

**THE INFLUENCE OF SUPPLEMENTARY FOOD ON THE RODENT
COMMUNITIES OF COASTAL SAND DUNES**

by

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The influence of supplementary food on the rodent communities of coastal sand dunes

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ABSTRACT

Earlier studies on the rodent community of a regenerating coastal dune forest north of Richards Bay, South Africa, indicate that unstable environmental conditions, rather than competitive interactions, are the major determinants of rodent community development. Therefore the present study investigates the effects of supplementary food provided to stabilise resource availability on rodent assemblages of a regenerating coastal dune forest. By increasing a portion of the resource spectrum, species diversity was reduced by increasing the abundance of *Mastomys natalensis*. As a competitively superior exploiter of the augmented resource, changes in its abundance rather than changes in the number of species or the abundance of other species, gave rise to changes in community characteristics.

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CHAPTER 1

INTRODUCTION

LITERATURE REVIEW

Review on community structure and interspecific competition

A community is considered to have structure or to be patterned if the species it contains are a nonrandom subset of those that could occur in it. Furthermore, if the community is patterned, species may be actively excluded because the community is not allowing other species to colonize (Pimm, 1991). By trying to explain either coexistence or the absence of species within a particular area, an indirect approach of looking for patterns attempts to infer processes from patterns. This approach, however, has always been highly controversial (Lewin, 1983a; 1983b).

The controversy stems from the difficulty in predicting the “ghosts”- the species that tried to invade a community, that failed (Pimm, 1991), and the effects that past competition has on present communities, known as “the Ghost of Competition Past” (Connell, 1980). Connell (1980) stated that competing species, which are not dependent on each other need not consistently co-occur or thus co-evolve. However, Colwell and Winkler (1984) noticed that community patterns from which we must draw inference about competition may already reflect the influence of competition. Species may not be competing at a particular time because selection in the past favoured an avoidance of competition and thus a differentiation of niches. Connell (1980) gave two general explanations as to why possibly competing species still co-exist. First, the species may have evolved separately and become adapted to different sets of environmental conditions. Each species would become established in a part of an area in which it is pre-adapted to do the best should they come together and have to co-occur for some reason. Second, competing species may have co-evolved under the pressure of competition. They would diverge from each other and

occupy different parts of an area. This is also known as “habitat shift”. For example, selective habitat selection is one of the principal therefore permitting species to coexist (Melton, 1987).

Rosenzweig (1981) provided a model on habitat selection as a method through which species avoid competition and coexist within the same community. Differential habitat selection is one of the principal ways in which species can coexist. However, theoreticians usually study it in a vacuum of one sort or another (Rosenzweig, 1981). Most have considered only the optimal choice which should be made by an individual (*e.g.* MacArthur & Pianka, 1966; Rosenzweig, 1974; Charnov, 1976), or allowed that choice to be influenced only by intraspecific competition (Fretwell & Lucas, 1970). In a major advance, Lawlor and Maynard Smith (1976) considered optimal habitat selection as a function of densities. Their model, however, assumes that habitat selection is free of costs (*i.e.*, the time and energy required to search for preferred habitats). Also their model affords a view of a system which is at or near equilibrium, making it difficult to predict the effects of perturbations (Rosenzweig, 1981). Rosenzweig’s own model, however, produces a conventional conclusion that habitat selection is indeed a way to achieve coexistence. Selective habitat selection therefore is a principal factor permitting species to coexist (Melton, 1987). Schoener (1974) suggested that it is likely that interspecific competition could result in species using resources differentially and consequently selecting habitats differentially.

Manipulation experiments have been used to test for the existence of competition between species. This includes both interference and exploitive competition. Interference or contest competition occurs when the organisms seeking a resource harm one another in the process, even if the resource is not short in supply. Exploitive competition is also known as resource or scramble competition and occurs when a number of organisms (of the same or different species) utilize common resources that are not short in supply (Krebs, 1994). Schoener (1983) considered an interspecific competition experiment to be a manipulation of the abundance of one or more

hypothetically competing species. Such manipulations may include removals, introductions, or both. Connell (1983) and Schoener (1983) independently published two reviews of competitor-removal experiments. Some of their conclusions are similar, but they disagree on a number of important issues. Schoener (1983) found that the great majority of competitor removals affected a change in the species for which population densities were measured. Connell (1983) had an alternative and quantitative approach in estimating how widespread competition might be. He counted the number of studies in which competitive effects had been found and related these to the number of pairs of species interactions studied. In studies where one experiment was done on only one species at one time and at one place, 14 (93%) recorded competition (see Connell, 1983). However, when more studies were reported by the experimenters, the percentage dropped. When there was more than one species studied by a given experimenter, only 48% of the studies found evidence of competition. When there were four or more experiments reported by each experimenter, only 22% of the studies found evidence for competition (Connell, 1983). This suggests that competition may not occur that often.

Disturbance and inconstancy in conditions

In the 1970's, the prevalent view among ecologists was that competition was of great importance in community development (MacArthur, 1972; Cody, 1975). The view that interspecific competition plays a central and powerful role in the shaping of communities was first fostered by the competitive exclusion principle which states that if two or more species compete for the same limiting resources, then all but one of the species will be driven to extinction. The same view has been underpinned by more sophisticated variants of the principle, namely the concepts of limiting similarity, optimum similarity and niche packing (Begon, Harper & Townsend, 1990).

More recently, the conventional wisdom in ecology has moved away from the monolithic

view to one giving more prominence to non-equilibrium and stochastic factors, such as physical disturbance and inconstancy in conditions (Diamond & Case, 1986; Gee & Giller, 1987). Bender, Case & Gilpin (1984) compared a community to a black box in the sense that the individual species grow and interact in complicated ways that are difficult to discern. Yet, by observing the response (output) of the system to natural or human-induced disturbances (input), information can be gained regarding the character and strength of species interactions. By definition, a perturbation is a selective alteration of the density of one or more members of the community. Two distinctly different kinds of perturbations are recognized, a pulse and a press perturbation (Bender *et al.*, 1984). The press perturbation which is a sustained alteration of species densities (often complete elimination of species) is important to the present study.

Studies on the effect of habitat disturbance on rodent populations have focussed on clearcutting (*e.g.* Kirkland, 1990) and fire (*e.g.* Swanepoel, 1981; Rowe-Rowe & Lowry, 1982; Fox, Quinn & Breytenbach, 1983; Clark & Kaufman, 1990) that result in “pulse” perturbations. These studies concentrated on survival during the disturbance period as well as the recovering and recolonisation of altered habitats.

Fire plays an important role in the development of forest ecosystems in Australia (Mount, 1964). Plant species seems to be adapted to a fire regimes rather than the occurrence of fire itself (Gill, 1975). Small mammal habitat selection relates to both structural and floristic components of the vegetation (Cheal, 1979; Fox & Fox, 1981). Small mammal abundance should then be thought of as a response to vegetational changes, rather than a response to a phenomenon like fire or habitat destruction that imply regeneration of vegetation and therefore succession (Fox & McKay, 1981). Successional changes within a rodent community can also be related to regeneration age (Fox & McKay, 1981; Van Aarde, Ferreira & Kritzing, 1996a; Van Aarde, Ferreira, Kritzing, Van Dyk, Vogt & Wassenaar, 1996b; Ferreira & Van Aarde, 1997).

Reports on recolonisation by small mammals of areas recovering from total habitat deconstruction are limited to volcanic eruptions (*e.g.* Anderson & MacMahon, 1985) and sand mining (*e.g.* Fox & Fox, 1978; Fox & Fox, 1984; Fox, 1990; Ferreira & Van Aarde, 1996; Ferreira & Van Aarde, 1997). Small mammal community recovery from habitat destruction after sand mining are described by Fox & Fox (1978), Fox & Fox (1984) and Fox (1990) of mined dunes in Australia, and Ferreira (1993); Ferreira & Van Aarde (1996) and Ferreira & Van Aarde (1997) of mined sand dunes in South Africa. The total destruction of these areas can be considered press perturbations. Recovery of these communities therefore depends on colonization through dispersal from adjacent areas, either by individuals that emigrated there as a result of the disturbance, or by individuals that were residents in adjacent areas (Ferreira & Van Aarde, 1996).

Supplementary feeding

Given the shortcomings of a passive, observational approach to the study of interspecific competition, ecologists have been turning to experimental approaches as a possible alternative to study community dynamics. In an attempt to study possible competitive effects, the density of one or more species was altered through the partial or total removal, or addition, of one or more species. It was hoped that the resulting community dynamics would produce conclusive proof regarding the presence or absence and strength of present-day biotic interactions, such as competition between species pairs.

MacArthur (1972) on the other hand, suggested a method of analysing resource utilization, competition and coexistence of species that exploit similar resources. According to his approach, species diversity can be increased by a decrease in average width of the species specific utilization curves, by an increase in average overlap of resource use between species, or by an increase in the resource spectrum.

