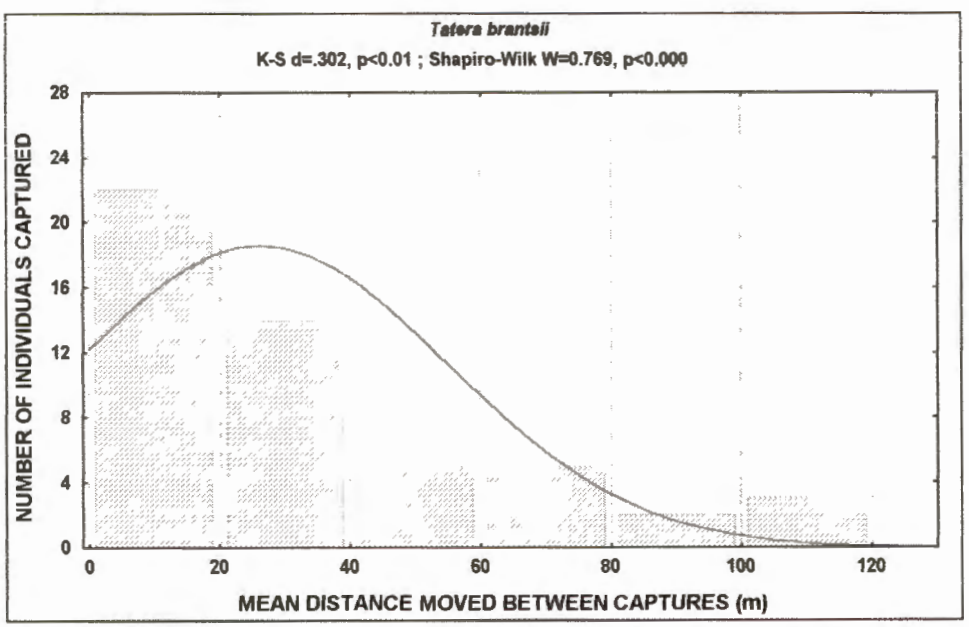


FIGURE 3.16: Histogram of the mean distances between recaptures for *T. brantsii*, based on all data (control and ash dam grids combined). A curve showing the normal expected frequency is superimposed.

The average distance moved between successive captures by the most common small mammal species varied markedly on a seasonal basis, and also between the ash dam and control grids (Table 3.10; Figure 3.17). The average distance moved between successive captures on the ash dams did not differ significantly among the five most common species. Data for the control grids were too limited for meaningful statistical analysis. In general, however, individuals tended to move over larger distances on the ash dams than on the control grids in any specific season.

R. pumilio was the only species which showed a significant difference ($H_{1,257}$=4.29; $p<0.05$) in distances moved on the control and ash dam grids, and only in autumn and summer (Table 3.10). The mean distance moved was significantly higher on the ash dam grids than on the control grids during autumn, whereas in summer this pattern was reversed.

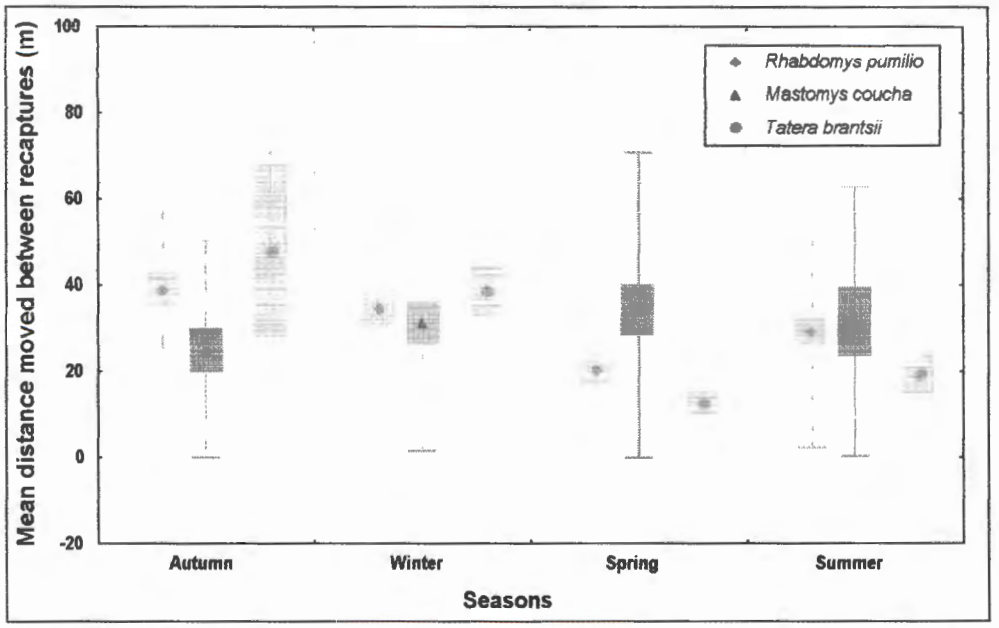


FIGURE 3.17: Seasonal variation in the average distance moved between successive captures by the three most common small mammal species, on the ash dam sites combined (Bars indicate ±1sd; boxes ±1se).

Statistically-significant seasonal differences in the mean distance moved were shown by

R. pumilio and *T. brantsii* on both the ash dams and the controls (Table 3.10). The mean distances moved by *R. pumilio* on the ash dams was significantly elevated during autumn and winter ($H_{1,83}$=15.8; $p<0.01$), a trend also evident in *T. brantsii*. On the controls, however, the mean distances moved by *R. pumilio* were significantly greater in summer ($H_{1,64}$=4.99; $p<0.01$).

It therefore appears that movement patterns (and thus presumably also home range size; Brant 1962) varied markedly in relation to both season and between survey areas. These differences probably relate to the extent of vegetative cover, which offers *R. pumilio* protection from predators (Brooks 1974). On the ash dam grids vegetation cover was significantly higher during autumn ($F_{3,96}$=5.85; $p<0.01$), while on the control grids no significant seasonal differences were evident (Morgenthal 1999).

The mean distance moved by *T. brantsii* between successive captures on the ash dams was significantly higher in autumn and winter than in any other season. The decrease in average distances moved from winter to summer also coincided with a decrease in the standard deviation, implying that variability in apparent home range size was also greater in winter. Gerbils are territorial and semi-colonial, with relatively restricted home ranges (De Moor 1969). These animals will, therefore, tend to be caught at the same trap station, or a closely neighbouring one because they usually feed close to their burrow entrances (De Moor 1969), a strategy typical of a central-place forager (Jackson 1998). During the dry winter months, when localized food resources become increasingly depleted, these animals may have to forage over greater distances than usual to satisfy their metabolic needs.

TABLE 3.10: Mean distance moved between successive captures by five species of small mammals on the ash dam and control sites in different seasons. Significant differences indicated by Kruskal-Wallis ANOVA are given in red. nc = not captured. n/a = sample sizes insufficient for statistical comparisons. nsd = no significant difference.

SPECIES	SEASON	ASH DAMS	CONTROLS	KW -ANOVA
R. pumilio	Autumn	38.5 ± 28.9 (54)	15.7 ± 16.1 (29)	$H_{1,83}$=15.8; p<0.01
	Winter	34.3 ± 31.7 (54)	31.4 ± 27.4 (13)	nsd
	Spring	20.2 ± 20.7 (36)	15.3 ± 12.0 (7)	nsd
	Summer	28.8 ± 26.4 (57)	54.4 ± 32.1 (7)	$H_{1,64}$=4.99; p<0.01
			$H_{3,56}$=12.40; p<0.01	
M. coucha	Autumn	24.7 ± 25.5 (26)	54.1 ± 0.0 (1)	n/a
	Winter	30.9 ± 29.4 (37)	31.1 ± 11.2 (10)	nsd
	Spring	34.1 ± 36.6 (38)	21.2 ± 0.0 (1)	n/a
	Summer	31.5 ± 31.2 (16)	50. ± 8.7 (3)	nsd
		nsd	n/a	
T. brantsii	Autumn	47.9 ± 39.4 (4)	nc	n/a
	Winter	38.4 ± 25.0 (18)	nc	n/a
	Spring	12.3 ± 9.0 (11)	nc	n/a
	Summer	19.2 ± 30.0 (31)	nc	n/a
		$H_{3,64}$=15.76; p<0.01	n/a	
M. varius	Autumn	35.6 ± 7.8 (4)	nc	n/a
	Winter	25.4 ± 12.1 (5)	15.0 ± 0.0 (1)	n/a
	Spring	43.8 ± 14.6 (2)	nc	n/a
	Summer	33.9 ± 29.5 (7)	12.1 ± 10.9 (3)	nsd
		nsd	n/a	
M. minutoides	Autumn	nc	nc	n/a
	Winter	33.5 ± 0.0 (1)	nc	n/a
	Spring	38.0 ± 6.3 (2)	nc	n/a
	Summer	29.4 ± 22.3 (4)	nc	n/a
		nsd	n/a	

3.4.2 Differences in movement patterns within the three dominant species

Rhabdomys pumilio

The average distance moved by the male and female of *R. pumilio* varied markedly on a seasonal basis, and also between the ash dam and control grids (Table 3.11). On the control grids, no significant differences in average distances moved between males and females were evident during any season. However, on the ash dam grids males tended to move over significantly greater distances than females during winter (Table 3.11). When the data for the seasons were pooled, males tended to move over significantly greater distances on both the control ($H_{3,39}$=9.06; $p<0.05$) and ash dam grids ($H_{3,109}$=10.44; $p<0.05$; Table 3.11).

TABLE 3.11: Average distance moved between successive captures (m±1sd) by male and female *R. pumilio* on the control and the ash dam grids during different seasons. Significant differences indicated by Kruskal-Wallis ANOVA and Mann-Whitney U tests are given in red. nc = not captured; n/a = sample sizes insufficient for statistical comparisons; nsd = no significant difference.

SEASONS	CONTROLS		MANN-WHITNEY	ASH DAMS		MANN-WHITNEY
	Males	Females		Males	Females	
AUTUMN	18.41 ± 17.22 (20)	9.71 ± 12.12 (9)	nsd	40.48 ± 28.60 (27)	36.54 ± 29.80 (27)	nsd
WINTER	32.44 ± 33.38 (6)	29.0 ± 23.56 (7)	nsd	40.67 ± 35.61 (35)	22.73 ± 18.48 (19)	U=223.5; p<0.05
SPRING	17.65 ± 10.97 (6)	*n/a* (1)	nsd	19.89 ± 21.62 (24)	20.80 ± 19.66 (12)	nsd
SUMMER	52.41 ± 32.12 (7)	nc	n/a	32.73 ± 24.24 (23)	26.09 ± 27.86 (34)	nsd
KW ANOVA	$H_{3,39}$=9.06; p<0.05	nsd		$H_{3,109}$=10.44; p<0.05	nsd	

Movement patterns may also have been affected by the breeding condition of individual animals. No significant differences were evident between non-breeding individuals in either males (Figure 3.18a) or females (Figure 3.18b) on either the controls or ash dam grids during any season. During summer no non-breeding males were captured on the control or ash dam grids, and no non-breeding females were recaptured on the control grids.

No significant differences in the average distance moved between successive captures were evident for breeding males and females between the control and ash dam grids during all seasons. However, on the control grids breeding males moved over significantly greater distances during summer ($H_{1,10} = 4.23$; $p<0.05$), a phenomenon evident also on the ash dam grids during autumn ($H_{2,44} = 13.24$; $p<0.01$; Figure 3.18c). No significant differences were evident in average distance moved by breeding females on the control and ash dam grids (Figure 3.18d), but samples were very limited. No breeding individuals were recaptured during winter on both the ash dam and the control grids, while on the controls, breeding males were only captured during spring and summer, and breeding females during autumn.

Mastomys coucha

No significant differences in movement patterns of male or female *M. coucha* were evident in relation to either season or the control vs. ash dam grids (Table 3.12). Sex-related differences in the average distance moved were thus negligible in this species. No significant differences in average distance moved between recaptures were evident for breeding and non-breeding males or females on either the controls and ash dam grids (Figure 3.19 a-b). During the summer months, no non-breeding individuals were captured on the control grids. Non-breeding males tended to move over greater distances during spring on the ash dam grids (Figure 3.19a), but these differences were not statistically significant. Breeding individuals tended to move over greater distances during summer

on both the ash dam and control grids (Figure 3.19 c-d), but again these differences were not statistically significant owing partly to small sample sizes.

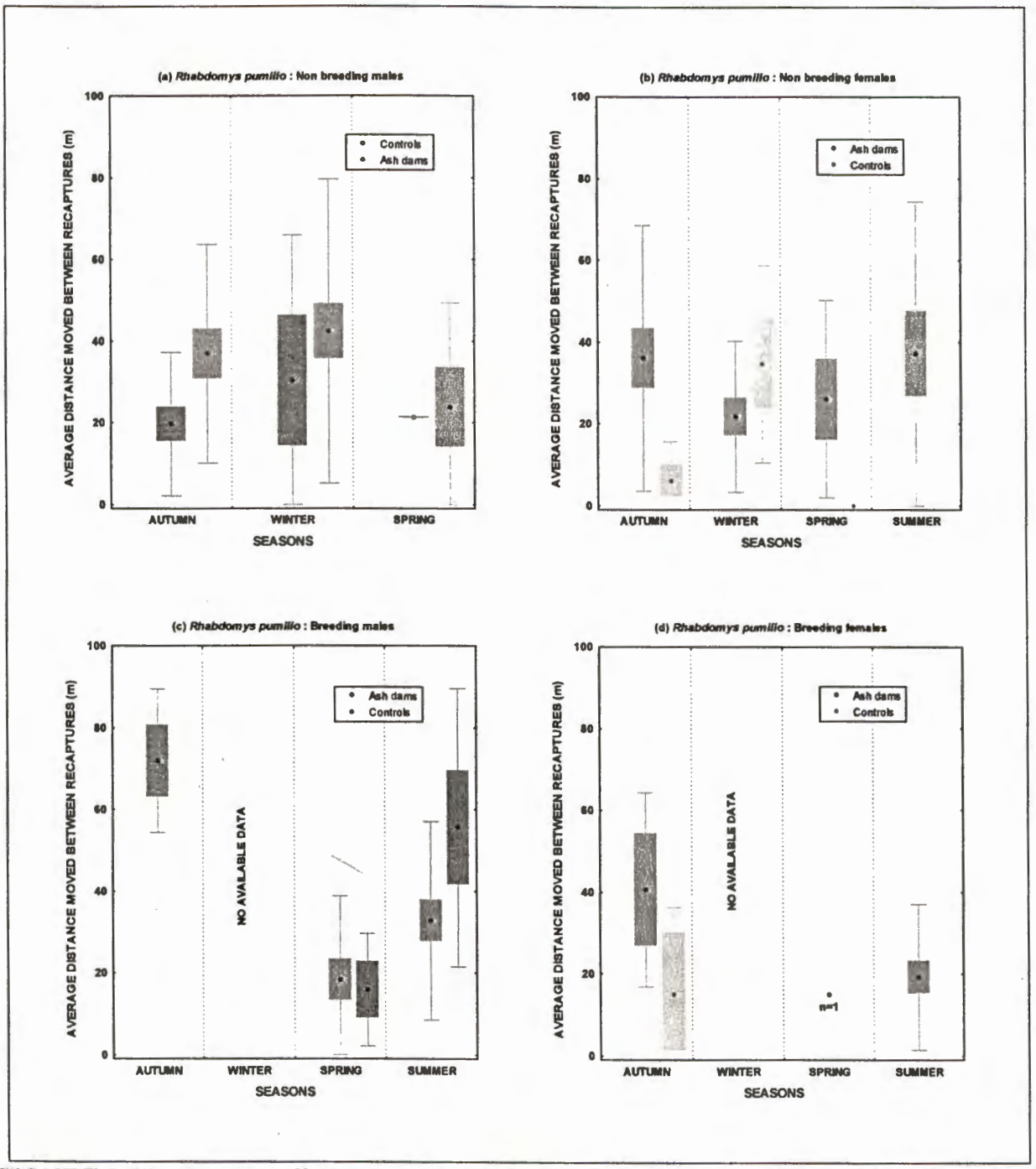


FIGURE 3.18: Average distance moved by non-breeding (a) male, (b) female and (c) breeding male and (d) female individuals of *R. pumilio* on the control and ash dam grids (Bars indicate ±1sd; boxes ±1se).

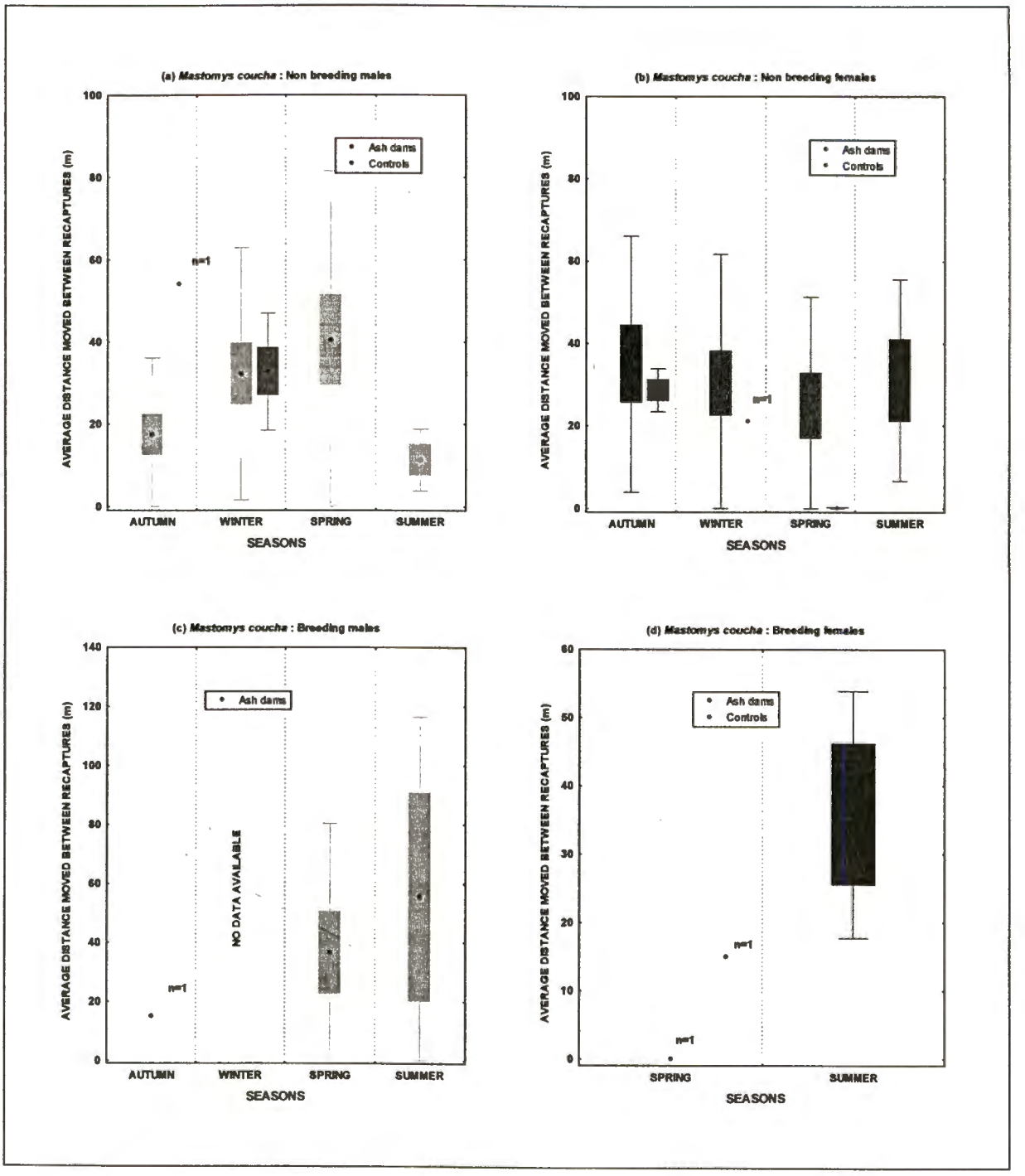


FIGURE 3.19: Average distance moved by (a) non-breeding male, (b) female and (c) breeding male, (d) female individuals of *M. coucha* on the control and ash dam grids (Bars indicate ±1sd; boxes ±1se).

TABLE 3.12: Average distances moved between successive captures by male and female *M. coucha* on both the controls and the ash dam grids. Significant differences indicated by Kruskal-Wallis ANOVA and Mann-Whitney U test are given in red. nc = not captured; n/a = sample sizes insufficient for statistical comparisons; nsd = no significant difference.

SEASONS	CONTROLS		MANN-WHITNEY	ASH DAMS		MANN-WHITNEY
	Males	Females		Males	Females	
AUTUMN	54.1 ± 0.0 (1)	nc	n/a	17.22 ±18.02 (15)	34.97 ±31.17 (11)	nsd
WINTER	32.7 ± 14.18 (6)	28.68 ± 5.25 (4)	nsd	30.37 ±29.38 (19)	31.52 ±30.33 (18)	nsd
SPRING	nc	21.2 ± 0.0 (1)	n/a	39.39 ±39.89 (26)	22.77 ±26.13 (12)	nsd
SUMMER	nc	5.0 ± 8.66 (3)	n/a	30.13 ±42.74 (7)	32.62 ±21.49 (9)	nsd
KW ANOVA	nsd	nsd		nsd	nsd	

Tatera brantsii

Only ten individuals were captured on the control grids and no average distance moved could therefore be calculated. On the ash dams, no significant differences in the average distance moved by male and female *T. brantsii* were evident in any season (Table 3.13). When data for the seasons were pooled, however, the average distance moved by females was significantly greater ($H_{1,67}$ =4.26; $p<0.05$) than for males. Male *T. brantsii* tended to move over greater distances during the summer periods, while females moved over significant greater distances during the colder periods of the year (autumn and winter; Table 3.13).

On the ash dam grids non-breeding males were too few caught for statistical comparisons, while breeding males moved over significantly greater distances during winter ($H_{3,24}$ =9.5;

$p<0.05$; Figure 3.20a). Breeding females, however, moved over small distances during spring and summer (Figure 3.20b), but these differences were not significant. Non-breeding females were captured throughout the year, and moved over greater distances during autumn, but again these differences were not significant.

TABLE 3.13: Average distances moved between successive captures by male and female *T. brantsii* on the ash dam grids. Significant differences indicated by Kruskal-Wallis ANOVA are given in red. nsd = no significant differences.

SEASONS	ASH DAMS		MANN-WHITNEY
	Males	Females	
AUTUMN	0.0 ± 0.0 (1)	63.93 ± 28.98 (3)	nsd
WINTER	32.7 ± 19.6 (8)	42.87 ± 28.84 (10)	nsd
SPRING	7.5 ± 10.61 (2)	13.33 ± 9.01 (9)	nsd
SUMMER	7.68 ± 10.23 (13)	27.48 ± 36.68 (18)	nsd
KW-ANOVA	$H_{3,24}=9.5$; $p<0.05$	$H_{3,40}=12.09$; $p<0.01$	

3.4.3 Edge-effects

Edge-effects refer to the capture of individuals whose home ranges overlap only slightly with trapping grids, or those of temporary residents. Such effects may lead to the over-estimation of population size, and are indicated if the capture rate on the outer border of a grid differs significantly from that within. Statistical comparison of capture frequencies in the outer (4950m^2) and inner (3150m^2) zones revealed no significant differences between the inner and outer sampling zones during any season on either the control or ash dam grids (Table 3.14), or for any of the particular ash dam or the control grids (Table 3.15). Any edge-effects that may have been manifested during this study were, therefore negligible.

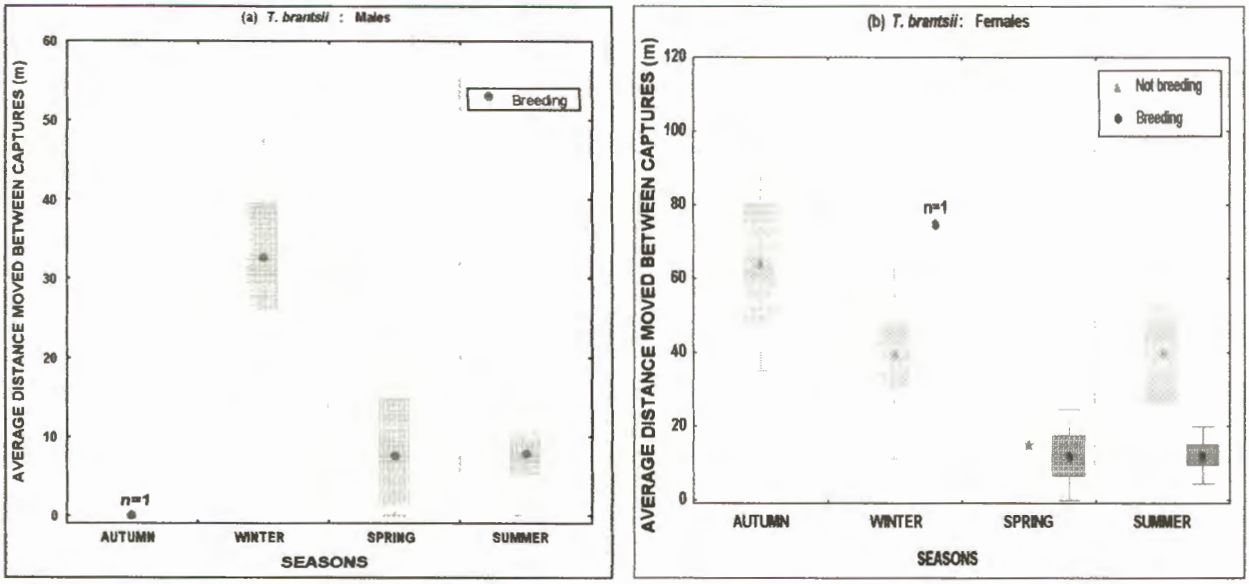


FIGURE 3.20: Average distance moved by (a) breeding male, (b) breeding and non-breeding female individuals of *T. brantsii* on the ash dam grids (Bars indicate ± 1sd; boxes ± 1se).

TABLE 3.14: Seasonal distribution of captures of all the species over the two capture zones on control and ash dam grids. The hypothesis of equal distribution of captures (correlated to a standardized zone surface area) was tested with a chi-square test. Expected values are given in parentheses.

SITE	SEASON	OUTER ZONE	INNER ZONE
ASH DAM GRIDS	AUTUMN	227.2 (217.5)	194 (209.38)
	WINTER	200.5 (208.38)	213 (200.64)
	SPRING	140.7 (144.8)	146 (139.46)
	SUMMER	175.7 (173.3)	163 (166.82)
CHI-SQUARE		$\chi^2 = 3.11$; p>0.05	
CONTROL GRIDS	AUTUMN	61.1 (55.5)	47 (55.77)
	WINTER	44.6 (46.6)	50 (46.8)
	SPRING	33.7 (39.2)	48 (39.39)
	SUMMER	44.6 (41.5)	37 (41.73)
CHI-SQUARE		$\chi^2 = 5.59$; p>0.05	

TABLE 3.15: Distribution of all the species over the two capture zones based on data for all control and ash dam grids (all surveys combined). The hypothesis of equal distribution of captures (expressed per standardized surface area) was tested with a chi-square test. nsd = no significant differences. Expected values are given in parentheses.

SITES	OUTER ZONE	INNER ZONE	CHI-SQUARE
GRID 1	25 (25.01)	16 (15.99)	nsd
GRID 2	104 (103.09)	65 (65.91)	nsd
GRID 3	130 (111.02)	52 (70.98)	nsd
GRID 4	126 (132.98)	92 (85.02)	nsd
GRID 7	123 (120.17)	74 (76.83)	nsd
GRID 8	166 (167.14)	108 (106.86)	nsd
GRID 9	141 (117.12)	51 (74.88)	nsd
GRID 10	81 (95.77)	76 (61.23)	nsd
GRID 11	100 (114.02)	87 (72.93)	nsd
GRID 12	173 (163.48)	95 (104.52)	nsd
TOTAL CHI-SQUARE			$\chi^2 = 12.63$; $p>0.05$
CONTROL 1	114 (122.61)	87 (78.39)	nsd
CONTROL 2	120 (123.22)	82 (78.78)	nsd
TOTAL CHI-SQUARE			$\chi^2 = 6.66$; $p>0.05$

TABLE 3.16: Distances moved between successive captures (m) for the three dominant small mammal rodent species on the control and ash dam grids.

SPECIES	CONTROL GRIDS			ASH DAM GRIDS		
	MEDIAN	MEAN ± 1sd	N	MEDIAN	MEAN ± 1sd	N
R. pumilio	15.0	23.9 ± 24.2	56	21.2	31.4 ± 28.3	201
M. coucha	30.0	26.7 ± 16.2	15	15.0	30.68 ± 31.2	117
T. brantsii	54.1	50.1 ± 27.1	3	15.0	25.2 ± 28.6	64

One of the conventional methods for calibrating trapping data to reflect actual densities is to add a boundary-strip to the grid, equivalent to the average distance between successive recaptures. Density estimations should then be calculated on a species-specific basis, unless there are no significant differences in distances moved (Flowerdew

1976). One limitation of the above-mentioned technique is that a minimum of 15 successive recaptures are needed to obtain a reasonably accurate estimate of home range areas.

During this study, sufficient recaptures for the estimation of boundary strip width were available for only three of the species, namely *R. pumilio, M. coucha* and *T. brantsii*, (Table 3.16). Moreover, the standard deviation for the mean distances moved by these species were large owing to seasonal differences in home range size and presumably also reproductive status. Considerably more recaptures are ideally needed before season and species-specific calibrations for effective trapping area can be calculated. However, the median distances moved by the three dominant rodents may be used to calculate a general calibrating factor, since median values are not as susceptible to distortion by extremes as are mean values. The median distances moved by *R. pumilio*, *M. coucha* and *T. brantsii* differed significantly on the control ($H_{8,274}$=17.35; $p<0.05$) and ash dam grids ($H_{9,382}$=19.33, $p<0.05$). Thus, on both the control and ash dam grids the above-mentioned technique could not be used. This posed no difficulties since edge-effects were, in any event, apparently minimal. Population sizes, as used hereafter, refer to numbers of individuals captured on each grid during each survey, and are indices of relative densities. To express population sizes as absolute densities, the grid trapping area (8100 m^2) can be used to derive a calibration factor (1.235) whereby numbers can be expressed per hectare for comparison with other published studies.

3.5 Population size

3.5.1 Methods for estimating population sizes

Since small mammals, especially rodents, comprise a large proportion of the vertebrate primary consumers in many habitats, and because of their important role they play in ecosystem functioning (Chapter 1) ecologists have devoted much time to devising methods

for estimating their numbers (Southern 1973). The most recent work of Krebs (1989) was referred to for methodological details in this study.

The accurate estimation of small mammal population size is notoriously difficult. Most of the assessment methods available rely on certain assumptions which are seldom satisfied. Assumptions commonly made by estimation methods are:

(1) animals do not lose their individual marks;

(2) captures are correctly recorded as marked or unmarked;

(3) marking does not affect the probability of survival;

(4) the population is either open or closed, therefore

(i) there is no gain or loss of members during sampling;

(ii) there is recruitment and immigration but death and emigration affect marked and unmarked animals equally;

(iii) knowledge is available from other sources which permits an allowance to be made for migration, birth and death prior to the analysis of the data.

(5) the population is randomly sampled so that:

(i) marked and unmarked animals intermingle freely;

(ii) every animal has the same probability of capture.

(Bronner & Meester 1987; Smith *et al.* 1975)

The following methods were used to estimate population sizes:

3.5.1.1 Enumeration methods

To simply count the number of individual animals captured is the easiest way to estimate the size of a population, but it is clear that not all individuals present at a given time are caught. Krebs (1966) therefore devised the Minimum Number Alive (MNA) method, which includes all individuals trapped in a particular session, plus those marked previously which were recaptured at a later date. According to Bronner & Meester (1987), this method is

generally to be preferred over statistical estimates since it is assumption-independent, but Leirs (1994) concluded that this method tends to underestimate the actual population size. For this study, Minimum Number Alive equals the number of individuals present during a particular survey period. The periods between surveys were too long (2-3 months) to assume that the populations were closed.

3.5.1.2 Statistical population estimation techniques

a) Schnabel method

This method is an extension of the classical Petersen estimate for circumstances with more than two samples. One of the assumptions of this method is that the population is closed. Since seasonal surveys involved trapping over 3 days/nights, during which recruitment, emigration, immigration and mortality was presumably negligible, the populations studied were regarded as closed and thus amenable to analysis via this technique.

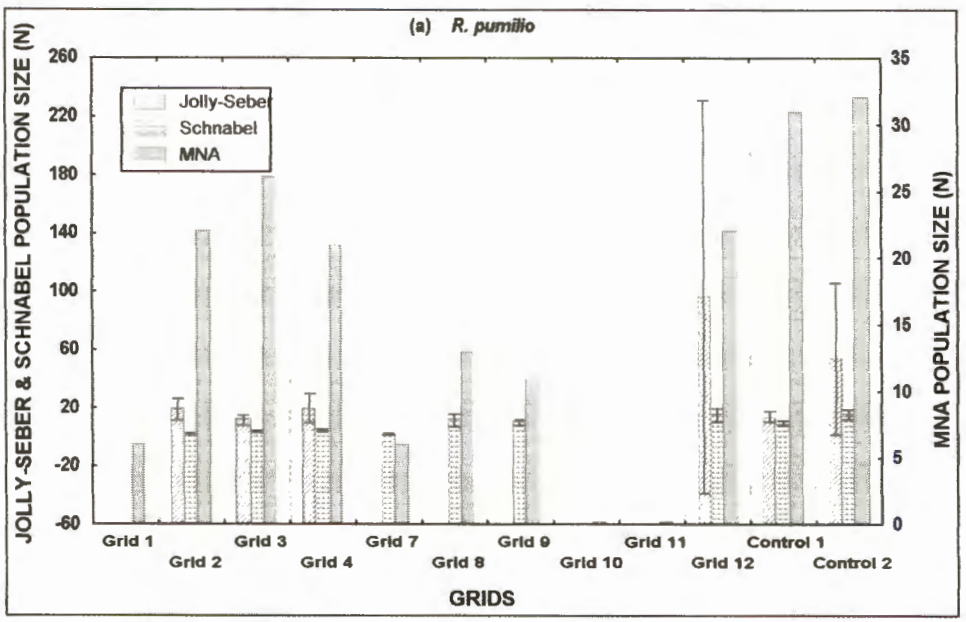
b) The Jolly-Seber method

This method can be applied to open populations in which births, deaths, immigration and emigration occur. The time interval between samples need not be constant, and any number of samples can be accommodated. Survival should be age-independent and equal catchability for marked and unmarked individuals is assumed by this method. The calculations are more complex and results in population size estimators for every sampling moment, except for the first one and the last one (Krebs 1989). This method for estimating survival rate tends to be robust to heterogeneity in detection probability but its abundance estimator is not (Krebs 1989).

Figure 3.21, based on the data for July 1997, showed that MNA is the most robust and

realistic indicator of demographic trends. The two statistical estimation techniques required equal trapability, an assumption that was violated throughout the study period. In some cases Jolly-Seber could not be used because no recaptures were documented (Grid 1, 10 & 11; Figure 3.21b) or the number of individuals captured was insufficient (Grid 1, 7, 8, 9, 10 & 11; Figure 3.21a). There was little agreement between the three techniques and Schnabel estimates were consistently lower than the minimum number of individuals captured (MNA), indicating that this method under-estimated population sizes. Similarly, Jolly-Seber estimates were generally lower than MNA, and only infrequently did upper confidence limits exceed MNA. However, there was a positive correlation between MNA and Jolly-Seber ($r=0.67$; $p<0.05$) and between Schnabel and Jolly-Seber ($r=0.68$; $p<0.05$) when the data for all species were combined, while there was a positive correlation between Jolly-Seber and Schnabel ($r=0.82$; $p<0.05$) when only the data for *R. pumilio* were used.

Flowerdew (1976) concluded that MNA estimates are usually accurate when trapping is intensive and recapture rates are high. Although this was not the case during this study, the MNA method was the only method that could be relied on here. The MNA method has the advantage of being exact number, not an estimate associated with a given probability (Leirs 1994), and is therefore assumption-free. MNA also seems to be the method with the greatest accuracy and widest applicability, since derived estimates are not as susceptible to distortion by minor fluctuations in sample sizes resulting from, for example, weather; while Jolly-Seber and Schnabel estimates often overestimate population sizes to some degree (Bronner & Meester 1987). Although the MNA method always underestimate real population size, other authors such as Christian (1979; 1980); Perrin (1979); Ascaray (1986) and David & Jarvis (1985) have used this method successfully to estimate rodent numbers, while Cheeseman & Delany (1979) concluded that it is the best of the five techniques they compared.



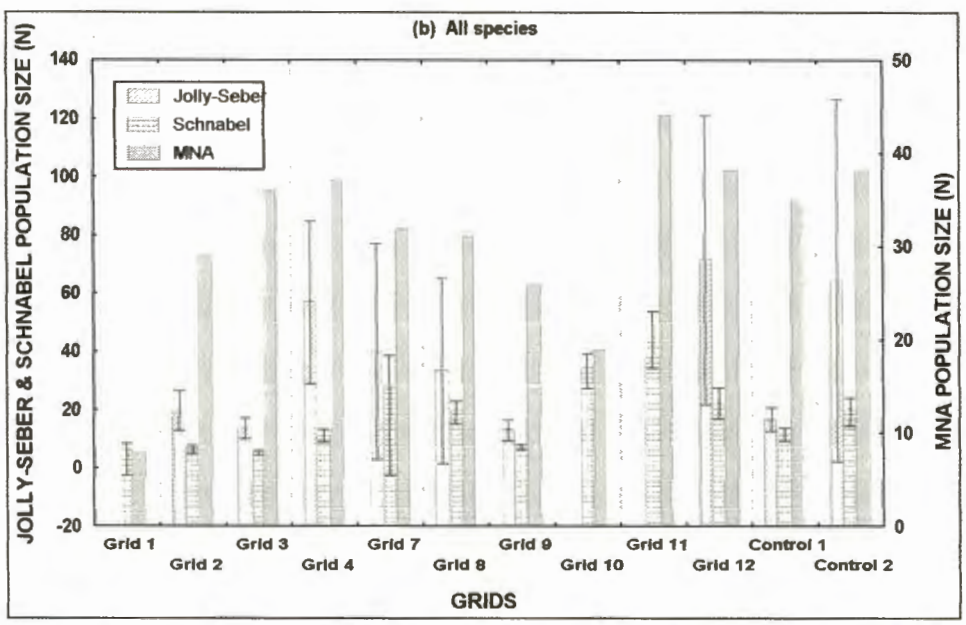


FIGURE 3.21: Population size estimated by the three methods mentioned earlier and their 95% confidence intervals (whiskers) for (a) *R. pumilio* and (b) all species (Bars indicate ±1sd).

3.6 Community structure

3.6.1 Population sizes and biomass

The demography of small mammals may be influenced by intra- and inter-specific interactions, as well as the structure of each species' environment, especially in grasslands which are highly-variable environments (Fa, Lopez-Paniagua, Romera, Gomez & Lopez. 1990). The main factors influencing the abundance and number of species of small mammals appear to be the seasonal abundance, floristic composition and physiognomy of vegetation resources, and the extent to which the habitat is modified by external factors such as fire and grazing (Delany 1964). Population sizes of small mammals therefore tend to fluctuate seasonally and features such as soil type, food availability, rainfall and vegetation structure may have a strong influence on their demography (Chidumayo 1980; Oguge 1995; Monadjem 1997; Monadjem & Perrin 1998).

Population sizes and biomass vary considerably from one vegetation type to another, even within different types of savanna (Delany 1972) and tend to be relatively constant in stable environments, but highly variable in harsh and unstable environments (Willan 1992). According to Grant, Birney, French & Swift (1982), biomass is the most appropriate descriptor of community structure and provides the best basis for calculating community productivity when emphasis is placed on the functional relationships that affect structure and productivity. These authors also concluded that the functional role of small mammals in the community is more directly related to biomass than to numbers.

The mean population size and biomass of small mammals did not differ significantly between the control and ash dam grids in any season (Figure 3.22), but marked and similar seasonal changes were evident in both areas. Mean population size (MNA) on both the ash dam grids ($H_{3,100}$=37.28; $p<0.001$) and the controls grids ($H_{3,20}$=8.99; $p<0.05$) decreased significantly during spring and summer. The same trend was evident for the

biomass of the small mammals on the ash dam grids ($H_{3,99}$=27.48; p<0.001), but no significant seasonal variability was evident on the control grids.

The significant decline in total population sizes in spring through summer was due mainly to a progressive, almost linear decrease (r=-0.484; p<0.001) in the number of *R. pumilio* (Figure 3.23) on both the control ($H_{3,20}$=7.69; p<0.05) and the ash dam grids ($H_{3,100}$=18.46; p<0.001).

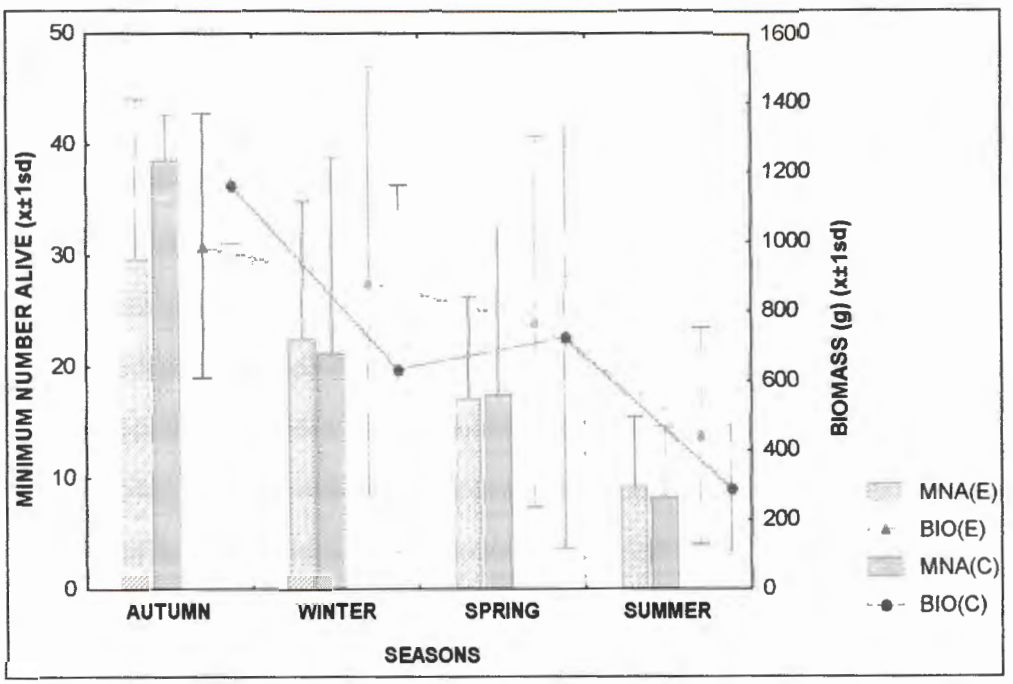
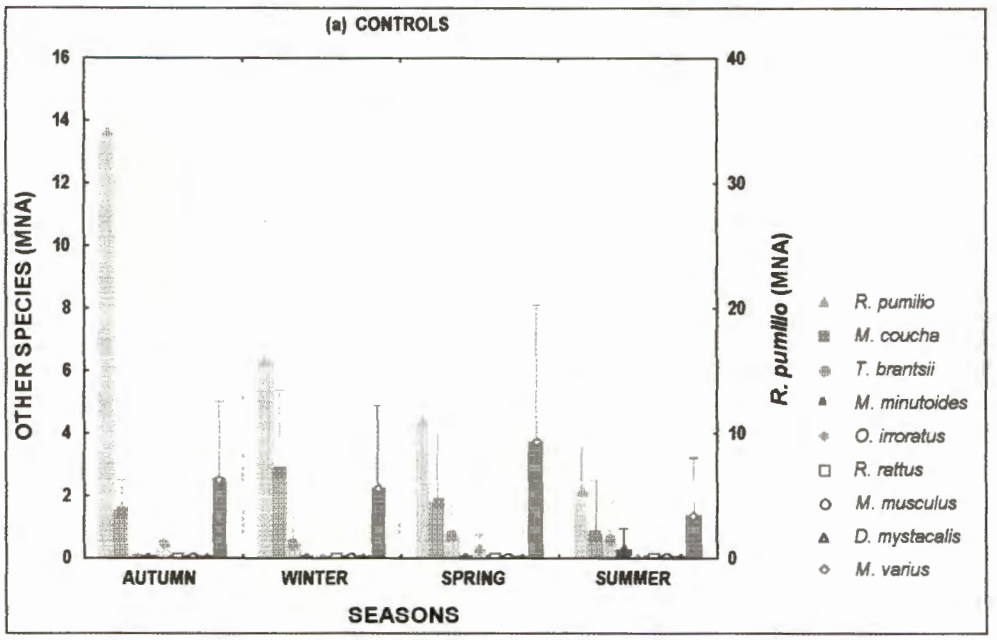


FIGURE 3.22: Seasonal variation in population sizes (minimum number alive) and biomass of small mammal communities resident on the ash dams (E) and the controls (C) (Bars indicate ±1sd).