In small mammal communities species diversity often is positively correlated with the breadth of the resource spectrum (usually expressed as foliage height diversity or horizontal patchiness) (*e.g.* Rosenzweig *et al.*, 1974). High production of an area, on the other hand, is associated with high or low species numbers and diversity. For instance, in southwestern North America the species diversity of seed-eating rodents increases with rainfall, since the increased rainfall result in increased production of seeds (Brown & Davidson, 1977). An opposite relationship has been found in studies on other taxa. For example, species diversity of diatoms decreases as production increases (Patrick, Hohn & Wallace, 1954). The differences in response to increased production was suggested to be dependent on the pattern of increase in production (MacArthur, 1972). An increase in the total resource spectrum would result in increased diversity because resources that were formerly too scarce to form an adequate diet, and therefore not counted as part of the resource spectrum, are now sufficient to support species survival (MacArthur, 1972). However, diversity may also be decreased through dominance by those species that are competitively superior in exploiting an augmented resource when only a small part of the total resource spectrum is increased. This implies that species in the community will only coexist if the overlap of resource use between these species is relatively small (MacArthur, 1972). Different responses to increased production of resources are therefore dependent on the pattern of the increase in production and can shed light on mechanisms responsible for community structure, such as competitive interactions.

Most food addition studies thus far have addressed questions of population regulation and limitation (see Boutin, 1990 and references therein). Only a few experiments have dealt with effects of food supplementation at the community level for rodents (Abramsky, 1978; Brown & Munger, 1985; Bowers, Thompson & Brown, 1987; Dickman, 1988; Monadjem & Perrin, 1996; 1998). No one would question that individuals and populations are ultimately limited by food

supply (e.g. White, 1978; Ford & Pitelka, 1984; Brown & Munger, 1985). However, many ecological factors can act to reduce the proximate importance of food supply, and controversy continues to exist as to the role that food availability plays in shaping the patterns of life history, population dynamics, and community structure (see Boutin, 1990).

Abramsky (1978) studied the response of small mammal species, inhabiting natural short grass prairie, to experimental perturbations. In one perturbation primary production was increased, which changed the nature of the habitat. In the other, the availability of one type of food source (a scarce resource) was increased without modifying habitat characteristics. Abramsky (1978) showed that as a result of the habitat manipulations, different small mammal communities were formed on the different treatment areas. The small mammal species naturally inhabiting the manipulated food plot did not respond in either their density or weight to the supplemented food. However, a new specialized seed-eating species invaded the food plot and persisted in relatively higher densities. As a result of the colonization, species diversity was significantly higher on the food plot relative to the unmanipulated control plot. Therefore an increase in a scarce or new resource that increases the resource spectrum on experimental plots results in an increase in diversity, supporting MacArthur's (1972) theory.

Brown and co-workers (Brown & Munger, 1985; Bowers *et al.*, 1987) added seeds of varying size to a desert rodent community. Millet seeds (*Panicum miliaceum* L.) were provided as whole seeds that represent the large seeds, cracked seeds representing small seeds and a combination as mixed sizes. The result was an increase in density of the largest seed eater (*Dipodomys spectabilis*) and a subsequent reduction in the second largest species (*D. merriami*, *D. ordii*), independent of size of seed added (small, large, mixed) or the method of administration (constant or pulsed). The addition of seed also had no effect on the spatial use of microhabitats by seed-eating rodents in the community (Bowers *et al.*, 1987). These results support the

argument that the desert rodent community is organized largely by competition, with the density of smaller granivorous rodents being inversely related to the density of the largest granivore.

Dickman (1988) examined the effects of a major competitor, *Antechinus swainsonii*, on the sex ratio of *Antechinus stuartii*, an inferior competitor; both small dasyurid marsupials, in Canberra, Australia. Higher densities of *A. swainsonii* lead to more female-biased sex ratios in *A. stuartii*, and the removal of *A. swainsonii* individuals or food addition reversed this pattern. Sons of mothers that received additional food were heavier and had higher survival rates than those from the control females. Dickman (1988) argued that the addition of food allowed females to increase the amount of parental investment and thus produce more costly males (see Maynard Smith, 1980).

Monadjem and Perrin (1996) investigated the effects of additional food (rolled oats and rabbit pellets) on the demography of three rodent species in a tropical grassland in Swaziland, southern Africa. Here only the multimammate mouse, *Mastomys natalensis*, responded to the supplementary food provided while the other two species present, *Mus minutoides* and *Lemniscomys rosalia* did not respond to the supplementary food. In another paper Monadjem and Perrin (1998) noted that an increased food supply resulted in an increase in small mammal biomass on the experimental plots. They concluded that food is clearly a limiting factor in this animal community. Although *M. natalensis* increased in density in response to the supplementary food, once again none of the seven other species increased significantly in density. As a result of the increase in *M. natalensis* densities, a decline in diversity was recorded. Species richness did not change and by raising the proportional representation of one species (*M. natalensis*) the diversity decreased on the experimental plots (Monadjem and Perrin, 1998).

With most of the food addition studies that have addressed questions of population regulation and limitation some general conclusions can be drawn. There are two constant

outcomes. The first is that in temperate environments at least, terrestrial vertebrate populations are frequently altered by food supply. The second consistent outcome of food supplementation experiments is that even though birth rate, immigration and survival are frequently altered by food supplementation, populations do not continue to increase in the presence of presumably unlimited food (see Boutin, 1990).

RATIONALE FOR THE PRESENT STUDY

Ferreira (1997) investigated the role of competition and habitat structure on the structure of rodent communities in rehabilitating coastal dune forests. He suggested that interspecific competition shape rodent communities during early stages of succession, while habitat changes shape communities during later stages of succession. The patterns of early colonization suggest that competitive interactions are not important within the first ten weeks of habitat rehabilitation. High variation of equitability on younger rehabilitating areas older than ten weeks, together with the stronger contribution of equitability to diversity on these areas, suggest selective resource advantages for *Mastomys natalensis*. It is possible that *M. natalensis* competitively excluded *Saccostomus campestris* and *Aethomys chrysophilus* from young rehabilitating stands older than ten weeks. If this is the case, *S. campestris* and *A. chrysophilus* numbers should change with the removal of *M. natalensis* from young rehabilitating stands. However, from the removal trials that Ferreira (1997) conducted it was apparent that intraspecific, rather than interspecific interactions play an important role in habitat selection within a particular site. This suggests that habitat suitability is the driving force behind the composition of rodent communities within coastal dune forests (Ferreira, 1997). Therefore, compositional differences in rodent communities between stands of different ages were related to habitat differences and not to interspecific interactions. The mechanism through which this observation is manifested is most likely through the provision

of seeds by trees in the different serial stages of succession (Ferreira, 1997). Seedbank composition had a slightly greater explanation value for rodent community composition than habitat structure. The association between rodent community composition and tree composition may therefore not be a result of habitat structure leading to differential microhabitat provision for rodents in different rehabilitating stands. It is more likely that trees provide microhabitats for successful seed production by grasses and herbs or the accumulation of seeds (Ferreira, 1997).

Rosenzweig's (1979) argument that habitat specialization of species has been moulded by previous competitive interactions is quite likely since all three species in question in the present study are native to Africa. This suggests that past competitive interactions cannot be discounted. Habitat age-related changes in densities of *M. natalensis*, *A. chrysophilus* and *S. campestris* (Ferreira & Van Aarde, 1996), suggested that low densities of these rodents recorded on older rehabilitating stands may potentially reflect on one of the assumptions of competition. Competition is not only a species attribute, but also depends on environmental stability (Keddy, 1989). The changes in vegetational characteristics and habitat structure associated with the rehabilitation of coastal dune forests (Van Aarde *et.al.*, 1996b) likely present an unstable system even for rodents. Here densities of potential competitors never reach equilibrium densities, a prerequisite for competition and consequently, result in habitat changes rather being the major determinant of rodent communities in coastal dune forests.

It therefore seems that with an increase in age of rehabilitating stands, conditions and habitat characteristics change, becoming progressively more suitable for rodent habitation. On older stands, rodent densities are too low for competition to occur.

The present field experiment was designed to investigate the effect of supplementary food on the rodent community in newly rehabilitated areas in coastal dune forests north of Richards Bay. It is proposed that with supplementary food, a relative constant environment in terms of food

availability could be created. However, it is expected that species diversity may be decreased through dominance by those species that are competitively superior in exploiting an augmented resource when only a small part of the total resource spectrum is increased. This implies that species in the community will only coexist if the overlap of resource use between these species is relatively small.

AIMS OF THE STUDY

- To investigate the diet of rodent species occurring on stands of rehabilitating coastal dune forests through an analysis of their stomach contents.
- To investigate the potential influence of additional food availability on the rodent community composition, species richness and species diversity of newly established rehabilitating stands through manipulation of food resources by providing additional food resources.
- To investigate the potential influence of additional food availability on the species specific survival and reproductive rate by providing additional food resources.

GENERAL NULL HYPOTHESES

- The diets of rodent species that occur on the newly established rehabilitating coastal dune forests do not differ from each other.
- Species composition, species richness and species diversity of rodent assemblages on newly established rehabilitating stands is not influenced by an increase in food availability.
- The species specific survival for rodents in the rehabilitating stands is not affected by food availability.
- The species specific reproductive rate for rodents in the rehabilitating stands is not

affected by food availability.

KEY QUESTIONS

- What is the diet of each species?
- Does the structure (densities, richness and diversity) of the community change on newly established rehabilitating stands with an increase in food availability?
- Do the species specific survival rates of rodent species on newly established rehabilitating stands change with an increase in food availability?
- Do the species specific reproductive rates of rodent species on newly established rehabilitating stands change with an increase in food availability?

CHAPTER 2

THE STUDY AREA AND MINING PROCEDURES

LOCATION

The study area is situated in northern Kwa-Zulu Natal, South Africa between the coastal town Richards Bay (28°43'S, 32°12'E) and the Mapelane Nature Reserve (32°25'S, 28°27'E) (Fig. 1).

The current land-use within the region includes mining, forestry, subsistence agriculture, industry and recreation. This area forms part of the Mozambique coastal plain directly south of Maputaland (Tinley, 1985). It stretches from the Mlalazi River northwards to the Rovuma River and forms a narrow coastal strip (two to four kilometres wide) of sand dunes with various types of vegetation. The sand dunes are characteristically narrow, bipolar and parabolic in shape. Dunes rise to an elevation of between 40 m and 90 m above sea level and are formed by strong north-east anticyclonic winds (Tinley, 1985).

CLIMATE

The climate is humid and warm to hot with little seasonal differences. The mean daily maximum temperatures range from 22.6°C in June to 30°C in January with the mean minimum temperatures ranging from 10°C in June to 20.6°C in January. Frost does not occur and the relative humidity is high, ranging from 59% in August to 72% in April and November, respectively (Avis, 1992). It rains throughout the year with a mean annual rainfall of 1292 mm (Van Aarde *et.al.*, 1996b). Winds occur throughout the year blowing parallel to the coast with the wind direction 39% of the time north-easterly and 37% of the time south-westerly (Avis, 1992).

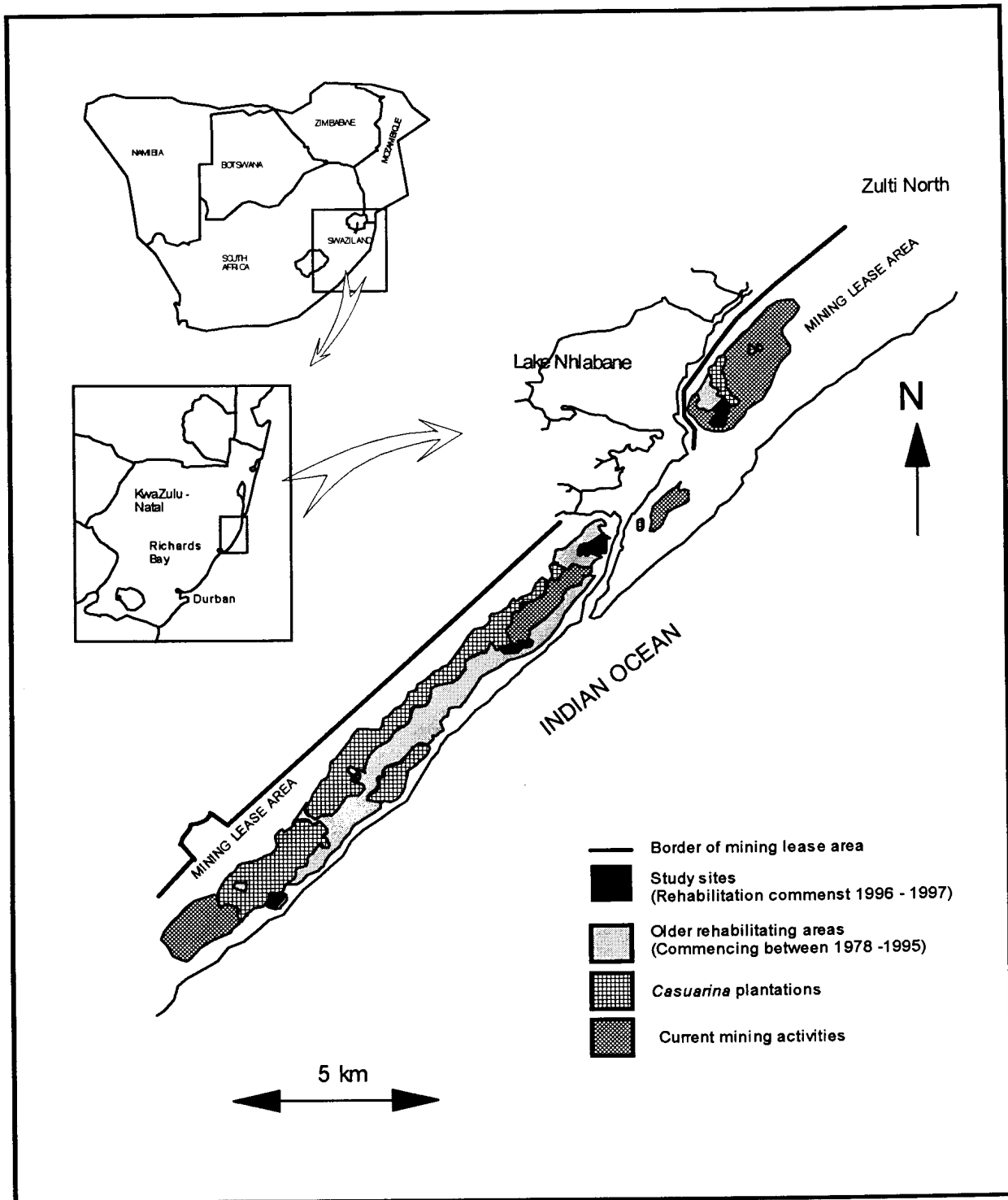


Figure 1. Map of the study area north of Richards Bay ($28^{\circ}43'S$, $32^{\circ}12'E$) showing the location of the study sites, older rehabilitating areas, *Casuarina* plantations and the current mining activities.

MINING AND THE REHABILITATION PROCESS

The mining company, Richards Bay Minerals (RBM), was established in 1976 and has been using a wet-mining process to extract ilmenite, zircon and rutile from coastal sand dunes north of Richards Bay. The mining commenced during July 1977, with rehabilitation of the first mined sites being initiated during 1978 (Ferreira, 1997).

In accordance with the policy of the landowners, the rehabilitation program is directed at establishing an indigenous coastal dune forest on one-third of the area exposed to mining. The subsequent re-establishment of indigenous vegetation where it had previously existed before mining has resulted in a continuous rehabilitation program. The remaining two-thirds of the area are revegetated with stands of exotic *Casuarina equisetifolia* trees which are used in the charcoal industry (Van Aarde, Coe & Niering, 1996c).

The re-establishment of the indigenous vegetation involves various steps so as to initiate ecological processes. Prior to any mining or clearing operations, seeds are collected from several indigenous plants (Ferreira, 1997). The areas are cleared from all vegetation and the seed-bearing topsoil is collected. Sand mining then takes place as described by Ferreira (1997). This is followed by the reconstruction of dunes to their topography prior to mining. Following the reshaping of dunes to their pre-mining topography, the topsoil is spread over the mined sand (to a depth of approximately 10 -15 cm) in areas demarcated for indigenous forests. The topsoil is harrowed and a cover crop of fast growing grasses are then sown in order to protect and augment the seeds contained within the topsoil (Ferreira, 1997). Wind-breaks (1.5 m high) which reduce erosion are erected across the dune facing the prevailing winds. They are removed three months after grass seeds have been sown and after the establishment of a cover crop. Management is limited to the initial topsoiling and seeding, after which the emergent *Acacia karroo* woodland is left to develop on its own accord (Van Dyk, 1996). The development of the woodland can be described as a

dense, almost unpenetrable shrub layer in the younger stands (\approx 2-6 years old), but in older stands (\approx 7-11 years old) it forms a canopy with very little undergrowth. Later stages (\approx 12-17 years old) are characterised by the development of an undergrowth layer with increasing number of broad-leafed saplings under the *Acacia karroo* canopy (Van Aarde *et.al.*, 1996b).