Mean population sizes of *T. brantsii*, the second most dominant species on the ash dams, also tended to be lower in spring and summer, but this effect was not statistically significant. The same pattern was evident on the control grids, but numbers were too low for statistical comparison. Numbers of *M. coucha* on the ash dam grids also showed a significant decrease in summer ($H_{3,100}$=17.43; p<0.001). Numbers of the forest shrew (*M.*



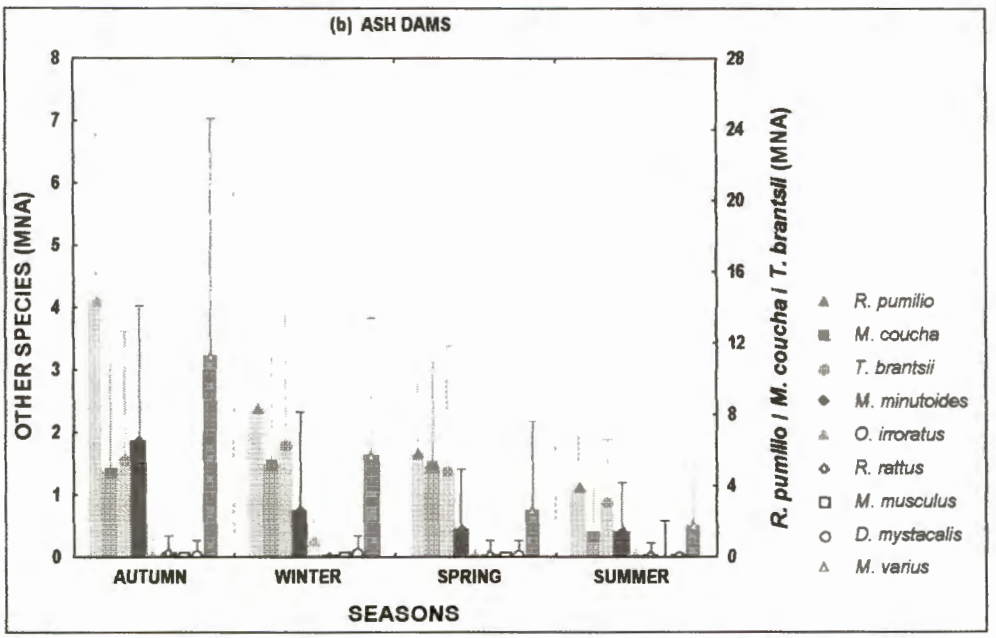
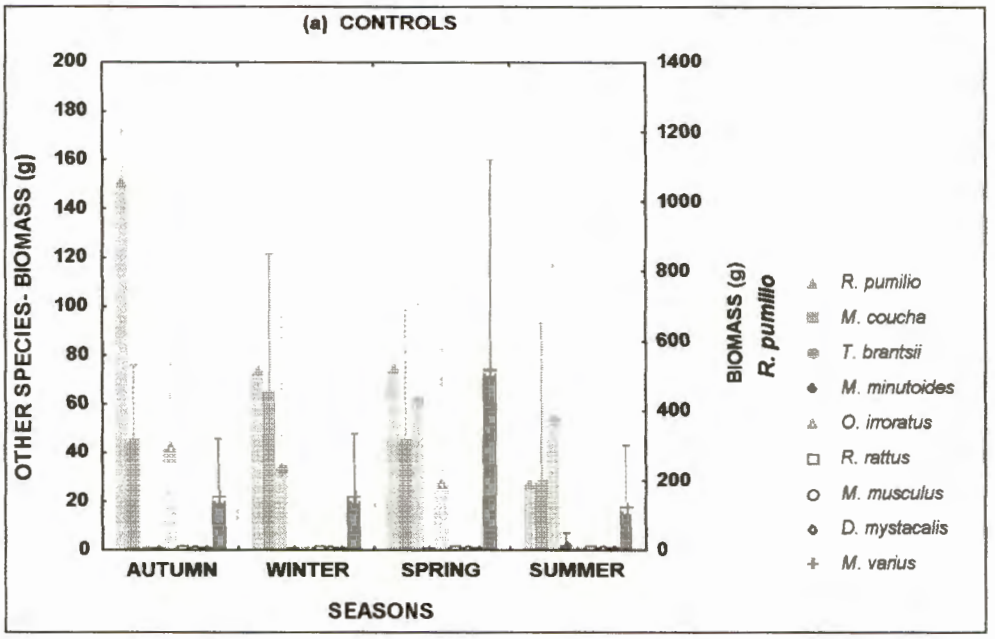


FIGURE 3.23: Population sizes of small mammal species in different seasons on the controls (a) and ash dam (b) grids (Bars indicate ±1sd).



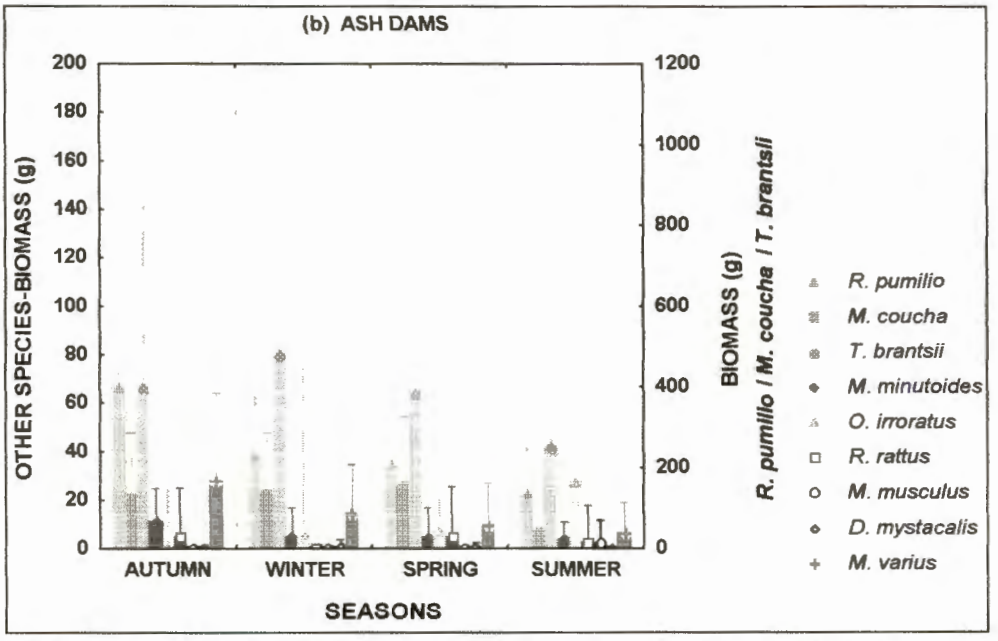


FIGURE 3.24: Biomass of small mammal species in different seasons on the controls (a) and ash dam (b) grids (Bars indicate ±1sd).

varius) on the ash dam grids were significant higher in autumn and winter ($H_{3,100}$=17.29; p<0.001), but on the control grids seasonal variability in populations of these two species were not significant (Figure 3.23). Total biomass similarly declined significantly from autumn through summer on the ash dam grids ($H_{3,99}$=27.48; p<0.001), owing to a significant decline in biomass of both *R. pumilio* ($H_{3,100}$=13.34; p<0.01) and *M. coucha* ($H_{3,100}$=15.6; p<0.001).

On the control grids, however, seasonal variability in biomass of these two species was not statistically significant (Figure 3.24), although the same pattern could be seen. The same trends were evident for *M. varius*, where biomass also declined significantly in summer on the ash dam grids ($H_{3,100}$=13.31; p<0.01), but peaked in summer on the control grids. This peak on the control grids was not, however, significant.

The seasonal decline in population sizes and biomass contrasts with the typical seasonal variation in grassland micro-mammal communities from summer-rainfall zones in South Africa, which have repeatedly been shown to decrease, (both in population size and biomass), during winter owing to high mortality and localized migrations, and to increase in spring and summer with the onset of reproductive activities and an influx of individuals from elsewhere (Davis 1973; Brooks 1974; Bronner 1986; Happold & Happold 1992). Since this atypical seasonal variation was evident also on the control grids, any effects associated with ecological rehabilitation, such as increased mortality or decreased ecological buffering, were apparently not involved. The decline in population size and biomass of *R. pumilio* from the dry winter to the wet summer season, at least on the ash dam grids, may be ascribed to either seasonal differences in trapability (Section 3.3.2), which varied significantly on a seasonal basis (Table 3.2), or a decrease in average distance moved (Table 3.10), with an attendant reduced probability of capture.

The reduction in the numbers of *M. varius* in winter on the control and the ash dam grids may be attributed to decreased movement patterns and to a reduction in activity rates

associated with lowered ambient temperatures. This species has a high mass-specific metabolic rate (Baxter, Goulden & Meester 1979), making it susceptible to cold periods when the availability of its invertebrate prey is greatly reduced (Skinner & Smithers 1990). The increase in the numbers of *M. varius* on the ash dam grids in autumn and winter may have been due to the significant increase in trapability and movement patterns during this period (Section 3.4). The control grids have greater vegetational heterogeneity, and hence also elevated resource abundance, and presumably were ecologically more buffered, so that individuals did not have to forage over longer distances, as observed on the ash dam grids (Table 3.10).

An atypical seasonal variation in numbers and biomass was also recorded by Gliwicz (1985) in a dry African savanna and she ascribed this atypical pattern to the seasonal migration of rodents. This same hypothesis could hold true for the present study. Small mammal species spread for short times all over the adjoining areas, when conditions suitable for reproduction prevail in these areas, and gather again on the ash dams, which they use as a refuge area, during the dry season.

Two other factors could also account for the low trapping success during these seasons, namely dispersal and weather. Animals may disperse into adjoining areas when conditions suitable for reproduction prevail, and gather in refugia, (in this case the ash dams), where they live in relatively high densities during the dry season (Kern 1981; Gliwicz 1985). Such dispersal may have taken place in response to the recovery of adjoining natural areas that are burned every winter (Section 3.3.2). Such dispersal would not necessarily have been detected by the trapping regime used.

Weather also has a marked effect on trapping success (Smith *et al.* 1975), particularly rain which tends to reduce the activity of small mammals and the effect of the weather is influenced by the type of habitat, day of trapping and the density of the population (Gentry *et al.*1966). Rain has an opposite influence on the forest shrew, whose probability of being

captured increases (Skinner & Smithers 1990). This effect may have been marked during the spring and summer surveys, during which thunderstorms occurred almost every night, and would also explain the tendency for the shrew samples to increase in summer when rodent samples were reduced. The relationship between population sizes and rainfall is an indirect one, whereby increased rainfall acts to increase plant cover and food availability, thus enabling rodents to reproduce (Taylor & Green 1976; Whitford 1976; Monadjem & Perrin 1997). The influence of the weather on the activity of animals would not necessarily be detected by trapability rates, which instead reflect only the catchability of individuals that are active, as opposed to those who remain inactive during inclement periods.

3.6.2 Population sizes and biomass in relation to macro-environmental parameters

3.6.2.1 Rehabilitation age

The structure of small mammal communities on the ash dam grids varied in relation to rehabilitation age (Figure 3.25). In general, communities were dominated by the striped mouse, *R. pumilio*, whose numbers increased progressively and significantly ($F_{9.81}$= 7.05; $p<0.001$) with increasing rehabilitation age to peak at 9 years. Since only one of the survey grids (Grid 12) had achieved a rehabilitation age of 9 years by the end of this study, no variance estimates were available and the statistical significance of this increase could not be evaluated.

Numbers of *M. coucha* ($F_{9.81}$ = 3.76; $p<0.001$) and other species ($F_{9.81}$= 5.96; $p<0.001$) also increased significantly with rehabilitation age, but peaked at 7 years, and then declined significantly. The decrease in the numbers of *T. brantsii* on the younger grids, and the increase on the older grids, were not statistically significant (Figure 3.25).

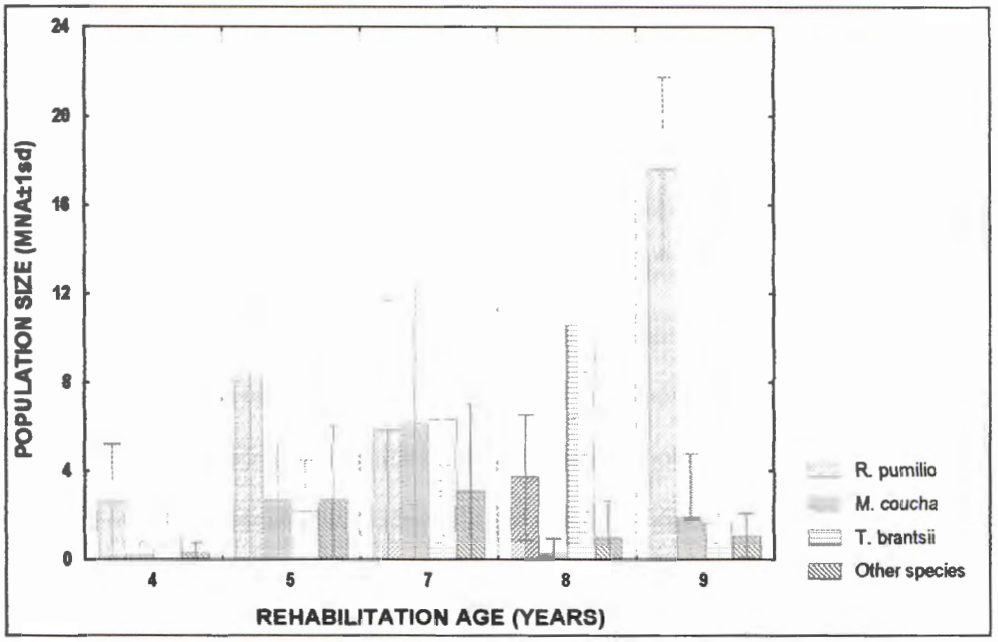


FIGURE 3.25: Community structure and population sizes of small mammals on the ash dam grids (all data pooled) in relation to rehabilitation age (Bars indicate ±1sd).

The biomass of small mammal communities varied similarly in relation to rehabilitation age (Figure 3.26). Biomass of *R. pumilio* increased significantly with rehabilitation age ($F_{9,81}$ = 5.82; $p<0.001$) to peak at nine years after rehabilitation. The biomass of *M. coucha* also increased significantly for up to seven years after rehabilitation ($F_{9,81}$ = 3.33; $p<0.01$), whereafter it decreased. The biomass of *T. brantsii* showed the same trend described above for *M. coucha*, but these changes in biomass with increasing rehabilitation age were not statistically significant. The biomass of other species on the ash dam grids was low, but showed a significant increase ($F_{9,81}$ = 2.45; $p<0.05$) on grids that were five to seven years old (Figure 3.26).

The high MNA and biomass of small mammals at 7 years post-rehabilitation presumably reflected optimal habitat suitability for small mammal communities (Figure 3.27), due to the

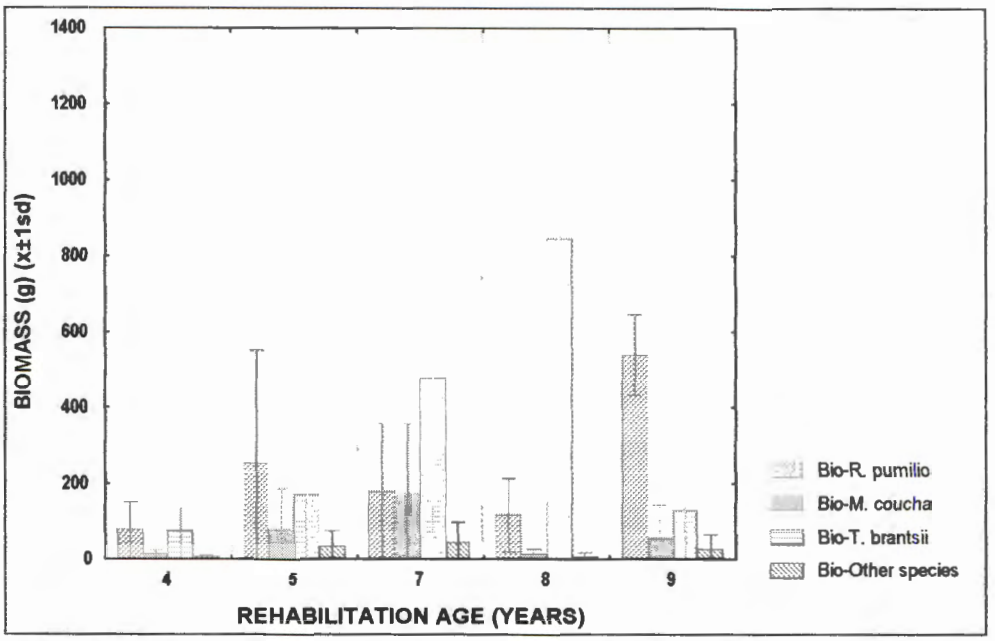


FIGURE 3.26: Variation in biomass of small mammal communities on the ash dam grids (all data pooled) in relation to rehabilitation age (Bars indicate ±1sd).

significantly higher plant diversity ($F_{9.36}$=7.05; $p<0.001$) during the same period (Morgenthal 1999). Biomass was dominated by *T. brantsii*, despite it not being numerically dominant, because of its larger body size.

These results agree with the results of Parker (1989), who found that small mammal density was lowest within the oldest areas after rehabilitation, while species diversity was greatest in the younger areas. According to Ferreira & van Aarde (1996), certain species can enter newly rehabilitated grids from older rehabilitating grids, while other species may enter these grids from undisturbed adjoining areas. The same pattern could apply here due to movement patterns between grids or emigration / immigration rates based upon capture data (Section 3.7.2.1 & 3.7.2.2).

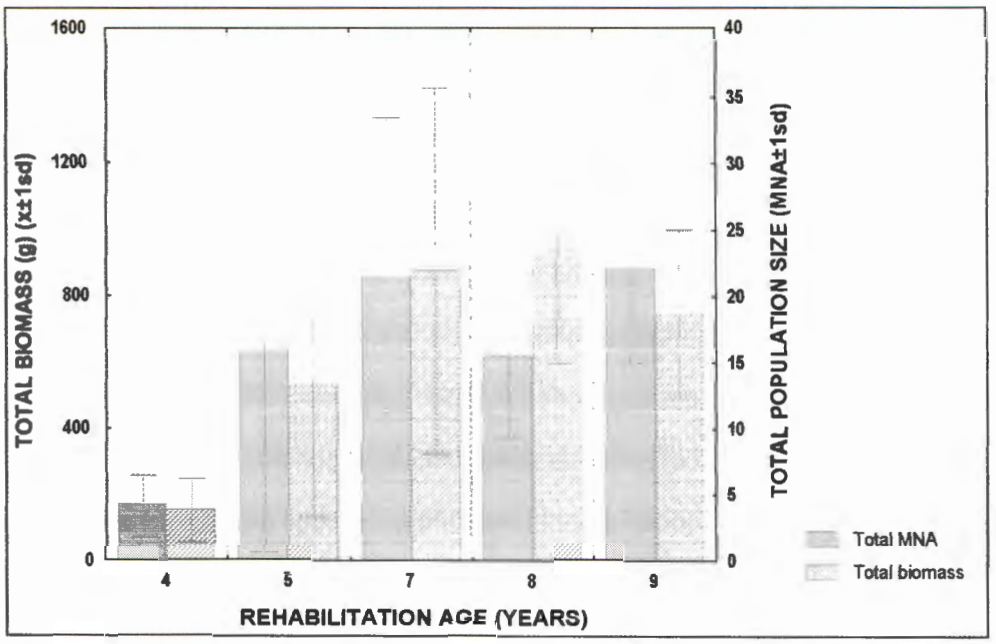


FIGURE 3.27: Variation in total biomass and total population size of small mammal communities on the ash dam grids (all data pooled) in relation to rehabilitation age (Bars indicate ±1sd).

3.6.2.2 Aspect and topography

The ash dams at Hendrina Power Station constitute artificial hills in an otherwise undulating landscape. Differences in the physical characteristics, such as aspect and topography, mediated via differences in micro climates, and also the ecological status of adjacent areas, may influence the rate at which re-vegetated communities recover, with an indirect effect on animal communities too.

Rhabdomys pumilio was dominant on all of the slopes of differing aspect, except on the west facing slope, as well as the plateaux grids of the ash dams where this species and *T. brantsii* were co-dominant (Figure 3.28). However, this dominance by *R. pumilio* was not statistically significant. Numbers of *M. coucha* were significantly higher on the slopes than on the plateaux ($H_{1,100}$=21.47; $p<0.001$), and also on the west-facing slopes

($H_{3,60}$=20.95; p<0.001). Population sizes of *T. brantsii*, on the other hand, were significantly higher on the plateaux than on the slopes of the ash dams ($H_{1,100}$=5.68; p<0.05), and this species was caught in significantly greater numbers on the grids facing east and west ($H_{3,60}$=18.74; p<0.001) than on the other slopes (Figure 3.28). The numbers of other, more specialized small mammal species captured during this study were significantly higher on the slopes than on the plateaux ($H_{1,100}$=25.43; p<0.001; Figure 3.28), which could reflect colonization from natural or unrehabilitated habitats adjoining the ash dams. The numbers of *T. brantsii* present on the ash dam grids was significantly higher ($H_{1,20}$=15.63; p<0.001) than on the control grids, while no significant differences were evident for the other species.

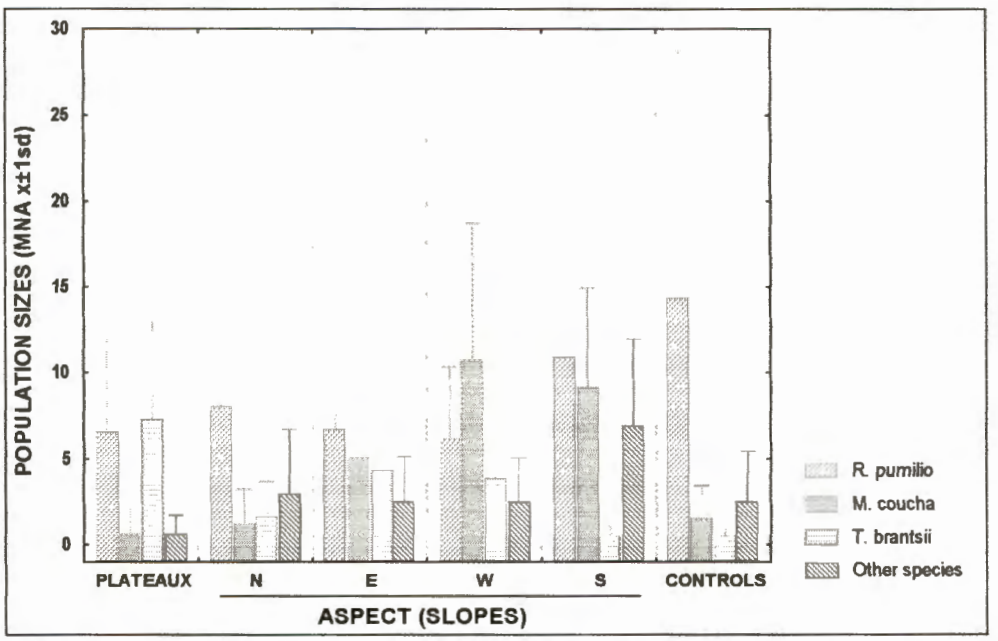


FIGURE 3.28: Community structure and population sizes of small mammals on the control and ash dam grids in relation to aspect and topography (Bars indicate ±1sd).

The same trends were evident for the biomass of the small mammal communities, with no significant differences in the biomass of *R. pumilio* in relation to topography or aspect on the ash dam grids. There was considerable variability in biomass on the slopes because

of a veld fire that destroyed vegetation on some slopes after May 1997, and also due to seasonal variation. These factors may have marked topographical - and aspect-related differences in small mammal biomass.

The biomass of *T. brantsii* was significantly higher on the plateaux ($H_{1,99}$=7.20; $p<0.01$) than on the controls, whereas the biomass of *M. coucha* ($H_{1,100}$=21.45; $p<0.001$), and other small mammals ($H_{1,100}$=25.88; $p<0.001$), was significantly higher on the slopes (Figure 3.29). The biomass of *M. coucha* was also significantly higher on the west- and south-facing slopes ($H_{3,60}$=10.66; $p<0.05$), while the biomass of *T. brantsii* was significantly elevated on the east- and west-facing slopes ($H_{3,60}$=25.18; $p<0.001$; Figure 3.29).

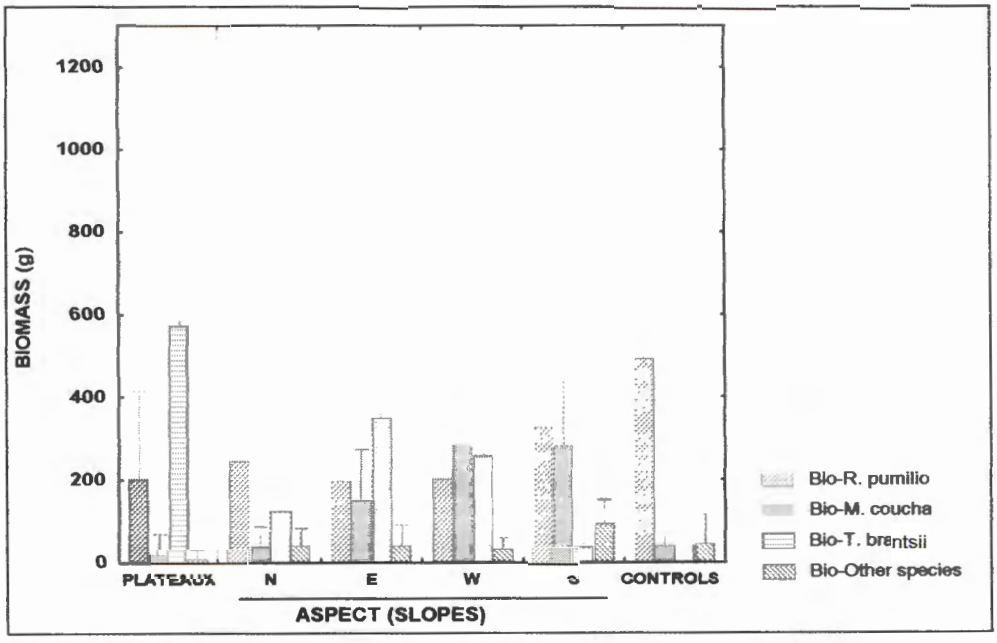


FIGURE 3.29: Variation in biomass of small mammal communities in relation to aspect and topography (Bars indicate ±1sd).

3.6.2.3 Ecological status of adjoining areas

The number of *R. pumilio* captured on the ash dam grids did not vary significantly in relation to the ecological status of the adjoining areas, but numbers of *M. coucha* were

significantly higher on slope grids adjacent to agricultural land and disturbed and - undisturbed grasslands ($H_{3,100}$=22.02; $p<0.001$). This supports previous reports of the predilection of *Mastomys* for disturbed habitats, crop fields and other habitats modified by man (Meester *et al.* 1979; Leirs 1994). Conversely numbers of *T. brantsii* were significantly higher on plateaux grids surrounded by other rehabilitated areas than on the ash dam slopes ($H_{3,100}$=9.82; $p<0.05$; Figure 3.30).

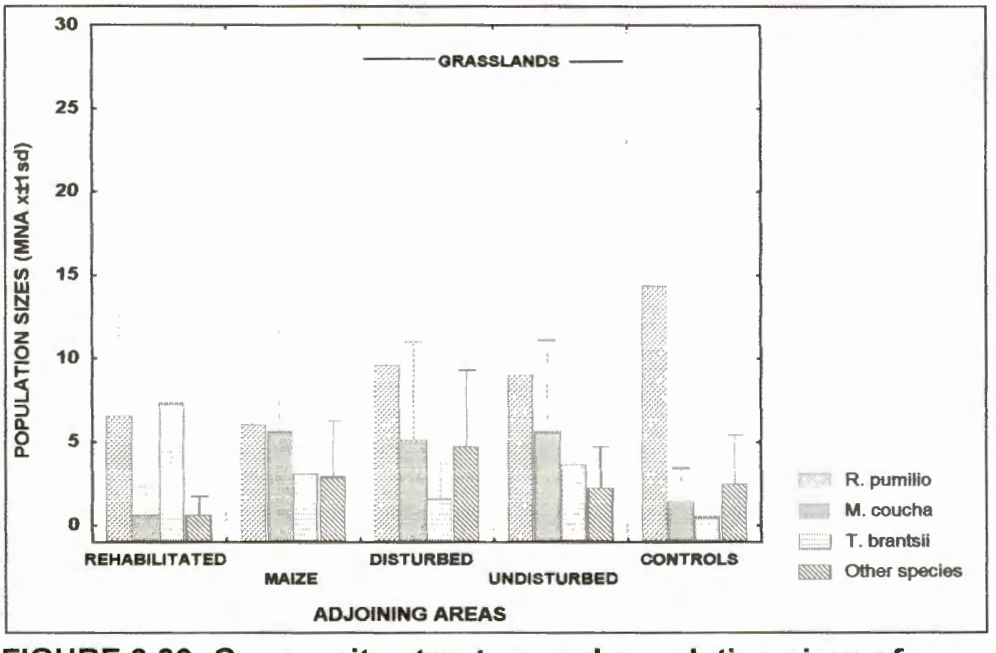


FIGURE 3.30: Community structure and population sizes of small mammals in relation to the ecological status of adjoining areas (Bars indicate ±1sd).

The biomass of small mammals showed the same trends as population sizes in relation to adjoining areas (Figure 3.31), with the highest biomass of *M. coucha* on the grids adjacent to maize fields and disturbed/undisturbed grasslands ($H_{3,100}$=21.99; $p<0.001$) and of other species on grids adjoining disturbed grasslands ($H_{3,100}$=30.52; $p<0.001$). Biomass of *T. brantsii* was highest on the rehabilitated ash dam plateaux grids ($H_{3,99}$=10.80; $p<0.01$).

The west- and south-facing slopes on the ash dams, represented by grids 7 & 8

respectively, and the high number of *M. coucha* captured here, may have been due to the nature of the adjoining area (agricultural lands). These fields may provide suitable food and cover for the highly-adaptable *M. coucha* during the summer period, whereafter these animals migrate to the ash dams (Grid 7 & 8) during the dry winter periods.

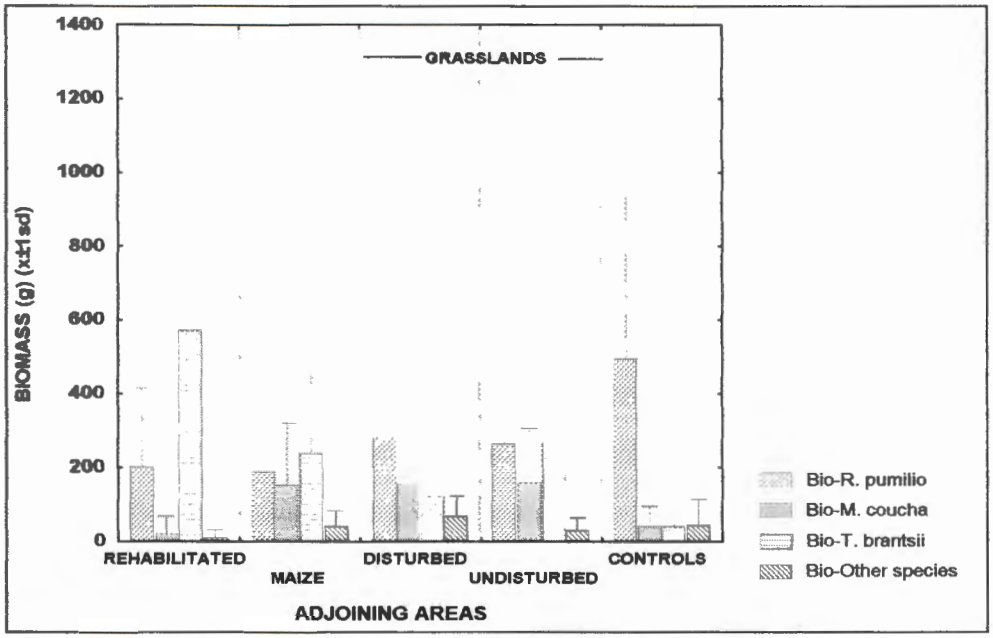


FIGURE 3.31: Variation in biomass of small mammal communities in relation to the ecological status of adjoining areas (Bars indicate ±1sd).

The highveld gerbil, *T. brantsii*, apparently preferred grids on the plateaux of the ash dams which were characterized by the *Chamaecrista biensis* variant (grids 10 & 11; Chapter 2; Table 2.3). This suggests that *T. brantsii* and *C. biensis* may coincide in the same areas, and that a symbiotic relationship may exist between them. *C. biensis* may play the same role as *Cyperus esculentus* in a study by De Moor (1969), whereby *C. esculentus* was found to be a early pioneer species, favoring disturbed areas where the mineral and nitrogen composition of the soil is changed. As secondary succession progresses and the soil compacts, the burrowing activity of some rodents favors the growth of *C. esculentus* around their colonies. In this study *Cyperus* and *Chamaecrista* may have similar roles and reactions during the secondary succession process.

The east-facing slopes on the ash dams, represented by grids 4 & 9, are characterized by the *Lespedeza cuneata-Hyparrhenia hirta* variant (Chapter 2). The high number of *T. brantsii* captured on these two grids may thus coincide with the appearance of *H. hirta* because significant positive associations were made between *T. brantsii* and *H. hirta* in a study in a sub-humid grassland in Kenya (Oguge 1995). The occurrence of the legume, *L. cuneata*, on these grids may play the same role as *C. biensis* on grids 10 & 11.

3.6.3 Diversity, equitability and richness in relation to macro-environmental parameters

Equitability (dispersion of individuals among species) and species richness (number of species) are both components of species diversity. The general term "diversity", as used in this study, includes equitability, species richness and Shannon diversity, but the latter terms are used *sense stricto* where necessary.

3.6.3.1 Rehabilitation age

Shannon diversity ($F_{1,108}$=10.58; $p<0.01$) and equitability ($H_{1,110}$=5.10; $p<0.05$) on the ash dam grids initially increased with rehabilitation age, and were significantly higher than on the controls from 5-7 years after rehabilitation (Figure 3.32). Thereafter, Shannon diversity ($F_{9.54}$=3.45; $p<0.01$) and equitability ($F_{9.54}$=2.74; $p<0.05$), declined steeply to levels approximating those on the controls. Species richness showed the same temporal trend, and increased significantly ($F_{9.81}$=4.17; $p<0.001$) with rehabilitation age and was also significantly higher on the ash dam grids than on the controls ($H_{1,120}$=4.05; $p<0.05$). The decline in diversity after 7 years therefore reflects increased domination of the small mammal communities, first by *T. brantsii*, mainly on the plateaux, and then by *R. pumilio*, especially on the slopes (Figure 3.28) of the ash dam grids, rather than any marked change in species richness.

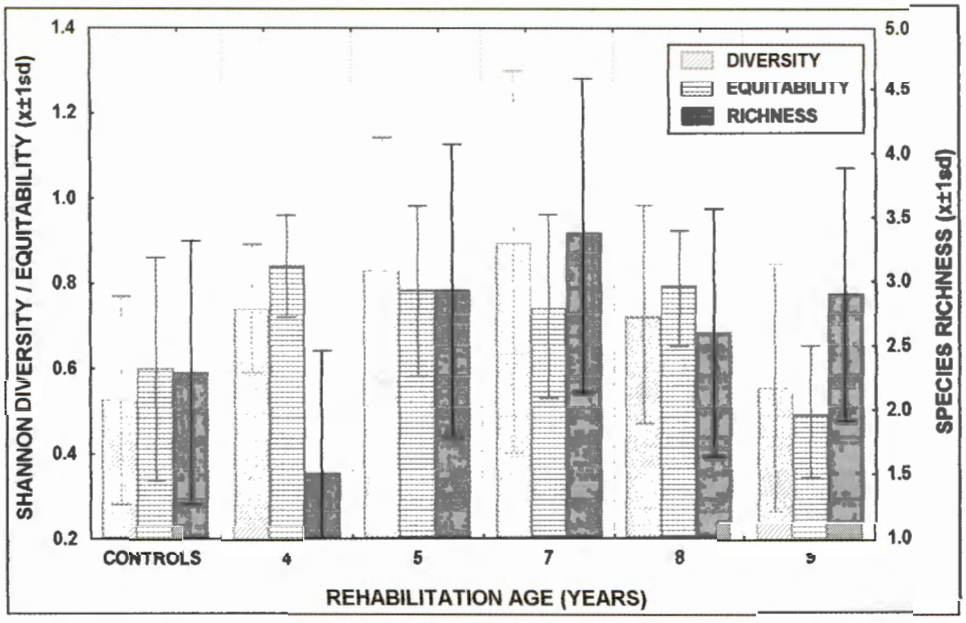


FIGURE 3.32: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age (Bars indicate ±1sd).

3.6.3.2 Aspect and topography

Diversity of the small mammal communities varied significantly in relation to aspect (diversity: $F_{3,55}=2.86$; $p<0.05$; equitability: $H_{3,59}=13.59$; $p<0.01$) and topography (diversity: $t=5.56$; $p<0.01$; equitability: $U=546.5$; $p<0.001$; richness: $U=611.5$; $p<0.001$; Figure 3.33). Diversity was significantly higher on the ash dam slopes than on the plateaux, where levels approximated those of the controls. Diversity and equitability were also significantly lower on the north-facing slopes, which probably reflects the hotter, drier micro-climates of these grids to some extent (Figure 3.33).

3.6.3.3 Ecological status of adjoining areas

Species richness ($H_{3,100}=19.10$; $p<0.001$), equitability ($H_{3,92}=13.81$; $p<0.01$) and diversity

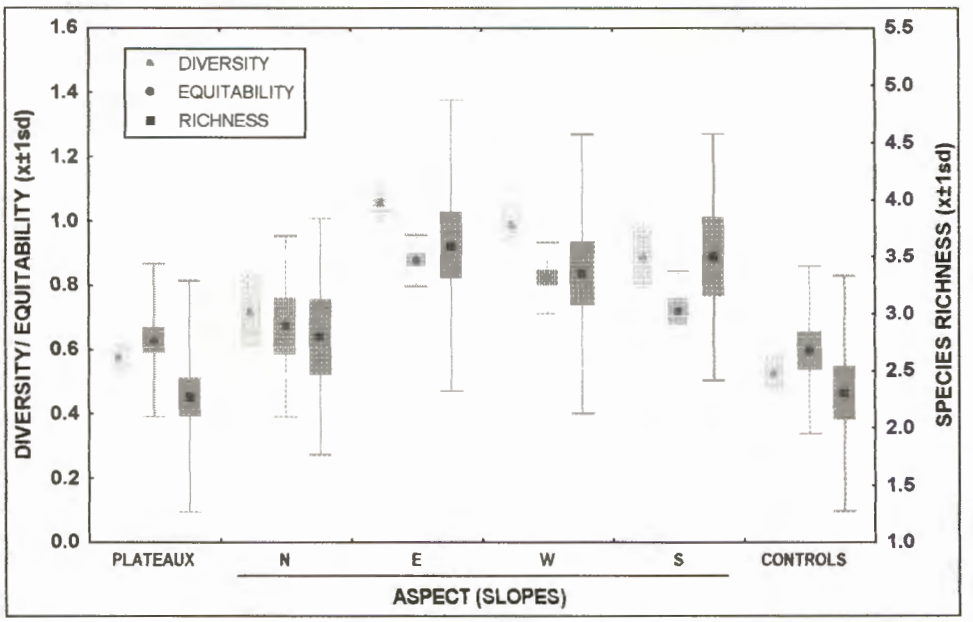


FIGURE 3.33: Variation in Shannon diversity, equitability and species richness in relation to aspect and topography (Bars indicate ±1sd; boxes±1se).

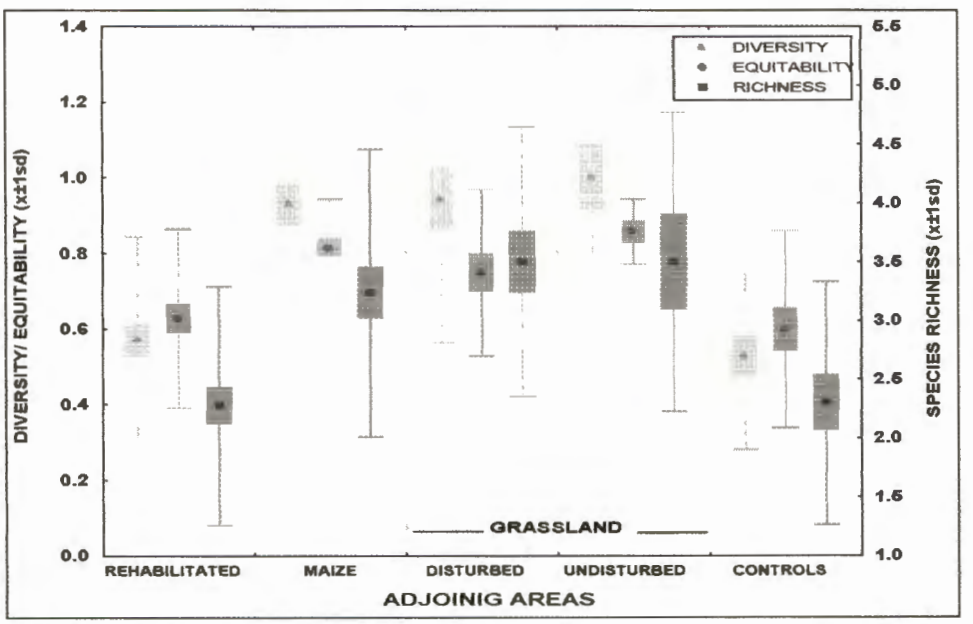


FIGURE 3.34: Variation in Shannon diversity, equitability and species richness in relation to the ecological status of adjoining areas (Bars indicate ±1sd; boxes ±1se).

($F_{3,88}$=10.23; p<0.01) were also significantly higher on the ash dam grids adjoining agricultural lands (maize fields) and disturbed or undisturbed grasslands than on the plateaux grids, which are surrounded by rehabilitated areas, or on the controls (Figure 3.34). The ecological status of adjoining areas (Table 2.2; Chapter 2) therefore apparently had some influence on small mammal diversity, probably via the determination of re-colonization opportunities or rates.

3.6.3.4 Vegetation variants

Diversity could also vary owing to factors, such as vegetation, that were unique to each grid. Grid 1 on ash dam A is here analyzed as a separate treatment due to its unique rehabilitation history (Chapter 2; Section 2.3). Species captured on this grid were not caught in sufficient numbers for the statistical analysis of patterns of diversity and equitability in relation to rehabilitation age, because no animals were captured during the January 1999 survey period (Figure 3.35).

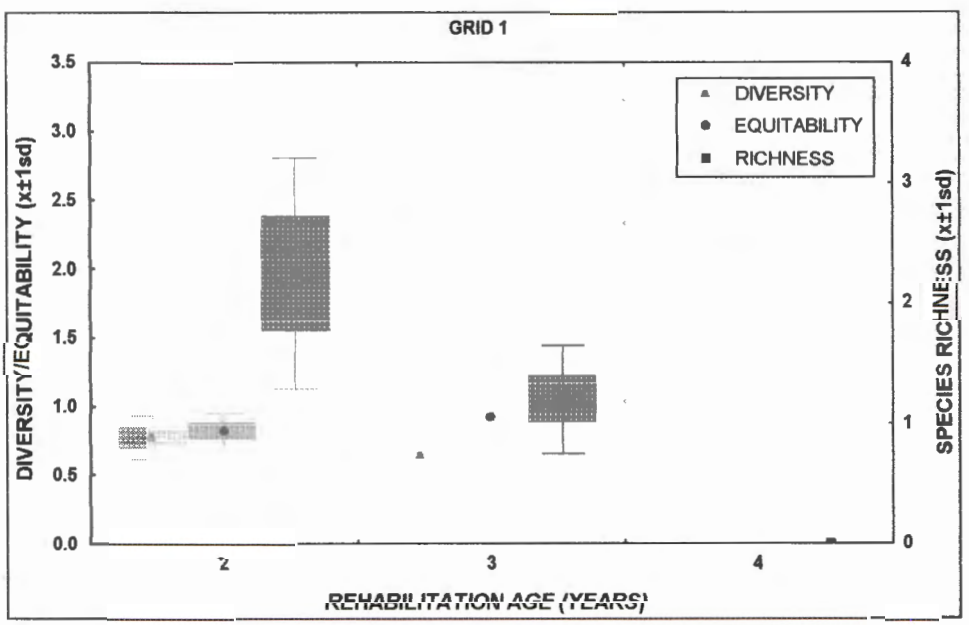


FIGURE 3.35: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 1 (Bars indicate ±1sd; boxes ±1se).

Species richness appeared to decline dramatically with increasing age of this grid, and this decrease was significant ($F_{2,7}$=4.88; $p<0.05$). This trend may have been an artefact resulting from a veld fire which destroyed the vegetation of this grid, leading to complete dominance of the small mammal community by *T. brantsii* (Section 3.6.4.2; Figure 3.49), rather than any age-related effect.

With rehabilitation treatment 3, comprising grids 2 and 3 (Table 2.2 & 2.3), no significant differences in diversity in relation to temporal succession were evident (Figure 3.36). Similarly, there was no significant temporal differences in these parameters on grid 4 (Figure 3.37). Since these three slope grids (2, 3 & 4) were rehabilitated in the same year (1994), but have different aspects, these grids were tentatively pooled as one treatment to assess if there were any aspect-related differences in small mammal community characteristics (Figure 3.38). ANOVA showed that any aspect-related differences were statistically non-significant, implying that aspect (mediated presumably via differences in micro-climates) had no major influence on community structure, at least on west-, east- and south-facing slopes.

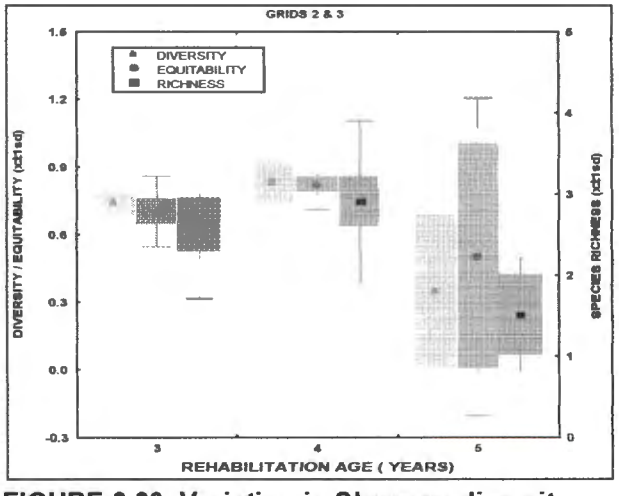


FIGURE 3.36: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grids 2 & 3 (Bars indicate ±1sd; boxes ±1se).

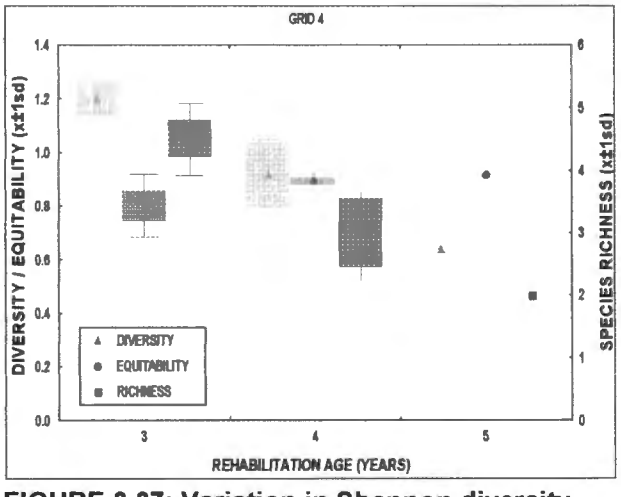


FIGURE 3.37: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 4 (Bars indicate ±1sd; boxes ±1se).

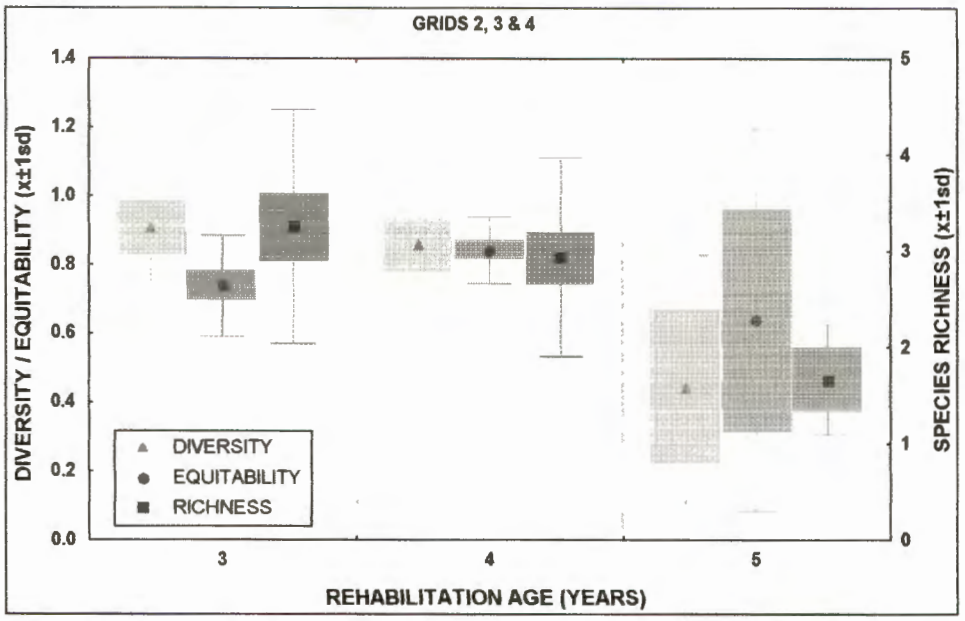


FIGURE 3.38: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grids 2, 3 & 4 (Bars indicate ±1sd; boxes ±1se).

Diversity decreased, albeit non-significantly, during the last survey period. This again was probably not an age-related effect but an afterfact resulting from a fire during 1998, whereafter *R. pumilio* disappeared and other pioneer species were captured in greater numbers (Section 3.6.4.2; Figure 3.50 & 3.51).

Although the grids on ash dam D, grids 7 and 8, were rehabilitated during the same period (Table 2.2) and are characterized by the same plant variants (Table 2.3), these two grids were regarded as representing two different rehabilitation treatments since they differ in aspect (south and west-facing slopes, respectively). No significant differences in diversity were evident for diversity in relation to rehabilitation age on grid 7 (Figure 3.39). The decline in all three parameters recorded in the last survey can be ascribed to the dominance of *T. brantsii* (Section 3.6.4.2; Figure 3.55), or to the atypical seasonal pattern in trapability that was evident during this study period.

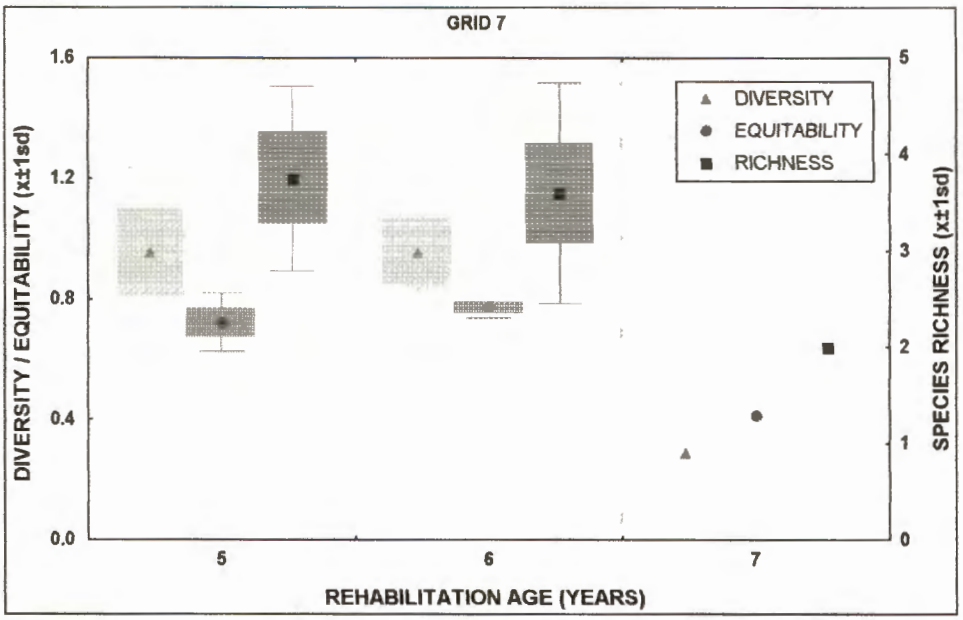


FIGURE 3.39: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 7 (Bars indicate ±1sd; boxes ±1se).

On grid 8, no significant differences in diversity in relation to increasing rehabilitation age were evident (Figure 3.40). All three of these parameters were relatively constant throughout the study period, reflecting a fairly even distribution of individuals between species (Section 3.6.4.2; Figure 3.56). This also explains why species richness on this grid was higher than on grid 7. These data suggest that aspect, mediated via micro-climates, may have had some influence on community characteristics.

No significant differences in diversity in relation to rehabilitation age were evident on grid 9 (Figure 3.41). The slight increase in diversity and species richness after 6 years of rehabilitation can be ascribed due to the appearance of *M. coucha* during the winter months of 1998. This species apparently migrates onto the ash dams during the cold winter when food is scarce in adjoining areas. The subsequent decrease in diversity and richness during the next year (7) may similarly reflect migration of *M. coucha* from the ash dams into more suitable habitats on the adjoining unrehabilitated areas (Section 3.6.4.2;

Figure 3.52).

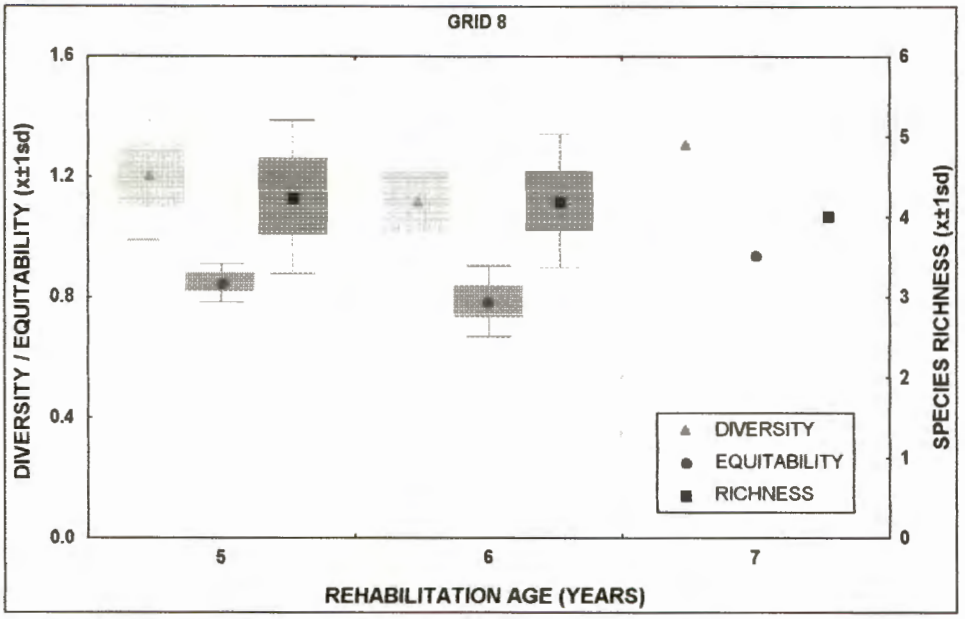


FIGURE 3.40: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 8 (Bars indicate ±1sd; boxes ±1se).

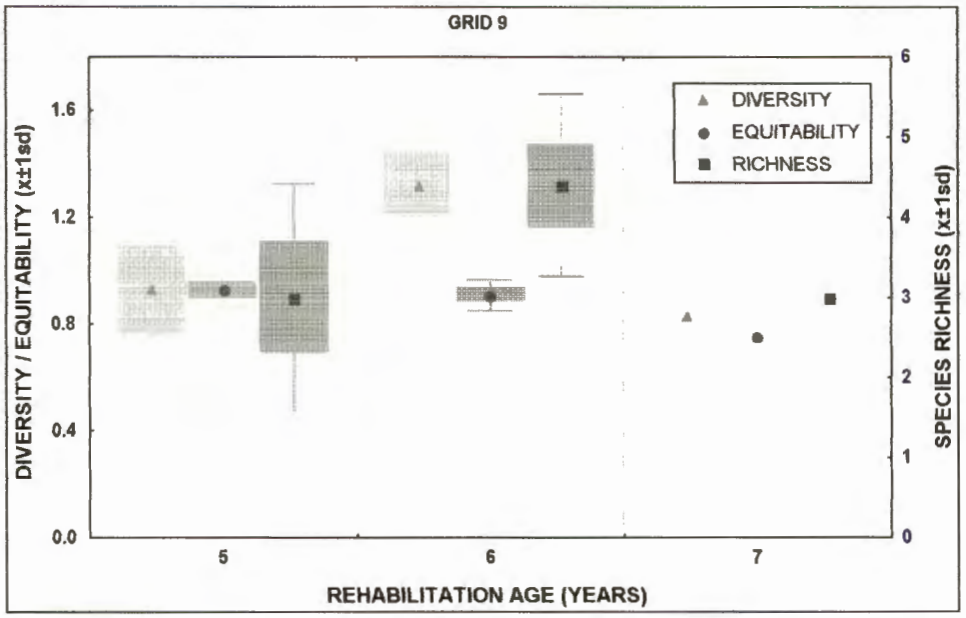


FIGURE 3.41: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 9 (Bars indicate ±1sd; boxes ±1se).

No significant differences in diversity were evident between grids 4 and 9, which have the same aspect (east facing), but differ in rehabilitation age (having been rehabilitated in 1994 and 1992, respectively). Similarly, when data for these two grids were pooled, again no significant age-related differences in diversity was evident (Figure 3.42).

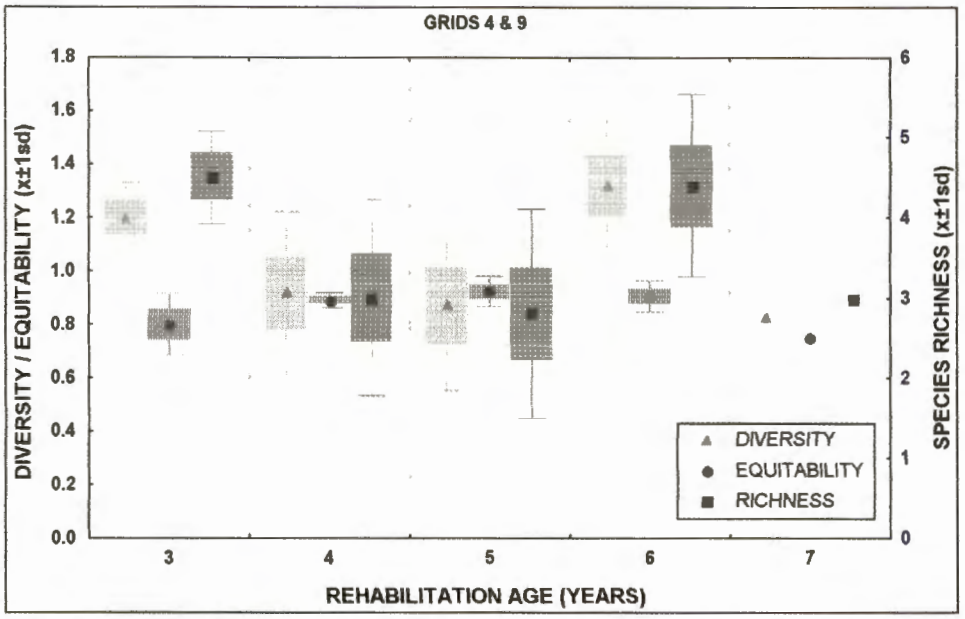


FIGURE 3.42: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grids 4 & 9 (Bars indicate ±1sd; boxes ±1se).

No significant differences in diversity were evident between grids 10 and 11, which are both located on the plateaux of ash dam C (*Chamaecrista biensis* variant), but differ in rehabilitation age (having been rehabilitated in 1991 and 1992, respectively). Similarly, when data for these grids were pooled, again no significant successional differences in diversity were evident during the study period. But, when data for the single 1999 survey were excluded (since no replicates were available) a significant increase in Shannon diversity ($F_{2,14}$=7.68; $p<0.01$) was evident between 5 and 7 years post-rehabilitation (Figure 3.43). Both these grids were dominated by the Highveld gerbil, *T. brantsii*, with *R. pumilio* as the second most dominant species. The increase in diversity after 7 years was due to the appearance of other rodent species and *M. coucha* as secondary succession

proceeded (Section 3.6.4.2; Figure 3.53).

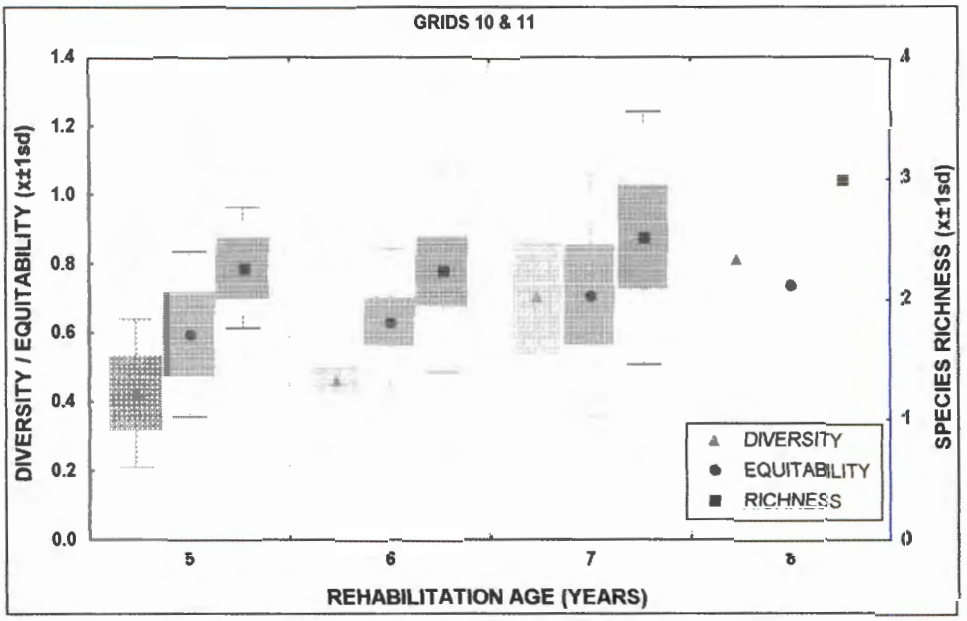


FIGURE 3.43: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grids 10 & 11 (Bars indicate ±1sd; boxes ±1se).

The oldest rehabilitated grid, grid 12, was regarded as a separate rehabilitation treatment because of topographic differences (situated on a lower level of the ash dam plateaux) and higher moisture levels of the soil. This grid showed a significant decrease in equitability ($F_{1,7}$=18.13; $p<0.01$) and Shannon diversity ($H_{1,9}$=4.86; $p<0.05$) 8 years after rehabilitation (Data for the single 1999 survey were again excluded due to a lack of replication). Species richness, however, did not vary significantly between the two years (1997 & 1998) (Figure 3.44). The temporal decline in Shannon diversity and equitability can be attributed to increased domination of the small mammal community by *R. pumilio*. Other species, notably *T. brantsii* and *M. coucha*, were captured in significant numbers only in 1997, and numbers thereof declined in 1998 (Section 3.6.4.2; Figure 3.54).

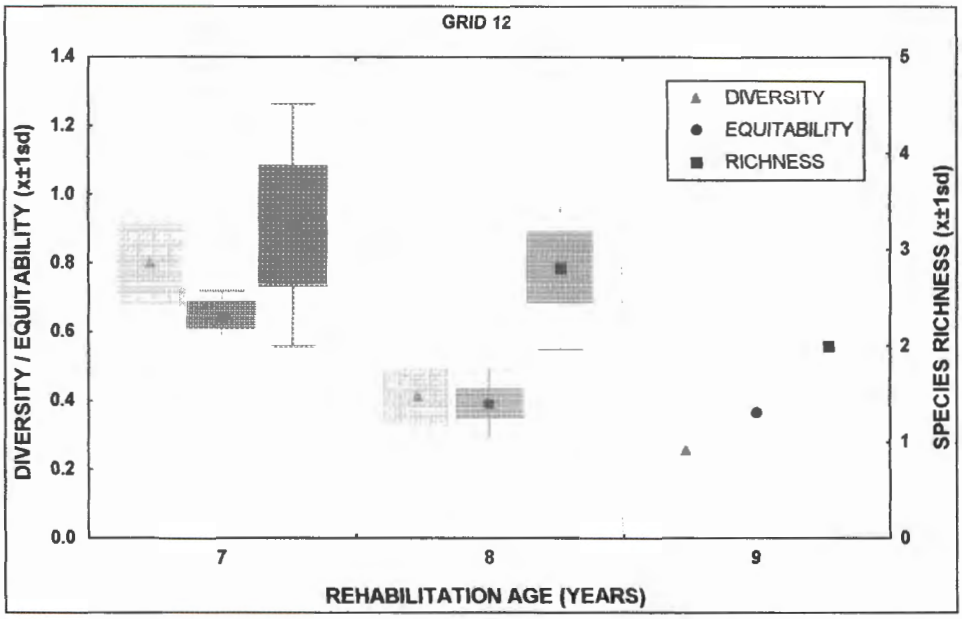


FIGURE 3.44: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for grid 12 (Bars indicate ±1sd; boxes ±1se).

Grids 10, 11 and 12 differed significantly in relation to Shannon diversity ($F_{3,22}$=7.69; $p<0.01$) and equitability ($F_{3,22}$=4.88; $p<0.01$). Again, data for the single 1999 survey were excluded due to a lack of replication (Figure 3.45). These differences could be due to grid 12, which had a significantly higher ($F_{3,23}$=4.26; $p<0.05$) vegetation cover and biomass ($F_{3,23}$=12.68; $p<0.001$) than grids 10 and 11.

3.6.4 General successional patterns

Habitat selection by small mammal species is related to factors such as soil texture and the amount of cover present (Nel 1978; Grant *et al.* 1982). According to Nel (1978), differences in soil types are responsible for much of the observed variation in plant species present (food resources), as well as for the amount and degree of plant cover present. This in turn influences the survival of certain species and also the number of species a habitat can support, and also furthermore provides cover for protection from predators

(Abramsky 1988; Kerley 1992; Monadjem 1997).

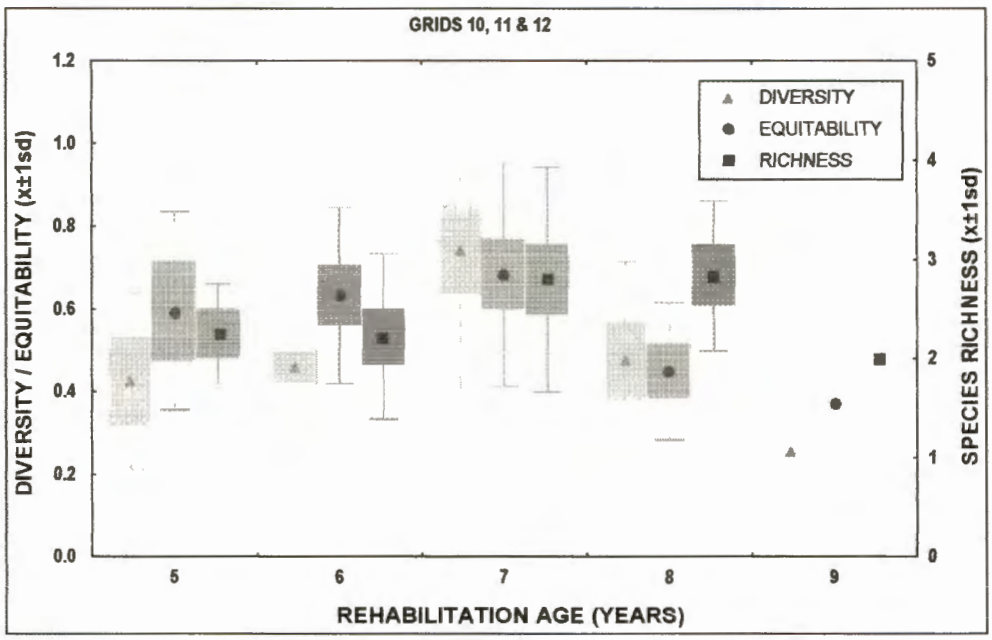


FIGURE 3.45: Variation in Shannon diversity, equitability and species richness in relation to rehabilitation age for the grids on the plateaux of ash dam C (grids 10, 11 & 12; Bars indicate ±1sd; boxes ±1se).

Burning is a regular occurrence in grassland habitats and results in a decline in the number of animals captured owing to food shortages and a lack of vegetative cover. Successional changes in the composition of small mammal communities within burnt areas are directly related to vegetational changes induced by fire, rather than a direct response to fire (Beck & Vogl 1972). The variety of reactions exhibited by different species suggests that the ability of a species to respond to fire, or to the post-fire environment, is part of a response continuum (Fox 1982). The result is a species-replacement sequence or succession that may facilitate coexistence, increase species richness, and determine species composition and community structure in a certain area (Fox 1982), as encompassed by the three models for ecological succession discussed in Chapter 1.

Numerous studies in forests, prairies and rangelands (Fox & McKay 1981; Parker 1989; Kirkland 1990; Ferreira & Van Aarde 1996) have shown that ecological succession is characterized by changes in species composition (species addition, species replacement or localized extinctions), species richness or equitability. Tramer (1969) concluded that succession occurs via variations in equitability in unstable environments, but through changes in species richness in more predictable habitats. Other authors, however, argued that species replacement, changes in density and competition effects, are the main factors following disturbance. Successional patterns following disturbance, therefore appear to be habitat-specific (Fox & McKay 1981; Parker 1989; Ferreira & Van Aarde 1996).

3.6.4.1 Successional trends on the control and ash dam grids

Different temporal patterns in community characteristics were evident on the ash dam plateaux, slopes and the control grids. On the controls, population sizes varied significantly among surveys ($H_{9,20}$=18.06; $p<0.05$). *R. pumilio* was dominant until the May 1998 survey after which a veld fire occurred on the controls (between May 1998 and July 1998), causing a dramatic decline in the numbers of *R. pumilio*, and therefore also in total population size, during the following survey periods ($H_{9,20}$=17.98; $p<0.05$). During this recovery phase there was a slight, but non-significant increase in the numbers of *M. coucha* and *T. brantsii* (Figure 3.46).

Population sizes did not vary significantly among surveys on the ash dam plateaux , and both *R. pumilio* and *T. brantsii* were co-dominant, with only a minor contribution to numbers by *M. coucha* and other species (Figure 3.47). On the ash dam slopes, however, there was a general and sequential decline in the numbers of *R. pumilio* ($H_{9,60}$=36.47; $p<0.001$) from autumn (1998) through winter to spring / summer (1999), coincident with a significant increase in numbers of *M. coucha* ($H_{9,60}$=21.27; $p<0.05$) and to a lesser, not significant extent, also of *T. brantsii* (Figure 3.48).

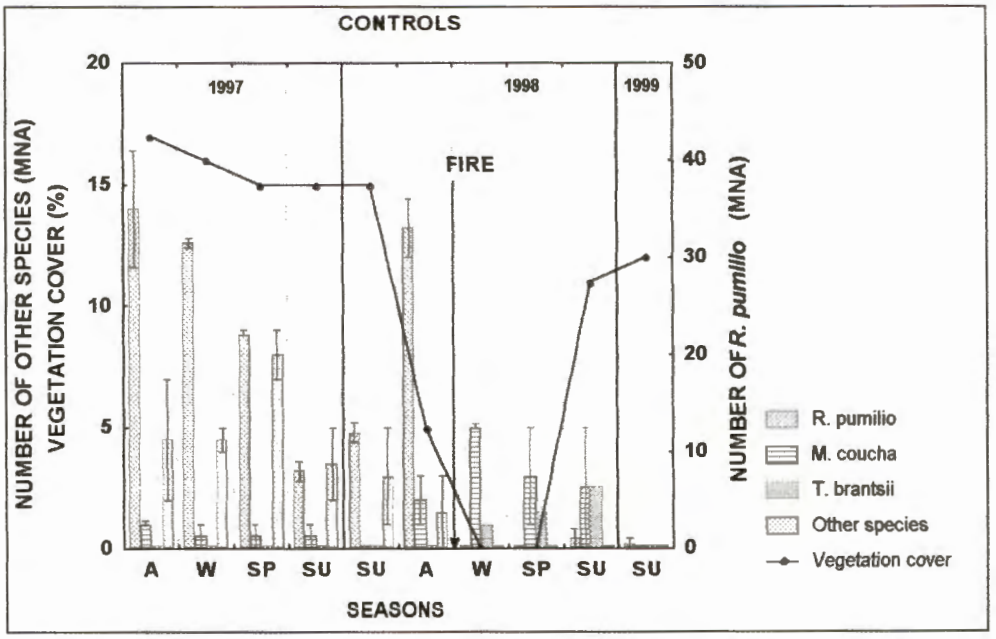


FIGURE 3.46: Variation in community structure and population sizes for each survey on the control grids (Bars indicate ± 1sd).

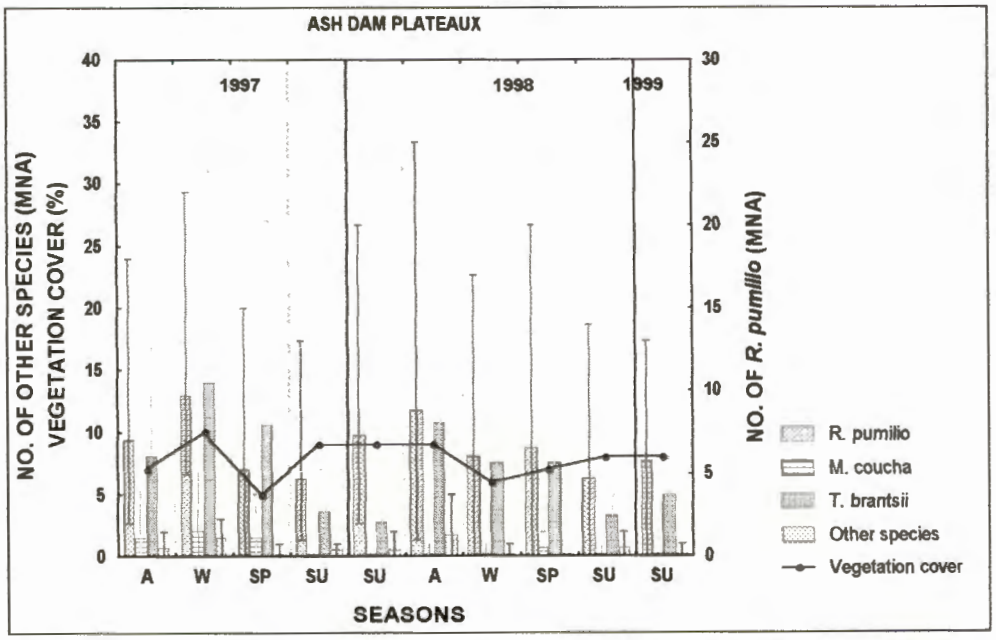


FIGURE 3.47: Variation in community structure and population sizes for each survey on the ash dam plateaux sites (Bars indicate ±1sd).

Small mammal communities on the ash dam slopes therefore showed similar temporal trends as those on the control grids, whereas those on the ash dam plateaux tended to be more stable and were dominated by *R. pumilio* and *T. brantsii*, especially on the older rehabilitated grids 10 & 11 of ash dam C.

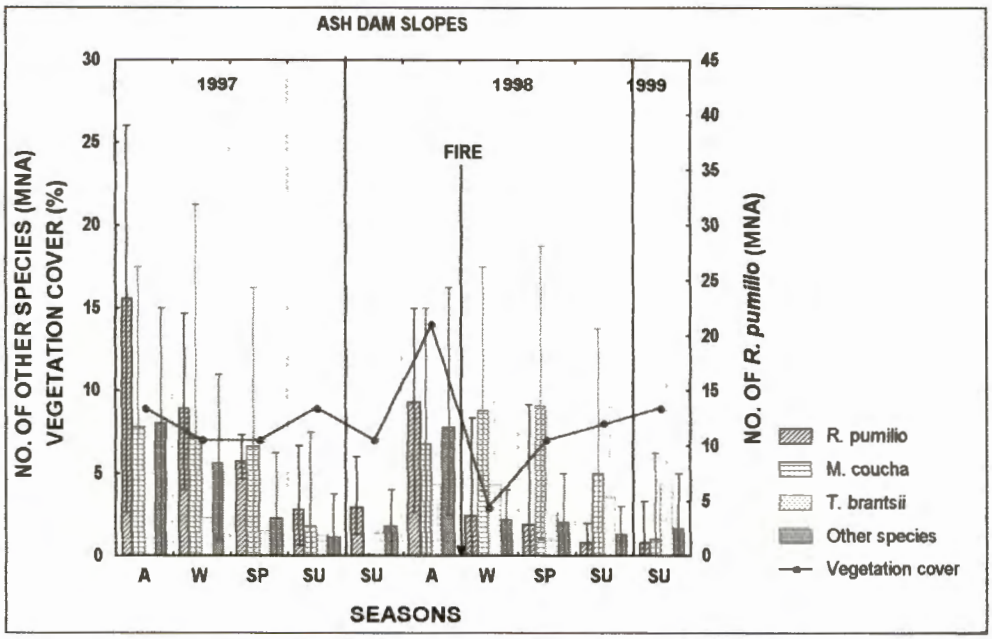


FIGURE 3.48: Variation in community structure and population sizes for each survey on the ash dam slope sites (Bars indicate ±1sd).

On the ash dam slopes, *R. pumilio* was dominant until a veld fire between the autumn and winter of 1998. As was evident on the controls, *R. pumilio* was replaced by *M. coucha* whereafter *T. brantsii* were captured in higher numbers towards the end of the study period (although this increase was not significant; Figure 3.48). A species-replacement successional pattern was thus evident following habitat destruction by fire.

Habitat preferences of small mammals are determined primarily by the type of cover available to them and areas with a dense plant cover generally support a higher diversity of animals (Oguge 1995; Monadjem 1997). *R. pumilio* dominated the controls during the first part of the study, but declined after the veld fire which had a marked effect on this

species. *R. pumilio* is a diurnal species whose movements and distribution appear to be depended upon the presence of adequate cover for protection from (particularly avian) predators (Christian 1977; Meester *et al.* 1979).

The appearance of *M. coucha* in this post-burn area may be due to the fact that this species is extremely adaptable and is likely to be one of the first species to become established in an area which is recovering from some form of habitat destruction, as was recorded for *M. natalensis* by Meester *et al.* 1979. It appears that these two species have a very similar ecology. The reduction in plant cover and biomass after the fire also favored species such as *T. brantsii*, which prefers open areas in the initial stages of plant succession (Kern 1981). As succession proceeded and more specialized plant communities became established after good rains, more specialized species replaced pioneer species, as was evident with the appearance of *R. pumilio* during the last two survey periods (Figure 3.46).

3.6.4.2 Successional trends within different rehabilitated treatments

The same pattern that was evident on the controls was observed on the four grids on ash dam A as well. A veld fire swept through these grids after the May 1998 survey period and thereafter the species composition changed dramatically on each grid. On grid 1, *R. pumilio* disappeared after the fire, while the pioneer species *M. coucha* and *T. brantsii* appeared in the traps (Figure 3.49). Vegetation cover decreased dramatically after the fire (Figure 3.49), suggesting that this area no longer fulfilled the habitat requirements of *R. pumilio*, and instead provided a habitat suitable for species more adaptable to a post-fire environment, such as *T. brantsii* (Kern 1981). These results concur with the findings of numerous other studies showing that the removal of vegetation by fire can create large patches of open habitat, accompanied by an increase in abundance of species having ecomorphological traits that enable them to exploit open areas, while species less specialized to cope with open areas tend to decrease (Ojeda 1989; Fa & Sanchez-Cordero

1993).

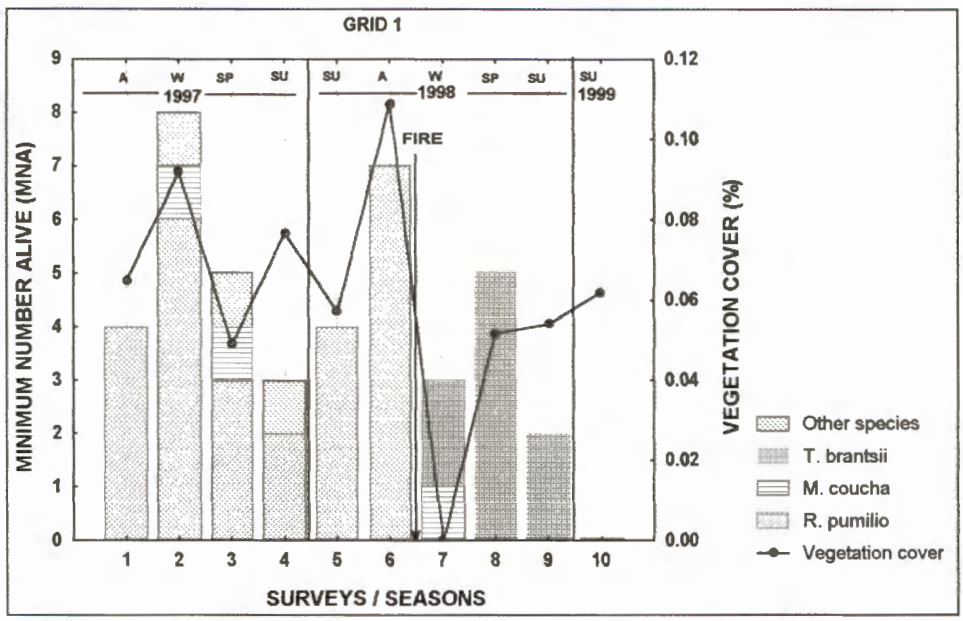


FIGURE 3.49: Population sizes of small mammal species and the average vegetation cover of grid 1 (Data for each survey combined).

Figure 3.50 shows the relative abundance of the small mammals captured on grids 2 and 3, which were also characterized by a dominance of *R. pumilio* until the May 1998 survey, whereafter this species was rarely captured following a veld fire in June 1998 . Again this can be ascribed to a not significant decline in the average vegetation cover during this period (Figure 3.50). The appearance of *M. coucha* in this area was presumably due to immigration into the burnt grassland soon after the fire (Meester *et al.* 1979) from adjoining unrehabilitated areas. Post-burning changes favour different species in succession and *T. brantsii* therefore entered the succession at a later stage. After the summer rains, *R. pumilio* was again captured on these areas, probably due to the increase in basal cover.

Grid 4 supported *R. pumilio*, *M. coucha* and *T. brantsii* before the fire, but after the fire *M. coucha* and *T. brantsii* dominated this area (Figure 3.51). The presence of other species on the grids on the slopes (Grids 2, 3 & 4), including taxa such as *M. varius*, which

prefers wetter areas, can be attributed to mesic habitats and dense vegetation associated with a drainage ditch along the bottom of each slope.

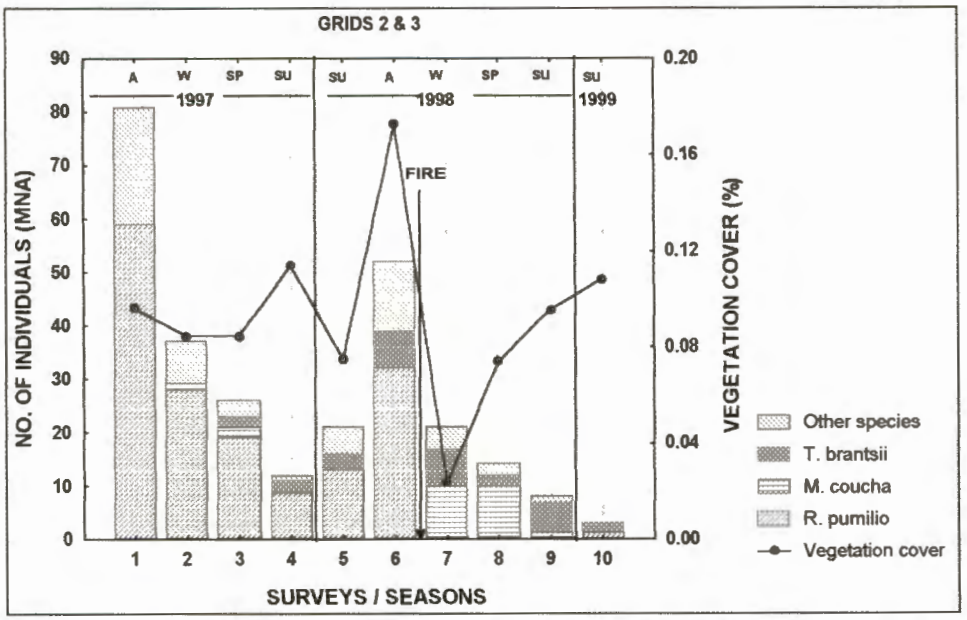


FIGURE 3.50: Population sizes of small mammal species and the average vegetation cover of grids 2 & 3 (Data for each survey combined).

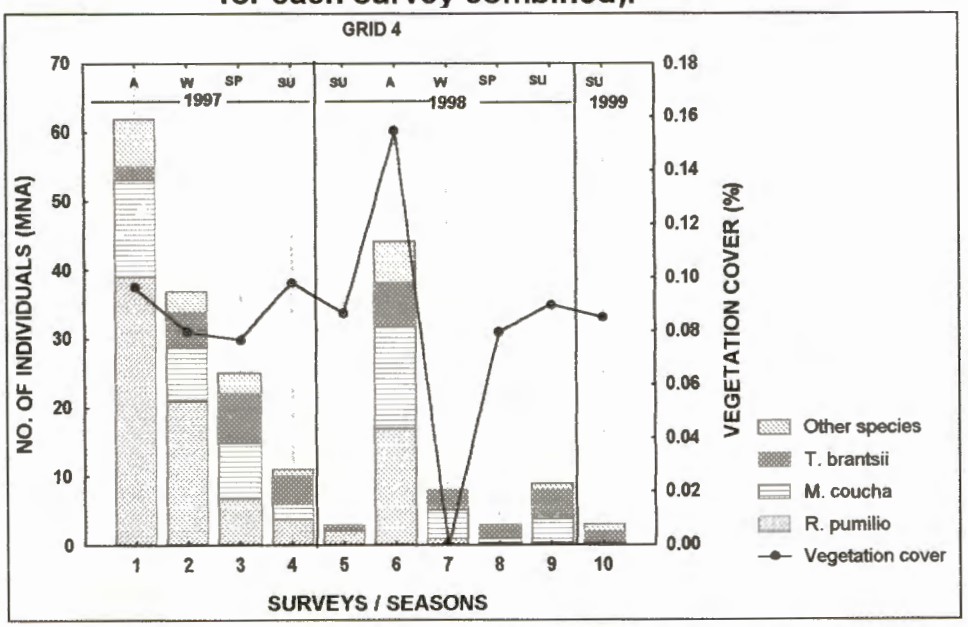


FIGURE 3.51: Population sizes of small mammal species and the average vegetation cover of grid 4 (Data for each survey combined).

On all three of the slopes on ash dam A the atypical seasonal pattern in population sizes discussed earlier (Section 3.6.1), was evident for all species before the fire. This implies that occurrence of a fire in 1998 was not solely responsible for the low numbers observed in the wet season of 1998/9, although it probably had some influence on population sizes and community structure during the following summer.

On ash dam C, grid 9 was dominated by *R. pumilio* and *M. coucha* during the first few survey periods (Figure 3.52), whereafter the number of *R. pumilio* tended to decline. Population sizes of *R. pumilio* were not significantly correlated with vegetation cover. The absence of any clear relationship between cover and population sizes of *R. pumilio* may reflect the aseasonal decline in numbers (Section 3.6; Figure 3.52). Numbers of *M. coucha* tended to increase towards the spring of 1998, but again there was no significant correlation with vegetation cover (Figure 3.52).

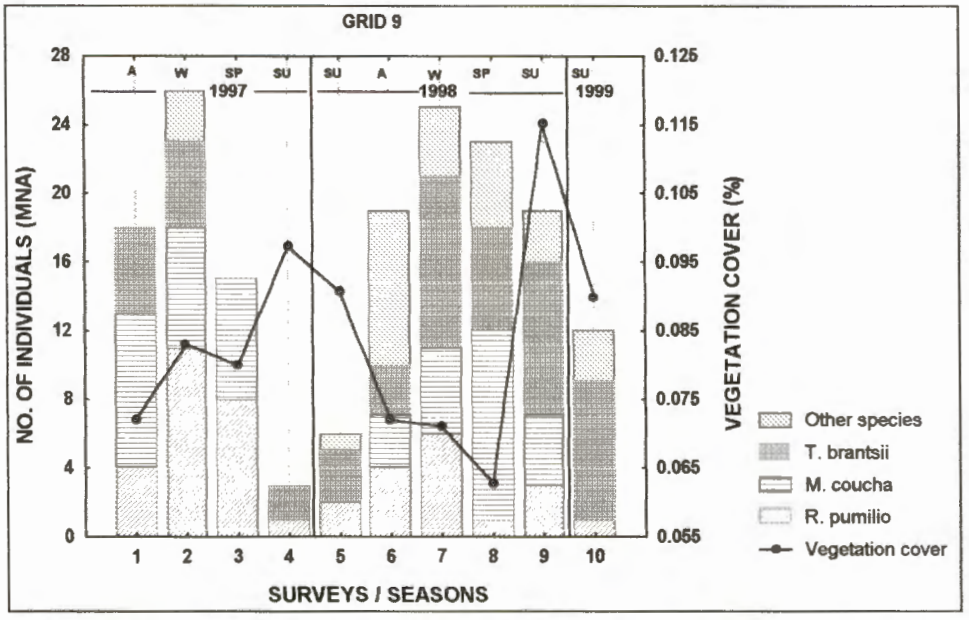


FIGURE 3.52: Population sizes of small mammal species and the average vegetation cover of grid 9 (Data for each survey combined).

Other taxa captured on this grid included species such as *O. irroratus* and *M. varius*. *O.*

irroratus is a specialized herbivore and seasonal migrant which retreats to more mesic adjacent (natural) grasslands in the dry season (Perrin 1980). This species entered the successional series relatively late after secondary succession started when the habitat fulfilled its stenoecious requirements (Meester *et al.* 1979).

Throughout the study period grids, 10 and 11 were dominated by the Highveld gerbil, *T. brantsii* (Figure 3.53). Species such as *R. pumilio* were not present in high numbers owing to the lack of adequate vegetation cover (Figure 3.53). The presence of *T. brantsii* in such high numbers can be attributed to other factors that are discussed in more detail in Section 3.6.5.

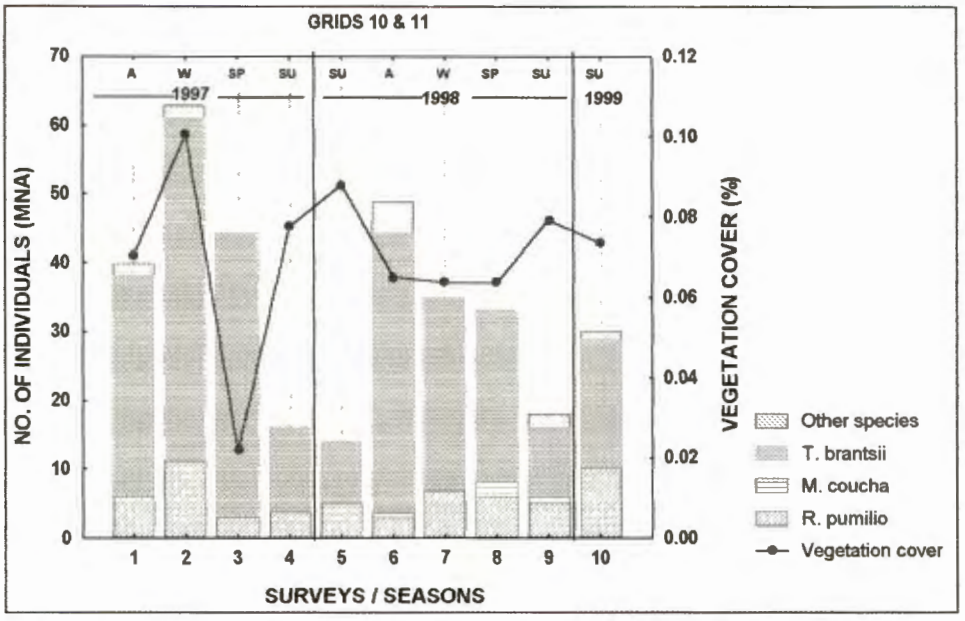


FIGURE 3.53: Population sizes of small mammal species and the average vegetation cover of grids10 &11 (Data for each survey combined).

The basal cover of grid 12 was relatively high during each survey period (Figure 3.54), and favoured *R. pumilio*, which was the dominant species on this grid throughout the study (Figure 3.54). The prominent atypical seasonal pattern in population sizes was evident on the grids of this ash dam as well, except on grid 12 where *R. pumilio* was present in

high numbers during every season. Grid 12 was characterized by less marked seasonal changes in cover, suggesting that vegetation characteristics and the different soil structure of grid 12 buffered small mammal community fluctuations.

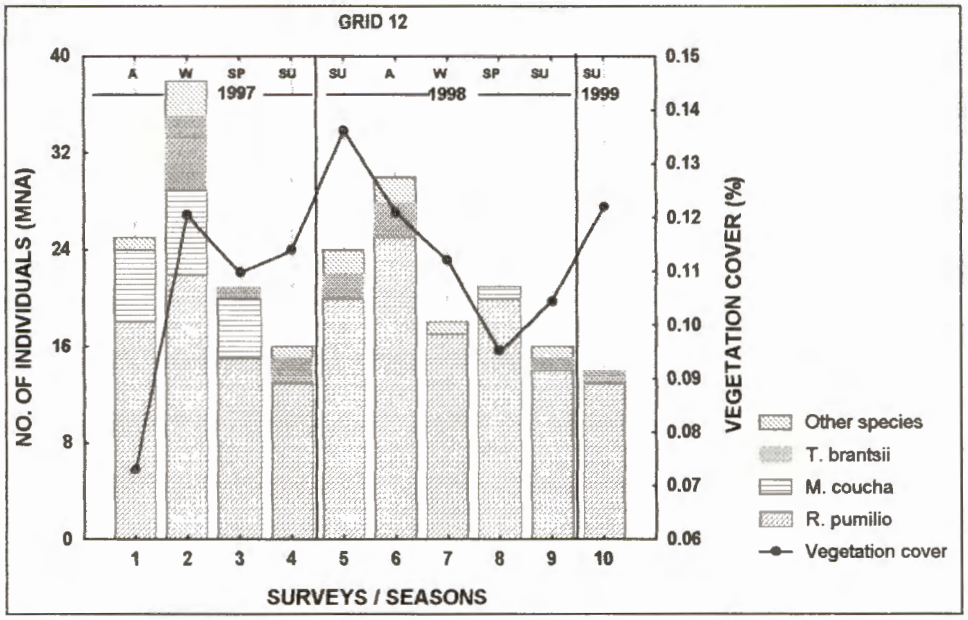


FIGURE 3.54: Population sizes of small mammal species and the average vegetation cover of grid 12 (Data for each survey combined).