STUDY SITES

The present study was conducted on pockets of newly rehabilitating coastal dune forest areas abutting older rehabilitating and forestry areas all located along a 18 km stretch of coast. Rehabilitation on four replicate sites, selected for the present study, commenced two years prior to the onset of the present study. The sites ranged between 7 ha and 21 ha in area and were characterised by the annual exotic plant species (*Pennisetum americanum*, *Crotalaria juncea*, *Sorghum* spp & *Helianthus* sp.) sown as part of the rehabilitation programme, being replaced by indigenous grasses such as *Eragrostis curvula* and *Cymbopogon validus* (Van Aarde *et. al.*, 1996b). Towards the end of the present study these grasslands had developed into a dense scrubland dominated by 30 to 80 cm high stands of *Acacia karroo* shrubs. These early stages of dune vegetation regeneration support relatively dense populations of rodents (Van Aarde *et. al.*, 1996b), probably as a consequence of the abundant seedcrop available in the topsoil spread over the dunes as part of the rehabilitation program. However, rodent densities drop dramatically after the first year of habitat regeneration (Ferreira & Van Aarde, 1999).

FACTORS AFFECTING THE STUDY

Subsistence farming and forestry are two of the current land-use practices in the region. Land available for cattle grazing and subsistence farming has decreased due to a continued increase in forestry activities. This has resulted in the illegal use of rehabilitated areas by surrounding cattle

owners for grazing. Cattle grazing was recorded on sites 1, 2 and 4. Sites 2 and 4 were more frequently grazed and therefore more degraded (personal observation). Furthermore cattle were seen to damage Sherman live traps and feeding stations while roaming on the study sites during the night.

None of the present study areas were spared by the present crime situation in South Africa. Feeding stations were stolen on several occasions. All those feeding stations were immediately replaced so as to keep the treatment the same over the different sites. Most of the theft occurred on sites 2 and 4.

CHAPTER 3

MATERIALS AND METHODS

DIETARY ANALYSIS

The food items taken by rodents were determined by the microscopic examination of the stomach content of animals caught in a Sherman live traps (H.B. Sherman Traps, Inc. Tallahassee, FL, USA) (8 x 9 x 23 cm) set on transect lines (90 m with traps 10 m apart) in areas adjacent to the four study sites. Snap traps were not used since the dead and exposed rodents were found to attract ants.

Animals were killed with diethyl ether and immediately dissected. Each stomach was removed and preserved in 70% alcohol for later analysis. Stomach contents were emptied onto two clear petri-dishes. Water and 1% hematoxylin were added and the fragments of stomach contents were left to absorb the stain. When the desired intensity of colour was achieved, the fragments were washed. The mixture was gently swirled until the fragments separated and were uniformly distributed (Williams, 1962). Excess fluids were then removed with a pasteur pipette and the stomach content examined at 10X magnification under a light microscope. Three 60 mm lines will be drawn randomly on the bottom of each petri dish and then each line was examined at 10X magnification under a light microscope. The number of insect, seed and vegetative particles touching each line was recorded. In each stomach the percentages of insect, seed and vegetation matter respectively, were then calculated by dividing the number of each particle type by the total number of particles counted (Watson, 1987). The diet composition within a given species was averaged to provide species mean values because of the instantaneous nature of the sampling method. Results should therefore only be treated as indicative because of the sampling method and the low sample sizes (see Watson, 1987).

FIELD EXPERIMENT

Experimental design

Each of the four study sites selected comprised a treatment and a control trapping grid. These grids were at least 200 m apart. Hundred Sherman live traps, arranged in a 10 x 10 configuration with 10 m intervals between trapping stations, were set on each of the 0.81-ha grids (90 x 90 m) (Fig. 2).

Monthly trapping (five consecutive nights per session) commenced during April 1997 and continued until August 1998. Thereafter the trapping took place at bimonthly intervals until April 1999. Treatment and control grids within a specific site were trapped simultaneously. Traps were baited with a mixture of raisins, rolled oats and peanut butter. Captured individuals were marked (uniquely toe-clipped), and the sex, weight and breeding condition noted. Individuals were released following inspection for previous marks and identification. Trapping commenced one month prior to the experimental supplementation of food on the treatment grids.

Supplementary food (sunflower seed) was placed on the treatment grids at seven day intervals for the full duration of the study, starting in May 1997. Seed was placed in feeders at feeding stations located at the centres of the squares formed by the trapping stations. Each grid had 81 feeding stations but those on the control grids received no seed. A feeder consisted of a plastic container inside a plastic plant pot holder (30 cm) turned upside down (Fig. 3). The sides of each plant pot had four evenly spread holes, each with a diameter of 5 cm, which allowed free access to rodents but limited access to larger granivores, such as vervet monkeys (*Cercopithecus aethiops*). Each feeding station received 200 g of seed weekly. The amount of seed taken from each feeder was also recorded weekly and an average calculated for each month. Sunflower seed was chosen as the supplementary feed as it forms part of the already existing resource spectrum since it is sown as part of the rehabilitation program (Ferreira, 1997).

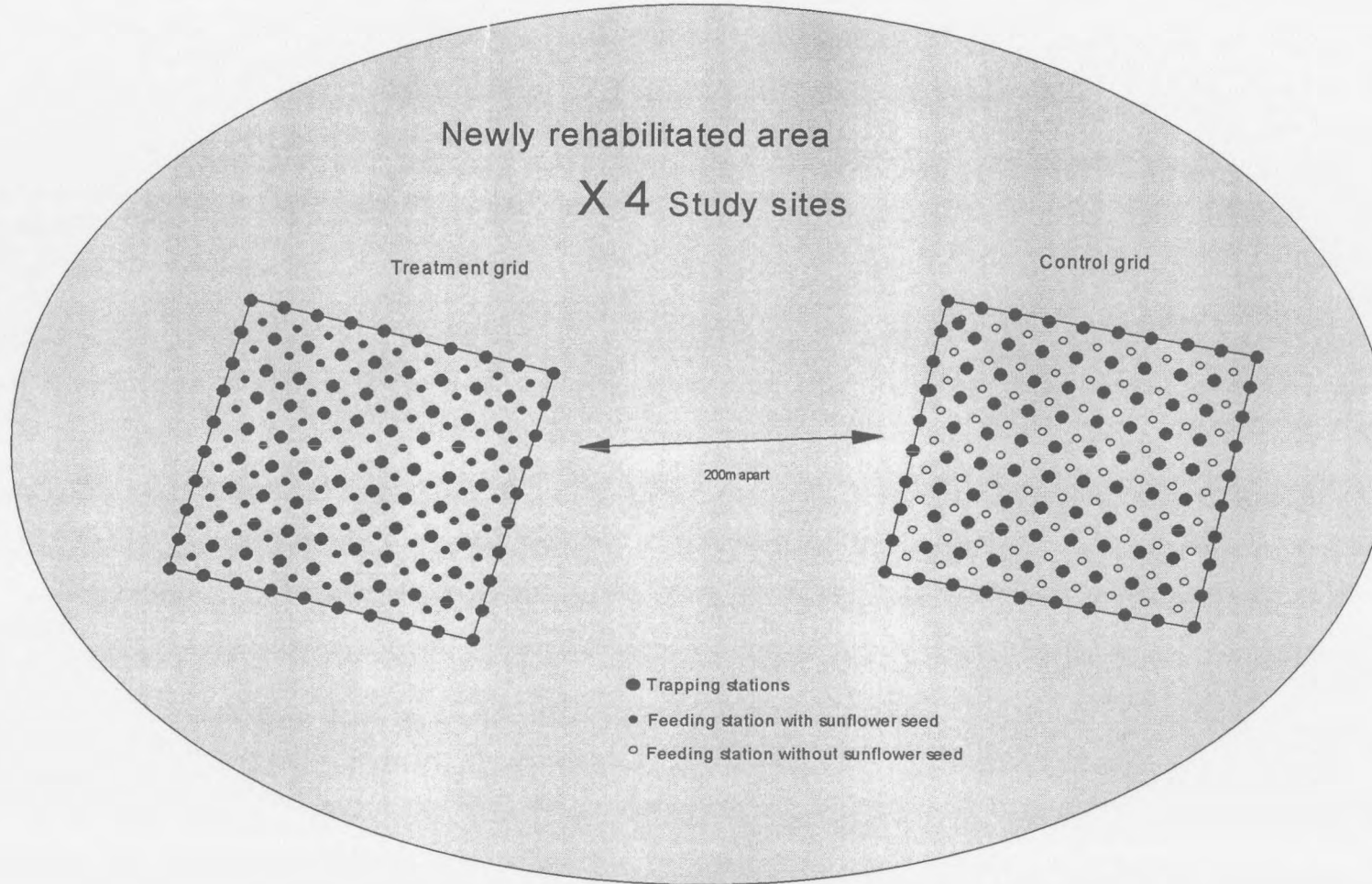


Figure 2. Line diagram of the arrangement of trapping grids on the four study sites. Each site comprised of a treatment and a control trapping grid, with grids at least 200 m apart. Trapping stations on each grid were arranged in a 10 x 10 configuration with 10 m intervals between trapping stations. The feeding stations were located at the centre of the squares formed by the trapping stations. Each grid thus had 81 feeding stations.