On ash dam D, *M. coucha* predominated the small mammal community on grid 7, except during the wet summer months when these animals disappeared and returned again during the subsequent dry winter months (Figure 3.55). Grid 7 is bordered by agricultural lands, and during the summer months food may be more readily available in these areas, whereas during winter the ash dams may serve as some sort of refugium. The decline in the number of *R. pumilio* captured towards the end of the study on grid 7 cannot be ascribed to a decline in vegetation cover, because the basal cover on grid 7 increased during the same period (Figure 3.55). There was no significant correlation with cover and numbers of any of the dominant species. The decline in the numbers of *R. pumilio* on this grid can instead be ascribed to the increase in the numbers of *T. brantsii* during the same period. Numbers of these species were inversely proportional, and although the negative

correlation was not significant, the r^2 value was 0.63 implying that 63% of the variance in the numbers of these species was explained by this inter-specific relationship. *T. brantsii* reduces vegetation cover and floristic composition (Bronner *et al.* 1999), and may thus negatively impact on the preferred habitat of *R. pumilio*.

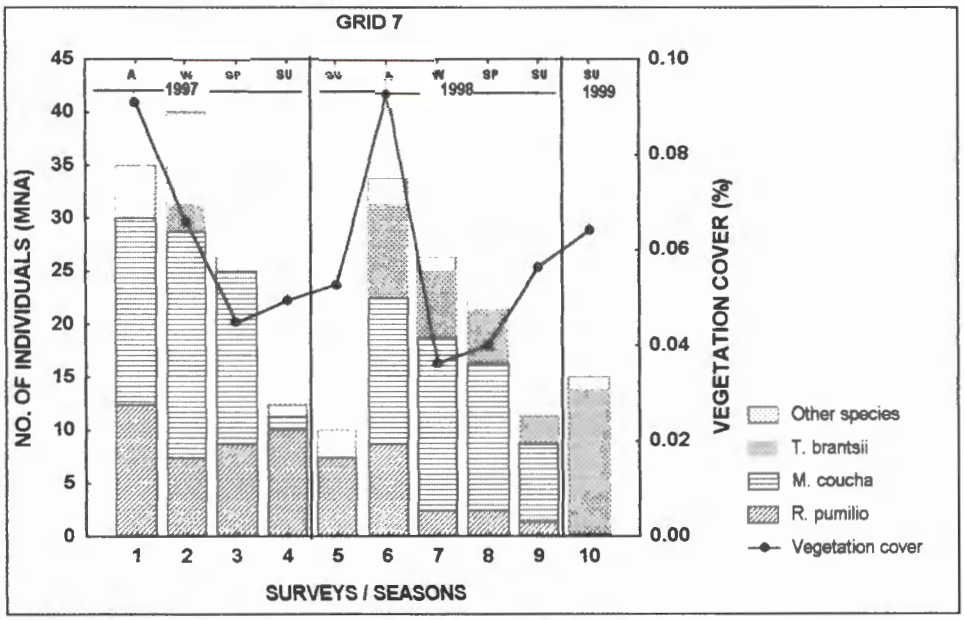


FIGURE 3.55: Population sizes of small mammal species and the average vegetation cover of grid 7 (Data for each survey combined).

While *R. pumilio* was generally the dominant species of small mammals on grid 8 in autumn and winter, other species, particularly *M. coucha* and *Mus minutoides*, predominated in the wet season surveys (Figure 3.56). Numbers of the latter tended to increase with a decrease in *R. pumilio,* but no significant correlation between population sizes of these species was evident. Numbers of *R. pumilio* were not significantly correlated with vegetation cover, which suggests that competition may have taken place between *R. pumilio* and other species. When vegetation cover is high, the *R. pumilio* population was large and inter-specific competition for resources may have been reduced. The increase in the number of *M. coucha* during the second part of the study may have been due to immigration onto the ash dams which apparently serve as a refugium during

this time of the year.

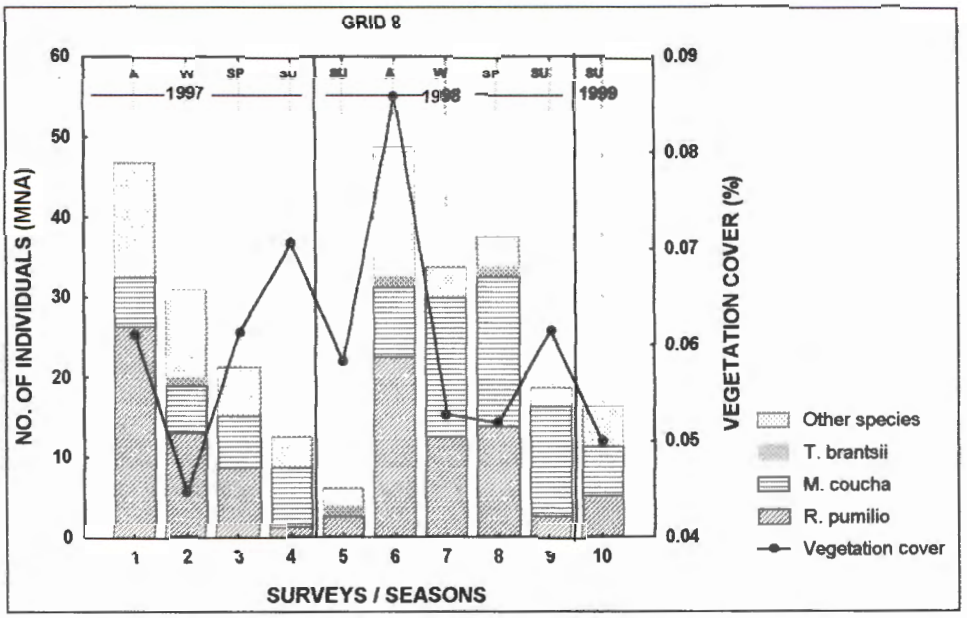


FIGURE 3.56: Population sizes of small mammal species and average vegetation cover of grid 8 (Data for each grid combined).

3.6.5 Ecological correlates of small mammal community structure

Intra- and interspecific interactions, as well as the structure of each species' environment, may influence the distribution of small mammals (Fa *et al.*1990). The role of microhabitat characteristics in determining patterns of co-existence and the within-habitat distribution of desert rodents has been well documented in South Africa (Kerley 1990) and in other parts of the world (Rosenzweig & Winakur 1969; Christian 1980; Abramsky 1988). In South Africa, however, little information is available on the influence of microhabitat characteristics on the distribution and abundance of grassland small mammals.

3.6.5.1 Small mammal communities and vegetation characteristics

3.6.5.1.1 Patterns of diversity

Small mammal diversity and plant diversity

On the ash dam grids small mammal species diversity correlated weakly but significantly with plant species diversity ($r=0.317$; $p<0.01$), plant equitability ($r=0.242$; $p<0.05$) and plant richness ($r=0.271$; $p<0.05$; Figure 3.57 a, c, e). Small mammal equitability also showed the same trend and was weakly correlated with plant species diversity ($r=0.369$ $p<0.001$), plant equitability ($r=0.267$; $p<0.05$) and plant richness ($r=0.327$; $p<0.01$; Figure 3.57 b, d, f). Small mammal species diversity and equitability therefore tended to increase with an increase in the diversity, equitability and richness of plant communities on the ash dam grids.

On the control grids, no significant correlations were evident between small mammal species diversity and plant species diversity, but small mammal equitability correlated strongly and significantly with plant species diversity ($r=0.718$; $p<0.01$) and plant species richness ($r=0.705$; $p<0.01$; Figure 3.58 a & b). Thus, small mammal equitability increased progressively with an increase in plant species diversity and equitability in the unrehabilitated plant community. Small mammal species richness, however, showed no significant correlation with plant species diversity on either the ash dam and control grids.

The tendency of small mammal diversity and equitability to increase with elevated plant diversity on the ash dam grids therefore appears to have been a response to increased equitability within the rehabilitated plant communities, reflecting reduced dominance by pioneer species and a more even distribution of individuals among plant species. This is to be expected during ecological succession (Tramer 1969). This relationship between small mammal diversity and plant diversity could reflect elevated resource availability, since increased plant diversity (particularly of forbs) leads to greater habitat heterogeneity and resource availability (Abramsky & Rosenzweig 1984). Conversely, increased small mammal equitability on the control grids was related to an increase in plant diversity, resulting from higher species richness. This indicates that successional patterns differed

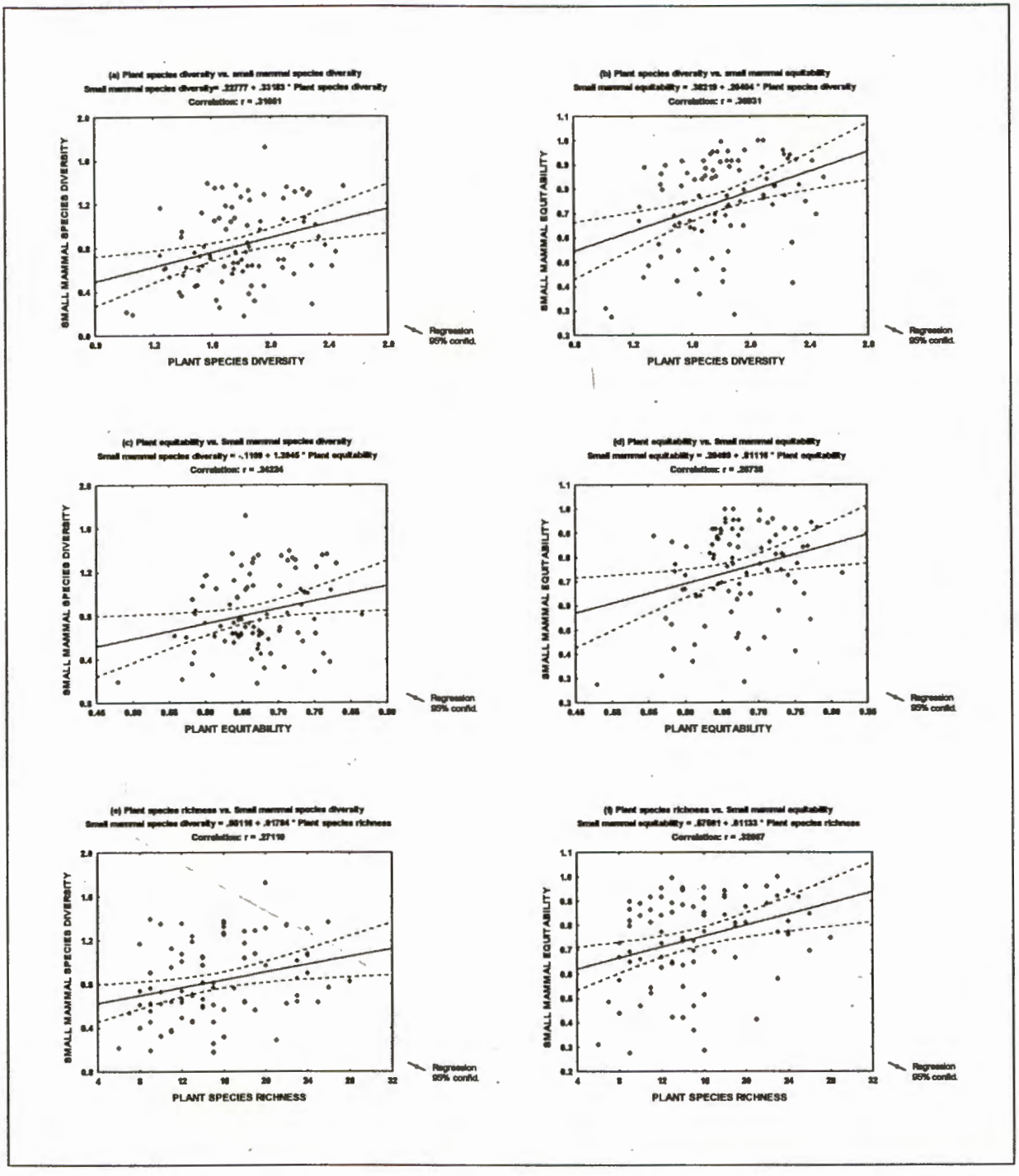


FIGURE 3.57: Linear regressions between small mammal species diversity and plant diversity (a-f) on the ash dam grids. All data were normally distributed, allowing the use of Pearson Product-Moment correlation coefficients.

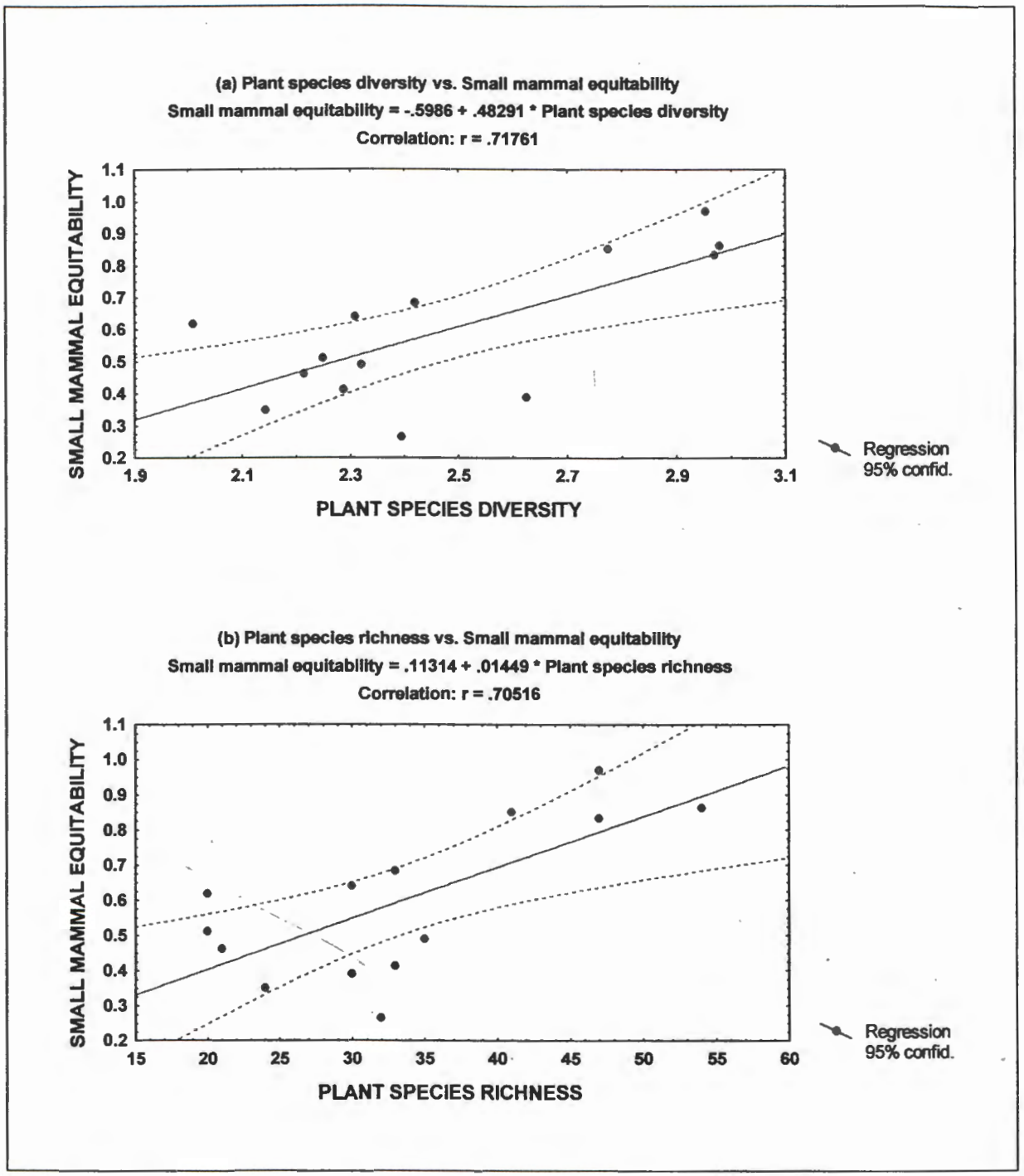


FIGURE 3.58: Linear regressions between small mammal species diversity and (a) plant species diversity and (b) plant species richness on the control grids. All data were normally distributed, allowing the use of Pearson Product-Moment correlation coefficients.

significantly between plant communities on the ash dam and control grids. On the ash dam, high dominance of the plant communities by species planted (e.g *Eragrostis curvula* and *Hyparrhenia hirta*) may have led to successional inertia; thus, any decrease in dominance would facilitate the establishment of other plant species and promote co-existence of small mammal species.

On the control grids, however, dominance (by annual grasses) was much lower, and the community contained many more forbs. Changes in the characteristics of the small mammal community were, apparently, less affected by dominance, and more responsive to changes in species richness of plants (= habitat heterogeneity), particularly following the veld fire in 1998.

The increase in small mammal species diversity with increasing resource availability may to be a result of more resources being available for more species to share and according to Rosenzweig & Winakur (1969), a more complex habitat will contain more niches which may be exploited by more species. A study in relatively moist savanna habitats in Swaziland by Monadjem (1997) also showed an increase in small mammal diversity with an increase in resource availability. However, small mammal diversity in desert habitats tended to increase with increase resource availability up to a certain level, above which diversity decreased (Abramsky & Rosenzweig 1984; Kerley 1992). A number of hypotheses have been suggested to explain this decline, one being that this resource availability gradient also represents a disturbance gradient. Other explanations are that the increase in all resources may not be symmetrical, so that some resources are limiting, and therefore the increasing resource base allows the competitive exclusion of the majority of species by a few competitive dominants (Abramsky & Rosezweig 1984; Abramsky 1988 Owen 1988).

Small mammal diversity and plant growth forms

On the ash dam grids small mammal diversity was weakly but significantly correlated with perennial forb species richness and annual grass species richness, while on the control grids diversity was significantly correlated with perennial grass species richness and annual grass species richness (Table 3.17). Small mammal equitability was weakly but significantly correlated with perennial forb species richness, perennial grass diversity and equitability (Table 3.17). On the control grids the same pattern was evident, but the correlations were slightly stronger; furthermore, small mammal equitability was positively correlated with of annual forb species richness. Small mammal species richness was positively correlated with annual grass species richness, and negatively correlated with perennial forb species diversity and equitability on the ash dam grids, but no significant correlations were evident on the control grids (Table 3.17).

As species richness of perennial forbs increased, small mammal diversity increased owing to an increase in equitability that more than offset a decrease in species richness. Small mammal diversity increased with increasing species richness of annual grasses despite a negative correlation between small mammal species richness and annual grass species richness. This suggests that any relationship that may exist between small mammals and annual grass species richness is mediated via changes in small mammal equitability, at least on the ash dam grids (but not on the control grids, since no negative correlations were observed).

Small mammal diversity increased with increased species richness of perennial grasses on the control grids (unrehabilitated areas), and small mammal equitability increased with increased equitability of perennial grasses and may be related to productivity.

TABLE 3.17: Pearson correlation coefficient (r) for the relationship(s) between small mammal species diversity, small mammal equitability, small mammal richness and plant growth forms on both the ash dam and control grids. Significant correlations are given in red ($p<0.05^{*}$, $p<0.01^{**}$ & $p<0.001^{***}$).

	SMALL MAMMAL DIVERSITY		SMALL MAMMAL EQUITABILITY		SMALL MAMMAL SPECIES RICHNESS	
PLANT GROWTH FORMS	ASH DAMS	CONTROLS	ASH DAMS	CONTROLS	ASH DAMS	CONTROLS
VEGETATION COVER	-0.051	0.131	-0.072	-0.223	0.038	0.316
PERENNIAL FORB DIVERSITY	-0.146	0.144	0.263	0.458	-0.315*	-0.409
PERENNIAL FORB EQUITABILITY	-0.155	0.116	0.185	0.269	-0.418**	-0.076
PERENNIAL FORB RICHNESS	0.388***	0.303	0.373***	0.596*	0.131	-0.432
PERENNIAL GRASS DIVERSITY	0.101	0.450	0.344**	0.590*	-0.018	-0.176
PERENNIAL GRASS EQUITABILITY	0.124	0.150	0.264*	0.458	0.050	-0.208
PERENNIAL GRASS RICHNESS	0.060	0.686**	0.149	0.494	0.050	-0.018
ANNUAL FORB DIVERSITY	0.041	0.347	0.144	0.463	-0.236	-0.097
ANNUAL FORB EQUITABILITY	0.137	0.203	0.156	0.022	-0.157	-0.196
ANNUAL FORB RICHNESS	0.070	0.216	0.175	0.745**	-0.077	-0.439
ANNUAL GRASS DIVERSITY	-0.044	-	-0.276	-	0.057	-
ANNUAL GRASS EQUITABILITY	-0.504	-	-0.343	-	-0.444	-
ANNUAL GRASS RICHNESS	0.321**	0.555*	0.192	0.457	0.276**	-0.297

Characteristically, small mammals associated with grasslands have to survive in an environment which fluctuates regularly (Fa *et al.* 1990). According to Hafner (1977), Abramsky (1988) and Owen (1988), small mammal diversity is a function of perennial plant cover. A hypothesis by Abramsky (1988) states that an increase in shrub cover may lead to less water and space for annual plants which then decrease in abundance. Most of the food utilized by rodents is produced by annuals and the establishment of a large number of shrubs lead to the decrease in the percentage of annual cover, and therefore the highest diversity of rodent species can be expected to occur in areas with low perennial cover (Abramsky 1988).

In the present study, the highest diversity of small mammals was found in areas with high species richness of perennial grasses and forbs, which might seen to contradict Abramsky's (1988) hypothesis. However, increased diversity and species richness of perennials do not necessarily equate to elevated cover, since many of the species concerned (particularly forbs like *Tagetes minuta*) may be small and provide little cover for small mammals. The increase in small mammal equitability with an increase in annual forb richness on the control grids (Table 3.17), may be due to the veld fire that occurred in this area during 1998. Annual forb plant species are the first pioneer species that appear after a veld fire (Morgenthal 1999), which in return may lead to a heterogenous habitat. Small mammal species richness on the other hand decreased during the same period, although this correlation was not significant. The lack of perennial grasses after the fire (post burn area) favour certain species like *T. brantsii* and *M. coucha* while the numbers of other species such as *R. pumilio* and *O. irroratus*, which rely on ground cover for specific resources, decline.

3.6.5.1.2 Associations between small mammal species and plant species

Patterns of association between small mammal and plant species were assessed using Detrended Correspondence Analyses. For the first analysis a DCA was applied to the

plant species data, whereafter small mammal species were chosen as supplementary species. According to Ter Braak & Šmilauer (1998), supplementary species differ from active species (plant species) because they do not influence the definition of the ordination axes. The relationships between plant species and small mammal species on both the ash dam and control grids are shown in Figure 3.59. The gradient distances between groupings along the two ordination axes both exceeded four, a value which as a general rule of thumb indicates that significant gradients existed in the data suite, implying that the plant assemblages were markedly divergent. The eigenvalues for these two ordination axes were 0.892 and 0.351 respectively, and together explained 70.2% of the observed sample variance. Two separate groups which separated along the first ordination axis were evident, and represented the control grids and the ash dam grids respectively. The ash dam grids also divided into two separate groups along the second ordination axis, namely the two grids of ash dam D (grids 7 & 8) vs. the other grids of ash dams A and C.

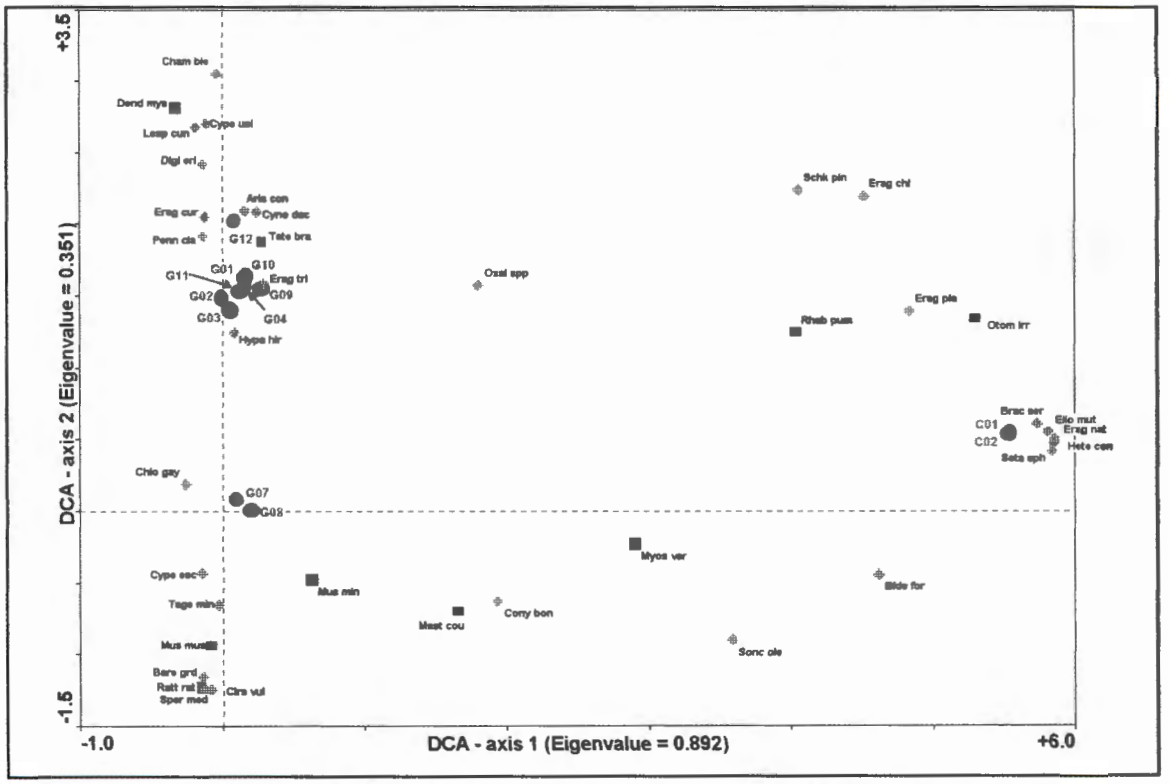


FIGURE 3.59: Detrended Correspondence Analysis (DCA) showing the relationship between small mammal species and plant species on the ash dam and control grids (Appendix 3.2).

The clear separation of the ash dam and control grids along the first axis reiterates that the vegetation communities in these areas are very different, both in floristic composition and physiognomy (Morgenthal 1999; see also Chapter 2). From Figure 3.59, it is apparent that the control grids are characterized by plant species such as *Brachiaria serrata*, *Elionurus myticus*, *Eragrostis* sp, *Heteropogon contortus* and *Setaria sphacelata*. The small mammal species most closely associated with this community were the vlei rat, *O. irroratus*, a grassland specialist that was uncommon on the ash dam grids. *R. pumilio* plotted in the middle of ordination axis 1 due to the fact that this species was dominant on both the control and ash dam grids, reflecting its opportunistic status and wide ecological tolerance.

Grids 7 & 8 are characterized by plant species such as *Chloris gayana*, *Cyperus esculentus* and *Tagetes minuta*. Small mammal species closely associated with these two grids included *M. musculus*, *M. minutoides*, *R. rattus*, and to a lesser extent, *M. coucha* (Figure 3.59). The grids on ash dams A and C, on the other hand, were characterized by plant species such as *Eragrostis curvula*, *Hyparrhenia hirta*, *Cynodon dactylon* and *Pennisetum clandestinum* (Figure 3.59). The small mammal species most closely associated with this plant species assemblage was the Highveld gerbil, *T. brantsii*.

In the second ordination the relationship between small mammal species and various plant species on the slopes of ash dam A and C were determined. For this ordination a DCA was applied again and small mammal species were selected as supplementary species (Figure 3.60). The eigenvalues of the first and second ordination axes were 0.159 (64%) and 0.071 (28.5%) respectively, and these axes accounted for 92.5% of the sample variance. Gradient distances along both axes exceeded four, indicating that significant gradients existed (Ter Braak & Šmilauer 1998). However, gradient distances between the four grids were small indicating that vegetation communities on these slopes were very similar, a result reported also by Morgenthal (1999; see also Chapter 2). Grid 9 plotted above the others along axis 2, which may reflect time since rehabilitation because grids

2, 3 and 4 were rehabilitated in 1994, two years after grid 9. Another possible explanation for the separation of grid 9 is that it was never burned, whereas grids 2, 3 and 4 were burned 1998. It is also likely that differences in aspect, mediated via microclimates, led to the separation of the grids along axis 1.

The small mammal species closely related with grid 9 were *O. irroratus*, *M. minutoides* and *T. brantsii*. *O. irroratus* and *M. minutoides* are species that avoid open areas denuded of vegetation, such as those that have been burned. This could explain their low frequency on grids 2, 3 and 4. Spatial factors could also account for the association pattern observed, since grid 9 is bordered by natural grasslands in which *O. irroratus* and *M. minutoides* were more frequently trapped. The western border of grid 9 also abutted the plateau of ash dam C where *T. brantsii* dominated the small mammal communities, thereby explaining the apparent association of this species with grid 9 instead of the grids burned in 1998 (Figure 3.60).

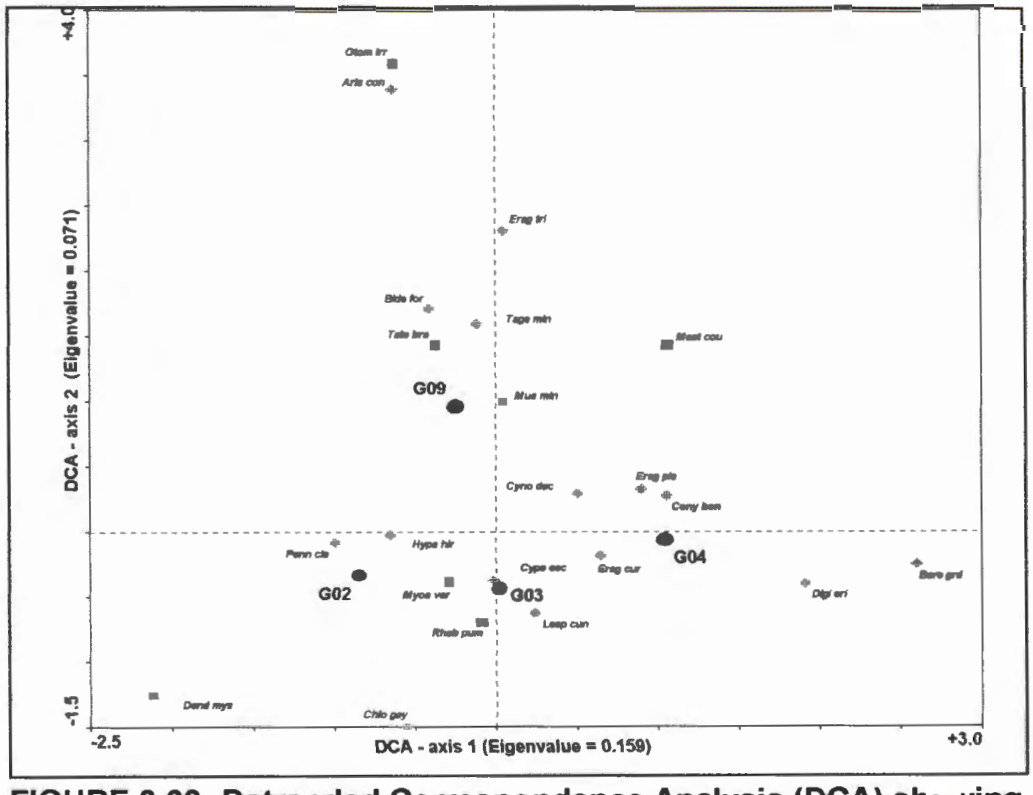


FIGURE 3.60: Detrended Correspondence Analysis (DCA) showing the relationship between small mammal species and plant species on the slope grids of ash dam A and C (Appendix 3.2).

The small mammal species most closely associated with grids 2, 3 and 4 were *R. pumilio* and *M. varius*. *M. coucha* plotted well to the right of other small mammal species along axis 1. This could reflect an aversion of this species for micro-habitats in which kikuyu grass (*P. clandestinum*) is common, as indicated by the wide gradient distance between these species on grid 2. This was supported further by the significant negative correlation that existed between the numbers of these species ($r = -0.962$; $p<0.01$; Figure 3.61).

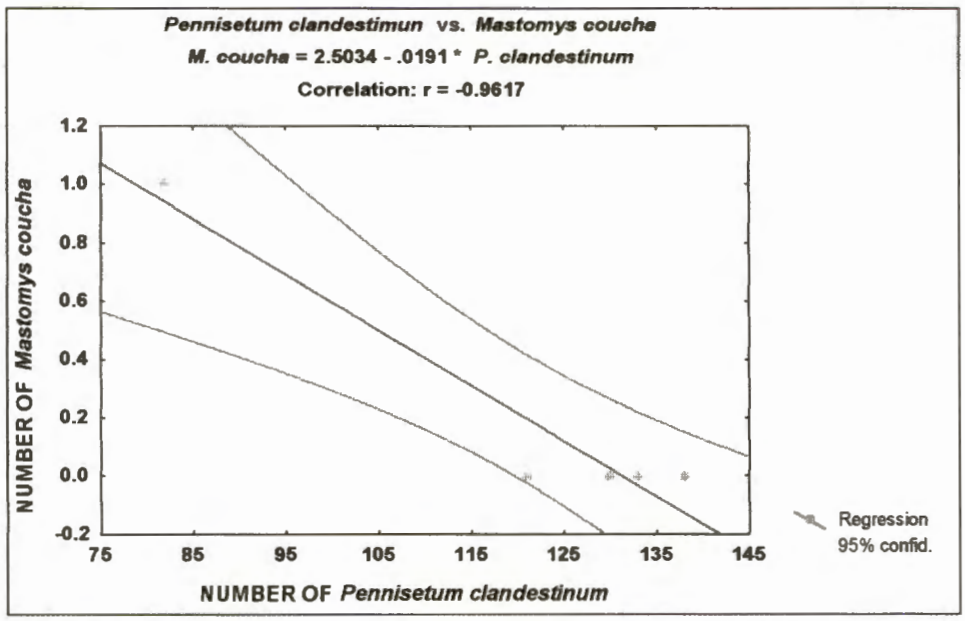


FIGURE 3.61: Linear correlation between the small mammal *M. coucha* and the number of *P. clandestinum* during five survey periods for grid 2.

Grid 3 was characterized by perennial forbs like *Cyperus esculentus* and *L. cuneata* and *E. curvula*, a perennial grass and by the two small mammals *R. pumilio* and *M. varius* (Figure 3.60). The number of *R. pumilio* correlated significantly with the number of *E. curvula* ($r=0.879$; $p<0.05$) and this small mammals' numbers increased with an increase in *E. curvula* (Figure 3.62). The Highveld gerbil, *T. brantsii*, was not present in substantial numbers on this grid and its numbers correlated negatively with *E. curvula* ($r= -0.881$; $p<0.05$). This correlation indicates that *T. brantsii* may prefer more open areas without a dense vegetation cover provided by *E. curvula*, or conversely that *T. brantsii* may have a

negative impact on the abundance of *E. curvula* (Figure 3.63). Based on field experiments (Bronner *et al.* 1999), showed that burrowing and feeding activities of *T. brantsii* have a marked impact on densities and biomass of *E. curvula*, effects which may make some of the rehabilitated habitats less suitable for other more specialized small mammal species.

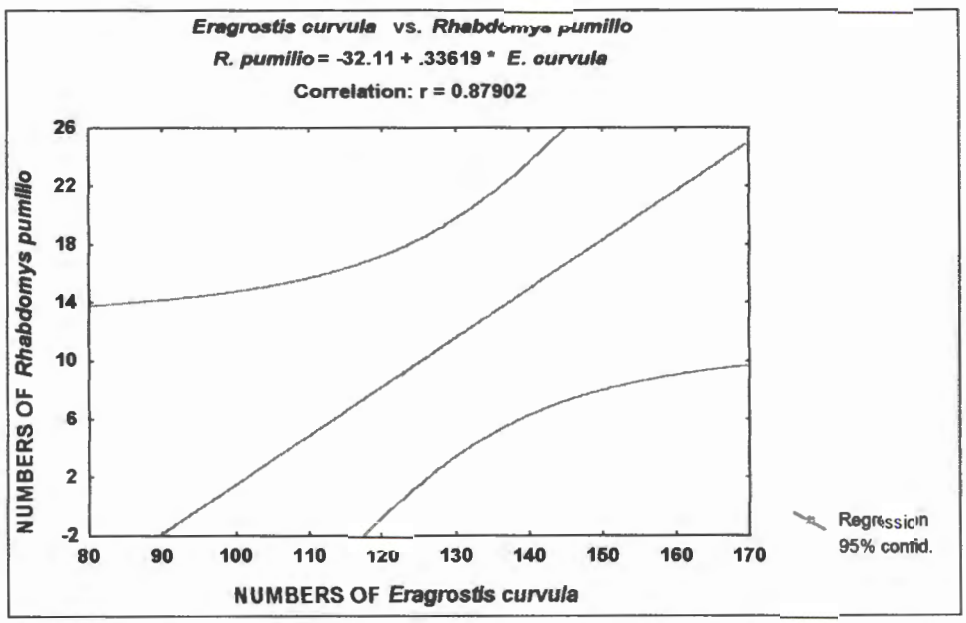


FIGURE 3.62: Linear correlation between the small mammal *R. pumilio* and the perennial grass *E. curvula* during five survey periods for grid 3.

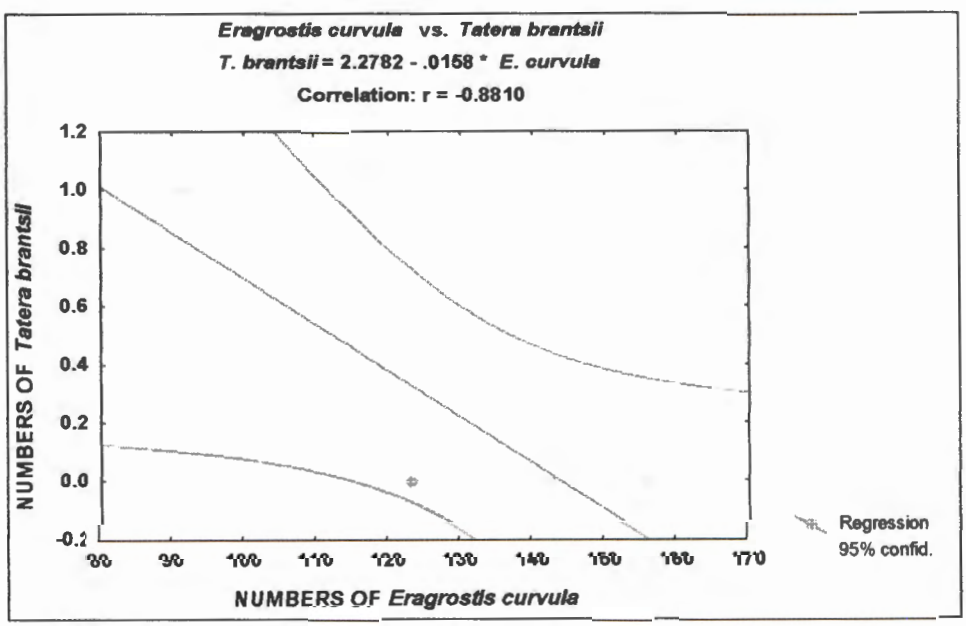


FIGURE 3.63: Linear correlation between the small mammal *T. brantsii* and the perennial grass *E. curvula* during five survey periods for grid 3.

Grid 4 was also characterized by plant species such as *E. curvula*, *L. cunneata* and *C. esculentus*, and the small mammals *R. pumilio* and *M. varius*. The other small mammal captured to a lesser extend on this grid were *M. coucha* (Figure 3.60). Patches of bare ground were also typical of this habitat.

Again, the number of *R. pumilio* was significantly correlated with numbers of *E. curvula* ($r=0.925$; $p<0.05$; Figure 3.64) on this grid, while the pioneer small mammal species, *M. coucha*, showed a significant correlation with frequency of bare ground ($r=0.978$; $p<0.01$). A part of grid 4 was destroyed by a fire during 1998 and the correlation between *M. coucha* and bare ground confirms published reports that this small mammal prefers areas recovering from disturbance (Meester *et al.* 1979).

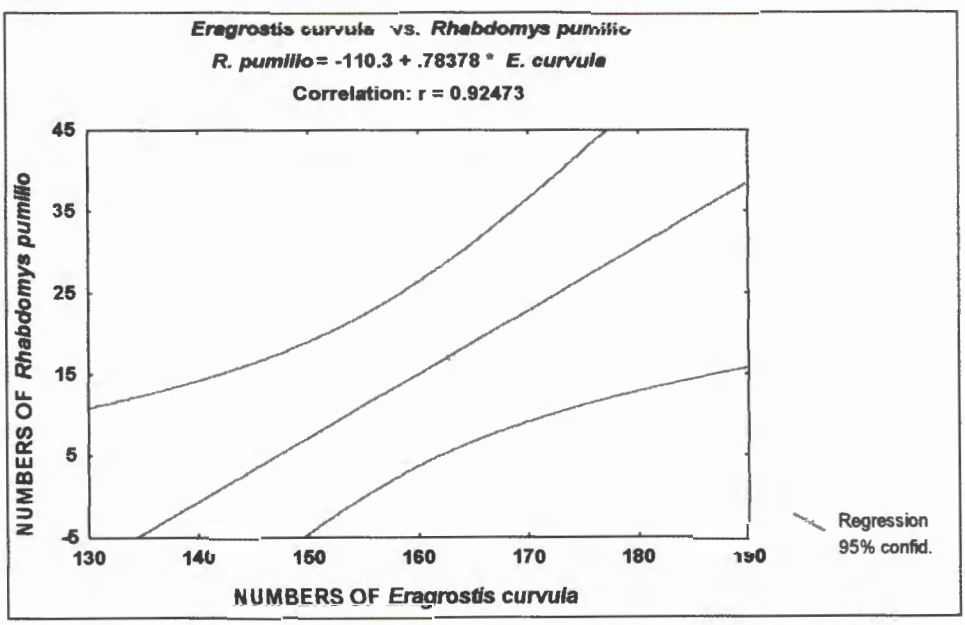


FIGURE 3.64: Linear correlation between the small mammal *R. pumilio* and the perennial grass *E. curvula* during five survey periods for grid 4.

Grid 9 was characterized by plant species such as *B. formosa*, *T. minuta* and to a lesser extend *H. hirta*, and by small mammal species like *T. brantsii*, *M. coucha* and *M. minutoides* (Figure 3.60). On this grid, the number of *T. brantsii* correlated significantly

with the annual forb *T. minuta* (r=0.924; p<0.05; Figure 3.65 c).

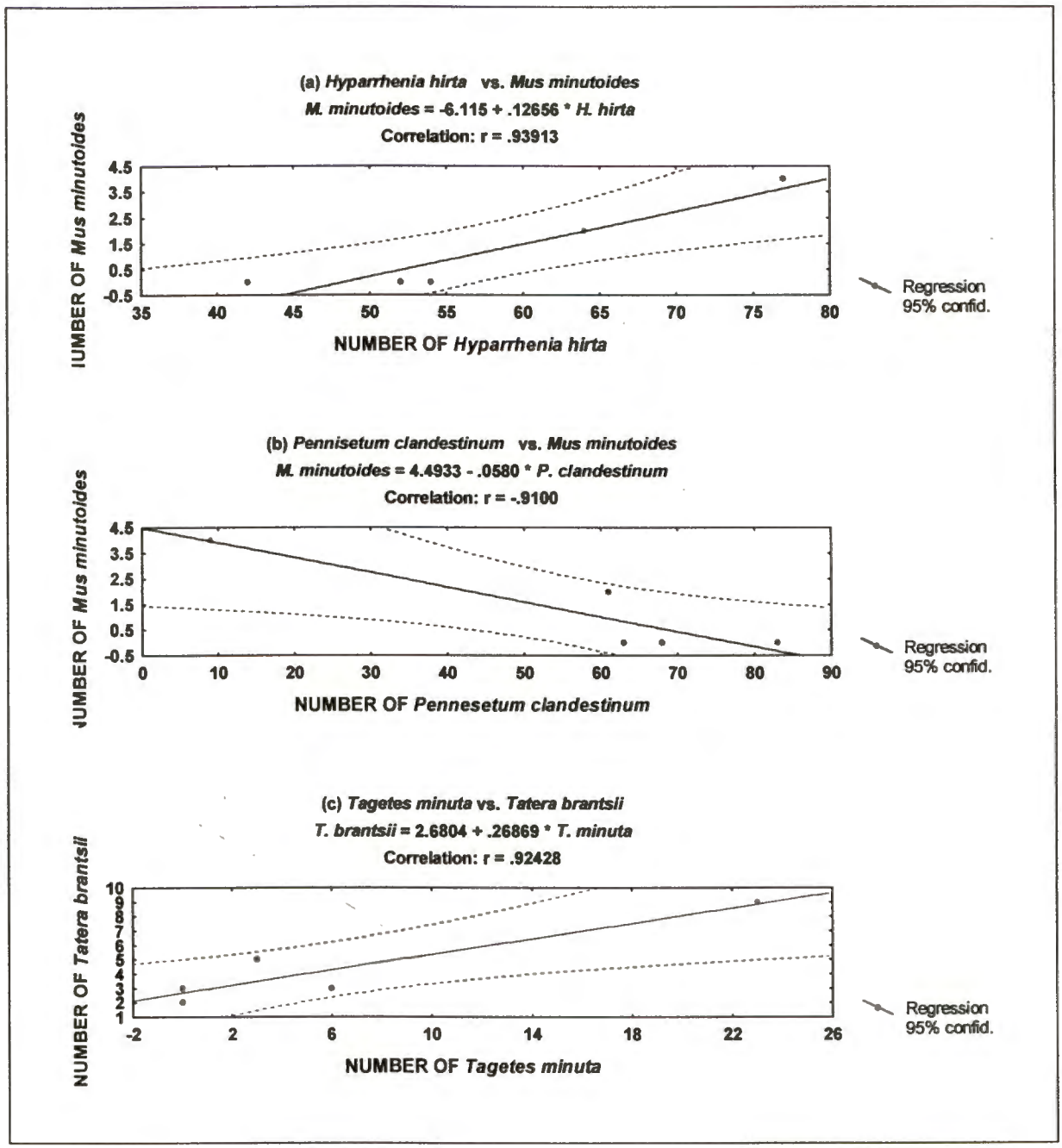


FIGURE 3.65: Linear correlations between the small mammal *M. minutoides*, (a) *H. hirta* and (b) *P. clandestinum* and between the small mammal *T. brantsii* and the annual forb (c) *T. minuta* during five survey periods for grid 9.

The numbers of *M. minutoides* increased significantly with an increase in the number of *H. hirta* ($r=0.939$; $p<0.05$; Figure 3.65 a), but the number of this species was inversely correlated with the number of *P. clandestinum* ($r= -0.909$; $p<0.05$; Figure 3.65 b). It is therefore clear that species such as *R. pumilio* and *M. varius* prefer areas with adequate vegetation cover, and will always be indicative of such areas (Els & Kerley 1996; Monadjem 1997). Species like *T. brantsii*, *M.coucha* and *M. minutoides* occur in areas with low vegetation cover, areas which, in this study, were characterized by plant species such as *H. hirta* and *B. formosa*. *M. coucha* is a highly adaptable small mammal species and can therefore inhabit a wide range of environmental conditions. According to Monadjem (1997), *M. minutoides* exhibits no obvious habitat preferences, but prefers areas with adequate vegetation cover. The presence of this species together with the other two dominant species on grid 9 can be ascribed to the fact that this grid was never burned and that this area represents a habitat available for a wide variety of species.

Relationships between small mammal species and certain plant species on the plateau grids (grids 10, 11 & 12) of ash dam C are shown in Figure 3.66. The eigenvalues of the first and second ordination axis were 0.150 (75.3%) and 0.049 (14.7%) respectively, and these two axes accounted for 90% of sample variance. The three grids plotted close together along these axes, indicate that the three survey areas on the plateaux of ash dam C were homogenous in terms of the floristic composition and abundance.

Along the first ordination axis, grid 12 tended to separate from grids 10 and 11 towards the right hand side of the scattergram. This separation reflects the dominance of the vegetation of this grid by the grass species such as *E. curvula* and small mammal species (*R. pumilio* and *M. coucha*) that are closely associated with this grass. This grid provided enough vegetation cover for the diurnal *R. pumilio* which prefer areas with enough vegetation cover for concealment from predators.

The dominance of *H. hirta* on grids 10 & 11, and the appearance of open areas (bare

ground) may be due to the fire that occurred in this areas in 1998, since it is known that fire stimulate the growth of this grass species (Morgenthal 1999). These two grids are also dominated by the Highveld gerbil, *T. brantsii*, which prefers open areas in the initial stages of plant succession (Kern 1981). The number of bare ground patches correlated significantly with the number of *T. brantsii* ($r=0.901$; $p<0.05$; Figure 3.67), indicating that the numbers of *T. brantsii* increase as the habitat became open with less cover.

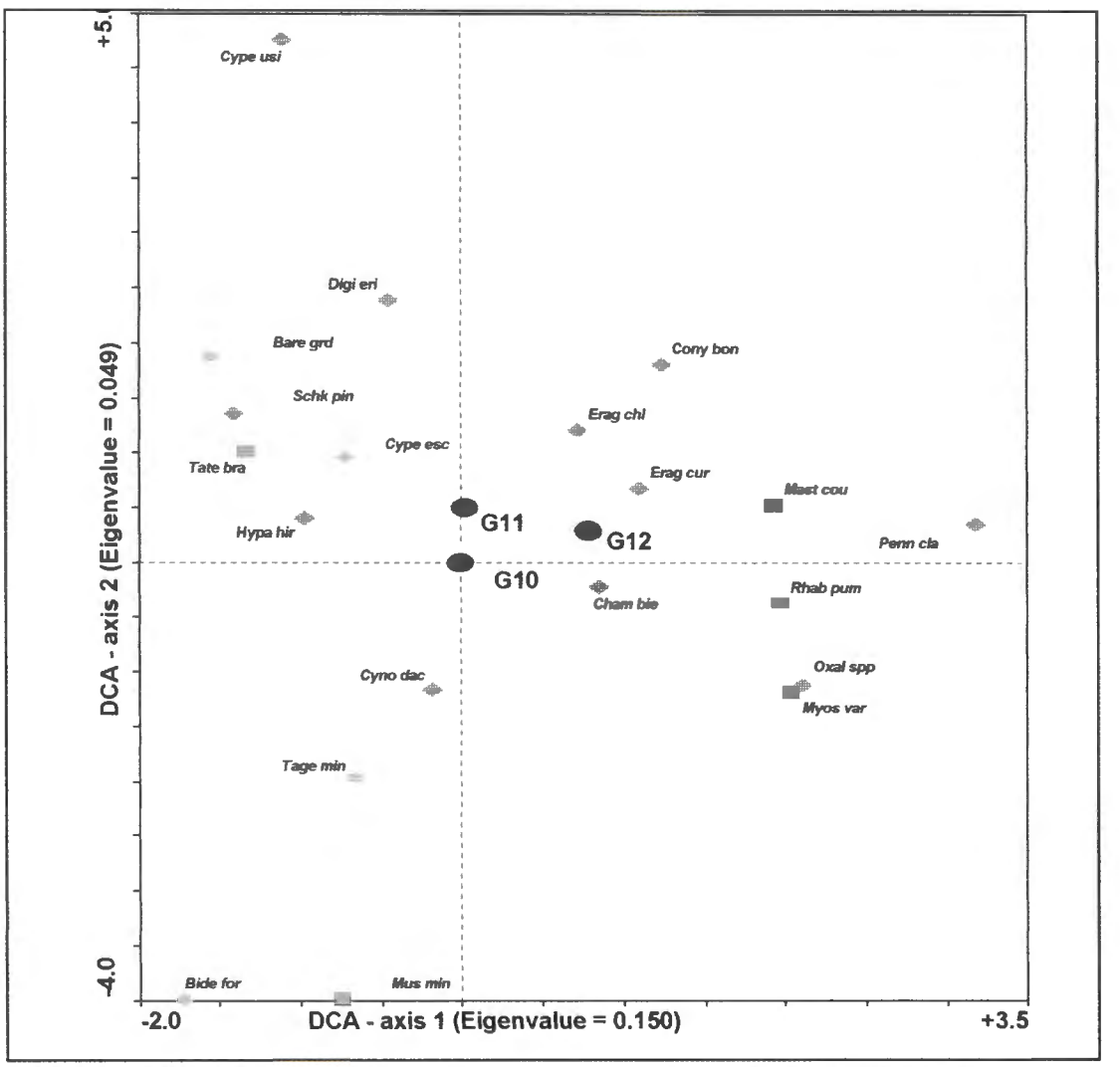


FIGURE 3.66: Detrended Correspondence Analysis showing the relationship between small mammal species and plant species on the plateaux grids of ash dam C (Appendix 3.2).

The abundance of *T. brantsii* may also have been due to the appearance of the annual forb, *Cyperus esculentus* (Figure 3.66). According to a study by De Moor (1969), this forb is a early pioneer species which favors disturbed areas. During this study, however, the number of *T. brantsii* increased with increased abundance of *C. esculentus*, but this correlation was not significant. No direct association between these species can therefore be assumed.

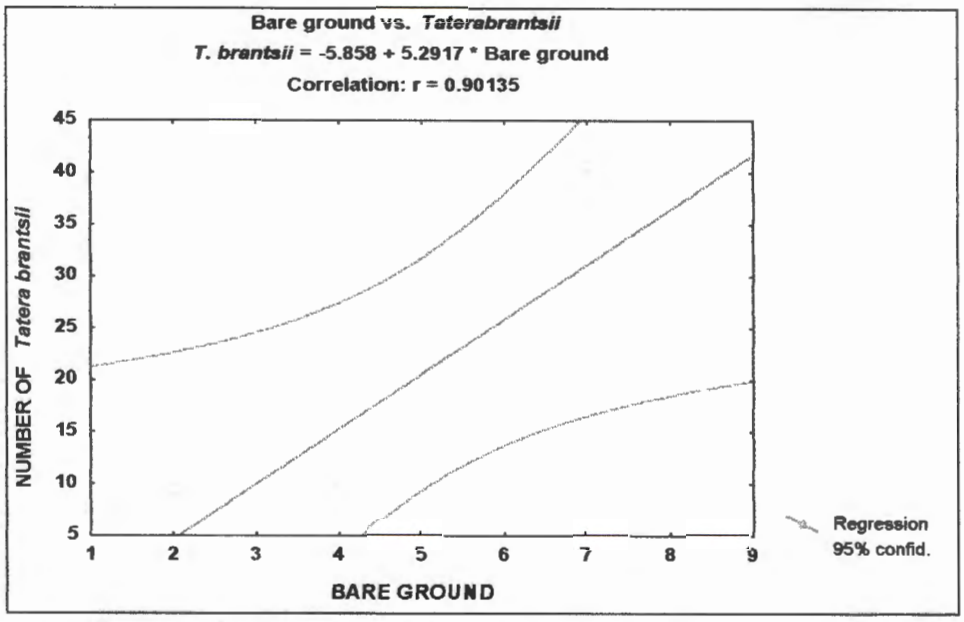


FIGURE 3.67: Linear correlation between bare ground and *T. brantsii* of grids 10 and 11 for five survey periods.

The number of *R. pumilio*, which was dominant on grid 12, showed a negative correlation with *Cynodon dactylon* ($r = -0.879$; $p<0.05$), a plant species characteristic of grid 10, indicating that this plant species does not provide an adequate habitat for *R. pumilio* (Figure 6.68). On the other, the number of *M. varius* correlated significantly with the number of *E. curvula* ($r=0.949$; $p<0.05$) on grid 12, suggesting a close association between these species.

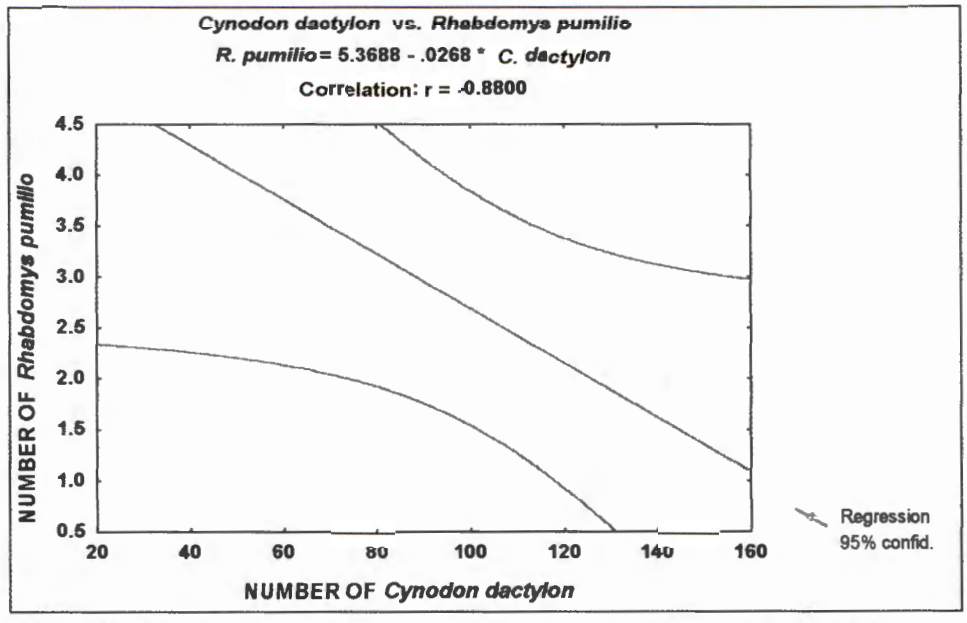


FIGURE 3.68: Linear correlation between *R. pumilio* and *C. dactylon* during five survey periods for grid 10.

3.6.5.1.3 Association between small mammal species and plant growth forms

The association between individual small mammal species and different plant growth forms were also determined using indirect gradient analysis, i.e. Canonical Correspondence Analysis (CCA). A survey area-species-environment triplot is used to illustrate these effects (Figure 3.69). In the ordination small mammal species were chosen as species data, while the different plant growth forms were selected as environmental data. The significance of a particular environmental variable can be assessed through a Monte Carlo test of the axis associated with that variable, using each axis's eigenvalue as the test statistic (Ter Braak & Prentice 1988).

Results of a forward selection of environmental variables which had the greatest influence on the small mammal community of the ash dam and control grids are summarized in Table 3.18. According to this table, the different plant growth forms did not have a significant influence on the distribution of small mammal species on either the control or ash dam grids.

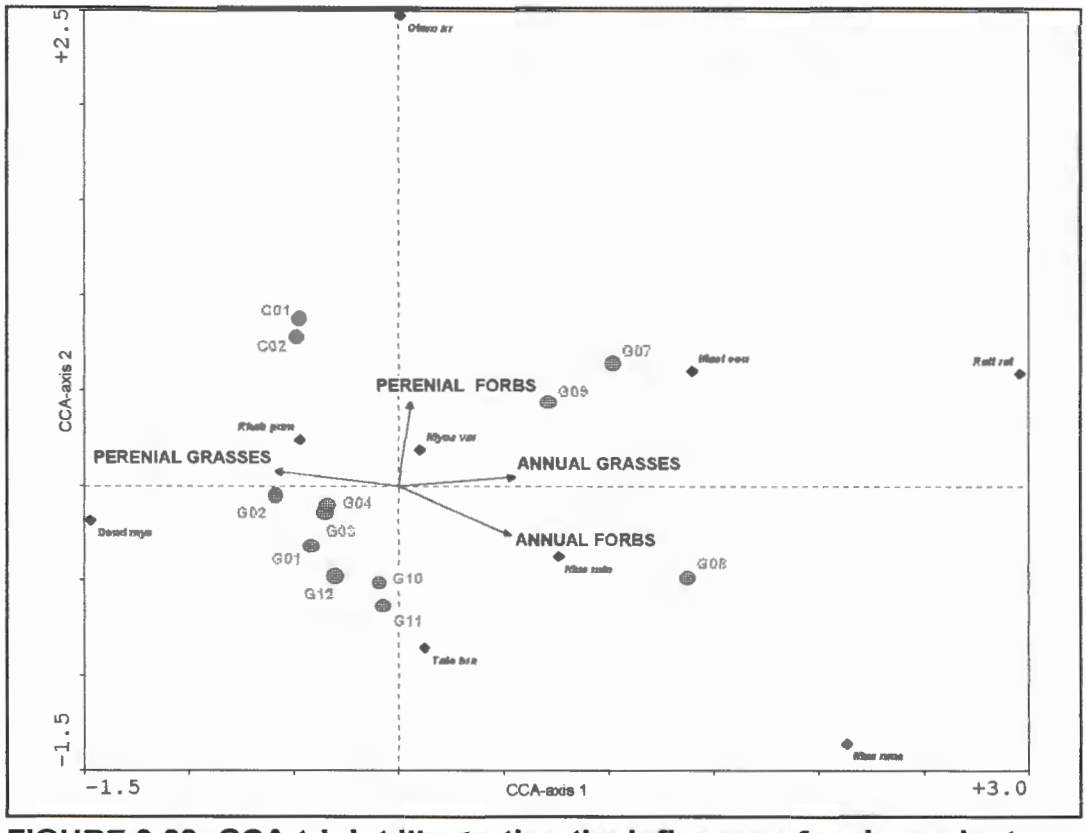


FIGURE 3.69: CCA-triplot illustrating the influence of various plant growth forms on the distribution and composition of the small mammal community on the ash dam and control grids for the summer surveys (Appendix 3.2).

TABLE 3.18: Forward selection showing the plant growth form which had the greatest influence on the distribution of small mammals on the ash dam and control grids.

PLANT GROWTH FORMS	λ	F-value	p-value
Perennial grasses	0.140	2.417	0.095
Annual forbs	0.133	2.262	0.120
Annual grasses	0.125	2.105	0.115
Perennial forbs	0.058	0.872	0.455

In the CCA (Figure 3.69) ordination triplot the arrows indicate the strength and direction of various environmental variables on the distribution of species along the ordination axes. The environmental factors indicated by long arrows are the ones most closely correlated with each ordination axis and indicate the most important factors that can influence the distribution of small mammal species.

The angle of each environmental arrow with respect to each axis indicates the correlation of the axis with the factor. Although the distributions of small mammal species were best predicted by percentage perennial grasses and annual forbs, the influence of these variables were not significant for the first axis' or for all the axes combined (Table 3.19). It can therefore be assumed that the distribution of small mammal species may be influenced by other environmental factors that will be discussed in the next section.

TABLE 3.19: Summary of the Monte Carlo test showing the influence of various plant growth forms on the distribution of the small mammal species on the control and ash dam grids.

AXES	λ	F-value	p-value
1st ordination axis	0.158	2.25	0.410
All axes together	0.247	1.392	0.280

The grids of ash dam A (grids 1, 2, 3 & 4) and grid 12 were characterized by perennial grasses such as *Hyparrhenia hirta* and *Eragrostis curvula*, while grids 10 and 11 on ash dam C are characterized by annual forbs such as *Cyperus esculentus*. The control grids, grid 7 and grid 9, on the other hand, were supported more by perennial forbs (Figure 3.69). The frequency of *R. pumilio* correlated weakly but significantly with the frequency of perennial grasses ($r=0.312$; $p<0.05$), and numbers of this species showed a progressive increase with an increase in the number of *E. curvula*, a perennial grass (Figure 3.70a). Frequency of most of the small mammal species, on the other hand, showed a negative correlation with the number of annual forbs ($r= -0.504$; $p<0.001$; Figure 3.70 c), lying in the

opposite direction as annual forbs (Figure 3.69).

According to Figure 3.69, grids 7 & 9 were characterized by perennial forbs, annual grasses and the small mammal species, *M. coucha*, the frequency of which was significantly correlated with both perennial forbs ($r=0.314$; $p<0.05$; Figure 3.70e) and annual grasses ($R=0.275$; $p<0.05$; Figure 3.70 b). Grids 10 & 11 were characterized by annual forbs and the small mammal, *T. brantsii*, the frequency of which correlated weakly and negatively with perennial forbs ($R= -0.397$; $p<0.01$; Figure 3.70 d), This correlation shows that this small mammal species may prefer areas characterized by annual forbs, which typically are pioneer plant species associated with disturbance (Figure 3.69), or in the case of *T. brantsii*, that burrowing by small mammals may facilitate the establishment of perennial forbs (mainly pioneer species) through the provision of germination sites. According to the ordination (Figure 3.69), *M. minutoides* was also closely associated with annual forbs, but no significant correlation were evident. The frequency of this species showed a weak negative correlation with perennial grasses ($R= -0.291$; $p<0.05$; Figure 3.70 f).

3.6.5.2 Small mammal communities and other environmental variables

3.6.5.2.1 Small mammal diversity and edaphic variables

Soil may affect small mammals via its influence on the plants and therefore may play an important role in the distribution of small mammal species. The possible influence of edaphic variables such as substrate structure(fraction of particle size distributions), pH of the substrate, electrical conductivity (EC) and percentage organic matter in the substrate on small mammal species diversity on the ash dam grids was assessed by regression analysis. Only one substrate data set (from the winter survey of 1997) was available for this analyses.

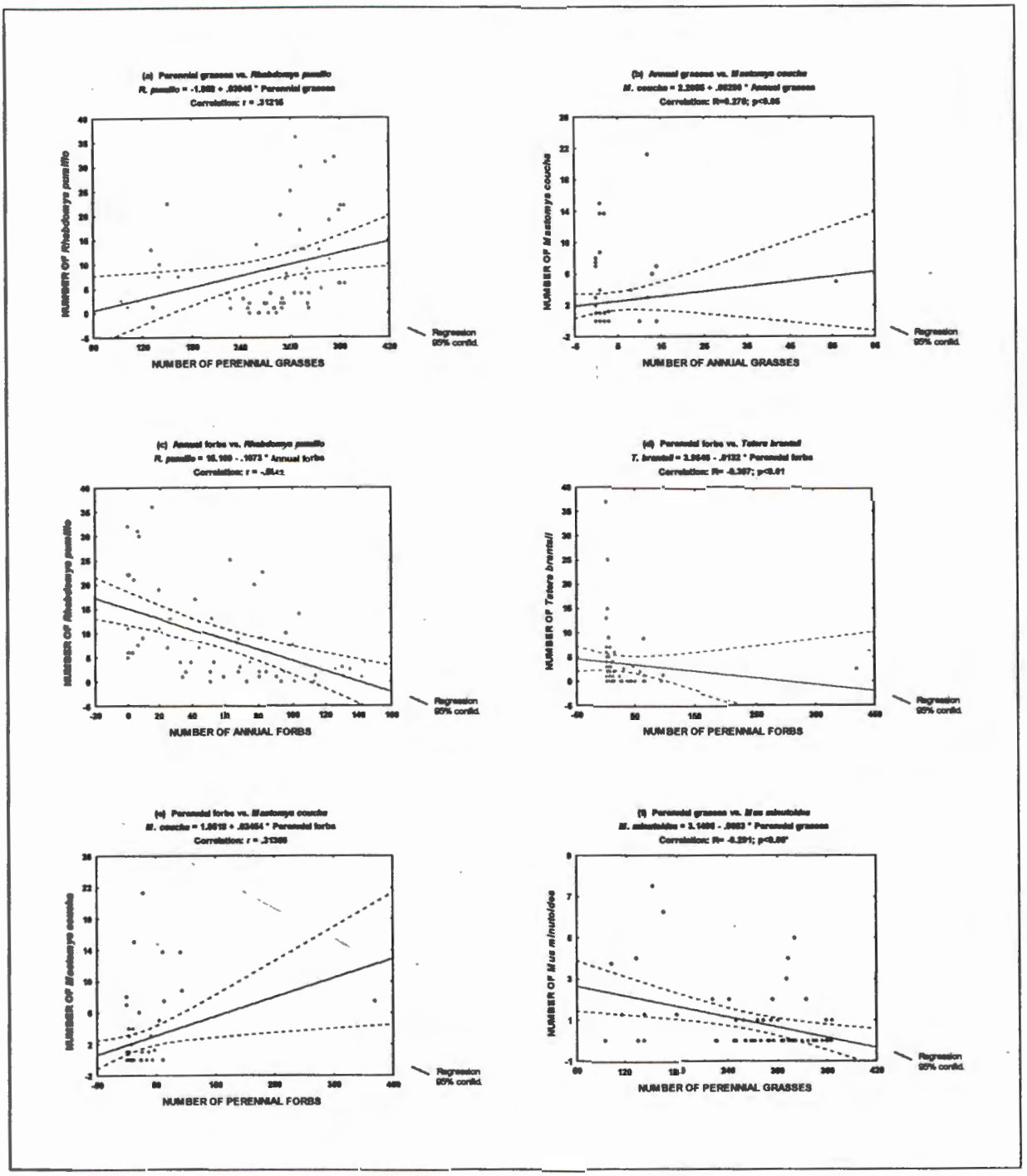


FIGURE 3.70: Linear correlations between small mammal species and different plant growth forms (a-f) during the summer survey periods.

Small mammal diversity on the ash dam grids was inversely correlated with pH of the substrate ($r = -0.665$; $p<0.005$; Figure 3.71), and therefore tended to decline as the alkalinity of the substrate increased. The same result was evident from a multiple (forward) stepwise regression based on six edaphic variables (Table 3.20), which showed that pH was the most important predictor of small mammal diversity, according for 28.7% of the observed variance. The percentage silt in the substrate was the second most important predictor, and accounted for 29.8% of the sample variance. Percentage gravel also made a significant contribution to the regression, but the partial correlation for this variable was not significant.

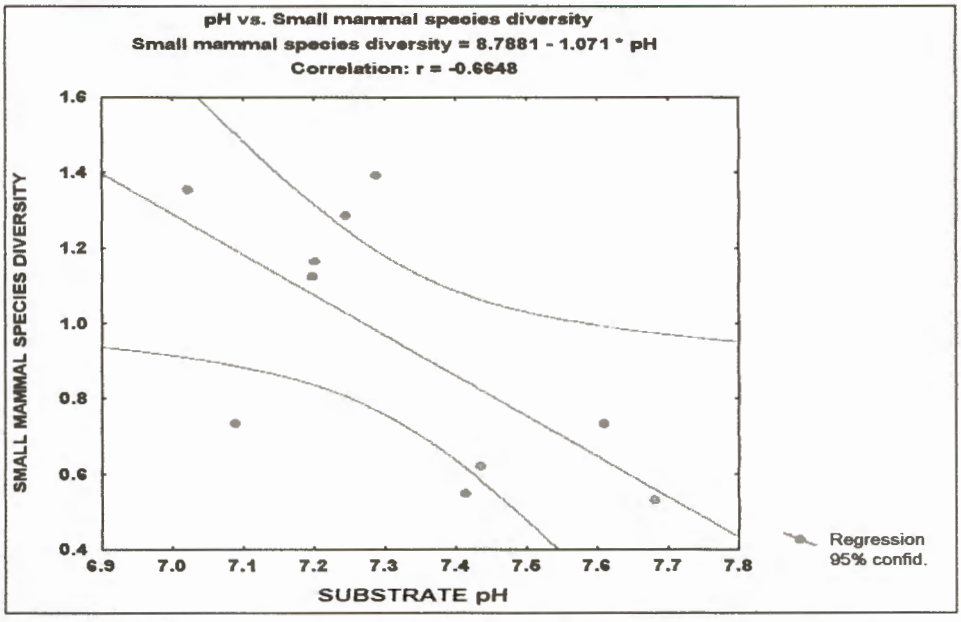


FIGURE 3.71: Linear correlation showing the relationship between small mammal species diversity and the pH of the soil on the ash dam grids during July 1997.

The influence of substrate pH and silt content on small mammal diversity collectively accounted for 58.5% of the observed variance in the diversity indices for small mammals. Since the observed range of values for all edaphic variables were within limits normally encountered in natural (unrehabilitated) habitats, including the control areas of this study,

any direct physiological or ecotoxicological effects of these factors on small mammal species can be discounted. The influence of substrate pH and silt content on resident small mammal communities must therefore been mediated via the effects of these variables on vegetation characteristics, and thereby on habitat characteristics and resource availability for small mammals. Also, the newer rehabilitated areas (grids 7 & 8) have a higher pH, thus the age effect could again be evident.

Substrate pH may directly influence which plant species become established during succession (Hayward & Phillipson 1982), and some influence of pH on plant diversity was also evident from the strong and significant correlation between these variables in my data suite ($r = -0.66$; $p<0.05$).

TABLE 3.20: Results of a forward stepwise regression analysis to assess relationships between small mammal diversity and six adaphic variables on the ash dam grids. The multiple regression was significant ($F_{5,22}=10.384$; $p<0.001$).

VARIABLE	PARTIAL CORRELATION	p	CO-EFFICIENT OF DETERMINATION	p	x ± 1sd
pH	-0.777	<0.001	0.287	0.003	7.317 ± 0.215
% SILT	0.480	<0.05	0.298	<0.001	0.315 ± 0.223
% GRAVEL	-0.236	>0.05	0.091	0.016	6.257 ± 2.672
TOTAL NUTRIENTS	0.281	>0.05	0.016	>0.05	4177.5 ± 2421
% SAND	0.180	>0.05	0.010	>0.05	51.77 ± 8.427
EC	-0.330	>0.05	<0.01	>0.05	0.760 ± 0.199
% C	-0.051	>0.05	<0.01	>0.05	6.257 ± 2.672
% CLAY	0.464	>0.05	<0.01	>0.05	25.9 ± 7.06

Silt content of the substrate may similarly influence plant community composition and viability via its effect on substrate moisture content. Silt particles are small with a relatively

high surface area for binding with water, thus increased silt content often coincides with elevated moisture content. Increased substrate moisture content in turn promotes the growth and establishment of plants and thereby influence vegetation communities with a concomitant indirect influence on the micro-habitats and resource availability to small mammals. This positive effect may, however, be offset by the direct relationship between silt content, pH and electrical conductivity (an index of salt content). These three variables were strongly correlated (% silt vs pH =0.77; % silt vs EC = 0.58; pH vs EC = 0.38; $p<0.05$), reflecting the capacity of small silt particles to provide a greater surface area for the binding of ions in solution. A synergistic effect on plant growth and establishment may thus take place.

3.6.5.2.2 Associations with other environmental factors

The effect of various other environmental variables on the composition and distribution of small mammal communities on the ash dam grids were determined with a CCA-triplot. (Figure 3.72). A forward selection of environmental variables which had the greatest influence on the distribution of the small mammals on the ash dam grids during the winter of 1997 are summarized in Table 3.21. The environmental variables showing the highest eigenvalues are those variables which had the greatest influence on small mammal species distribution.

According to Table 3.21, percentage clay made the largest contribution to the observed distribution of small mammal species on the ash dam grids. This is confined also in Figure 3.72, as indicated by the long arrow for this environmental variables. Other environmental variables represented by long arrows are vegetation cover and percentage carbon, but according to Table 3.21 these variables did not have any significant influence on the distribution of small mammals.

TABLE 3.21: Forward selection of environmental variables showing the influence of these variables on the distribution of the small mammal community on the ash dam grids during the winter of 1997.

ENV. VARIABLES	EIGENVALUE (λ)	F-value	p-value
% CLAY	0.204	3.122	0.035
% CARBON	0.177	2.604	0.065
% SAND	0.167	2.407	0.110
ELECTRICAL CONDUCTIVITY	0.142	1.979	0.110
pH	0.141	1.962	0.110
% SILT	0.131	1.795	0.150
VEGETATION COVER	0.119	1.609	0.215
% GRAVEL	0.095	1.609	0.190

TABLE 3.22: Results of a forward stepwise regression analysis to assess relationships between *R. pumilio* and certain edaphic variables on the ash dam grids during July 1997.

VARIABLES	PARTIAL CORRELATION	r^2	Change in r^2	p
% CARBON	0.685	0.236	0.236	0.257
pH	-0.701	0.309	0.193	0.479
% SLIT	0.685	0.506	0.177	0.262
% CLAY	-0.557	0.613	0.107	0.362
ELECTRICAL CONDUCTIVITY	0.409	0.622	0.090	0.776
VEGETATION COVER	0.379	0.647	0.024	0.694
% GRAVEL	0.297	0.678	0.013	0.703

A multiple stepwise regression was also used to assess the most important environmental variables that had an influence on the distribution of the dominant small mammal species. According to Table 3.22, % carbon and pH were the best predictors of the distribution of

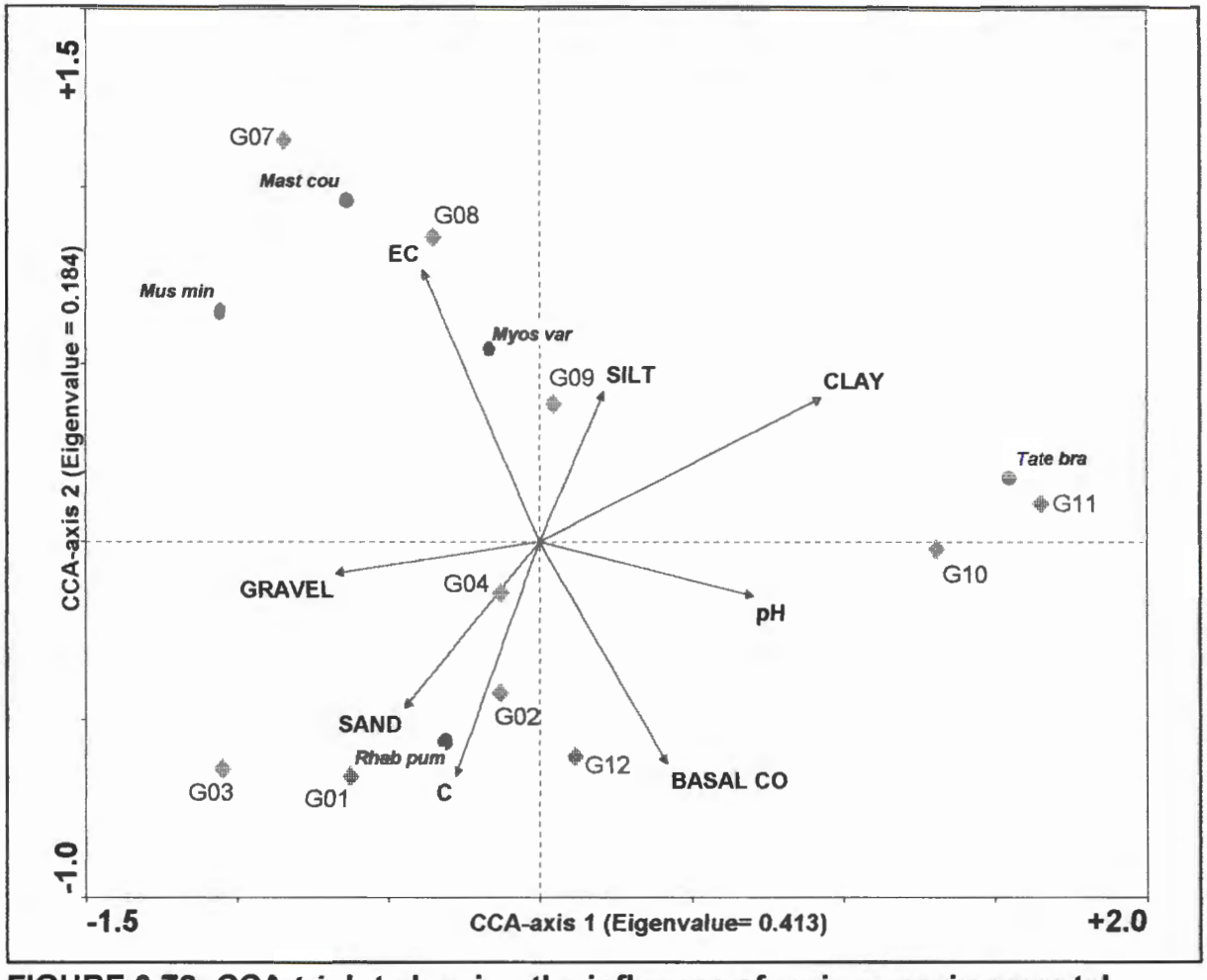


FIGURE 3.72: CCA-triplot showing the influence of various environmental variables on small mammal distributions during July 1997 (Appendix 3.2).

R. pumilio during July 1997, describing 23.6% and 19.3% of the variation respectively. This influence, however was not statistically significant and no significant correlations between *R. pumilio* and any of the individual environmental variables were evident. These influences are also reflected by Figure 3.72, which shows that *R. pumilio* preferred areas with a high gravel, sand, organic content and a suitable pH reflected by grid 12.

According to Table 3.23, % clay and % carbon in the substrate were the best predictors of variation in the distribution of *M. coucha*, describing 41% and 12 %, respectively, of the

observed variation. This influence was not, however, statistically significant, but a Pearson's correlation analysis with clay content showed that % clay ($r=0.641$; $p<0.05$) and the number of *M. coucha* were directly related (Figure 3.73 a). This effect, however is not so clear according to Figure 3.72, which indicate that electrical conductivity, as was reflected by grids 7 & 8, had a greater influence on the distribution of this species.

TABLE 3.23: Results of a forward stepwise regression analysis to assess relationships between *M. coucha* and certain edaphic variables on the ash dam grids during July 1997.

VARIABLES	PARTIAL CORRELATION	r^2	Change in r^2	p
% CLAY	0.733	0.410	0.410	0.078
% CARBON	-0.637	0.530	0.119	0.252
% SAND	0.558	0.623	0.093	0.290
VEGETATION COVER	-0.348	0.676	0.053	0.418
ELECTRICAL CONDUCTIVITY	-0.111	0.679	0.004	0.834

The numbers of *T. brantsii* was inversely correlated with % clay of the substrate ($r= -0.671$; $p<0.05$; Figure 3.73 c) and therefore tended to decline as the % clay of the substrate increased. The same result was evident from a multiple (forward) stepwise regression based on certain edaphic variables (Table 3.24), which showed that % clay was the most important predictor of *T. brantsii*, accounting for 42% of the observed variance.

The % sand of the substrate was the second most important predictor, and accounted for 22% of the sample variance. Electrical conductivity, % silt and the pH of the substrate, together with vegetation cover also made a significant contribution to the regression (Table 3.24). It is thus clear that during this study *T. brantsii* preferred areas characterized by a high clay content in the substrate, such as grids 10 and 11 (Figure 3.72).

TABLE 3.24: Results of a forward stepwise regression analysis to assess relationships between *T. brantsii* and certain edaphic variables on the ash dam grids during July 1997. The multiple regression was significant $F_{7,2} = 85.68$; $p<0.05$.

VARIABLES	PARTIAL CORRELATION	p	r^2	Change in r^2	p
% CLAY	-0.990	0.009	0.416	0.416	0.139
ELECTRICAL CONDUCTIVITY	0.985	0.015	0.528	0.111	0.328
% SLIT	-0.993	0.007	0.634	0.106	0.318
pH	0.992	0.008	0.729	0.095	0.317
% SAND	-0.982	0.018	0.948	0.219	0.054
VEGETATION COVER	0.949	0.051	0.995	0.047	0.031
% CARBON	0.518	0.482	0.997	0.001	0.481

Normally, this small mammal species, which are burrowers, prefer areas characterized by sandy loose substrate. However, their preference for areas with a high % clay content may be due to the fact that the top 10 cm of the substrate, which were sampled for the substrate analysis, was hard (high % clay), while the deeper parts of the substrate were still sandy and loose for easy burrowing by this species.

Variation in the number of *M. minutoides* was best described by the electrical conductivity (EC) of the substrate. According to Table 3.25, EC described 84% of sample variance, and this effect was statistically significant ($p=0.023$). However, the number of *M. minutoides* also correlated significantly with EC ($r=0.761$; $p<0.05$; Figure 3.73 e), but the partial correlation for this variable was not significant. This effect is also evident in Figure 3.72, as indicated by the abundance of this small mammal species on grids 7 & 8. The number of this species also correlated significantly with % clay in the soil ($r=0.754$; $p<0.05$; Figure 3.73 b) although this effect is not so clear according to Figure 3.72, and the partial correlation for this variable was not significant.

TABLE 3.25: Results of a forward stepwise regression analysis to assess relationships between *M. minutoides* and certain edaphic variables on the ash dam grids during July 1997.

VARIABLES	PARTIAL CORRELATION	r^2	Change in r^2	p
ELECTRICAL CONDUCTIVITY	0.605	0.838	0.838	0.023
% CLAY	0.938	0.937	0.099	0.08
% CARBON	-0.921	0.961	0.024	0.197
% SAND	0.836	0.972	0.011	0.291
% SLIT	0.651	0.975	0.003	0.557
VEGETATION COVER	-0.816	0.987	0.012	0.234
pH	0.601	0.992	0.005	0.399

According to Table 3.26, vegetation cover was the best predictor of variation (47%) in the number of *M. varius*, but this was not statistically significant. The % carbon in the substrate, which accounted for 11% of *M. varius* (Table 2.26). Numbers of this species, however, were negatively correlated with vegetation cover ($r = -0.817$; $p<0.01$; Figure 3.73 d), as indicated also by its tendency to plot in the opposite direction to vegetation cover in Figure 3.72. This effect is in contrast to the typical distribution pattern of this species, which prefers areas with dense vegetation cover (Skinner & Smithers 1990). Other habitat requirements, such as moisture and water availability may be more important in determining the numbers and localized distribution of this species.

It is therefore clear that the general composition of grassland small mammal communities is determined primarily by structural attributes of the habitat (Grant *et al.* 1982). During this study also found that certain edaphic variables individually or together with other factors may influence the distribution of small mammal species and by increasing the availability of the preferred habitat of a species results in an increase in the numbers of that species (Whitford, Dick-Peddie, Walters & Ludwig 1978).

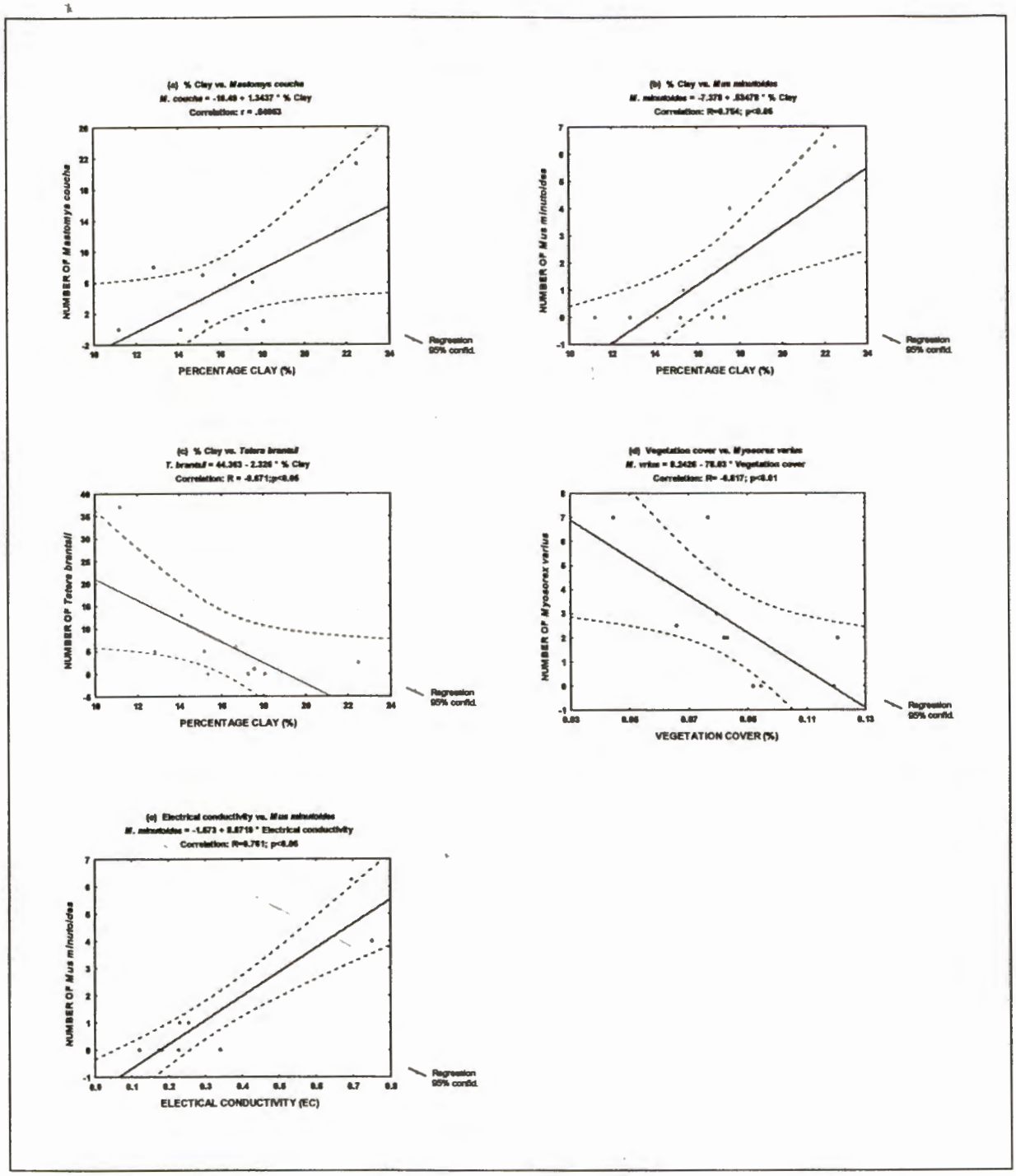


FIGURE 3.73: Linear correlations between small mammal species and other environmental variables (a-e) during the July 1997 survey.

TABLE 3.26: Results of a forward stepwise regression analysis to assess relationships between *M. varius* and certain edaphic variables on the ash dam grids during July 1997.

VARIABLES	PARTIAL CORRELATION	p	r^2	Change in r^2	p
VEGETATION COVER	0.586	0.414	0.472	0.472	0.116
% CARBON	0.956	0.044	0.578	0.106	0.316
% SLIT	0.947	0.053	0.659	0.081	0.356
% GRAVEL	0.903	0.097	0.737	0.079	0.346
ELECTRICAL CONDUCTIVITY	0.908	0.092	0.753	0.015	0.667
% CLAY	-0.910	0.089	0.863	0.111	0.259
pH	-0.838	0.162	0.959	0.096	0.162

3.7 Demography of dominant rodent species

3.7.1 Sex ratios

Trap-revealed sex ratios may deviate from the actual sex composition of a population owing to differences in trap-response, movement patterns and dispersion between the sexes (Brooks 1974; Bronner 1986). The marked avoidance of traps by one sex cannot be tested for or even anticipated, since some individuals may remain permanently untrapable. The similarity of male and female trapability rates for the three dominant species during this study (Section 3.3.2.2), however suggests that there was no differential trap response. On the other hand, differential movement patterns also affect trapability and thus bias sex ratios, although the precise influence of this factor on the trap-revealed sex ratio may be difficult to assess and will vary according to the sampling methods used (Brooks 1974). Differences in dispersion characteristics between sexes may also result in one sex colonizing sub-optimal areas more rapidly than the other, and increasing the likelihood of capture in such areas (Brooks 1974).

Rhabdomys pumilio

Of the 719 *R. pumilio* captured on the ash dam grids, 370 were males and 349 females, giving an overall sex ratio of 1.1 males : 1 female. This did not deviate significantly from an expected 1:1 ratio ($\chi^2 = 0.056$; df=1; $p>0.05$). Similarly, while sex ratios varied quite substantially between surveys, from as low as 0.6 males : 1 female (December 1997) to as high as 1.6 males : 1 female (July 1998), these differences were not statistically significant ($\chi^2 = 10.76$; df=9; $p>0.05$). The peak in sex ratios favouring males in July 1998 may reflect movement patterns, since males moved over significantly greater distances than females (Section 3.4.2) and therefore potentially had a greater probability of encountering a trap.

On the control grids, monthly sex ratios during surveys ranged from 0.9 males per female (December 1997) to a peak of 1.9 in July and September 1997 (Figure 3.74). A veld fire destroyed the control grids after the May 1998 survey and only 3 individuals (2 males and 1 female) were captured during the last four survey periods (July 1998 to January 1999); hence data for this period were not included in the analysis. Figure 3.74 also shows a transition from a male to a female predominance during the 1997 surveys, with evidence of more females during the summer months.