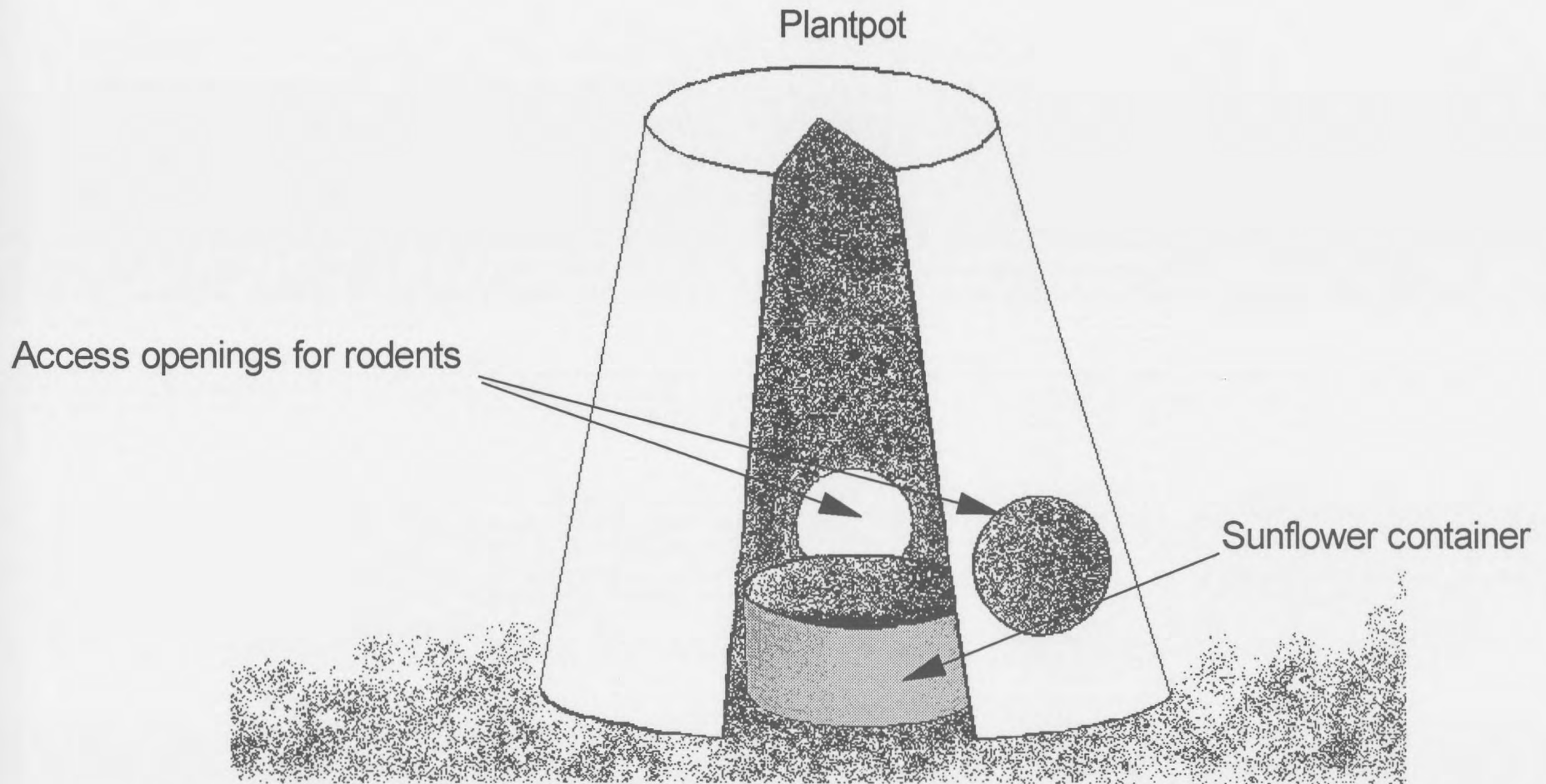


Figure 3. A schematic representation of a feeding station consisting of a plastic sunflower container inside a plastic plant pot holder (30 cm) turned upside down. The sides of each plant pot had four evenly spread holes that allowed free access to rodents. Pots were held in place by a steel peck through the centre of the pot.

Sunflower seed (22.2% digestible protein) is a high-protein seed that is attractive to rodents and supports a good breeding performance (Bomford & Redhead, 1987). Rodents prefer seed with a high energy content (Kerley and Erasmus, 1991) and remove proportionally more large seeds than small seeds (Hulme, 1998).

Measurement of responses

Density was estimated as the minimum number of animals known to be alive (MNA) during a trapping session per grid and was calculated for each species and rodents in total (Chitty & Phipps, 1966). The MNA assumes that an animal is present from its first to its last capture. This may result in an underestimate of population density. However, data for each five day trapping session was combined for the purpose of calculating the MNA. This index was also used to calculate other community variables. Species richness (S) was calculated as the total number of species present monthly. Shannon-Wiener diversity was calculated and used as a diversity index that incorporates both species richness (S) and equitability components. These variables were calculated using the program PRIMER Version 4.0 (Carr, 1996). The relative contribution of each species to the average Bray-Curtis dissimilarity (δ) between the treatment and control groups was calculated for each month using the program SIMPER from PRIMER Version 4.0 (Carr, 1996). Dominance was calculated by dividing the number of individuals of the two most abundant species by the total number of individuals in the community (McNaughton, 1968). Dominance is therefore the percentage contribution of the two most abundant species to the total number of individuals for the treatment and control grids.

The monthly survival rate was calculated for each species using the method described by Caughley (1977). Survival was calculated as $1-q$ where q represents the mortality estimate. A regression of $\log_e m$ on time (m = the number of recaptures; M = marked individuals during subsequent trapping sessions) with equal intervals (months) between trapping sessions (Caughley,

1977). Survival rates were calculated for the total rodent community, and for each species on each of the grids.

The proportion of reproductive adults was calculated for the total rodent community and for each species. At each capture individuals were weighed to the nearest gram using a fisherman spring balance (Salter Spring balance Abbey, Limited, Edmond, Suffolk, England). Individuals were classified as either adults or sub-adults depending on their weight. Individuals were considered to be sub-adults when weighing < 45 g (*Mastomys natalensis*), < 7 g (*Mus minutoides*) and < 50 g (*Saccostomus campestris*) as specified by Ferreira (1997). *Dendromus melanotis* and *Otomys angoniensis* individuals were considered as sub-adults if they weighed less than 8 g and 80 g respectively, following Skinner and Smithers (1990). The proportion of breeding individuals (B) was calculated as $B=b/t$; (b = the number of breeding individuals, t = the total number of individuals) for females and males separately (Bomford & Redhead, 1987). Males were considered to be breeding when their testes were scrotal while females were considered to be breeding if the vagina was perforated, or when they were visibly pregnant or lactating. The proportion of juveniles in the total rodent community and within each species was calculated by dividing the number of juveniles by the total number of individuals recorded.

Statistical analysis

The variability in the amount of seed taken over time was measured following the method described by Pimm and Redfearn (1988). The measure of variability was presented as the standard deviation of the logarithm of the monthly amount of seed taken (SDL). An increase in variability would indicate a cyclic pattern in the amount of seed taken. The amount of seed taken was related to rodent densities using least squares regression analysis (LSR) (Sokal & Rohlf, 1995).

The Bray-Curtis dissimilarity values were regressed against time (LSR) in an effort to assess the influence of the treatment on the rodent community. The relationships between species

densities were determined using LSR (Sokal & Rohlf, 1995).

The data used to measure various community parameters and responses was collected by sequential sampling of the same sites, because of the cumulative nature of the supplementary feeding experiment. This resulted in longitudinal data. The analysis of the data allowed for the repeated measure design where measurements on individual grids were dependent from one month to the next. The repeated measures analysis of variance (ANOVAR - Potvin, Lechowicz & Tardif, 1990) was therefore used to test for the effect of food supplementation on rodent density, species richness, diversity, dominance and the densities of individual rodent species. ANOVAR was also used to determine any differences between treatment and control grids using survival rates, female reproductive rates, male reproductive rates and the proportion of juveniles. All analyses were done with the statistical package SAS release 6.12 (SAS institute Inc., Cary, NC, USA) and were run from the SAS procedure GLM. Inferences about main effects and interactive effects were made from F -tests based on appropriate ratios of mean square terms (Kleinbaum, Kupper, Muller & Nizam, 1998). The ANOVAR method is based on a split plot design (Von Ende, 1993) and is generally regarded as a more powerful method because some relaxation of the restrictive assumptions are possible using corrected significance levels (Potvin *et.al.*, 1990). Huynh-Feldt adjusted probabilities based on the Huynh-Feldt epsilon were therefore used to determine any significant differences between treatment and control grids (Von Ende, 1993). Significance was taken at the 95% level ($P = 0.05$) in all cases.