On the ash dam grids, seasonal sex ratios ranged from 0.6 males per female (December 1997) to a peak of 1.6 in July 1998 (Figure 3.75). This peak in sex ratios favouring males may reflect the significantly greater distances moved by males during winter (Section 3.4.2). Figure 3.75 also shows a female predominance in May 1997 and July 1997 and then again during the December 1997 and 1998 survey periods.

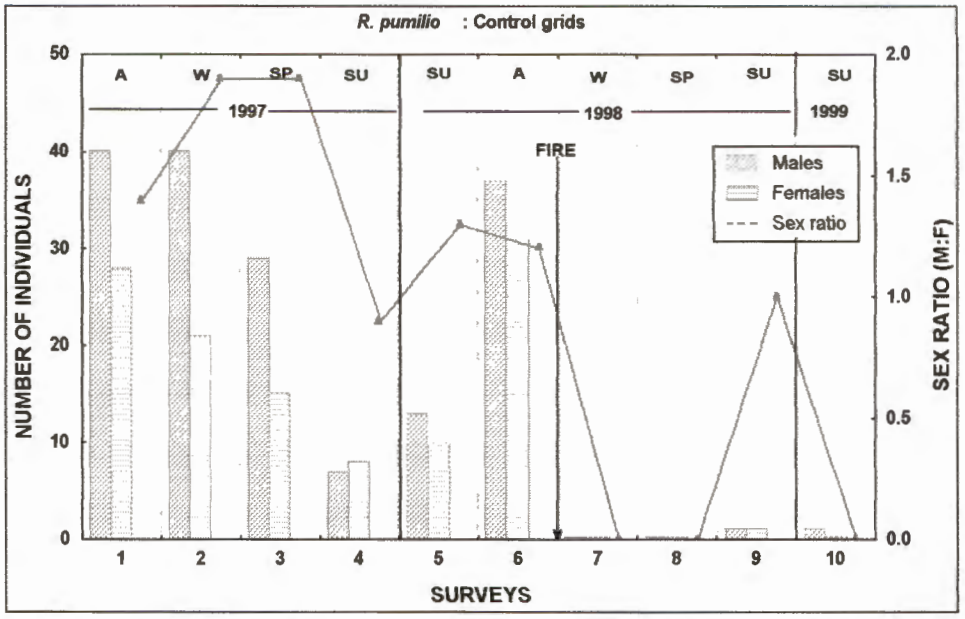


FIGURE 3.74: Sex structure and monthly variation in sex ratios of the population of *R. pumilio* on the control grids (Data for C1 & C2 combined).

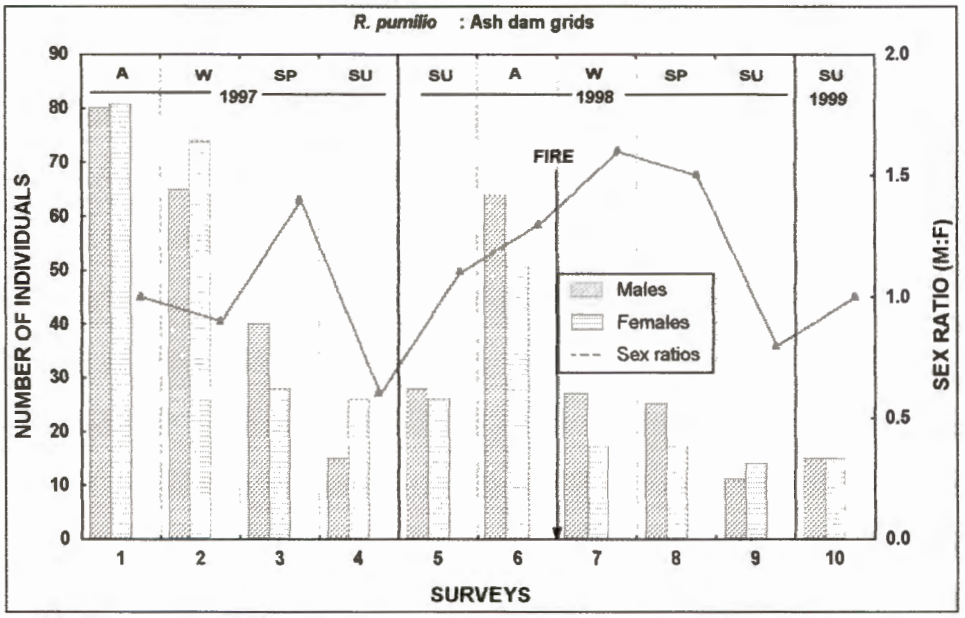


FIGURE 3.75: Sex structure and monthly variation in sex ratios of the population of *R. pumilio* on the ash dam grids (Data for all grids combined).

On a seasonal basis sex ratios on the ash dam grids favoured males in all seasons except during summer when females were favoured. These differences in sex ratios did not, however, deviate significantly from parity (Table 3.27)

TABLE 3.27: Seasonal variation in sex ratio of 719 *R. pumilio* captured on the ash dam grids over the period May 1997 - January 1999.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	144 : 132	1.09 : 1	0.96 (df=3)	ns
Winter	92 : 91	1.01 : 1	2.86 (df=3)	ns
Spring	65 : 45	1.4 : 1	0.01 (df=3)	ns
Summer	69 : 81	0.85 : 1	0.06 (df=3)	ns

On the control grids sex ratios favoured males during all seasons but again this did not deviate significantly from parity (Table 3.28). As stated earlier, trapping results will show heavy bias in favour of that sex exhibiting the greater movement pattern (Brooks 1974) and during this study, males moved over greater distances than females (Section 3.4.2), which may have contributed to their higher incidence in seasonal samples.

TABLE 3.28: Seasonal variation in sex ratio of 282 *R. pumilio* captured on the control grids over the period May 1997 - January 1999.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	77 : 59	1.3 : 1	0.28 (df=3)	ns
Winter	40 : 21	1.9 : 1	0.01 (df=3)	ns
Spring	29 : 15	1.9 : 1	0.001 (df=3)	ns
Summer	22 : 19	1.2 : 1	0.22 (df=3)	ns

The monthly variation in the sex structure of breeding and non-breeding individuals on the control grids and the ash dam grids are presented in Tables 3.29 and 3.30 respectively.

TABLE 3.29: Sex ratios of breeding and non-breeding *R. pumilio* captured on the control grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Breeding	46 : 19	2.4 : 1	9.16 (df=1)	ns
Not breeding	96 : 78	1.2 : 1	3.88 (df=1)	ns

The data relating to breeding and non-breeding individuals on the control grids give no indication of any significantly different sex ratio, although sex ratios in both reproductive categories tended to favour males.

The sex-ratios for breeding individuals on the ash dams were significantly skewed in favour of males, while the sex ratio for non-breeding individuals was significantly biased towards females (Table 3.30).

TABLE 3.30: Sex ratios of breeding and non-breeding *R. pumilio* captured on the ash dam grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Breeding	115 : 61	1.9 : 1	18.30 (df=1)	$p < 0.05$
Not breeding	219 : 252	0.87 : 1	18.34 (df=1)	$p < 0.05$

This again could reflect differential movement patterns, since reproductive males move over larger distances, and were active for longer periods, presumably in search of mates during the breeding season (Section 3.4.2). The average distance moved by breeding males on the ash dam grids was significantly greater than the average distance moved by breeding females (Section 3.4.2). No non-breeding males were recorded to move over a large distance during summer, while non-breeding females moved over relatively great distances during the same period (Section 3.4.2). These movement characteristics could explain the above differences as results will show heavy bias in favour of that sex

exhibiting the greater movement pattern and may in fact also indicate differential use of sub-optimal areas (Brooks 1974).

Mastomys coucha

Of the 315 *M. coucha* captured on the ash dams, 158 were males and 157 were females, giving an overall sex ratio of 1.01 males : 1 female. This did not deviate significantly form an expected 1:1 ratio (χ^2= 6.62; p>0.05). Similarly, the overall sex ratio on the control grids (1.14 males : 1 female) did not deviate significantly from an expected 1 : 1 ratio.

Sex ratios on the control grids during the study period ranged from 1 male per female (May 1997) to a nadir of 0.5 males per female in spring 1998 (Figure 3.76). From July 1997 to December 1997, no female *M. coucha* were captured on the control grids, while after the veld fire females appeared in the traps. During this period (September 1998 - December 1998) sex ratios were skewed in favour of females, but this deviation from parity was not significant (Table 3.32).

On the ash dam grids, seasonal sex ratios ranged from 0.2 males per female (January 1999) to a peak of 1.35 males per female in winter 1998 (Figure 3.77). On the ash dam grids there was a transition from female to male predominance between the surveys in 1997 (May 1997 - December 1997) and 1998 (May 1998 - December 1998), with evidence of predominance by females again during the January 1999 survey (Figure 3.77; Table 3.32).

The similarity of male and female *M. coucha* trapability rates suggests that there was no differential trap response (Section 3.3.2). Although no statistically-significant sex-related differences in local movement patterns on either the control and ash dam grids were apparent during this study, males moved over greater distances during autumn and winter on the control grids, while on the ash dam grids females moved over greater distances

during all seasons except spring (Section 3.4.1).

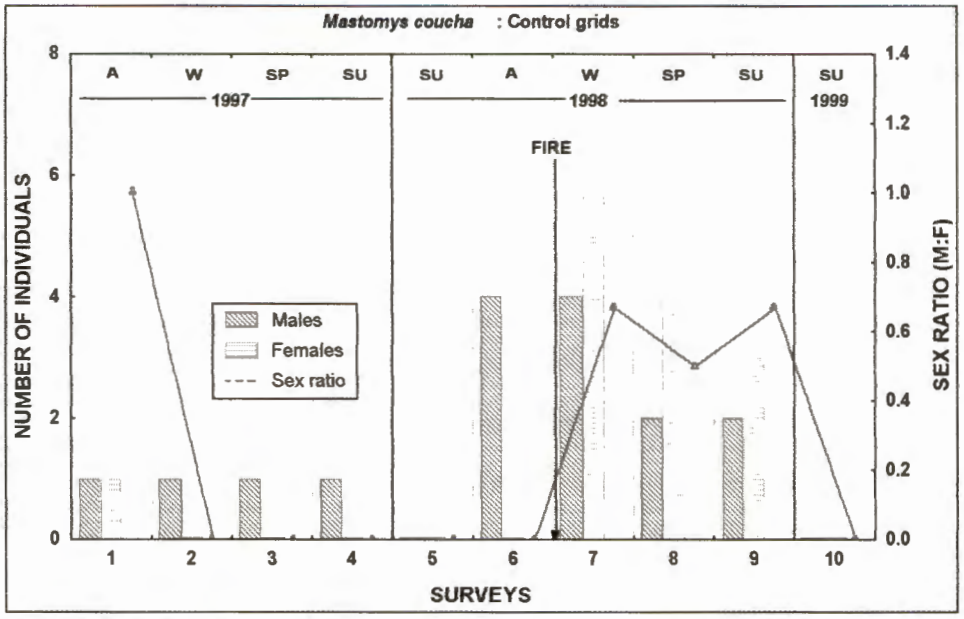


FIGURE 3.76: Sex structure and monthly variation in sex ratios of the population of *M. coucha* on the control grids (Data for C1 & C2 combined).

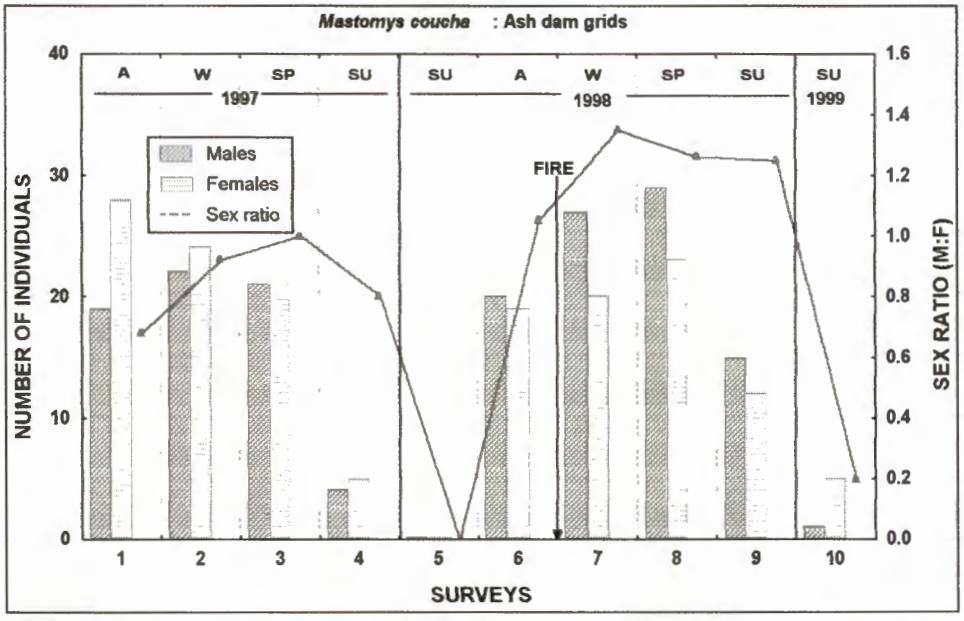


FIGURE 3.77: Sex structure and monthly variation in sex ratios of the population of *M. coucha* on the ash dam grids (Data for all grids combined).

These differences in trapability and movement characteristics could explain the above differences. On the control grids seasonal variations in sex ratios did not differ significantly from parity during any season (Table 3.31). Males predominated during autumn whereas females were favoured during winter and spring.

TABLE 3.31: Seasonal variation in sex ratio of 30 *M. coucha* captured on the control grids over the period May 1997 - January 1999; n/a = sample sizes insufficient for statistical comparisons.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	5 : 1	5 : 1	n/a (df=3)	n/a
Winter	5 : 6	0.83 : 1	n/a (df=3)	n/a
Spring	3 : 4	0.75 : 1	n/a (df=3)	n/a
Summer	3 : 3	1 : 1	n/a (df=3)	n/a

On the ash dam grids, seasonal sex ratios favoured males slightly during winter and spring, but during autumn and summer sex ratios were biased slightly in favour of females. These differences were not, however, statistically significant (Table 3.32).

TABLE 3.32: Seasonal variation in sex ratio of 315 *M. coucha* captured on the ash dam grids over the period May 1997 - January 1999.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	39 : 47	0.83 : 1	1.02 (df=3)	ns
Winter	49 : 44	1.11 : 1	0.87 (df=3)	ns
Spring	50 : 44	1.14 : 1	0.31 (df=3)	ns
Summer	20 : 22	0.91 : 1	0.05 (df=3)	ns

The control and ash dam grids showed opposite trends in sex ratios on a seasonal basis, and therefore, a fundamental demographic difference between the rehabilitated community

and the control community is evident and can thus be related to rehabilitation. De Wit (1972) noted a slight preponderance of males in all seasons except winter, while Coetzee (1967), who worked with mice excavated from burrows, found a significant overall preponderance of females. Similar sex ratios were recorded by Bronner (1986), who found that sex ratios favoured males in all seasons except autumn and that only in summer were males significantly more numerous than females.

On the control grids no significant differences in sex ratios were evident for either breeding and non-breeding individuals (Table 3.33). However, males tended to dominate samples of breeding and non-breeding individuals.

TABLE 3.33: Sex ratios of breeding and non-breeding *M. coucha* captured on the control grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Breeding	3 : 2	1.5 : 1	2.92 (df=1)	ns
Not breeding	13 : 11	1.18 : 1	6.81 (df=1)	ns

The sex ratios of breeding *M. coucha* on the ash dam grids was significantly biased in favour of males when data for all surveys were pooled (Table 3.34). Although there were no statistically significant differences in trapability or local movement patterns between males and females (Section 3.3.3), overall however, males were more trapable than females and therefore could be able to colonize sub-optimal areas more rapidly than females which increase the likelihood of capture in such areas.

TABLE 3.34 Sex ratios of breeding and non-breeding *M. coucha* captured on the ash dam grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Breeding	39 : 14	2.79 : 1	17.12 (df=1)	$p<0.05$
Not breeding	110 : 134	0.82 : 1	16.14 (df=1)	ns

Tatera brantsii

Of the 448 *T. brantsii* captured on the ash dams, 168 were males and 280 were females, giving an overall sex ratio of 0.6 males : 1 female, which departed significantly (χ^2=22.4; p<0.05) from an expected 1 : 1 sex ratio. The overall sex ratio on the control grids (1.5 males : 1 female) did not, however, deviate significantly from parity (χ^2= 1.01; p>0.05).

On the control grids *T. brantsii* was first captured during the July 1998 survey, probably because of a veld fire that occurred after the previous survey. Thereafter sex ratios ranged from a 1 : 1 sex ratio to as high as 2 males per female (September 1998) (Figure 3.78). The sex structure on the control grids show a dominance of males where after this species disappeared again during the last survey period (Figure 3.78).

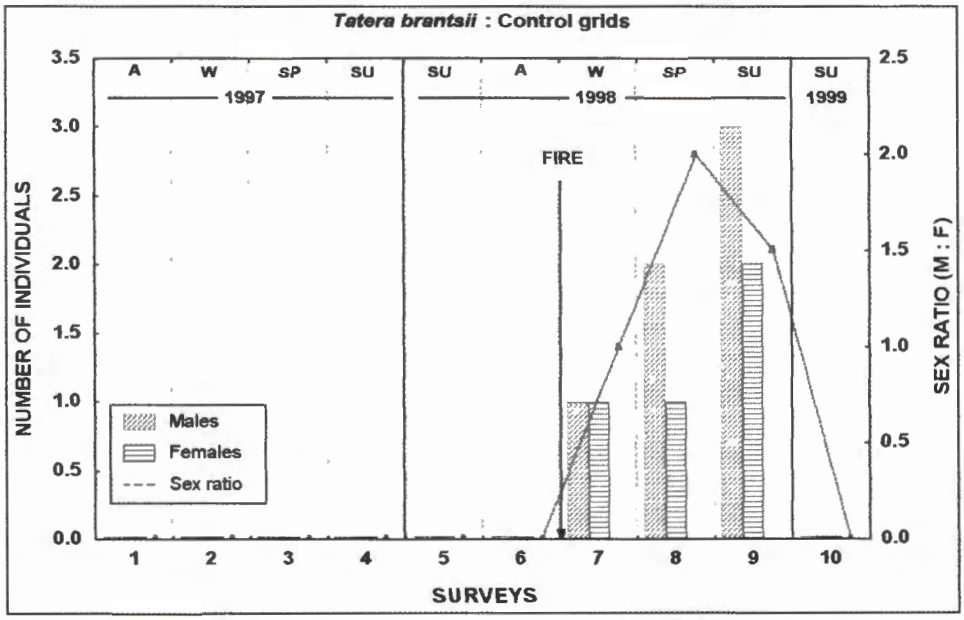


FIGURE 3.78: Sex structure and monthly variation in sex ratios of the population of *T. brantsii* on the control grids (Data for C1 & C2 combined).

On the ash dam grids monthly sex ratios during the study period ranged from 0.19 males per female (January 1998) to as high as 1.3 males per female (December 1998) (Figure

3.79). Figure 3.79 shows that females predominated throughout most of the study period, with evidence of male predominance only during the last two survey periods (December 1998 and January 1999). The dominance of females may be due to the fact that females were more trapable than males (Section 3.3.2).

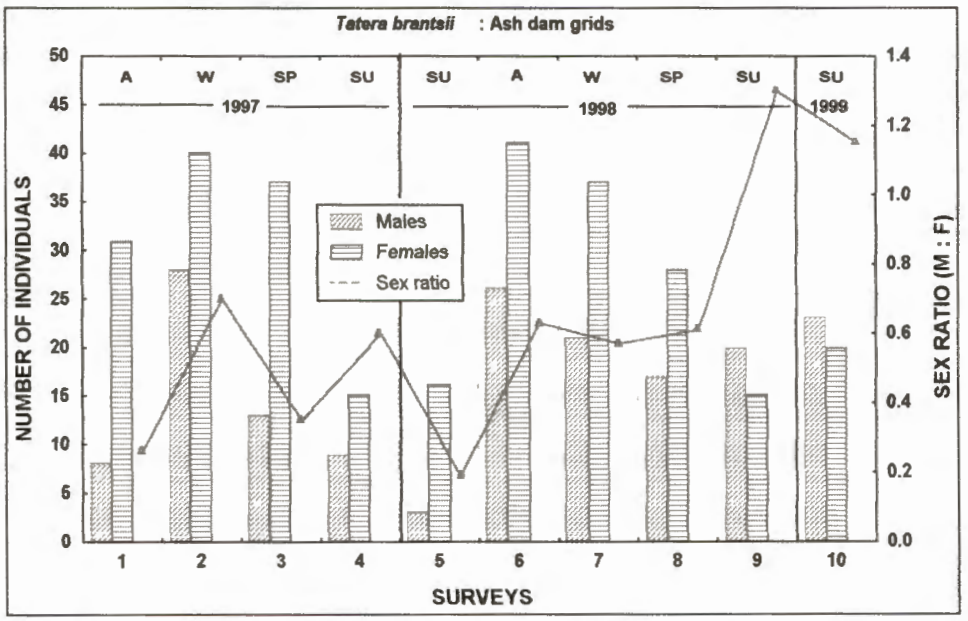


FIGURE 3.79: Sex structure and monthly variation in sex ratios of the population of *T. brantsii* on the ash dam grids (Data for all grids combined).

TABLE 3.35: Seasonal variation in sex ratio of 10 *T. brantsii* captured on the control grids over the period May 1997 - January 1999; n/a = sample sizes insufficient for statistical comparisons.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	0 : 0	-	-	n/a
Winter	1 : 1	1 : 1	-	n/a
Spring	2 : 1	2 : 1	-	n/a
Summer	3 : 2	1.5 : 1	-	n/a

Sample sizes on the control grids were too small for meaningful statistical analyses of sex ratios. However, males were favoured over females during every season except autumn when no individuals were captured (Table 3.35).

TABLE 3.36: Seasonal variation in sex ratio of 448 *T. brantsii* captured on the ash dam grids over the period May 1997 - January 1999.

SEASON	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	χ^2	p
Autumn	34 : 72	0.47 : 1	3.79 (df=3)	ns
Winter	49 : 77	0.64 : 1	0.33 (df=3)	ns
Spring	30 : 65	0.46 : 1	1.52 (df=3)	ns
Summer	55 : 66	0.83 : 1	8.31 (df=3)	$p<0.05$

On the ash dam grids seasonal variations in sex ratios tended to favour females in all seasons, but only in summer were females significantly more numerous than males (Table 3.36). This probably reflects the pronounced bias resulting from sexual differences in movement patterns where females moved over greater distances in summer than males (Section 3.4.2), perhaps to satisfy higher energetic costs associated with pregnancy, or as could be expected of a r-selected opportunistic species like *T. brantsii*, the more females, the quicker the population can expand to take advantage of the abundant resources in summer and therefore, tended to be more trapable during early summer than males (Section 3.3.2).

On the control grids, sex ratios of breeding individuals were biased slightly in favour of males, whereas sex ratios for non-breeding individuals were skewed slightly in favour of females. These differences did not, however, vary significantly from a 1:1 ratio (Table 3.37).

TABLE 3.37: Sex ratios of breeding and non-breeding *T. brantsii* captured on the control grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	CHI^2	p
Breeding	5 : 2	2.5 : 1	0.86 (df=1)	ns
Not breeding	1 : 2	0.5 : 1	3.02 (df=1)	ns

Sex ratios for breeding individuals on the ash dam grids were skewed significantly in favour of males, while sex ratios for non-breeding individuals did not differ significantly from parity (Table 3.38). The significant difference between breeding individuals may reflect sexual differences in trapability, although this is unlikely since breeding male and female mean trapability rates were similar (Section 3.3.2). Alternatively, it may have resulted from movement patterns, because breeding males moved over significantly greater distances than females during all seasons, especially during winter. Breeding females only moved around over substantial/long distances during spring and summer.

TABLE 3.38: Sex ratios of breeding and non-breeding *T. brantsii* captured on the ash dam grids over the period May 1997 - January 1999.

	NUMBER OF MALE : FEMALE	SEX RATIO MALE : FEMALE	CHI^2	p
Breeding	135 : 84	1.61 : 1	52.19 (df=1)	$p<0.05$
Not breeding	31 : 180	0.24 : 1	6.98 (df=1)	ns

For both *R. pumilio* and *M. coucha* sex ratios were more in favour of males on both the control and ash dam grids, while sex ratios for *T. brantsii* were more in favour of females. As stated earlier, trap-revealed sex ratios will show heavy bias in favour of that sex exhibiting the greater movement pattern, as was evident for the males of *R. pumilio* and *M. coucha*. Evidence from previous studies, however, suggested that differences in sex ratios may in fact also indicate differential use of sub-optimal areas, which may explain the sex ratios favouring females of *T. brantsii*.

3.7.2 Recruitment and population losses

Fluctuations in population size result from differences in the rate at which animals are recruited to, and disappear from, a population. Known rates of these variables are therefore vital for the critical examination any species demography.

3.7.2.1 Recruitment

Recruitment rates, here defined as the proportion of animals present at one trapping session that have entered the population since the previous session, reflects two distinct processes: birth and immigration. These two elements can be differentiated by assuming that the percentage of newly-captured immature mice represents the breeding increment, and that the addition of older animals results from immigration (Brooks 1974).

Rhabdomys pumilio

Recruitment of *R. pumilio* varied seasonally on both the control (Figure 3.80) and ash dam grids (Figure 3.81) and was related to breeding activity and also land-use practices in adjoining areas. Recruitment was highest in the summer and autumn months (December - May) of all years. To some extent, this reflected the surge of reproductive activity in the warm, wet summer months, and the subsequent maturation of young which only became trapable a few weeks after birth. However, during the spring and summer of 1997 high recruitment was due mainly to immigration, with rates varying from 22.74 % to 46.7% on the control grids, and from 27.93% to 29.3% on the ash dam grids, and/or elevated trapability of animals resident on these grids (Section 3.3.2).

Immigration rates, shown in Figures 3.80 and 3.81 as the difference between breeding increments and total recruitment, varied from as low as 5% (during winter, July 1997), to 100% (during late summer 1998/9; Figure 3.80) on the control grids. A dramatic increase

in immigration was evident in spring and early summer (September and November) of 1998, before any marked increase in the breeding increments. This may be attributed, in part, to a veld fire which destroyed vegetation in areas adjoining two sides of the control grids in July 1998, shortly after the survey was undertaken. This may have caused an influx of unmarked animals onto the control grids during the next few months, since the destroyed vegetation did not start recovering until after the onset of the summer rains in early November.

Another factor that might explain the marked 1997 spring / summer increase in immigration is dispersal from the ash dams into adjoining unrehabilitated areas, including the control grids. However, no movements of marked animals between these two survey areas were ever recorded, and no marked population losses were evident on the ash dams during this period (Section 3.7.2.2), suggesting that any such dispersal (involving unmarked animals) was negligible. Recruitment declined to 0% during winter (July) and spring (September) 1998, following a veld fire which destroyed vegetation on the control grids, leading to large-scale emigration and/or mortality (Section 3.7.2.2). This was followed by high immigration (50%) and natality in summer, coincident with the recovery of vegetation on the control grids following the onset of the summer rains.

On the ash dam grids, a similar pattern of recruitment was observed. Breeding increments were highest in autumn and winter of both years, following the summer surge in reproductive activity, and declined in spring and early summer (September to November) as a result of decreased reproduction in the winter months. Immigration increased markedly between September 1997 and January 1998, which again may be attributed to veld fires on adjoining unrehabilitated areas, leading to an influx of animals seeking refuge on the ash dams (Figure 3.81).

Mastomys coucha

On the control grids recruitment peaked at 100% in September 1997 & December 1997 (Figure 3.82), reflecting large-scale immigration following the burning of many adjoining

unrehabilitated areas.

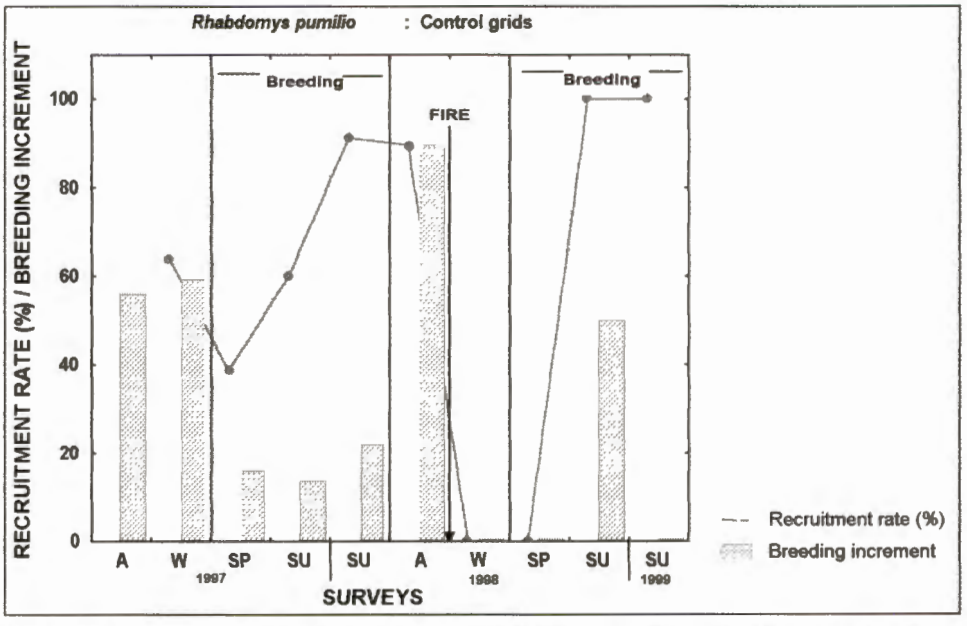


FIGURE 3.80: Recruitment rates of *R. pumilio* on the control grids over the period May 1997 - January 1999.

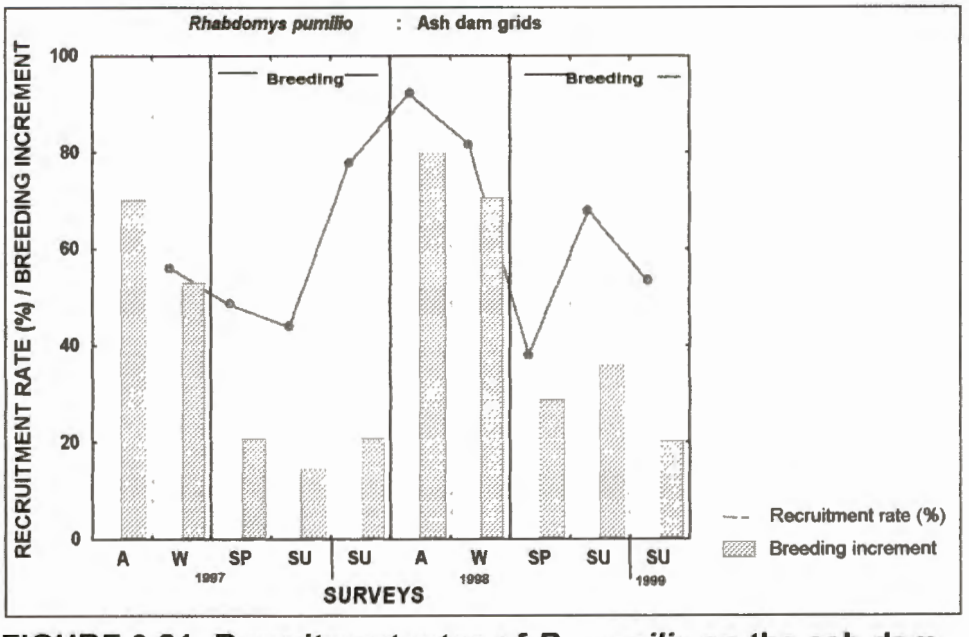


FIGURE 3.81: Recruitment rates of *R. pumilio* on the ash dam grids over the period May 1997 - January 1999.

A second peak in recruitment was observed in May 1998, but this was due to a dramatic increase in the breeding increment following the onset of breeding in spring and early summer of 1998. Breeding increments declined during the winter and spring of 1998, reflecting reduced reproduction in the dry, cold winter months. No peak in breeding increments was evident in January 1999, possibly because of the disappearance of these animals from the survey areas during the summer months which was accompanied by low trapability rates (Section 3.3.2), shorter distances moved by these animals, especially on the control grids (Section 3.4.2), and concommitantly small population sizes (Section 3.6.1).

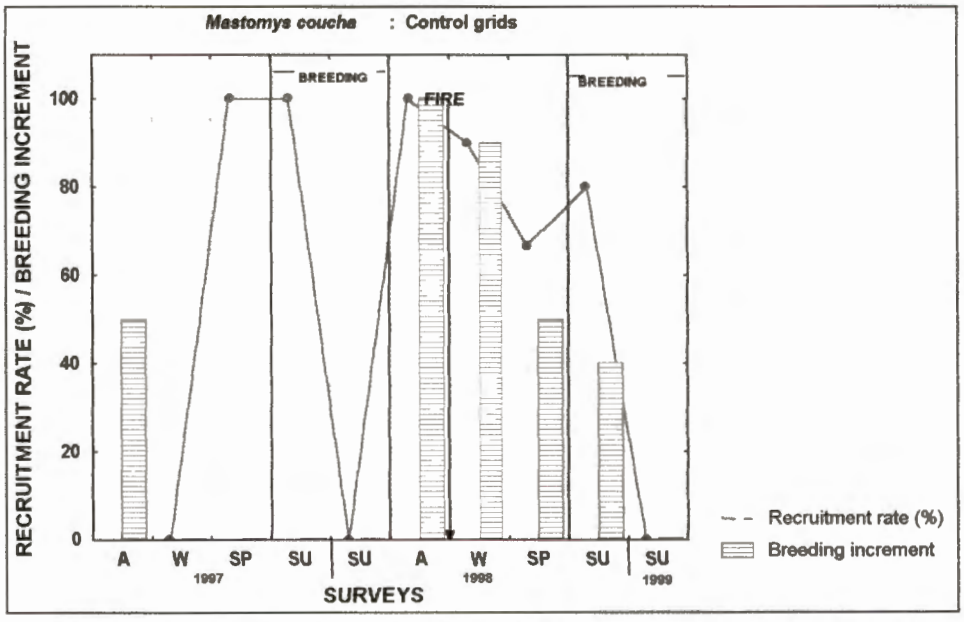


FIGURE 3.82: Recruitment rates of *M. coucha* on the control grids over the period May 1997 - January 1999.

On the ash dam grids recruitment was related to female breeding activity, being greatest at the end of the main breeding season in May 1998 and least during the breeding period (Figure 3.83). Increments from breeding declined from relatively high levels to zero from winter to summer, and increased to former high levels in May 1998, after the peak breeding period by adult females. Immigration varied between an estimated 2% and 33%,the greatest number of mice entering the population during summer 1999 (Figure

3.83). Recruitment due to birth exceeded immigration during almost every survey period, except during the last two surveys where recruitment may have been due mainly to immigration from surrounding areas, but no evidence for this was available.

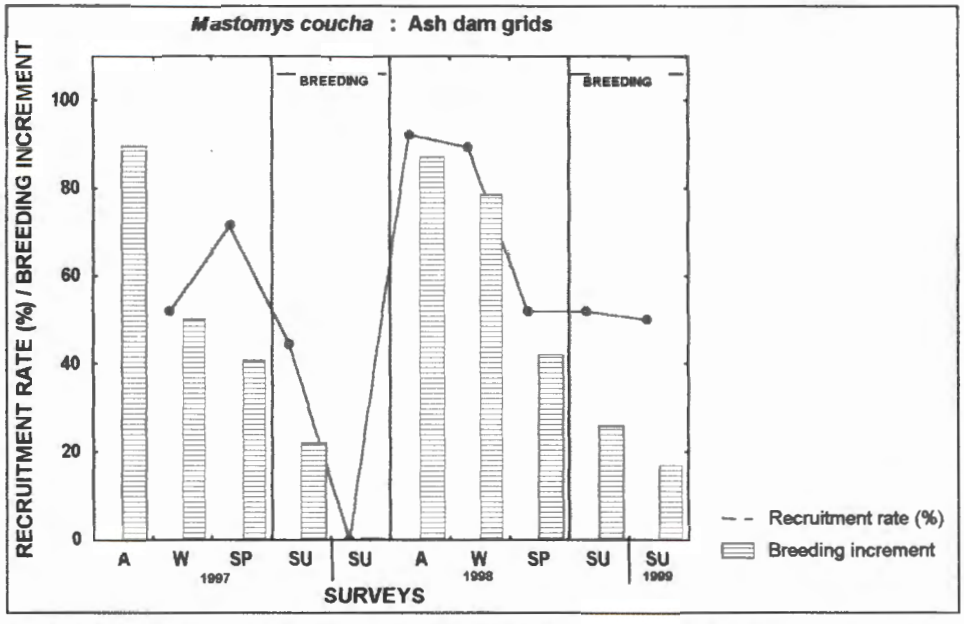


FIGURE 3.83: Recruitment rates of *M. coucha* on the ash dam grids over the period May 1997 - January 1999.

Tatera brantsii

Only ten individuals of *T. brantsii* were captured on the control grids after a veld fire during the winter of 1998 and only two of these were recaptured, so no trends in recruitment could be elucidated. On the ash dam grids, recruitment peaked in May 1997 and 1998 and December 1998 (Figure 3.84), reflecting mainly increased breeding increments following elevated levels of reproduction activity in the wet summer months, as well as immigration ($\bar{x}$ = 40%; mean immigration rate for this period). Immigration levels were generally high (28.8% to 48.6%) throughout the study period, and perhaps reflect movement between colonies. It is, however, unlikely that much immigration from adjacent areas occurred, because of the absence of this species in the unrehabilitated areas, including the control grids (Section 3.1).

Recruitment due to birth exceeded immigration during the winter of 1998, and in the spring of 1998, while recruitment during the other survey periods was mainly due to immigration.

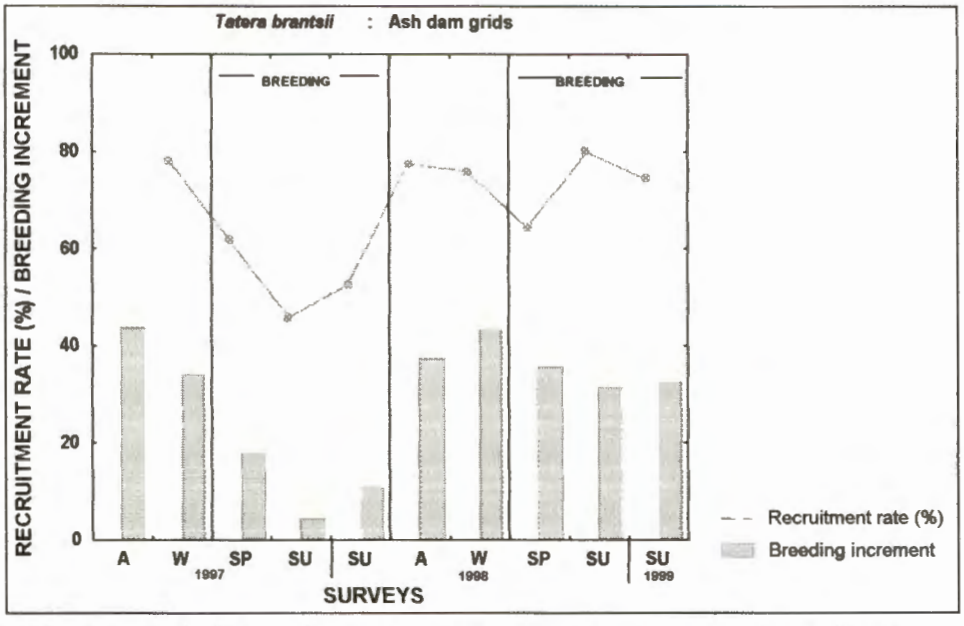


FIGURE 3.84: Recruitment rates of *T. brantsii* on the ash dam grids over the period May 1997 - January 1999.

3.7.2.2 Population losses

The rate of disappearance, as here defined, is the proportion of the population present at one trapping session which was not captured the following session. The rate as used here does not distinguish between real mortality and losses due to emigration from the grids (Brooks 1974). Mortality may operate at various developmental stages in the life of the individual. Pre-natal losses, either prior to or after implantation, and post-natal losses of individuals before they leave the nest and enter the trapable population cannot be detected by trapping (Brooks 1974).

Rhabdomys pumilio

The rates of disappearance of all *R. pumilio* trapped on the control and ash dam grids

between May 1997 and January 1999 were high, and generally exceeded 70% (Figure 3.85). On the control grids, the disappearance rate of *R. pumilio* increased from autumn (May) through winter (July) and spring (September) in 1997, and thereafter remained very high until the veld fire in May 1998. The initially low rate of disappearance may be attributed to an abundance of cover and resources in autumn (Brooks 1974), at the end of the growing season. It is probable that the rates of disappearance between May and December 1997 involved mortality rather than emigration, since areas adjoining the control grids were burned in July 1997, thereby curtailing emigration possibilities, and relatively harsh environmental conditions prevailed. High rates of disappearance from December 1997 to May 1998 cannot be attributed to changes in trapability, due to the relatively high and stable trapability rates evident during this period (Section 3.3.2).

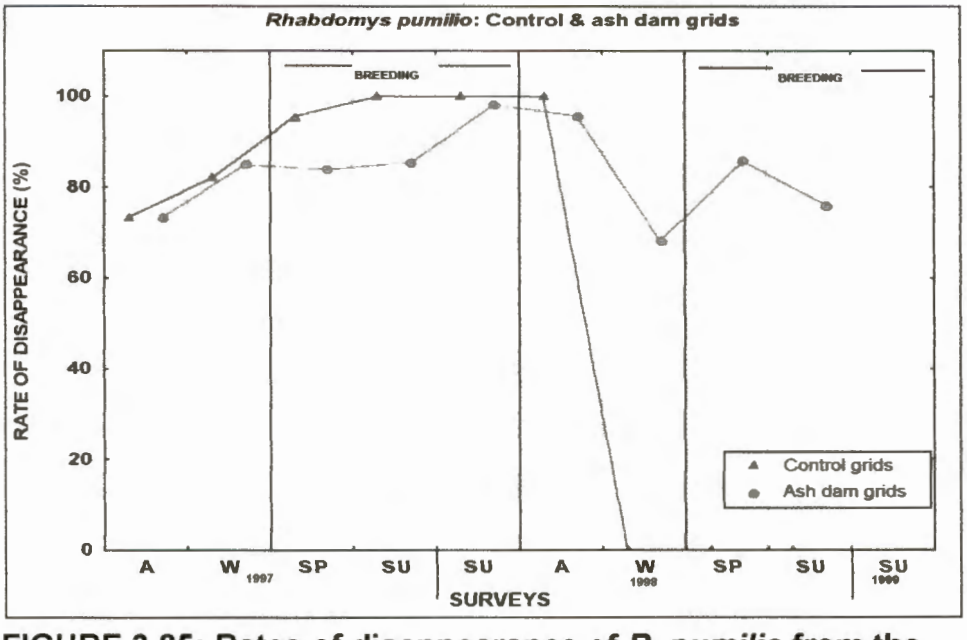


FIGURE 3.85: Rates of disappearance of *R. pumilio* from the control & ash dam grids over the period May 1997 - January 1999.

On the ash dam grids the rate of disappearance was relatively stable in spring and summer of 1997, but overall it was still high, probably due to emigration. An increase in the rate of disappearance from January 1998 to May 1998 was evident , with a decline in

winter (July 1998) which is congruent with the hypothesis that emigration rates were low owing to a veld fire after the May 1998 survey (Figure 3.85). Conversely, population losses during spring and summer probably involved emigration rather than mortalities, since this period coincided with the recovery of vegetation on adjacent areas and the return of more favourable environmental conditions. High rates of disappearance suggest rapid population turnover rates, especially during the summer months, and was related to a decline in population sizes.

Mastomys coucha

Rates of disappearance of *M. coucha* were very high, except in May 1997, and fluctuated markedly on both the control and ash dam grids (Figure 3.86). Population losses on the control grids during May 1997 were exceeded by those in the subsequent survey periods, except in January 1998 when no individuals were captured.

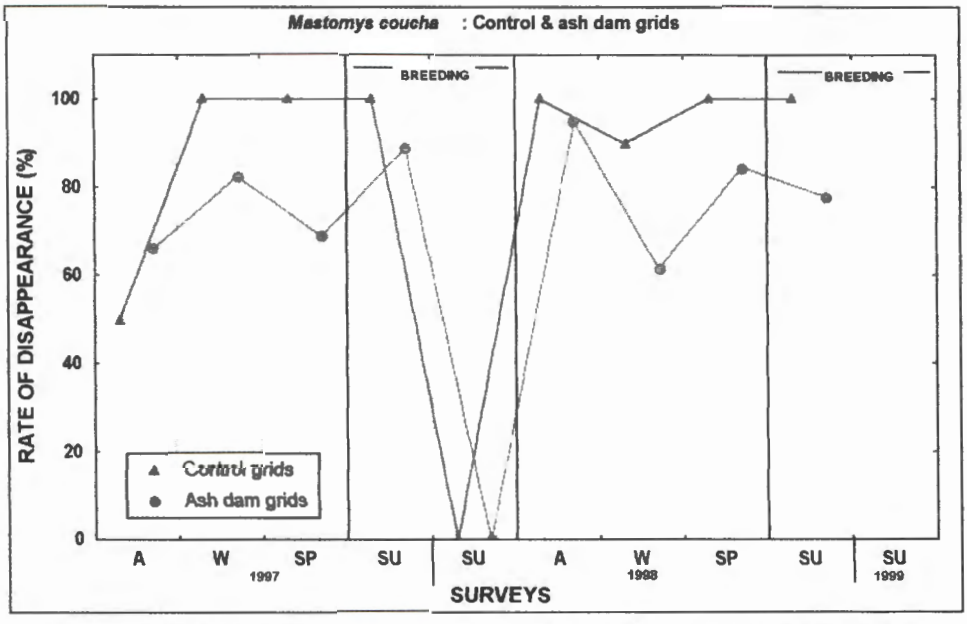


FIGURE 3.86: Rates of disappearance of *M. coucha* from the control & ash dam grids over the period May 1997 - January 1999.

On the ash dam grids population losses were lowest during May 1997, September 1997 and July 1998 (Figure3.86), and may have been due to real mortalities because of the prevailing harsh environmental conditions. The higher values during spring, summer and May 1998 probably involved emigration rather than death, as surrounding areas recovered from winter burning.

Tatera brantsii

The rates of disappearance of all *T. brantsii* trapped on the ash dam grids are presented in Figure 3.87. Population losses were lowest during the autumn and winter of 1997 and may be attributed to the high population sizes (Section 3.6.1) during this period due to the abundance of resources in autumn, at the end of the growing season, and were exceeded by those in the subsequent survey periods. The high values in the summer and autumn of 1998 could have been due to density-dependant emigration, with animals leaving established colonies to excavate new ones and to extend their range in search of food (De Moor 1969).

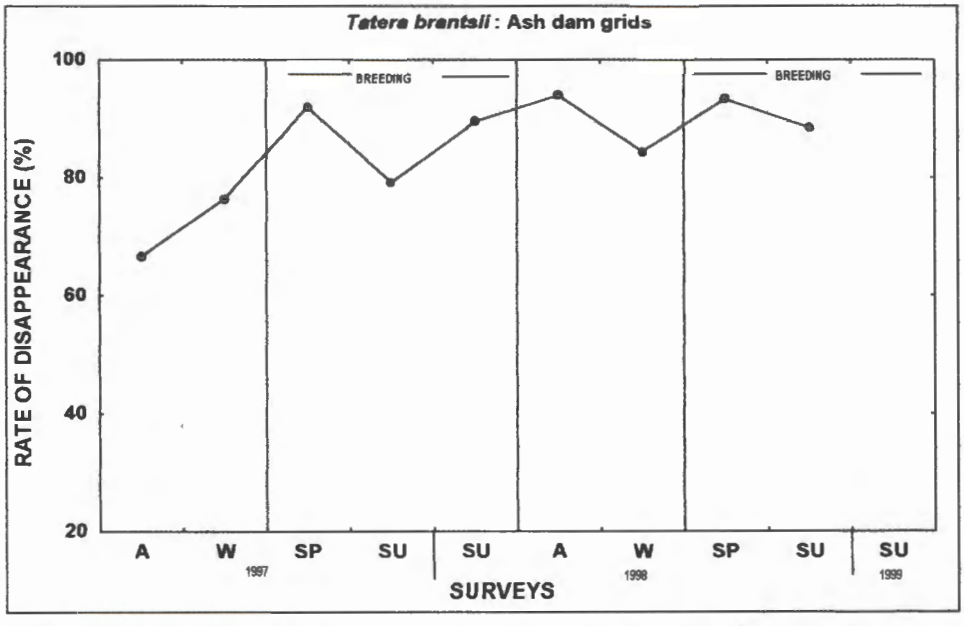


FIGURE 3.87: Rates of disappearance of *T. brantsii* from the ash dam grids over the period May 1997 - January 1999.

3.7.2.3 Population gains and losses

Rhabdomys pumilio

On the control grids population losses exceeded recruitment throughout 1997 until May 1998, whereafter *R. pumilio* disappeared from the area due to the destructions of the habitat by a veld fire (Figure 3.88). During the summer of 1998 & 1999 recruitment exceeded mortality as a result of immigration into the area coincident with the recovery of vegetation after the onset of the summer rains (Section 3.7.2.1). On the ash dam grids population losses exceeded gains throughout the study period except during July 1998 when recruitment was slightly higher, mainly as a result of large breeding increments to the population during this period (Figure 3.81).

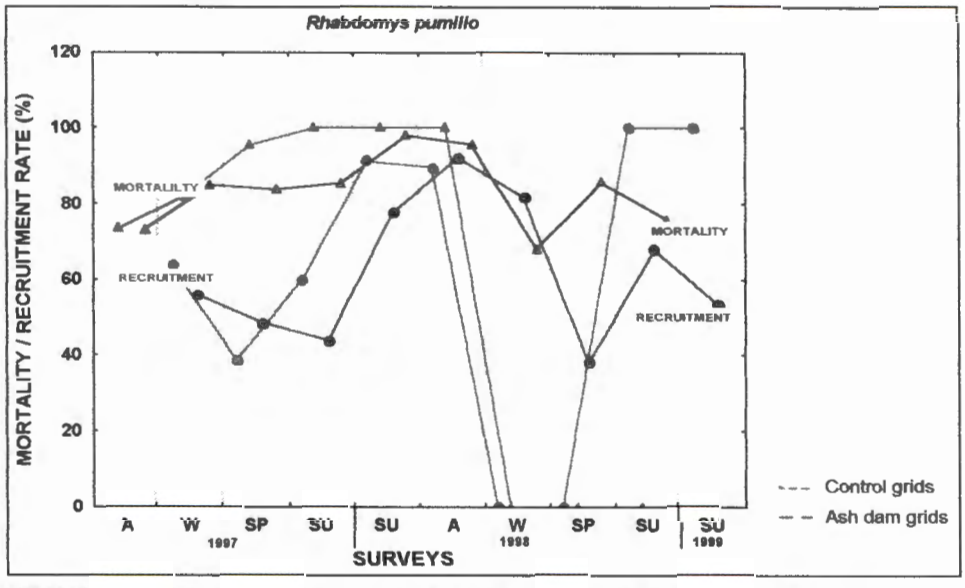


FIGURE 3.88: Monthly variation in the recruitment and disappearance rates of *R. pumilio* at Hendrina Power Station.

Mastomys coucha

On the control grids population losses exceeded gains at the beginning and end of the

study period, this presumably being due to high levels of emigration. During the rest of the study period, however, recruitment and disappearance rates were roughly equal (Figure 3.89). On the ash dam grids the same pattern was evident except in July 1998 when population gains exceeded losses slightly, mainly as a result of large breeding increments to the population after the breeding season (Figure 3.83).

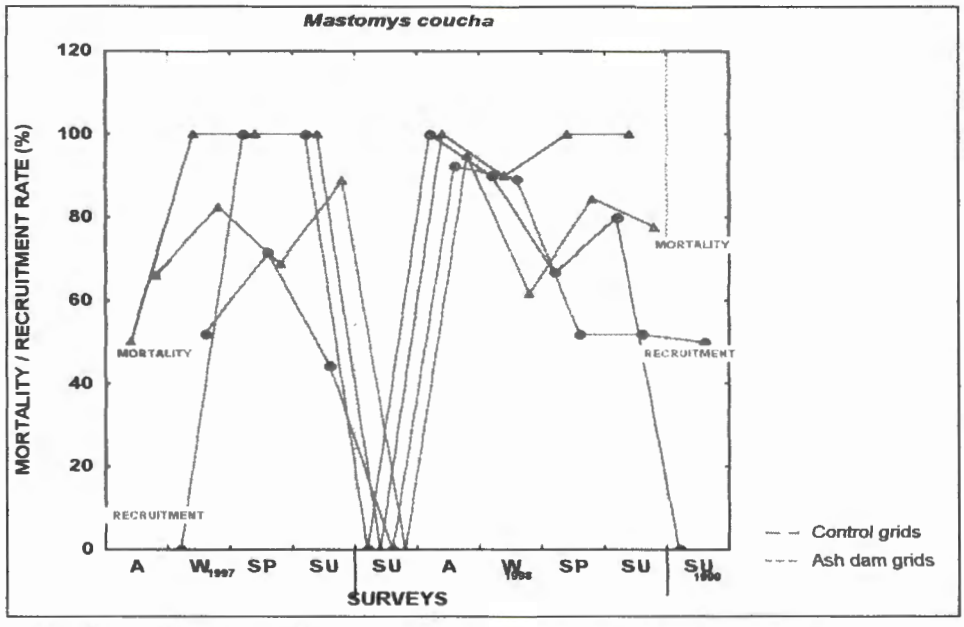


FIGURE 3.89: Monthly variation in the recruitment and disappearance rates of *M. coucha* at Hendrina Power Station.

Tatera brantsii

For *T. brantsii* disappearance rates were higher than recruitment rates, except in May 1997 (Figure 3.90). The high disappearance rates may have been due to density-dependant emigration by individuals in search for food and mates (De Moor 1969), and *T. brantsii* colonies also tend to move around across an area over time (Korn & Korn 1989).

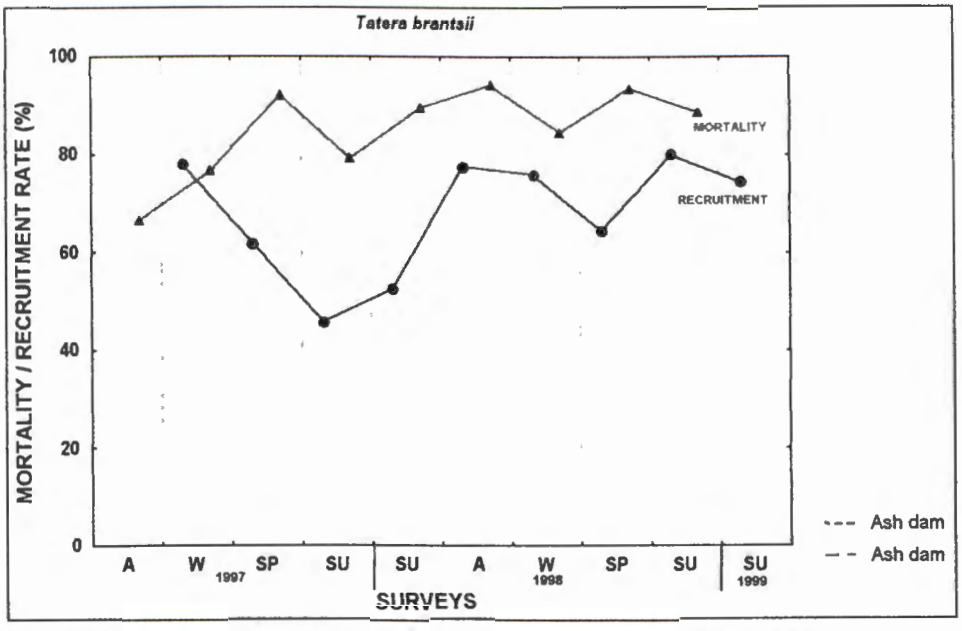


FIGURE 3.90: Monthly variation in the recruitment and disappearance rates of *T. brantsii* at Hendrina Power Station.

3.7.3 Age determination

Age determination of small mammals during ecological studies is notoriously difficult. The ideal situation would be to know the exact date of birth of each individual and monitor it throughout its entire life-span. This is almost always impossible owing to the cryptic lifestyle of most species. Therefore, age determination is restricted to more or less confident estimates based on trapped animals (Leirs 1994).

Many parameters have been used to estimate age in ecological studies on small mammals. Characters which are available only from dead, preserved material, such as cranial dimensions, tooth eruption sequences and eye lens masses are not applicable to CMR studies of demography based on a live-trapping experimental design.

Most field workers have used body mass as an index of age, either alone or in combination

with body length and pelage characteristics (Brooks 1974). As the dominant species in this study all show quite marked intra-populational variability in fur colour, and no clear-cut differences in pelage characteristics in relation to age were observable, this parameter was of little use. The ageing system was therefore restricted to only body mass. The use of body mass for ageing small mammals is complicated by the fact that mass does not depend on age alone, but also on nutritional status, which is in turn affected by food availability, social status, water retention and the physiological milieu during growth (Brooks 1974; Leirs 1994).

Furthermore, body mass varies in relation to reproductive status, most notably in females, and in some species mass may also vary seasonally in an adaptive manner related to food availability. Despite these confounding factors, body mass can, and often is, successfully used for the delimitation of broad age-classes providing that reproductive status is also taken into consideration. Such age classes do not have any clear-cut biological significance, and seem only to explore temporal variation in population structure.

Rhabdomys pumilio

The observed mass distribution of all females captured during all the survey periods on both the ash dam and control grids, conformed to normality (Figure 3.91), but some indications of polymodality were evident with nadirs (observed frequencies much lower than expected) at 16 -18g, 26 -28g and 36 - 38g.

The minimum mass of breeding (pregnant and / or lactating) females during the breeding season(s) was 28 g (Figure 3.92), which coincided with one of the nadirs identified above. An adult : immature mass boundary of 28g was thus adopted, and could be used with at least 95% confidence ($Z = 1.61$; $p = 0.0537$).

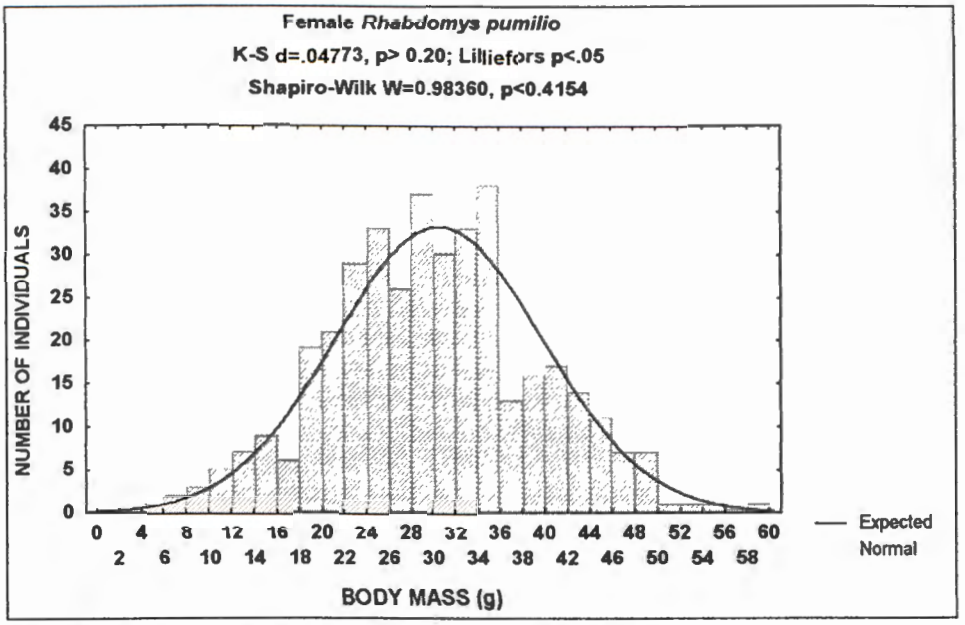


FIGURE 3.91: Mass distribution of female *R. pumilio* individuals during all the survey periods on the ash dam and the control grids.

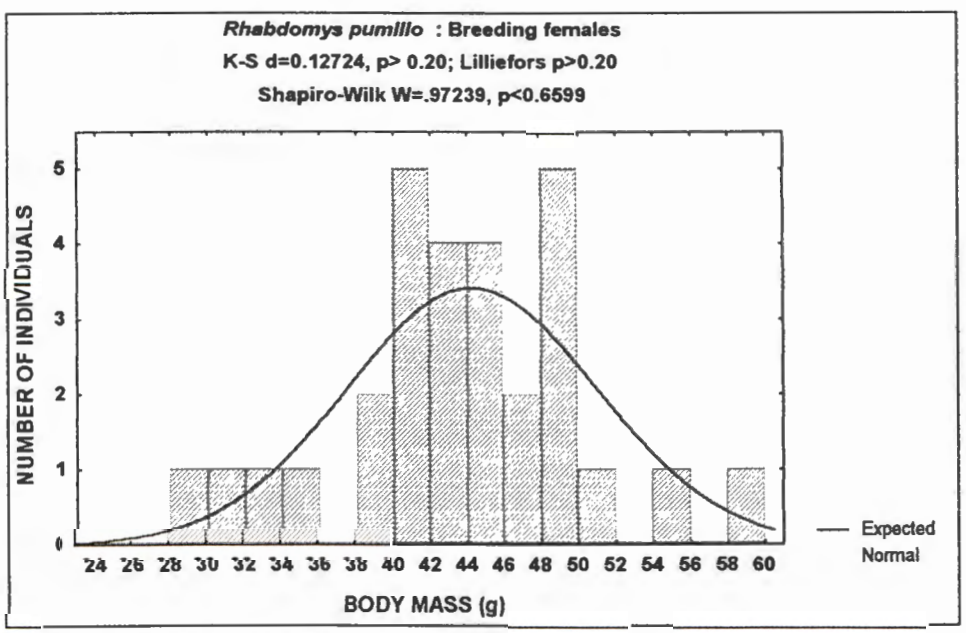


FIGURE 3.92: Mass distribution of breeding female *R. pumilio* individuals during the breeding season (December & January) on the ash dam and control grids.

Observed mass frequencies of immature (non-breeding) females with a body mass less than 28g deviated significantly form normality (Figure 3.93), and showed evidence of bi-modality. Observed frequencies for the 16 -18g mass range were significantly lower than expected, thereby providing a convenient (if somewhat arbitrary) mass limit of 18g to distinguish two subadult age / mass cohorts: subadult class 1 (<18g), representing the newest cohorts in the population; and subadult class 2 (18 -27g).

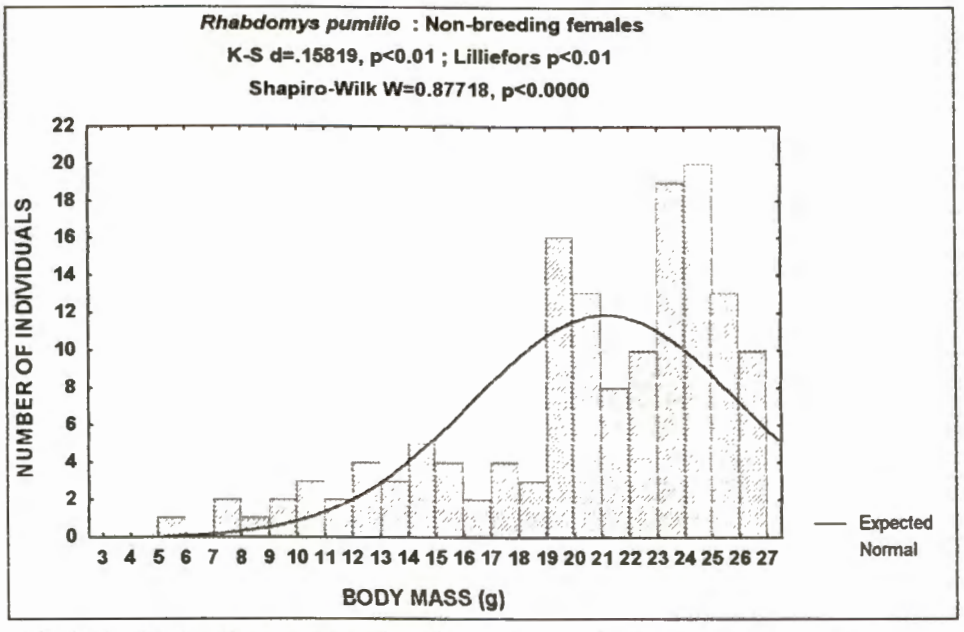


FIGURE 3.93: Mass distribution of non-breeding female *R. pumilio* individuals for all survey periods on the ash dam and control grids.

While the mass frequency of breeding females conformed to a normal distribution during the main breeding season(s) (Figure 3.92), when data for all surveys were combined, the mass distribution deviated significantly from normality (Figure 3.94). Observed frequencies for the 36 -38g mass range, in particular, were markedly lower than expected, suggesting that this mass range distinguished two cohorts. A mass limit of 36g was therefore used to distinguish between two adult age/mass classes, namely: adult class 1 (28 -35g); and adult class 2 (>36g).

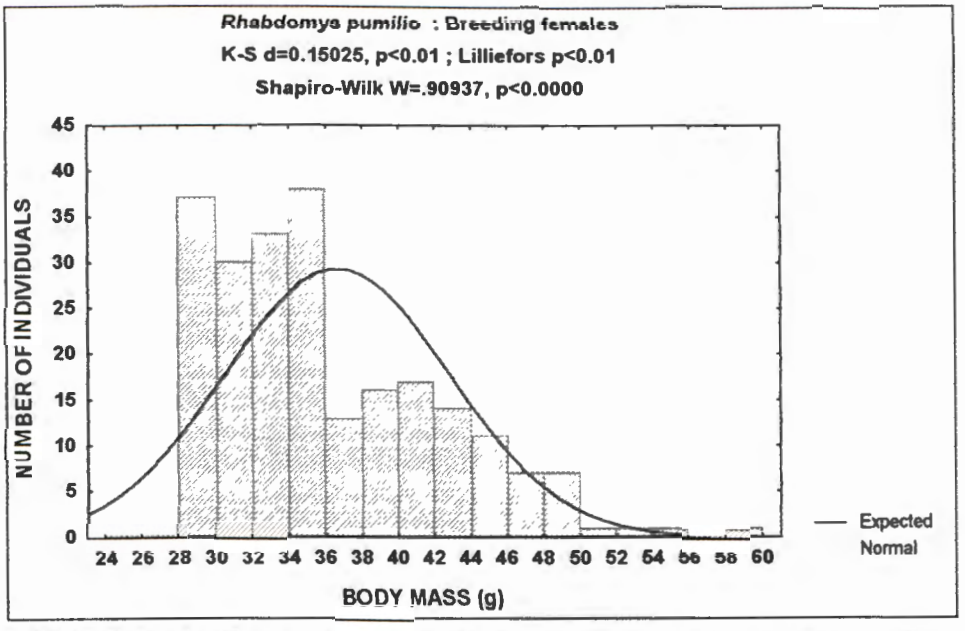


FIGURE 3.94: Mass distribution of breeding female *R. pumilio* individuals for all survey periods on the ash dam and control grids.

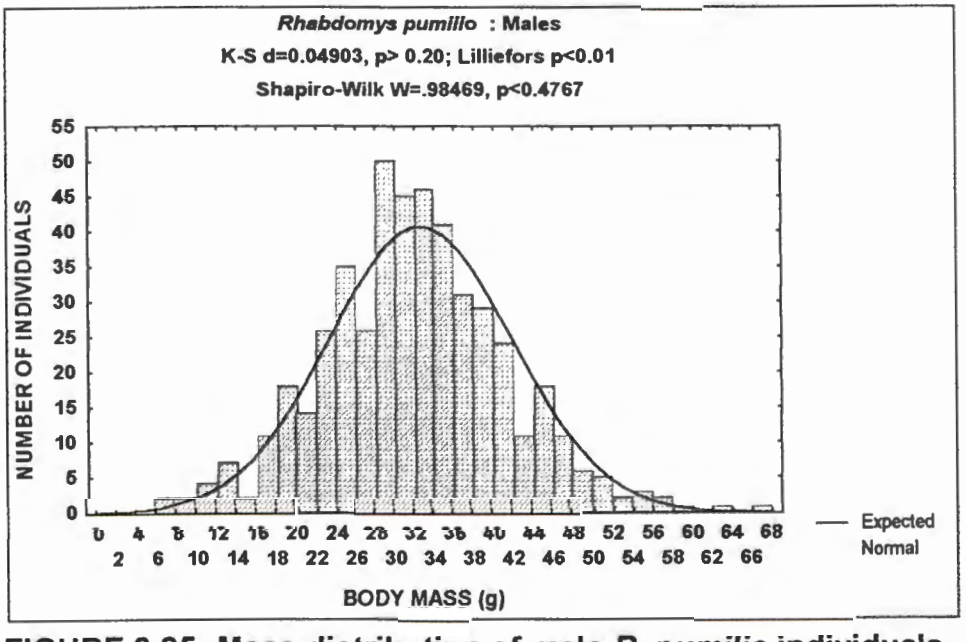


FIGURE 3.95: Mass distribution of male *R. pumilio* individuals during all the survey periods on the ash dam and control grids.

Observed mass frequencies of male *R. pumilio* conformed to normality (Figure 3.95), but there was evidence of polymodality with lower than expected frequencies at especially 14 -16g, 26 -28g and 42 - 44g. The minimum mass of scrotal males during the main breeding season(s) was 22g (Figure 3.96), but only 8% of scrotal males weighed less than 28g (Z = 1.39; p= 0.0823) .

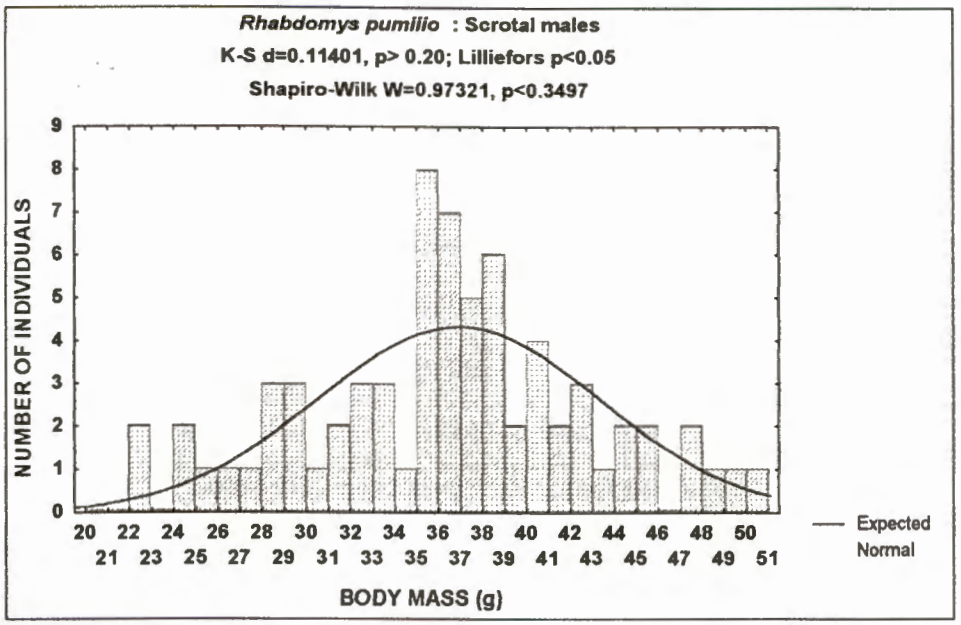


FIGURE 3.96: Mass distribution of scrotal male *R. pumilio* individuals during the breeding season (December & January) on the ash dam and control grids.

An adult : immature mass limit of 28g was thus adopted, and could be used with at least 90% confidence. When data for all surveys were combined, the observed mass frequencies of immature males deviated significantly from normality (Figure 3.97), and a nadir at 14 -16g was again evident. This provided a convenient (although arbitrary) mass limit of 16g to distinguish between two subadult age / mass classes, namely subadult class 1 (<16g) and subadult class 2 (16 -27g). Similarly, the mass distribution of scrotal males during all seasons deviated significantly from normality, with observed frequencies for the 42 -44g range being markedly lower than expected. A mass limit of 44g was thus used to

distinguish between two adult classes (Figure 3.98).

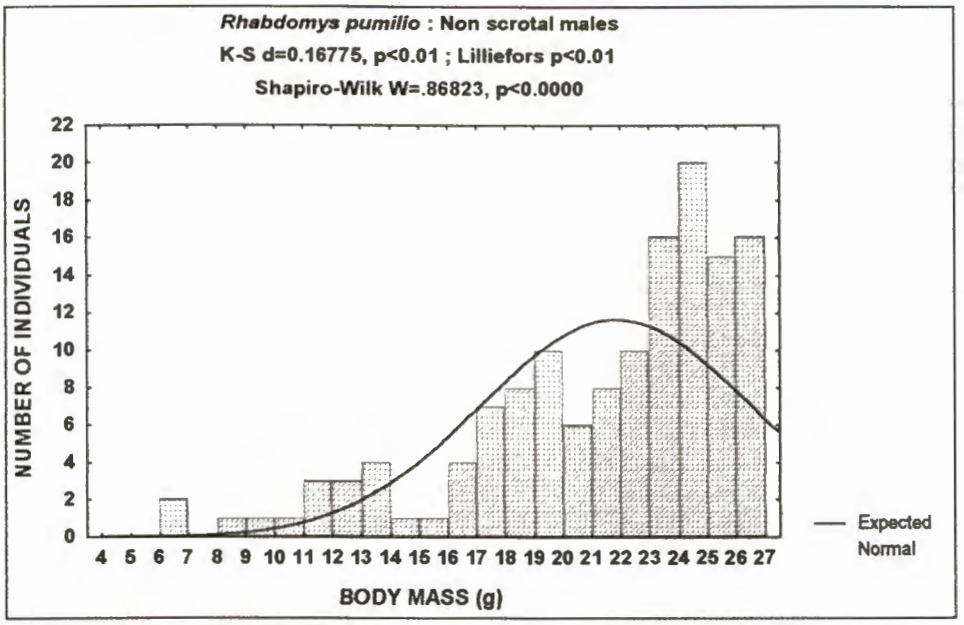


FIGURE 3.97: Mass distribution of immature male *R. pumilio* individuals for all survey periods on the ash dam and control grids.

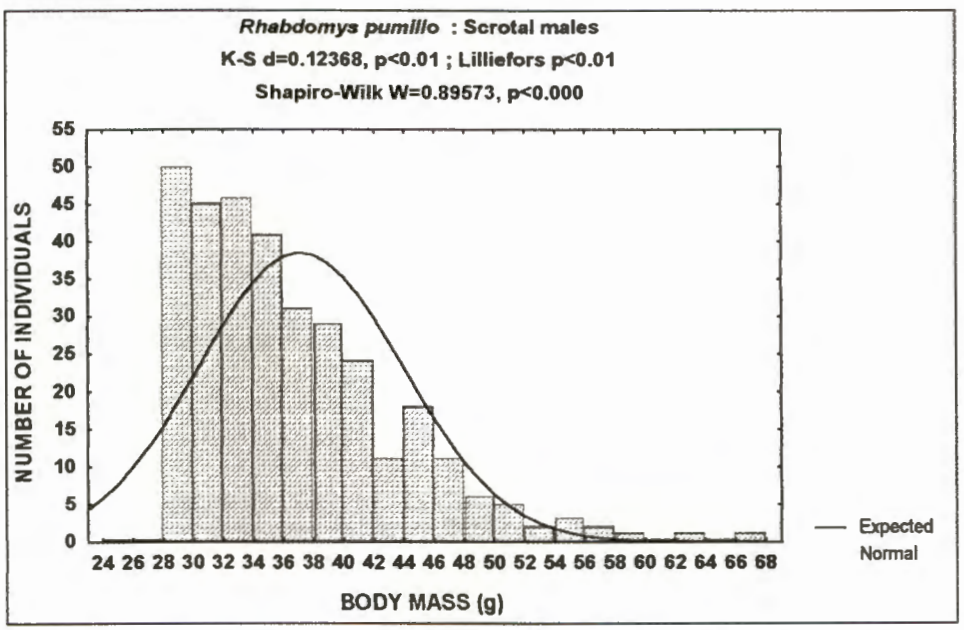


FIGURE 3.98: Mass distribution of scrotal male *R. pumilio* individuals for all survey periods on the ash dam and control grids.

David & Jarvis (1985) found that females weighing 30 g and more were mature, while males weighing 36 g or above were sexually mature. During this study, however, 28g was adopted as the mass boundary between adult (mature) and immature individuals for both males and females. Brooks (1974), however, found that the mean age of breeding maturity was nine weeks (range 22 -36g) and that 56% of these female individuals were reproductively active. David & Jarvis (1985) on the other hand found that 92% of Cape Flat females in the weight range 27 -36g were pregnant and lactating. Since 6 out of 137 (4%) of Hendrina Power Station females in the weight range 28 - 35g were pregnant or lactating, these individuals at Hendrina appear to mature much later than on the Cape flats (David & Jarvis 1985), and in other natural grassland habitats (Brooks 1974).

For males, however, the mass class distribution identified for this study, varied markedly from the mass classes identified by David & Jarvis (1985) and from Brooks (1974). Males at Hendrina Power Station appeared to mature much later than males in other grassland areas, since 37% of these males in the weight range 28 -44g were scrotal, while Brooks (1974) found that 53% of two month old (27 -36g) males were reproductively active. David & Jarvis (1985), on the other hand estimated that only 31% of males in the weight range 27 -36g were reproductively active, which compared well with the data for active males during the present study.

It is therefore clear that there are mass-age related differences for both males and females in different areas, which can be due to the fact that *R. pumilio* shows marked geographical variations in size (Skinner & Smithers 1990) and the fact that the ash dams are not a natural habitat compared to other studied areas in South Africa.

Mastomys coucha

The observed mass frequencies of female *M. coucha* conformed to a normal distribution (Figure 3.99), although there were indications of polymodality with lower than expected

frequencies at 14 -16g, 24 -26g and 34 -36g.

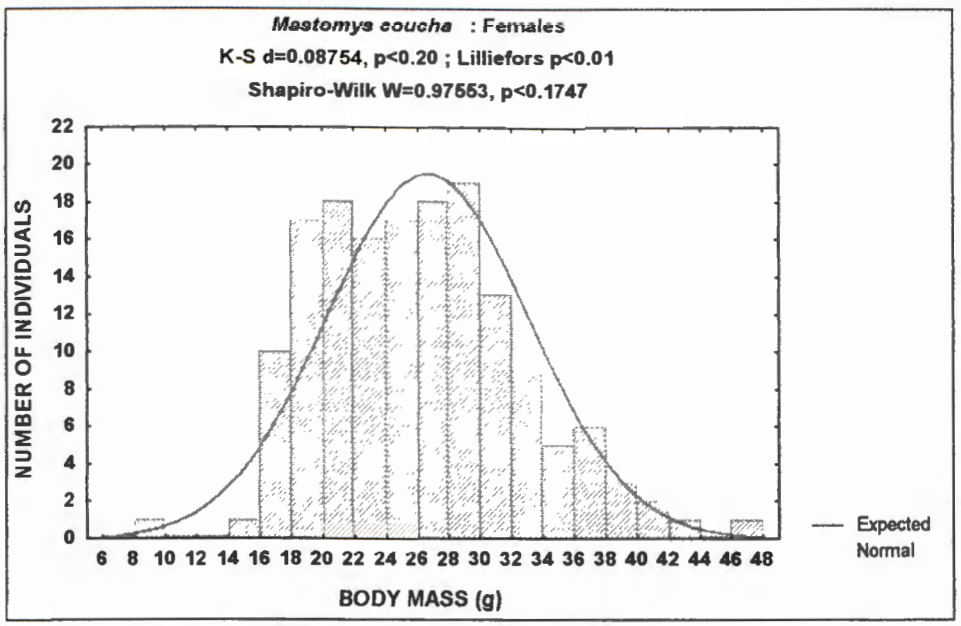


FIGURE 3.99: Mass distribution of female *M. coucha* individuals during all the survey periods on the ash dam and control grids.

The lowest recorded mass of a breeding (pregnant/lactating) female was 24g (Figure 3.100), and only 5% of breeding females could be expected to have a mass lower than this ($Z = 1.60$; $p = 0.0548$). An adult : immature mass boundary of 24g was thus assumed, and could be used with 95% confidence.

Although sample sizes were small, the mass distribution of non-breeding females (Figure 3.101) deviated from normality (Shapiro-Wilk $W = 0.885$; $p<0.001$), and observed frequencies in the 17 -18g mass range were lower than expected. A (somewhat arbitrary) mass limit of 18g was therefore used to distinguish between two subadult classes, namely subadult 1 (<18g) and subadult 2 (18 -23g). Similarly, the mass distribution of breeding females throughout all seasons deviated from modality, with observed frequencies for the 34 -36g mass range being markedly lower than expected (Figure 3.101). A mass limit of 36g was therefore used to recognize two adult classes, namely adult class 1 (14 -35g) and adult class 2 (>35g).

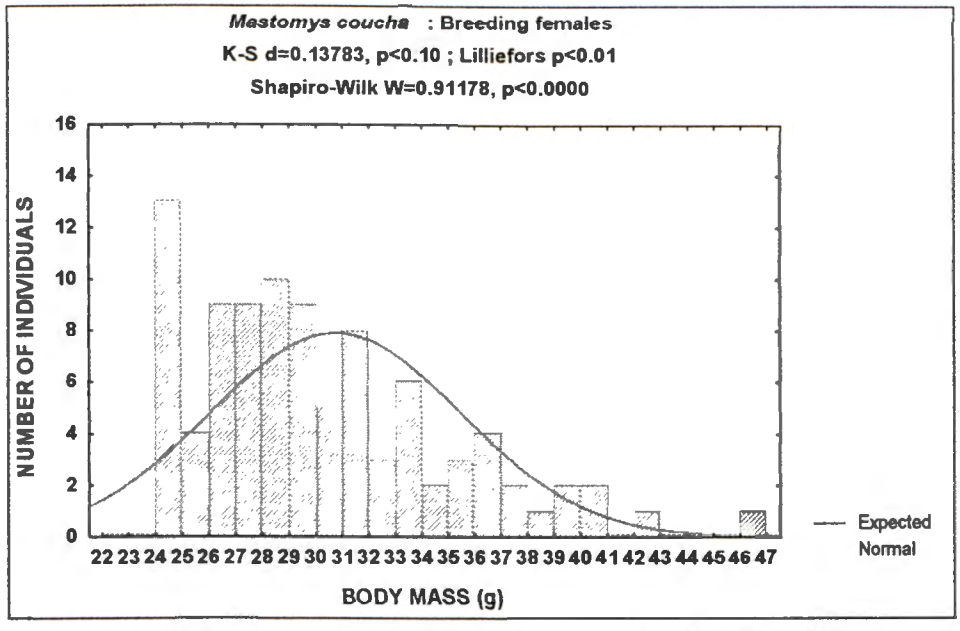


FIGURE 3.100: Mass distribution of breeding female *M. coucha* individuals for all survey periods on the ash dam and control grids.

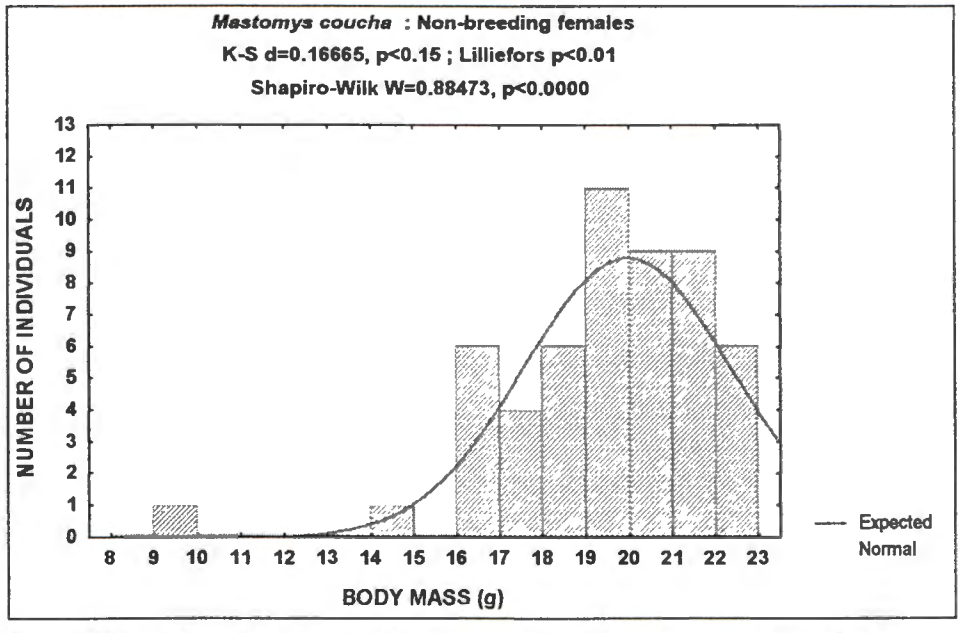


FIGURE 3.101: Mass distribution of non-breeding female *M. coucha* individuals for all survey periods on the ash dam and control grids.

The mass distribution of male *M. coucha* did not conform to normality (Figure 3.102), and distinct bi-modality was evident with nadirs at 28 -30g and 36 -38g.

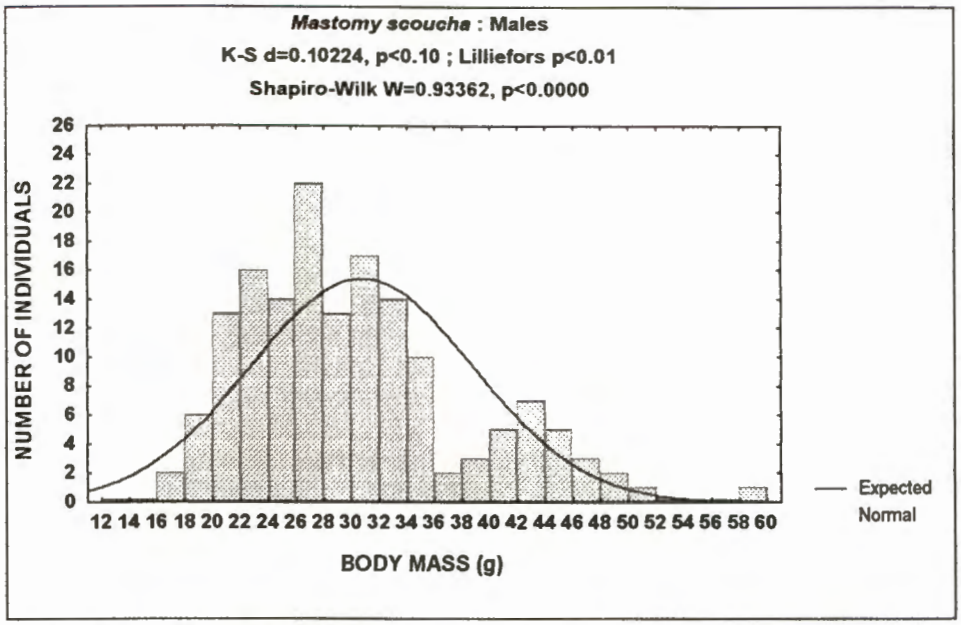


FIGURE 3.102: Mass distribution of male *M. coucha* individuals during all the survey periods on the ash dam and control grids.

The minimum mass of scrotal males was 28g (Figure 3.103), and only 9.6% of scrotal males could potentially be expected to weigh less than this ($Z = 1.30$; $p = 0.0968$). A mass boundary of 28g could thus be used to differentiate adult and immature males with at least 90% confidence.

Among the breeding males, no scrotal individuals weighing between 36 -38g were captured, thereby providing a convenient (though arbitrary) boundary for the recognition of two adult classes. Observed mass frequencies for non-scrotal males (Figure 3.104) deviated significantly from normality (Shapiro - Wilk $W = 0.921$; $p<0.001$), and there was clear evidence of bi-modality with a nadir at 23 -24g. A mass limit of 23g was thus used to distinguish between 2 subadult cohorts, namely subadult 1 (<23g) and subadult 2 (23 -28g).

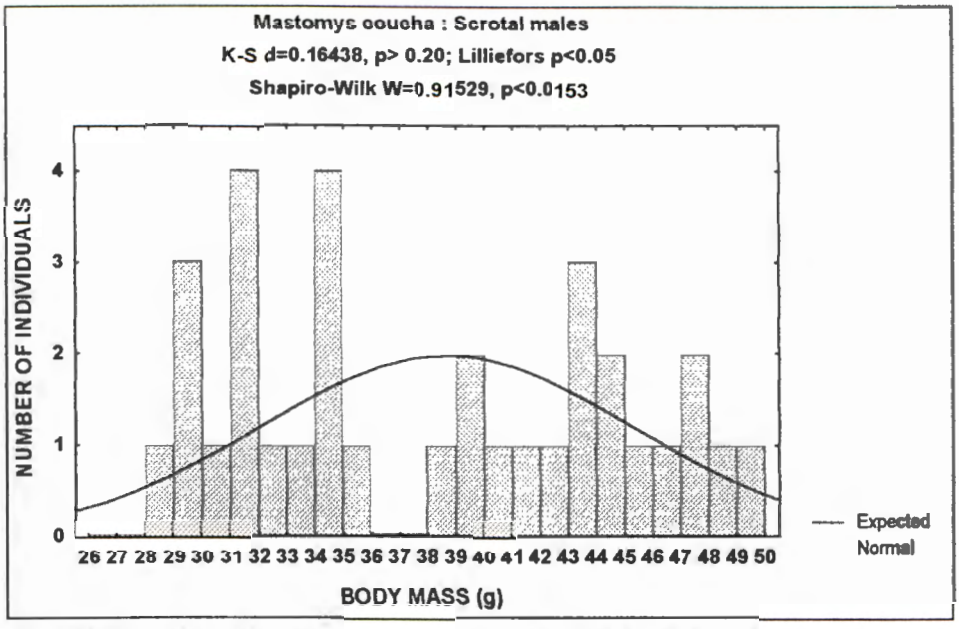


FIGURE 3.103: Mass distribution of scrotal male *M. coucha* individuals during the breeding season (September to December) on the ash dam and control grids.

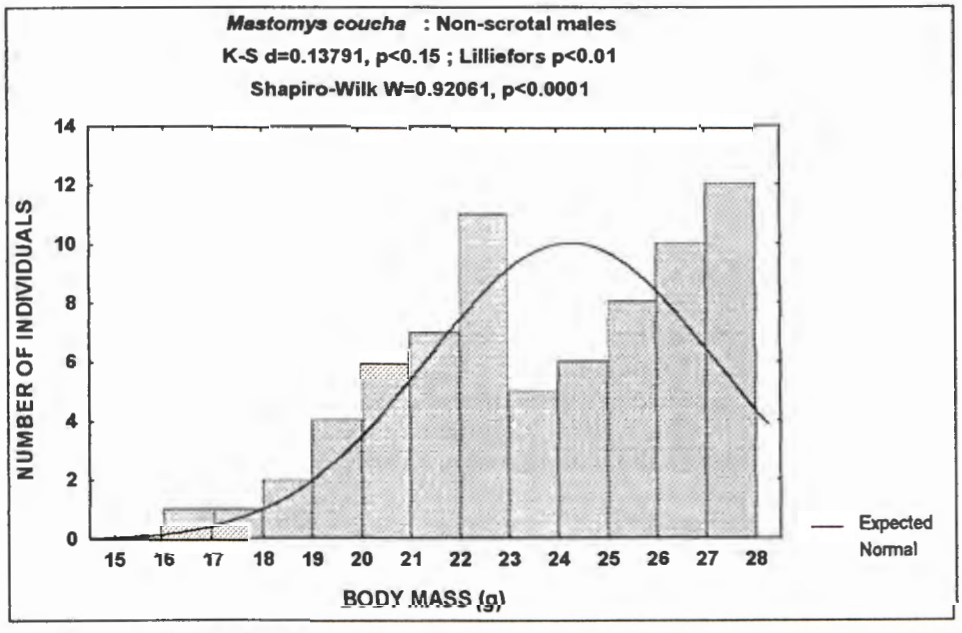


FIGURE 3.104: Mass distribution of non-scrotal male *M. coucha* individuals for all survey periods on the ash dam and control grids.

The *M. coucha* individuals captured during this study; weighed less than the *M. natalensis* individuals captured during a study in Natal, where 40g represented the adult-immature boundary (Bronner 1986). During the same study, non-breeding individuals were subdivided into two groups, namely juveniles (0 -25g) and subadults (25 -40g), while breeding individuals represented three groups, namely adult 1 (40 -50g), adult 2 (50 -70g) and adult 3 (>70g; Bronner 1986). The differences in weight between these two species can be attributed at least partly to differences in climate, whereas the winters in Kwazulu-Natal are relatively warm compared with that in Mpumalanga, and also to differences between these two closely related species.