CHAPTER 4

RESULTS

DIETARY ANALYSIS

Five rodent species (*Mastomys natalensis* (Smith 1834), *Mus minutoides* (Smith 1834), *Dendromus melanotis* (Smith 1834), *Saccostomus campestris* (Peters 1846), and *Otomys angoniensis* (Wroughton 1906)) were present on the newly rehabilitating areas. Only two of these species were sampled in areas allocated to the sampling of individuals examined in the dietary analysis. Skinner and Smithers (1990) report that *M. minutoides* and *M. mastomys* both take seed as part of their diet. Results of the present study and the survey of Kreiner (1993) suggest that seeds form the main part of their diet (Table 1).

It is also clear from the literature that most of the species present in the study area feed on seeds with the exception of *Otomys angoniensis*, which as a herbivore, prefers succulent stems and rhizomes of grasses and fine reeds (Skinner and Smithers, 1990) and *Dendromus melanotis* which mainly feeds on insects but occasionally consume seeds (Skinner and Smithers, 1990) (Table 1).

RESOURCE USE

About 85.2 g (s.e. = 7.0) of the 200 g of sunflower seeds provided per feeding station was taken per week. The calculated variability (SDL) increased over time, suggesting a cyclic pattern in the amount of seeds consumed. The amount of seed consumed weekly, increased significantly with the number of *M. natalensis* individuals present on the grid (LSR: $F = 13.85$, $r^2 = 0.52$, $P < 0.05$) (Fig. 4a). However, the amount of seed taken did not increase significantly with rodent numbers (LSR: $F = 0.78$, $r^2 = 0.05$, $P > 0.05$) (Fig. 4b) or as time progressed (LSR: $F = 3.27$, $r^2 = 0.16$, $P > 0.05$) (Fig. 5).

Table 1. Summary and results of specific diet preferences for rodent species occurring in newly rehabilitating areas during summer. Summary taken from Skinner and Smithers (1990). Results taken from Skinner and Smithers (1990), Kreiner (1993) and the present study. The values in brackets represent the number of individuals sampled.

Species	Food type %	Skinner & Smithers (1990)	Kreiner (1993)	Present study
<i>Otomys</i>	Insect	-	-	-
<i>angoniensis</i>	Seed	-	-	-
	Foliage	-	-	-
<i>Mus</i>	Insect	-	-	18.33 % ± 16.5
<i>minutoides</i>	Seed	-	-	55 % ± 14.1
	Foliage	-	-	16.67 ± 6.2 (3)
<i>Mastomys</i>	Insect	5%	17% ± 18.4	26% ± 21.3
<i>natalensis</i>	Seed	63%	71 % ± 18.8	58.62% ± 19.5
	Foliage	32% (12)	0.1% ± 1.3 (20)	8.58% ± 7.0 (13)
<i>Saccostomus</i>	Insect	9-31%	7.6 % ± 16.3	-
<i>campestris</i>	Seed	57-79%	90.4% ± 16.3	-
	Foliage	12% (14)	0.1% ± 0.3 (19)	-
<i>Dendromus</i>	Insect	-	-	-
<i>melanotis</i>	Seed	-	-	-
	Foliage	-	-	-

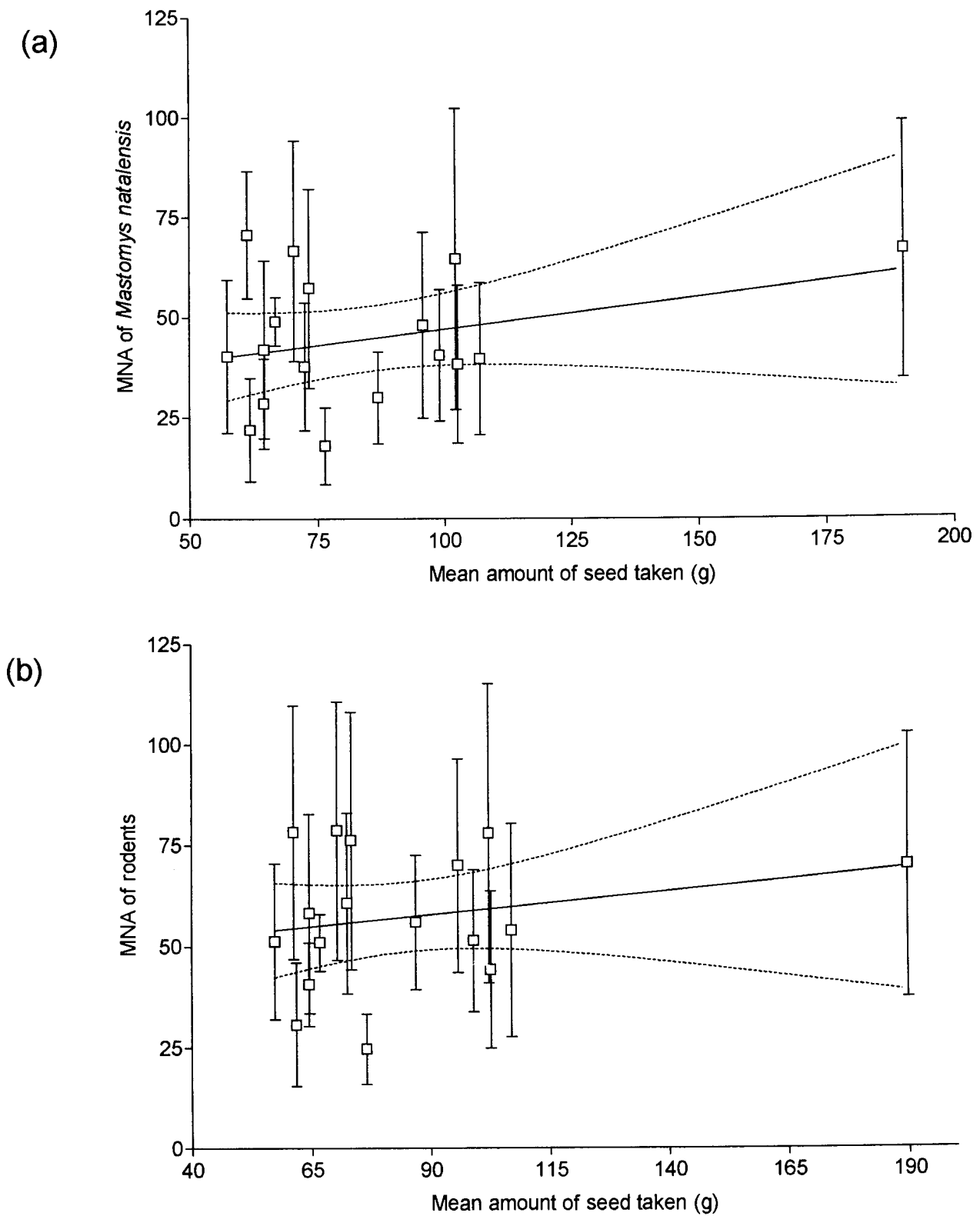


Figure 4. The relationship between the amount of seed taken (mean \pm s.e. in grams) and (a) the minimum number of *Mastomys natalensis* individuals alive and (b) the minimum number of rodents alive. The line were fitted through a least square regression analysis.