Coetzee (1965; 1967), on the other hand, derived juvenile-subadult and subadult-adult boundaries of 15g and 25g respectively for *M. coucha* (see Bronner 1986) from the Transvaal highveld, using more accurate indicators of age (toothwear, histological examination of testis and ovaries). The subadult-adult mass limits determined during the present study therefore are in close agreement with those used by Coetzee (1965; 1967). The lower mass values for *M. coucha* evident during the present study may also be influenced by age-related difference in trapability (more young individuals were captured), as was evident during a study on *M. natalensis* by de Wit (1972).

Tatera brantsii

The observed mass distribution of female *T. brantsii* during this study (Figure 3.105), deviated significantly from normality (Shapiro-Wilk W= 0.955; $p<0.001$), with observed frequencies that were markedly lower than expected at 45 -50g and 100 -105g. The minimum recorded mass of breeding females was 50g (Figure 3.106), and based on the normal expected curve only 0.2% of breeding females could be expected to weigh less than this ($Z = 2.91$; $p= 0.0018$). An adult : immature mass boundary of 50g could thus be used with at least 99% confidence. The mass distribution of breeding females also showed a nadir at 100 -105g, thereby providing a convenient (but arbitrary) mass

boundary for distinguishing between two adult classes, namely adult class 1 (50 -100g) and adult class 2 (>100g).

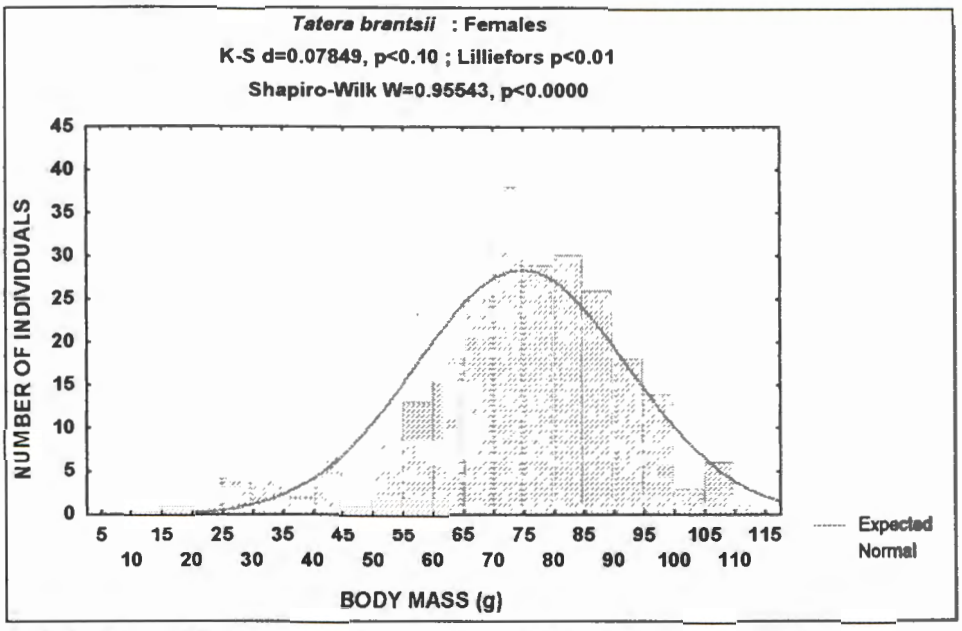


FIGURE 3.105: Mass distribution of female *T. brantsii* individuals during all the survey periods on the ash dam and control grids.

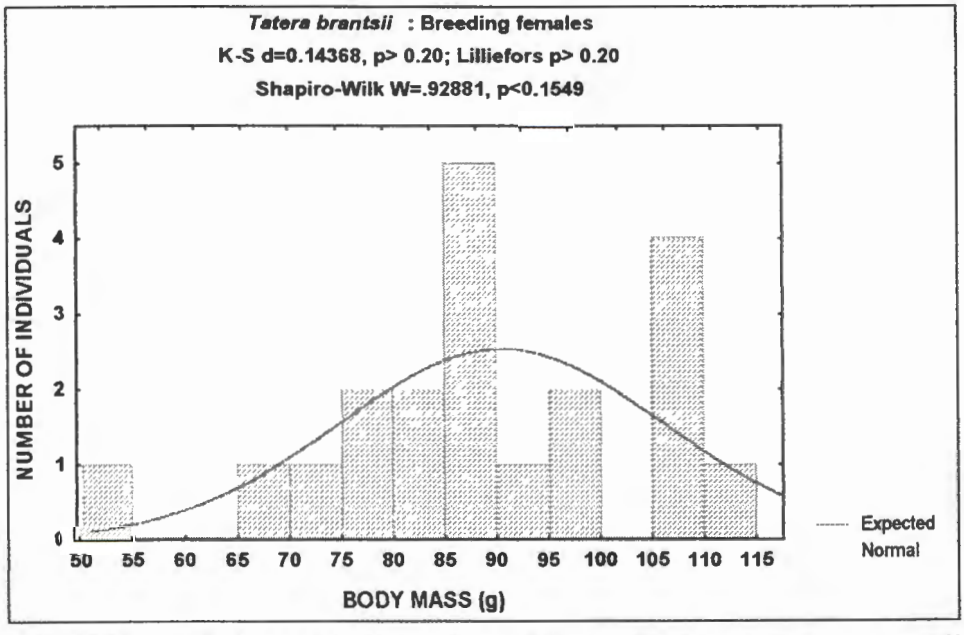


FIGURE 3.106: Mass distribution of breeding female *T. brantsii* individuals during the breeding season (December & January) on the ash dam and control grids.

Observed frequencies of non-breeding females conformed to normality, but sample sizes were small with the result that any potential bi-modality may have been obscured. No animals in the 36 -38g mass range were captured (Figure 3.107). A mass boundary of 36g was thus used to divide the immature population into two groups, namely subadult class 1 (<36g) and subadult class 2 (37 -50g). This latter mass boundary was wholly arbitrary, and lacks any statistical or clear-cut biological significance; it served only to delimit relative age classes for the examination of population age structure (Section 3.7.5).

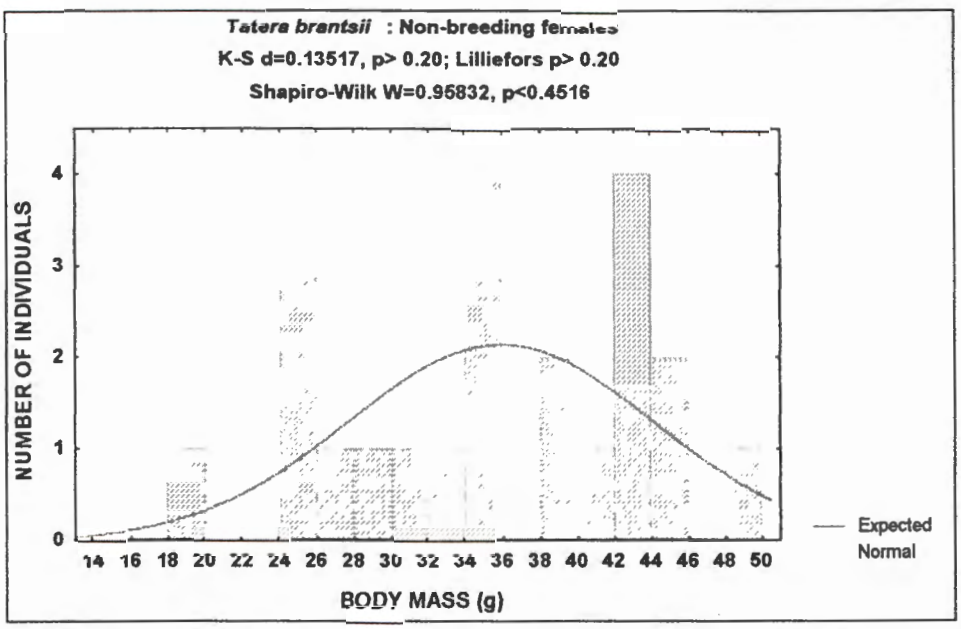


FIGURE 3.107: Mass distribution of non-breeding female *T. brantsii* individuals for all survey periods on the ash dam and control grids.

The mass distribution of male *T. brantsii* captured during this study deviated significantly from normality (Figure 3.108), and polymodality was suggested by nadirs at 50 -55g, 60 -65g and 100 -105g. The minimum recorded mass of a scrotal male was 55g (Figure 3.109), and based on the normal curve only 2% of breeding males could be expected to weigh less than this (Z = 2.07; p= 0.0192). An adult : immature mass boundary of 55g was thus assumed and would be used with 95% confidence. The observed frequency for the 100 -105g mass range were considerably lower than expected, thereby providing a

convenient, but arbitrary mass limit of 100g to distinguish between two adult classes.

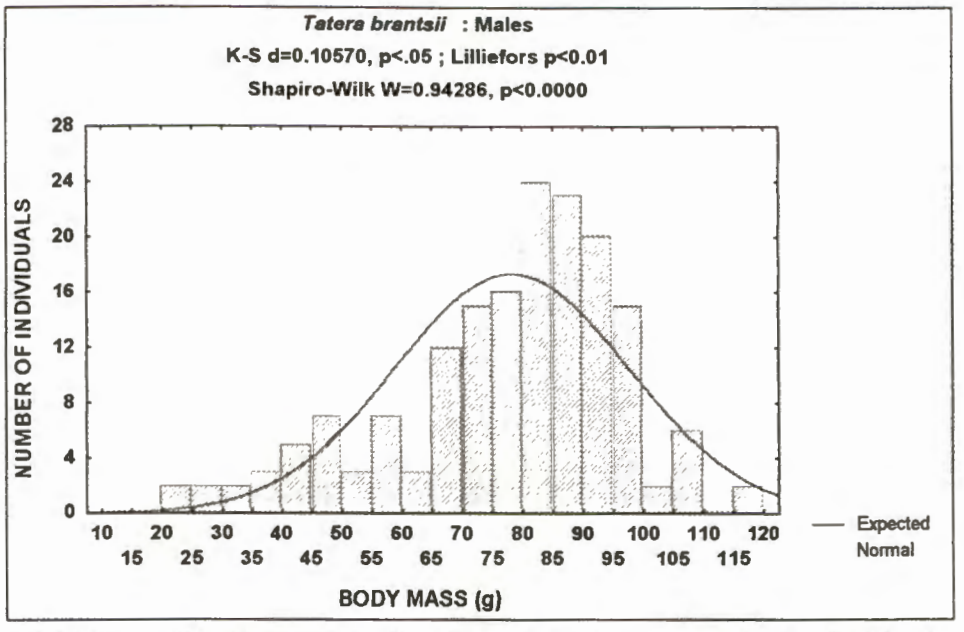


FIGURE 3.108: Mass distribution of male *T. brantsii* individuals during all the survey periods on the ash dam and control grids.

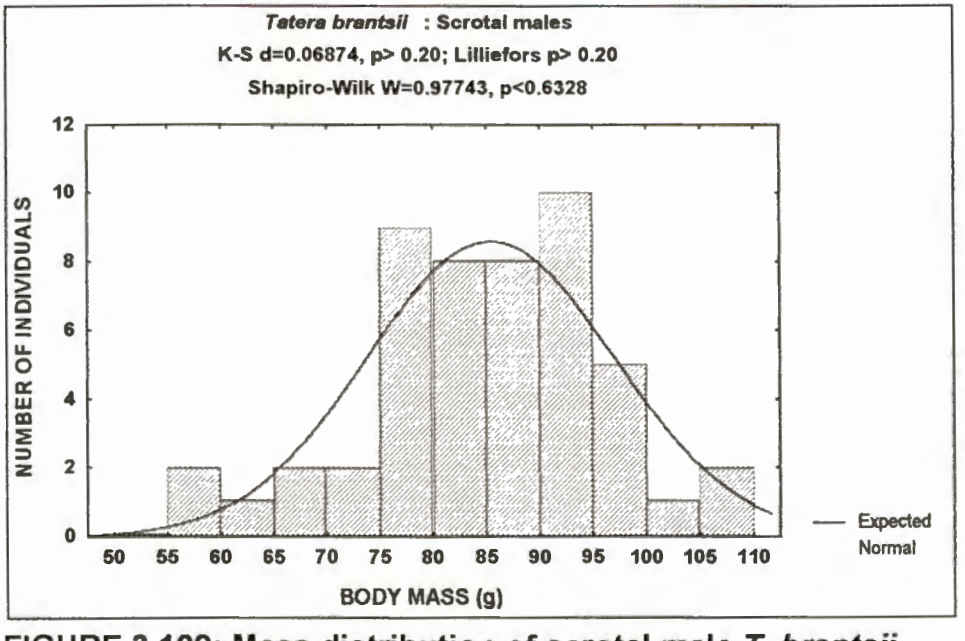


FIGURE 3.109: Mass distribution of scrotal male *T. brantsii* individuals during the breeding season (December & January) on the ash dam and control grids.

While the mass distribution of immature males conformed to normality, sample sizes were low and no clear-cut bi-modality was evident (Figure 3.110). Observed frequencies for the 30 -40g mass range were, however, lower than expected, and an arbitrary mass boundary of 35g was used to delimit two subadult age classes.

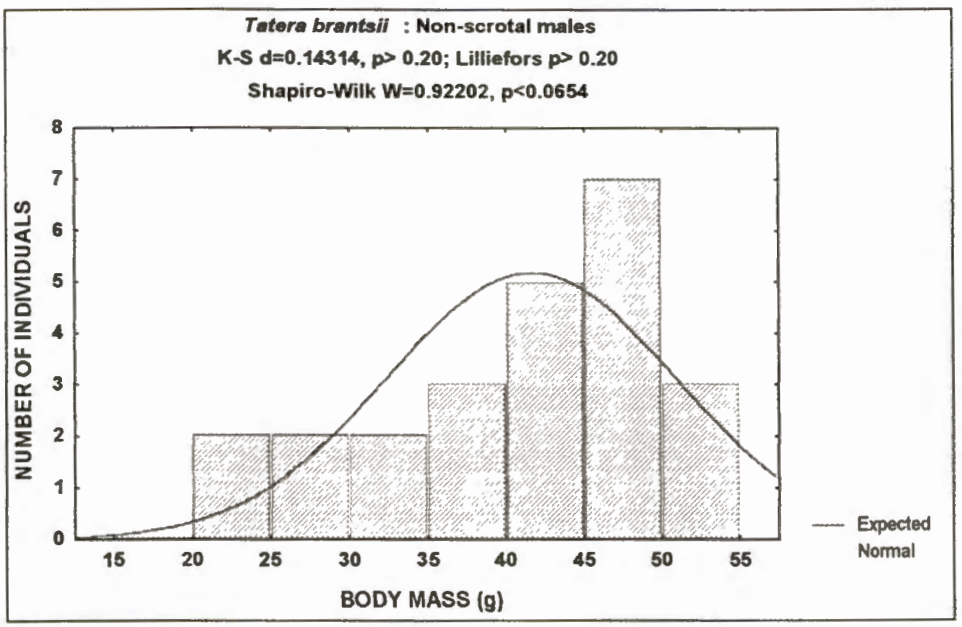


FIGURE 3.110: Mass distribution of non-scrotal male *T. brantsii* individuals of all survey periods on the ash dam and control grids.

Measroch (1954) found that the majority of immature female *T. brantsii* weigh less than 55g and that only two adult females weighing less than 50g were ever captured during her study. This compareswell with the adult : immature mass boundary of 50g of the present study. For males, Allanson (1958) determined that below 50g, all males were immature, while for the present study, 55g were used as an adult-immature mass boundary. Individuals captured on the ash dams, however, generally weighed less than the individuals captured by Davis (1953), who captured males and females weighing up to 112g and 102g, respectively. Body weight or the nature of a species growth is an intrinsic property of the species and varies slightly unless the environment is grossly deficient or abnormal De Moor (1969), as in the case of the ash dams.

3.7.4 Age & mass structure

Rhabdomys pumilio

The age = mass structure of the *R. pumilio* population varied markedly on a seasonal basis for female (Figure 3.111) as well as male individuals (Figure 3.112). These variations were in response to fluctuations in recruitment, mortality and maturation rates, which in turn resulted from changes in environmental conditions. The first young female (subadult class 1; <18g) of the year appeared in the traps during December and the last at the end of July, while subadult class 2 individuals (18 -27g) were trapped throughout the study period with peak appearances from May to September (Figure 3.111). Adult class 1 females (28 -35g) were also present throughout the study period, while adult class 2 females (>36g) were trapped in high numbers from spring (September) to autumn (May). However, the peak months were from September to January (Figure 3.111).

The first young male (subadult class 1; <16g) of the year appeared in the traps during January and the last at the end of May; while sudadult class 2 individuals (16 -27g) peaked in numbers from May to September (Figure 3.112). Adult class 1 males (28 -44g) on the other hand were present in higher numbers than the adult class 1 females throughout the study period and during every survey 60% or more of the male population were adult class 1 males (Figure 3.112). Adult class 2 males (>44g) were captured from September to May, with a peak during spring 1997 (Figure 3.112).

It is therefore clear that in the transition from winter to spring, older individuals became increasingly preponderant and this may be due to rapid maturation of immature individuals in response to the favourable environmental and climatic conditions which prevailed during spring. Breeding therefore, took place in the wet summer months of the year (September to April), which is in comparison with a study by Brooks (1974) in the Transvaal highveld for *R. pumilio*

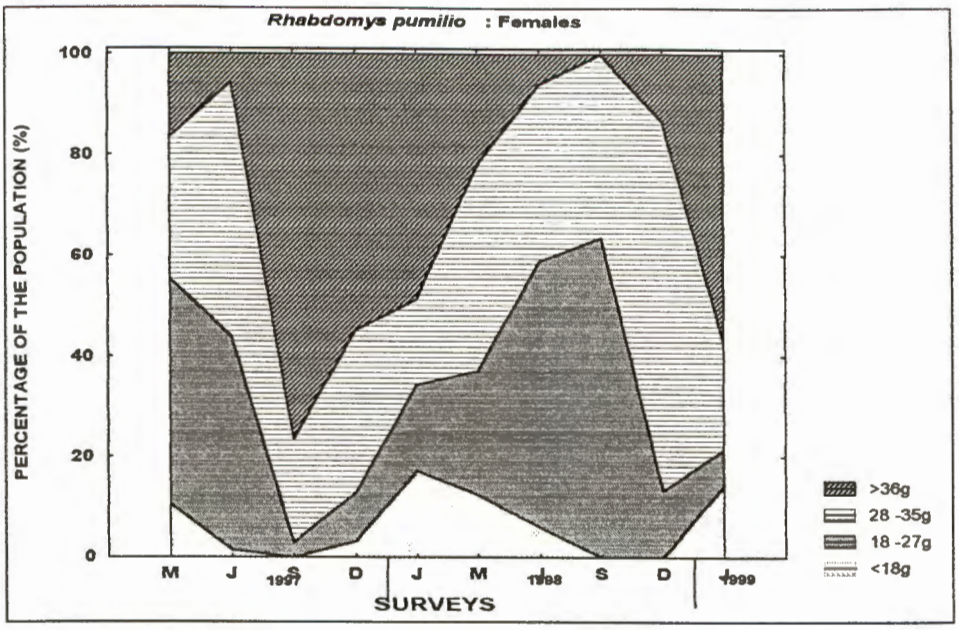


FIGURE 3.111: The age distribution of female *R. pumilio* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

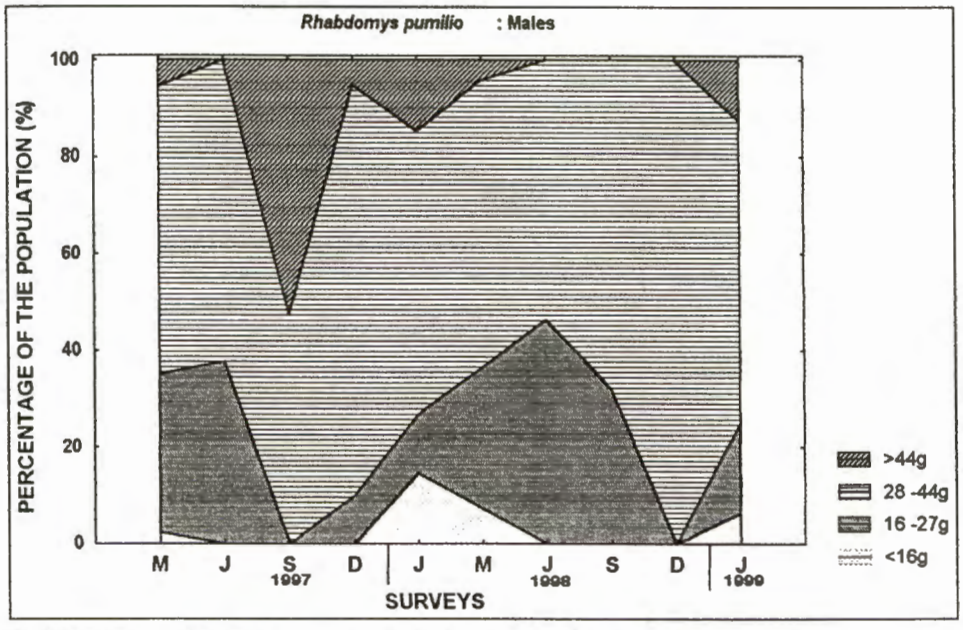


FIGURE 3.112: The age distribution of male *R. pumilio* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

Temporal variation in the age structure of the *R. pumilio* populations therefore reflected seasonal breeding with younger cohorts appearing in early summer following elevated levels of reproduction in spring, followed by rapid maturation through autumn when subadults became increasingly predominant. In winter these cohorts, now young adults, dominated the populations and older adults tended to disappear. The young adults which dominated in winter formed the breeding stock for renewed reproduction and a repetition of this temporal cycle the following wet season.

In the Cape Flats, with its Mediterranean-type climate, *R. pumilio* retained its summer breeding pattern in a winter rainfall region, presumably due to an increased summer food supply (David & Jarvis 1985). As might be expected from this breeding pattern, the proportion of immature individuals increased during the second half of the breeding season (late summer) and rose to a maximum during the winter (Figure 3.11 & 3.112). Younger (subadults 1 & subadults 2) individuals, thus, became dominant as a result of increased recruitment due to birth and probably as a result of immigration.

Mastomys coucha

The age-mass structure of both male and female *M. coucha* populations varied markedly on a seasonal basis (Figure 3.113 & 3.114). The first young females (subadult class 1; <18g) of the year were captured in May and the last during September, while the same pattern was evident for individuals in the subadult class 2 mass range (18 -23g; Figure 3.113). Female individuals in the mass range, 24 -35g (adult class 1) were captured throughout the year. Adult class 2 females (>35g), on the other hand, appeared in the traps from September (spring) to January (summer; Figure 3.113).

As with the young females, the first young males (subadult class 1; <23g) of the year were captured in May, and the last during September, while the subadult class 2 (23 -28g) individuals followed the same pattern (Figure 3.114). Individuals in the adult class 1 mass

range (28 -38g) were also present in the traps throughout the year, while older individuals (adult class 2; >38g) first appeared in the traps in September (spring) through to January (summer; Figure 3.114).

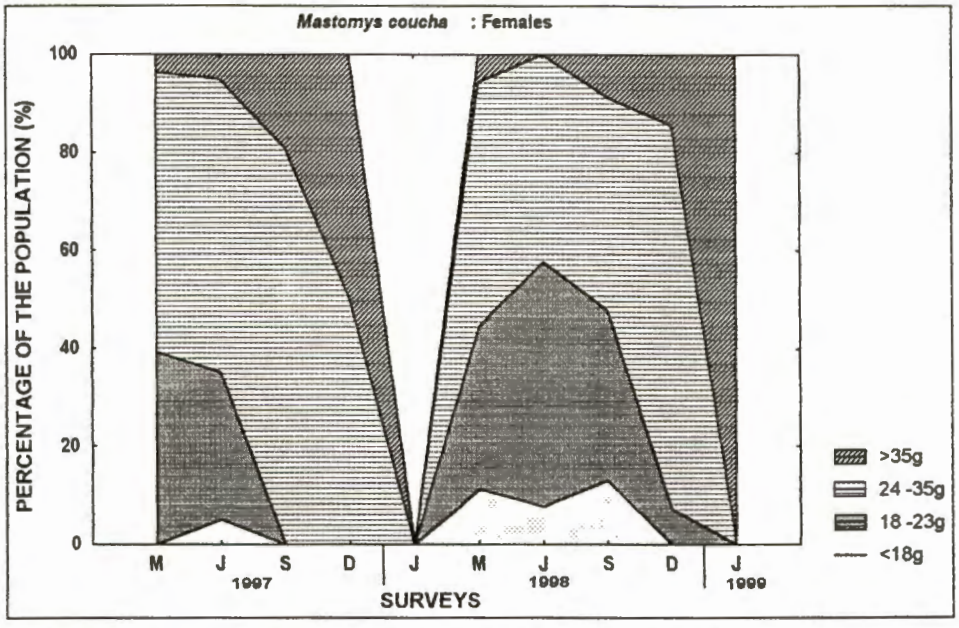


FIGURE 3.113: The age distribution of female *M. coucha* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

It is therefore clear that in the early autumn and throughout the following spring, the population comprised mainly younger animals (subadult class 1 & 2) for both males and females while with the transition from winter to spring, older individuals became preponderant, coincident with a decrease in population size (Section 3.6.1).

This can be due to the maturation of immature individuals, presumably in response to the favourable environmental conditions which prevailed during spring, or because of a reduction in breeding increments to the population following decreased reproduction by adults in the dry winter months (Section 3.7.2.1; Bronner 1986). Breeding therefore, occurred during the wet summer months, as was found by Coetzee (1967).

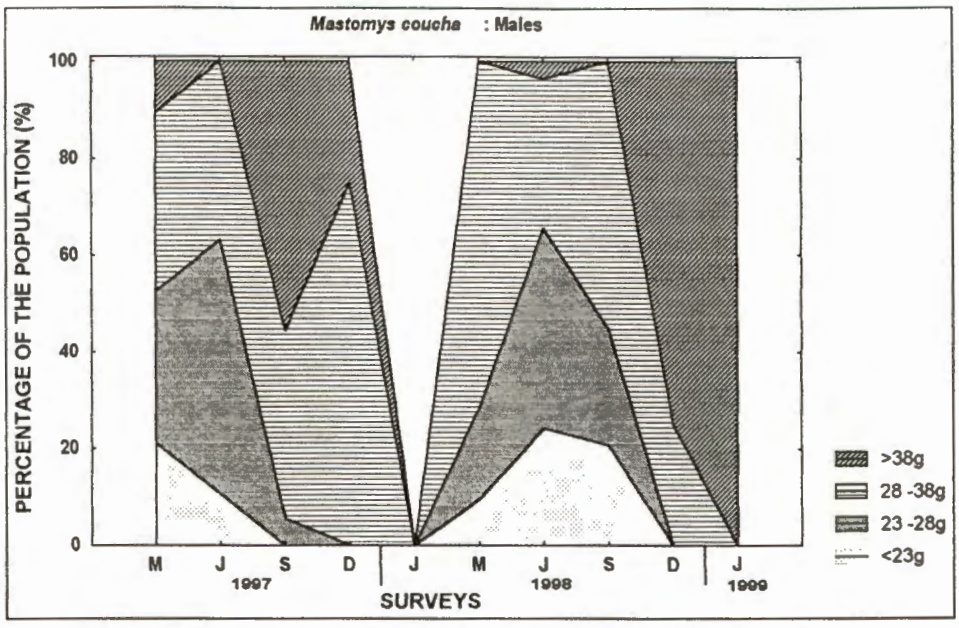


FIGURE 3.114: The age distribution of male *M. coucha* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

Tatera brantsii

For the *T. brantsii* population the age-mass structure also varied markedly on a seasonal basis for both female and male individuals (Figure 3.115 & 3.116). The first young females (subadult 1; <36g) of the year appeared in the traps during May until July, while females weighing 37 -50g (subadult class 2) were captured from autumn through to spring, and as late as summer (January 1999; Figure 3.115).

The female population consisted of mainly individuals in the adult class 1 mass range (50 -100g), which contributed more than 75% of the population during every survey period (Figure 3.115). The first older females weighing more than 100g (adult class 2) of the year appeared in the traps from September to July, with peaked appearances during January (Figure 3.115).

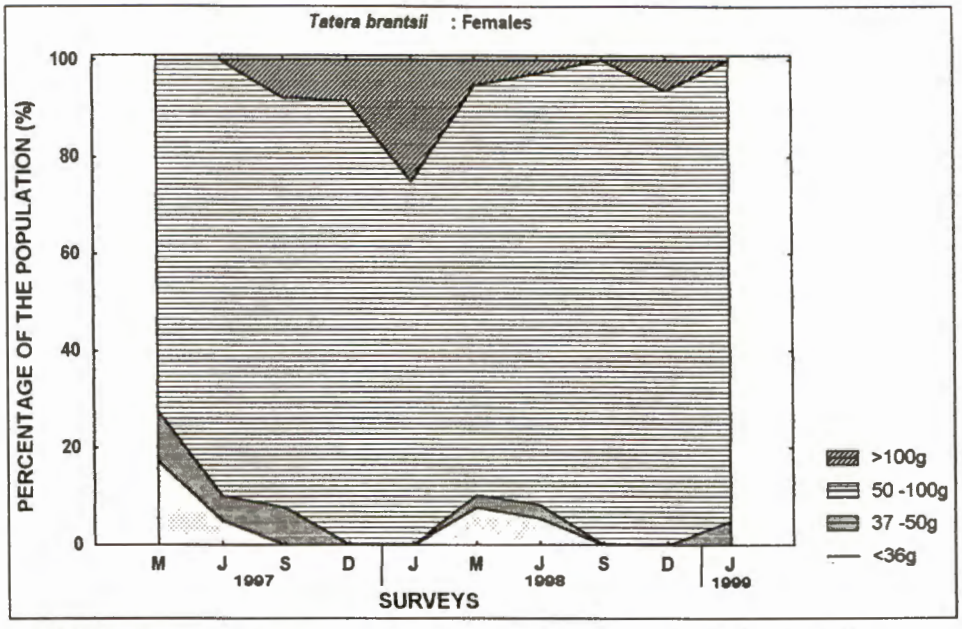


FIGURE 3.115: The age distribution of female *T. brantsii* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

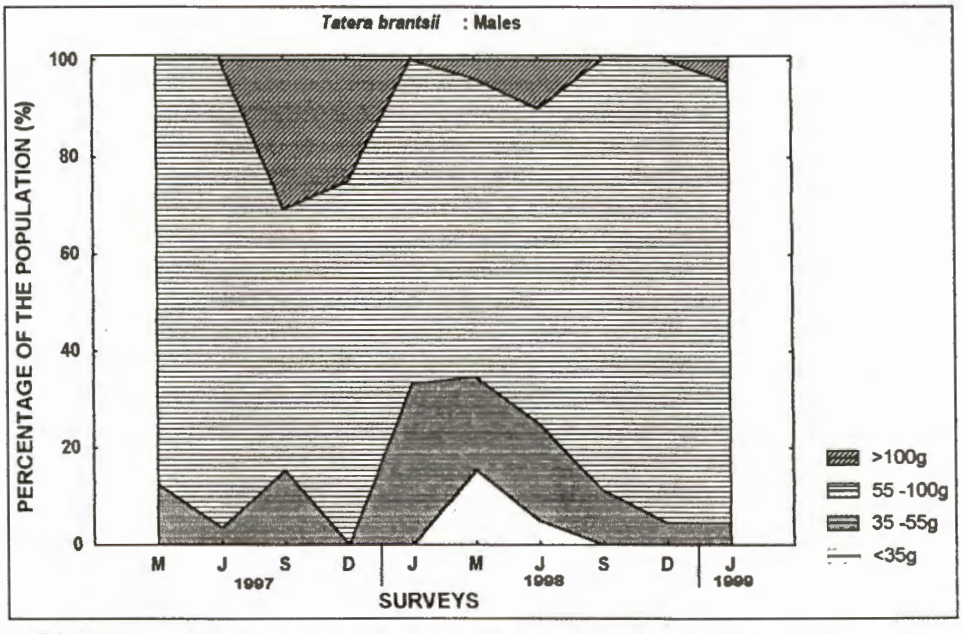


FIGURE 3.116: The age distribution of male *T. brantsii* individuals from Hendrina Power Station, based on reproductive condition and body mass (Data for all grids combined).

For males, young individuals (subadult class 1; <35g) were only captured during May and July of 1998, while individuals weighing 35 -55g (subadult class 2) appeared in the traps during every survey, except during the December 1997 survey, with peaked appearances in January 1998 (Figure 3.116). As with the female population, more than 50% of the population consisted of mainly older individuals weighing 55 -100g (adult class 1), while older males weighing more than 100g were trapped from September to July, with peaked appearances in September and December 1997 (Figure 3.116).

During autumn (May) and winter (July) the population of both males and females consisted of mainly younger animals (subadult class 1 & 2) and young adults (adult class 1). This can be due to an increase in the breeding increments to the population during autumn and winter (Section 3.7.2.1), or due to emigration by older individuals who extend their range in search of food (Section 3.7.2.2). Older adults (adult class 2), on the other hand became increasingly preponderant from winter / spring to summer. Measroch (1954) and Allanson (1958) found that *T. brantsii* individuals breed throughout the year but with periods of maximal and minimal reproductive activity. This was also evident during the present study, where young adults (adult class 1) were captured throughout the year, and older adults (adult class 2) appearing in the traps during the wet summer months.

The age and mass structure of the three dominant species varied on a seasonal basis in response to fluctuations in recruitment, mortality and maturation rates, which in turn were related to environmental changes. For both *R. pumilio* and *M. coucha* younger individuals were present in high numbers from early autumn to spring, with the main breeding period during the wet summer months, with older individuals becoming increasingly preponderant during this period. *T. brantsii* on the other hand showed smaller breeding increments throughout the study, with younger adults present all year round, due to the fact that this species' breeding period are not strictly seasonal, but occurring throughout the year with periods of maximal and minimal breeding activity.

CHAPTER 4

CONCLUSIONS

This study has demonstrated pronounced similarities in the composition of the small mammal faunas on the rehabilitated ash dams and the control (natural grasslands) grids at Hendrina Power Station, with both areas dominated by rodent species, such as *Rhabdomys pumilio*, *Mastomys coucha* and *Tatera brantsii*. The composition of the small mammal fauna at Hendrina Power Station compares well with other grassland areas on the highveld, suggesting that species diversity has not been severely impacted by local industrial activities.

In most small mammal communities from the summer rainfall zone of southern Africa, population sizes peak in the wet season, and decline during the autumn/winter (Perrin 1980; Willan 1992). Seasonal trends in numbers, which declined in the wet summer months during this study, were thus atypical. This cannot be attributed to rehabilitation factors since the same pattern was evident on both the control and ash dam grids. Instead, seasonal changes in trapability and use of the ash dams as refugia could explain these tendencies. Trapability of all species except *T. brantsii* was significantly higher in autumn and winter than in spring and summer, perhaps reflecting a tendency by animals to forage for longer periods, and over larger areas in response to limited food resources (Smith *et al.* 1975). Alternatively, the seasonal pattern may reflect immigration from surrounding areas (which are regularly burned) into the study area during winter, and subsequent dispersal during the wet season. *R. pumilio*, in particular is known to aggregate in mesic patches protected from fire during winter (Willan 1984).

The most important macro-environmental factors which appear to promote diversity on the ash dam grids were the ecological status of adjoining areas and topography. The nature of adjoining areas to a large extent determines recolonization rates, both for plants and small mammals (Ferreira & Van Aarde 1996; Olff & Ritchie 1998). The slopes of the ash dams were generally more heterogeneous in terms of substrate and plant characteristics (Morgental 1999), and habitat heterogeneity is thought to be a major factor affecting diversity (Kerley 1992). These conclusions are , however, equivocal since the layout of the study area prevented me from establishing sufficient grids to test all possible combinations of macro-environmental features.

Various grids of the ash dams show different patterns of small mammal species diversity, and could be divided into treatments according to the vegetation characteristics. Differences in the rehabilitation history of each grid were primarily responsible for the variation not only in plant species present and therefore food resources available to small mammals, but perhaps more crucially in different growth forms and thus the amount and degree of cover. This would affect not only the small mammal species able to survive in a given habitat, but also population sizes (Nel 1978). Increased vegetation cover, as was evident on grid 12, favoured species like *R. pumilio*, while *T. brantsii* preferred areas (Grids 10 & 11) with sufficiently patchy cover and a substrate amenable to digging. *M. coucha* occurred in higher numbers in areas recovering from some form of habitat destruction, like fire.

It is therefore clear that the presence or absence of a species in certain areas resulted from the degree of pre-adaptation of these species to prevailing conditions. Whether the differences between the grids of the ash dams-, and between the ash dams and the controls will prevail in the long-term as a result of different macro-environmental parameters, or vary to reflect differing successional patterns due to fire, with consequential effects on food and cover availability, is difficult to determine. Certainly the same species were not always dominant in the different areas. Therefore, certain areas seem more

favourable to some species than other areas. For the present study, the control and ash dam grids differed from each other in terms of vegetation and substrate composition. The control grids were characterized by high floristic diversity and crown cover and the soil was heavy and rocky, therefore more suitable for more specialized species such as *R. pumilio* and *Otomys irroratus*. The ash dam grids, however, were characterized by more open areas in the initial stages of plant succession with loose substrate more suitable for pioneer species such as *M. coucha* and *T. brantsii* and as succession proceeds on the ash dams, these species may be replaced within months by grassland specialists, such as *R. pumilio* and somewhat later by *Otomys* spp.

Small mammal populations fluctuate tremendously on a seasonal basis, particularly in temperate regions where annual primary productivity and breeding is concentrated in the warm/wet season. Certain species (such as *M. coucha*) also display cyclical changes in abundance over several years (Leirs 1994), and small mammal communities invariably show successional alterations in structure and composition that are related to climatic and vegetational factors (Smith *et al.* 1975). There are, therefore, no grounds to assume that the results of this study are definitive and more data, collected over several years, will be needed for this purpose.

Ecological succession on the ash dams was characterized mainly by a progressive decline in equitability, accompanied by a sustained increase in density, reflecting increasing domination of communities first by *T. brantsii*, and then by *R. pumilio*. Similar successional patterns occur in regenerating forests of the northern hemisphere (Parker 1989). These results support the finding that succession in unstable habitats is driven by variations in equitability (Tramer 1969). However, changes in species richness, and local extinctions of the less common small mammal species were also apparent. This could be due to competition, as recorded in rehabilitated coastal forests of South Africa (Ferreira & Van Aarde 1996). But, a more likely alternative is that the abundant dominant rodent species modified existing habitats to such an extent that other more specialized species were

excluded. Both *M. coucha* and *T. brantsii* are pioneer species, which thrive in disturbed areas with little cover (Willan 1984), and have a dramatic influence on both natural fauna and floral communities (Korn & Korn 1989) and ash dam grids (Bronner *et al.* 1999).

For the rehabilitation process in an area to be successful, the resulting ecosystem must strongly resemble the structure and composition of the so-called natural ecosystem, and must be sustainable and resilient enough to survive short-term unfavourable environmental conditions, such as droughts and fires (Higgs 1997). The rehabilitation process of the present study has been very successful in restoring small mammal populations, diversity and community structure to natural (control) levels within four to seven years after rehabilitation, whereafter total diversity declined, which suggests that rehabilitation strategies do not restore communities that are sustainable in the medium-long term.

Older rehabilitated areas were dominated by the three pioneer species which have a wide habitat tolerance, high reproductive potential and fast population turnover rates. Two of these species, *R. pumilio* and *M. coucha*, occurred in considerable numbers on the controls so their abundance on the ash dams can be assumed natural. *T. brantsii*, however, was restricted to the ash dams, and dominated the biomass of older rehabilitated areas with lower small mammal diversity. It can thus be regarded as an indicator of ecological retrogression for rehabilitation purposes. Since it thrives in open habitats, high densities of this species may signal the need for active management measures. *T. brantsii* is of management interest not simply because it may be a useful indicator of ecological retrogression to earlier successional stages with lower diversity, but indeed because this species contribute directly to habitat degradation in older rehabilitated areas. On the slopes of the ash dams, its burrow systems are often associated with erosion gulleys that have corroded right through the topsoil layer and several centimeters into the underlying ash. On the plateaux grids of the ash dams, *T. brantsii* carries large quantities of ash to the surface during its nocturnal excavations, which is worrisome particularly from a health perspective, since one of the prime aims of current rehabilitation strategies is to reduce

windborne air pollution. Furthermore, there are asbestos dumps on the ash dams, and burrowing by this species could potentially result in the airborne dispersal of asbestos fibers. The burrowing activities and trophic impacts of this species may also be considerable and impact negatively on vegetation succession after rehabilitation (Bronner *et al.* 1999).

Trap-revealed sex ratios for *R. pumilio* were similar in favouring males during all seasons on both the control and ash dam grids, mainly due to the greater distances moved by males in both areas. For *M. coucha*, however, the control and ash dam grids showed opposite trends in sex ratios on a seasonal basis which may indicate demographic differences related to rehabilitation. The differences in sex ratios between the ash dam and the control grids for *T. brantsii* might have been due to the fact that males moved over greater distances in search for food and, therefore, were the first individuals to exploit the controls after the fire in 1998. On the ash dams, however, more female individuals were present, which might have been adaptive in that this would allow the resident populations to expand rapidly to take advantage of the abundant resources and suitable habitat of the ash dams.

On both the ash dam and control grids population losses exceeded recruitment rates of *R. pumilio* throughout the study, except after the fire in 1998, recruitment rates on the controls increased mainly due to immigration into this area. For *M. coucha* recruitment rates on both the ash dams and the controls were related to female breeding activity, while the population losses on the controls were markedly higher than on the ash dams, mainly due to emigrations. Population losses for *T. brantsii* were higher overall than the recruitment rates, which shows that either the populations were not in an increase phase (perhaps due to high predation), or that substantive density-dependent emigration was taking place. The overall pattern which emerges from the mass-age structure of the dominant small mammal species was that *R. pumilio* and *M. coucha* breed during the wet summer months when food resources are readily available, while *T. brantsii* breeds

throughout the year with periods of minimal and maximal reproductive activity.

Given the lack of information on impacts of small mammals in the grasslands of South Africa, and the obvious need for management strategies to be holistic, it is impossible to make any concrete, short-term management recommendations. The use of fire in restoring community structures of older rehabilitated areas deserves special attention, since it has been shown to stimulate vertebrate diversity of Drakensberg grasslands (Rowe-Rowe 1995). However, annual burning tends to favour dominance by opportunistic species like *T. brantsii* and *M. coucha* (Kern 1981), so the fire regime used should be carefully planned and executed, and the rehabilitated areas should be protected from accidental burning during the common veld fires which occur in the area during winter. There is thus a clear need for further research on rehabilitation ecodynamics of temperate grasslands, particularly on the highveld which has been subjected to severe habitat degradation. Such research will not only further current scientific knowledge, but also facilitate the formulation of more effective environmental rehabilitation strategies.

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APPENDIX 3.1

CHECKLIST OF THE SMALL MAMMAL FAUNA AT HENDRINA POWER STATION

The list below includes 27 species and was compiled during small mammal surveys on the ash dam and control grids at Hendrina Power Station, from May 1997 - January 1999.

Species records were obtained from three sources:

- trapping data or sight records from the survey, denoted below by (+)
- potential species: which have been recorded in the same quarter degree square as Hendrina Power Station are denoted by (*), and can confidently be expected to occur on the reserve; whereas species recorded from the degree square are denoted by (?), and are possibly also resident there.

Order: Insectivora

Crocidura mariquensis (+)	Swamp musk shrew
Myosorex varius (+)	Forest shrew
Atelerix frontalis (?)	Hedgehog

Order: Chiroptera

Suborder: Microchiroptera

Eptesicus capensis (?)	Cape serotine bat
Rhinolophus clivosus (?)	Geoffroy's horseshoe bat

Order: Rodentia

Tatera brantsii (+)	Highveld gerbil
Mastomys coucha (+)	Multimammate mouse
Mus minutoides (+)	Pygmy mouse
Rhabdomys pumilio (+)	Striped mouse
Otomys irroratus (+)	Vlei rat
Cryptomys hottentotus (+)	Common molerat
Hystrix africaeaustralis (+)	Porcupine
Aethomys chrysophilus (?)	Red rock rat
Dendromys mystacalis (+)	Grey climbing mouse
Thryonomys swinderianus (?)	Greater cane-rat

Order: Carnivora

Canis mesomelas mesomelas (+)	Black-backed jackal
Galerella sanguinea (+)	Slender mongoose
Cynictis penicillata (+)	Yellow mongoose
Felis caracal (+)	Caracal
Ictonyx striatus (*)	Striped polecat
Felis nigripes (*)	Black-footed cat
Genetta tigrina (+)	Large-spotted genet
Vulpes chama (?)	Cape fox
Poecilogale albinucha (?)	Striped weasel

Order: Lagomorpha

Lepus capensis (+)	Cape hare

Order: Artiodactyla

Sylvicapra grimmia (+)	Grey duiker
Raphicerus campestris (*)	Steenbok

APPENDIX 3.2

The list below includes the abbreviations used for the small mammal species and plant species used in Section 3.6.5: Ecological correlates of small mammal community structure.

Small mammal species

Abbreviation	Species name
Dend mys	*Dendromys mystacalis*
Mast cou	*Mastomys coucha*
Mus min	*Mus minutoides*
Mus mus	*Mus musculus*
Myos var	*Myosorex varius*
Otom irr	*Otomys irroratus*
Ratt rat	*Rattus rattus*
Rhab pum	*Rhabdomys pumilio*
Tate bra	*Tatera brantsii*

Plant species

Abbreviation	Species name
Aris con	*Aristida congesta*
Bare grd	Bare ground
Bide for	*Bidens formosa*
Brac ser	*Brachiaria serrata*
Cham bie	*Chamaecrista biensis*
Chlo gay	*Chloris gayana*
Cirs vul	*Cirsium vulgare*

Cony bon	*Conyza bonariensis*
Cyno dac	*Cynodon dactylon*
Cype esc	*Cyperus esculentus*
Cype usi	*Cyperus usitatus*
Digi eri	*Digitaria eriantha*
Elio mut	*Elionurus muticus*
Erag chl	*Eragrostis chloromelas*
Erag cur	*Eragrostis curvula*
Erag nat	*Eragrostis* (natural grassland)
Erag pla	*Eragrostis plana*
Erag tri	*Eragrostis trichophora*
Hete con	*Heteropogon contortus*
Hypa hir	*Hyparrhenia hirta*
Lesp cun	*Lespedeza cuneata*
Oxall spp.	*Oxallis* species
Penn cla	*Pennisetum clandestinum*
Schk pin	*Schkuhria pinnata*
Seta sph	*Setaria sphacelata*
Sonc ole	*Sonchus oleraceus*
Sper med	*Spergularia media*
Tage min	*Tagetes minuta*