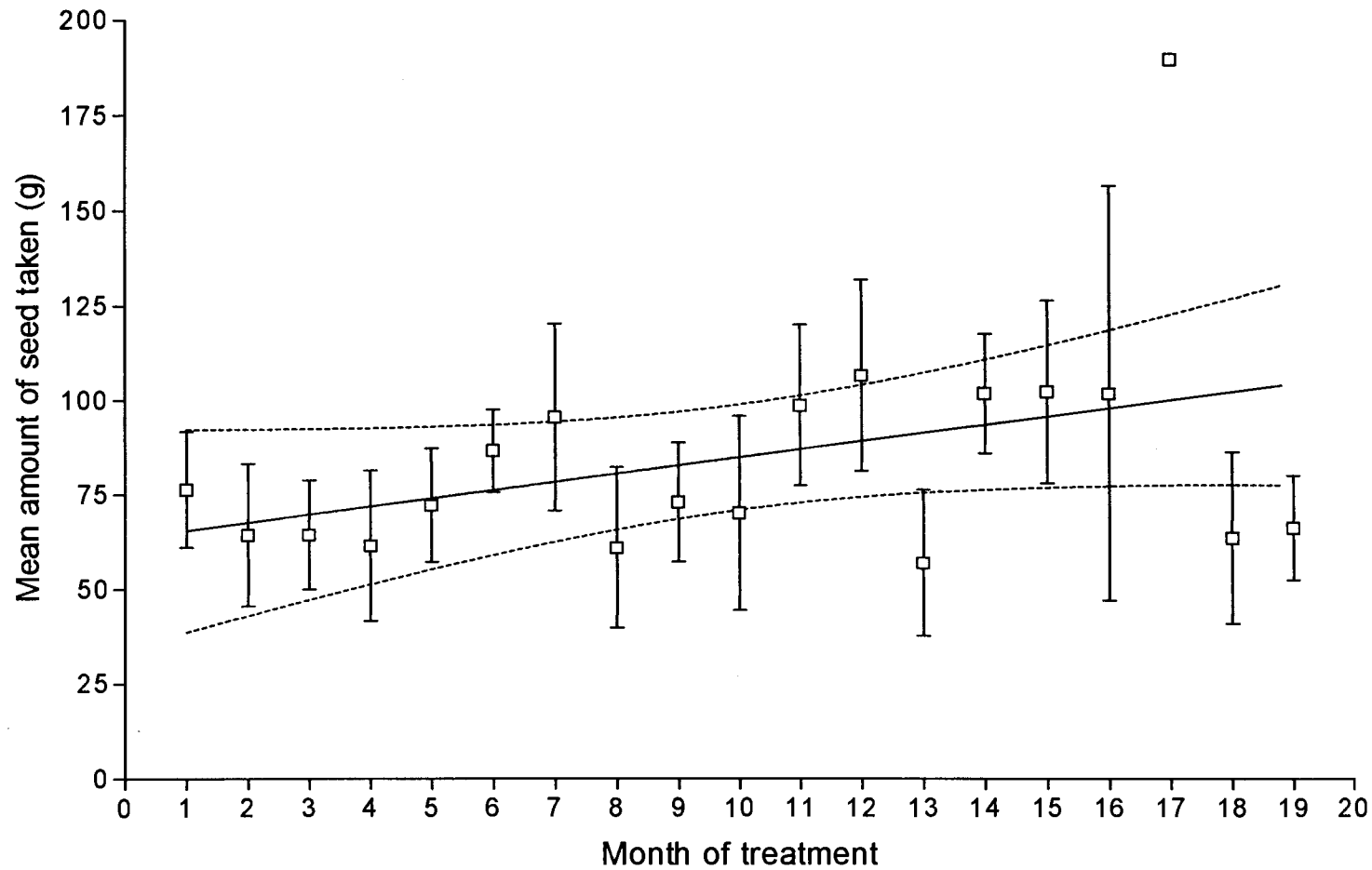


Figure 5. The relationship between the amount of seed taken (mean \pm s.e. in grams) and the month of the study period (treatment duration), where 1 represents October 1997 and 20 represents April 1999. The line were fitted through a least square regression analysis.

COMMUNITY

The Bray-Curtis dissimilarity between the treatment and control grids increased significantly with an increase in the treatment duration (LSR: $F = 4.71$, $r^2 = 0.2$, $P < 0.05$) (Fig. 6). The mean MNA of rodents on the treatment grids was higher than on the control grids but this difference was not significant (ANOVAR: $F = 0.92$, $P > 0.05$). At the onset of the study, the MNA on control and treatment grids were similar but after a five month period the MNA on the control grids decreased to a value lower than that on the treatment grids. MNA for the treatment and control grids increased and decreased concurrently during the study period, only differing in amplitude of the response (Fig. 7). The combined MNA of the treatment and control grids increased significantly with time since the onset of the study (ANOVAR: $F = 2.32$, $P < 0.05$). However, the univariate test that incorporates the effect over time, and differences between the different treatment levels showed no significant effect (ANOVAR: $F = 1.58$, $P > 0.05$). This indicates the treatment did not cause a significant response over time.

Species richness increased on the control grids after a 11 month period. Overall species richness on the treatment grids was significantly lower than the species richness on the control grids (ANOVAR: $F = 8.73$, $P < 0.05$) (Fig. 8). The combination of species richness for the treatment and control grids increased over time and was significantly different ($F = 2.29$, $P < 0.05$). Even though there is an apparent difference between the treatment and control grids when the mean species richness is compared, and the combination of the two show a significant change over time, it is still no indication that the treatment had an effect as time progress. This suggests that there was a similar response for both the treatment and control grids, but on two different levels and not due to the treatment. For species richness this seem to be the situation since there was no significant differences for the interaction between time and species richness (ANOVAR: $F = 0.46$, $P > 0.05$).

No significant difference was recorded between the mean diversities for the treatment and

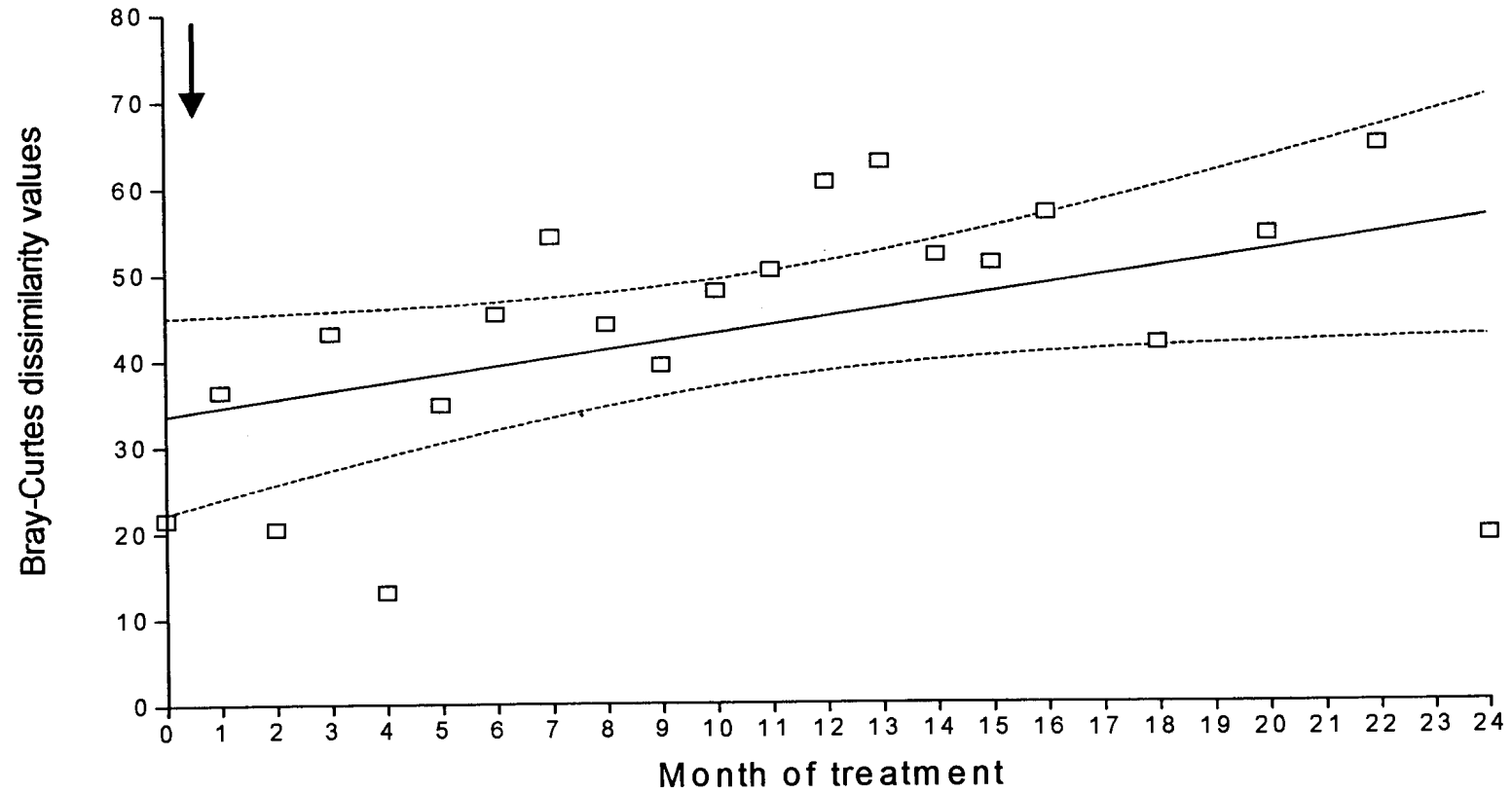


Figure 6. The least square regression line illustrating temporal trends in the Bray-Curtis dissimilarity values calculated to show differences in the community variables of the treatment and the control grids (↓ Start of treatment).

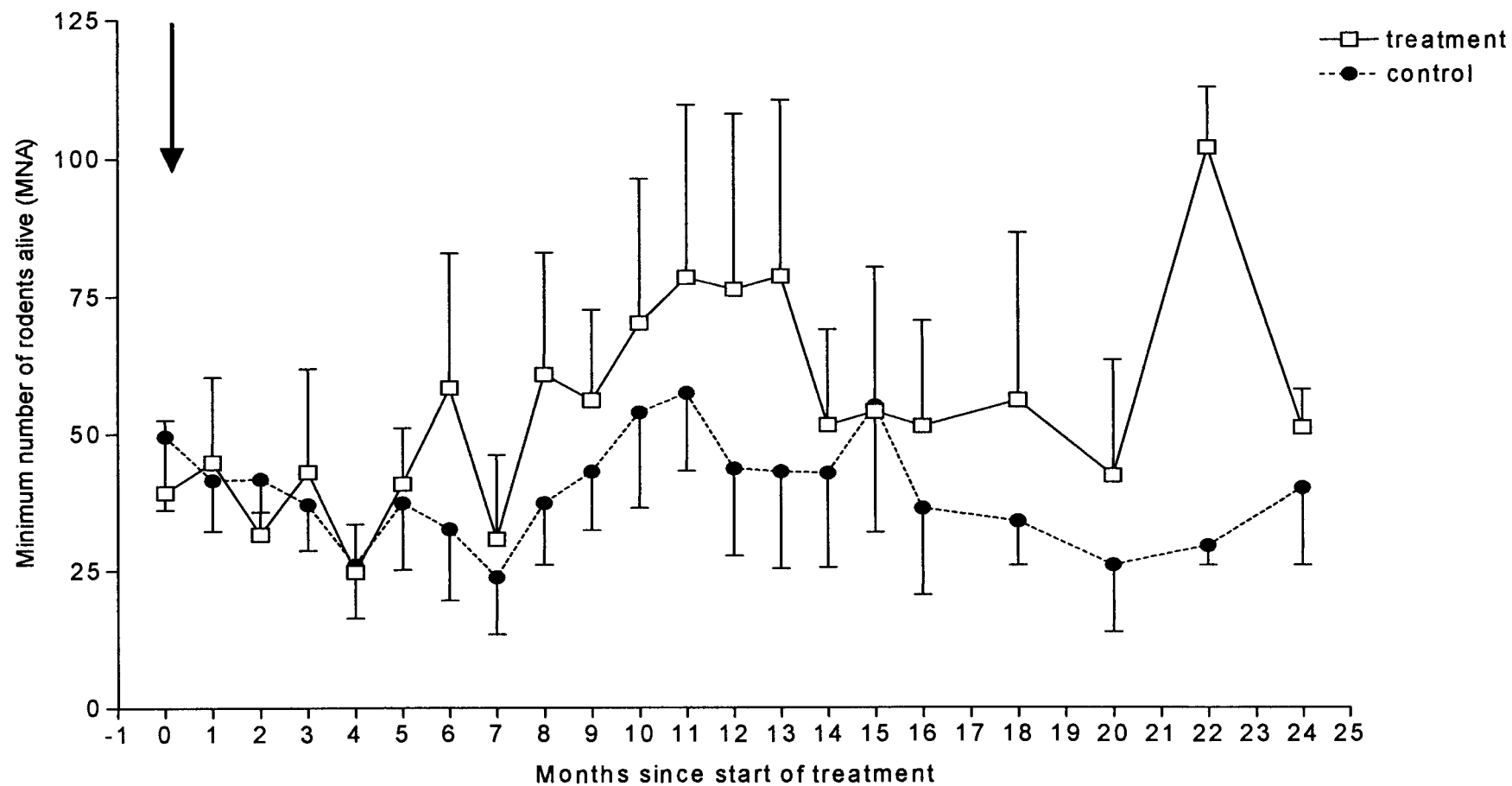


Figure 7. Temporal trends (mean \pm s.e.) in the minimum number of rodents alive (MNA) for four treatment (\square) and four control (\bullet) grids (\downarrow Start of treatment).

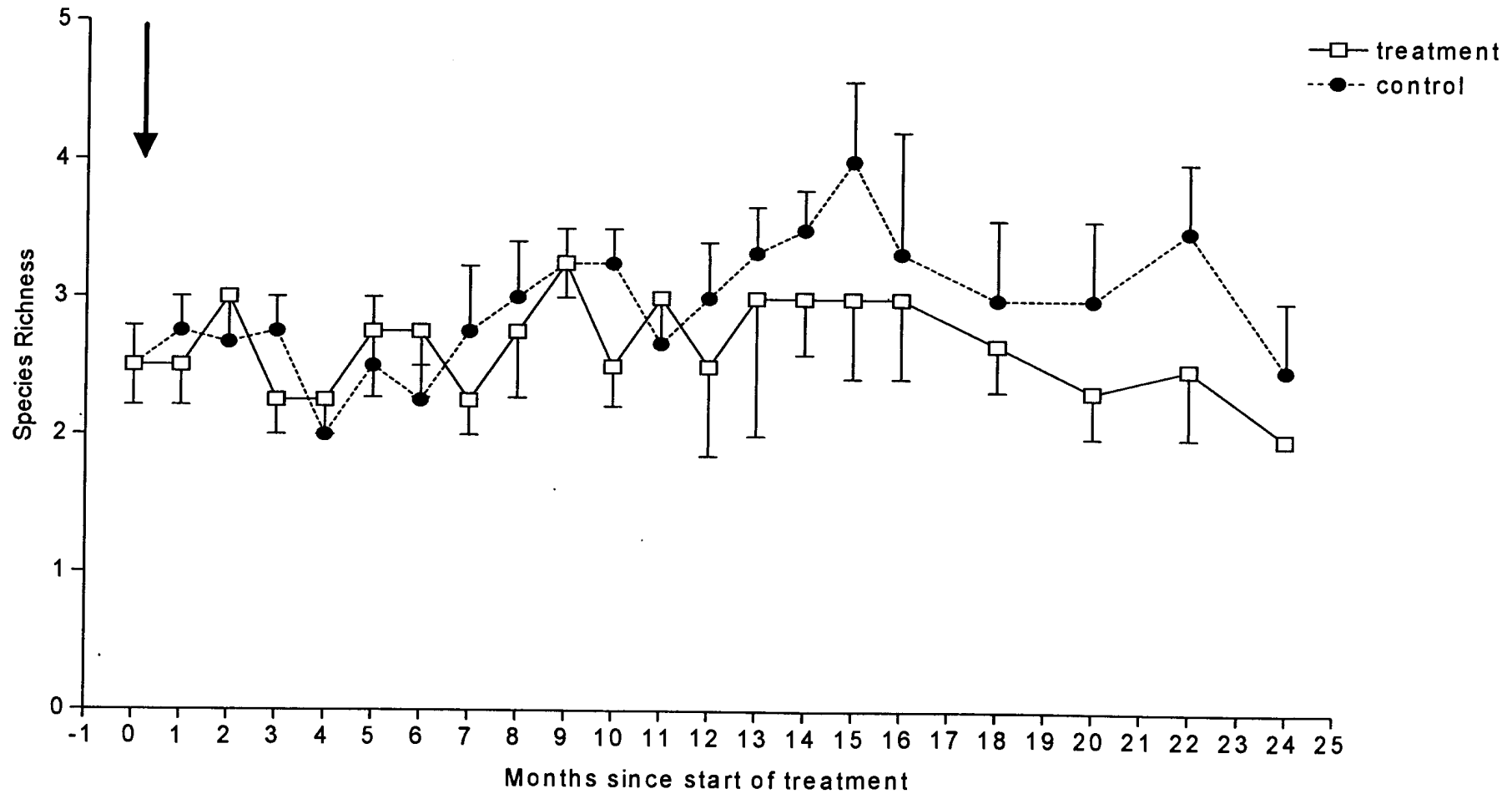


Figure 8. Temporal trends (mean \pm s.e.) in species richness on four treatment (\square) and four control (\bullet) grids (\downarrow Start of treatment).

control grids (ANOVAR: $F = 5.39$, $P > 0.05$) (Fig. 9). An increase in diversity on the control grids is more apparent after 10 months of food supplementation. However, diversity on treatment grids varied but decreased overall over time. The decrease in diversity on the treatment grids caused the mean diversity of the treatment and the control grids combined to decrease significantly, rather than to increase over time (ANOVAR: $F = 3.15$, $P < 0.05$). Supplementary food on the treatment grids caused a significant decline in the rodent community diversity (ANOVAR: $F = 2.24$, $P < 0.05$).

After a 12 month period, dominance started to decrease slightly on the control grids. The mean dominance for the treatment grids did not differ significantly from the mean dominance of the control grids (ANOVAR: $F = 0.93$, $P > 0.05$). With the combination of the dominance of the treatment and control grids, there was significant decrease over time (ANOVAR: $F = 3.02$, $P < 0.05$). In addition to the time effect, the interaction between the treatment effect and time showed a significant effect (ANOVAR: $F = 1.95$, $P < 0.05$) (Fig. 10).

SPECIES AND THEIR INTERACTIONS

The mean MNA for the five species that occur on the newly rehabilitated areas for treatment and control grids were similar (Table 2). However, all differences were significant when the MNA of treatment and control grids were combined and tested for significant differences over time (Table 2). For all of the species, MNA fluctuated over time, with some increasing in numbers, like *M. natalensis* (Fig. 11), and others such as *M. minutoides*, decreasing in numbers. For *S. campestris* values fluctuated, with a slow increase in numbers over time. *Otomys angoniensis* occurred in low numbers and their numbers fluctuated over the period with no specific patterns (Fig. 12). After a 12 month period, *D. melanotis* had a short period (five months) of increase in numbers, followed by a decrease in numbers. The interaction between the treatment effect and time was only significant for two species, namely *M. natalensis* (ANOVAR: $F = 2.65$, $P < 0.05$)

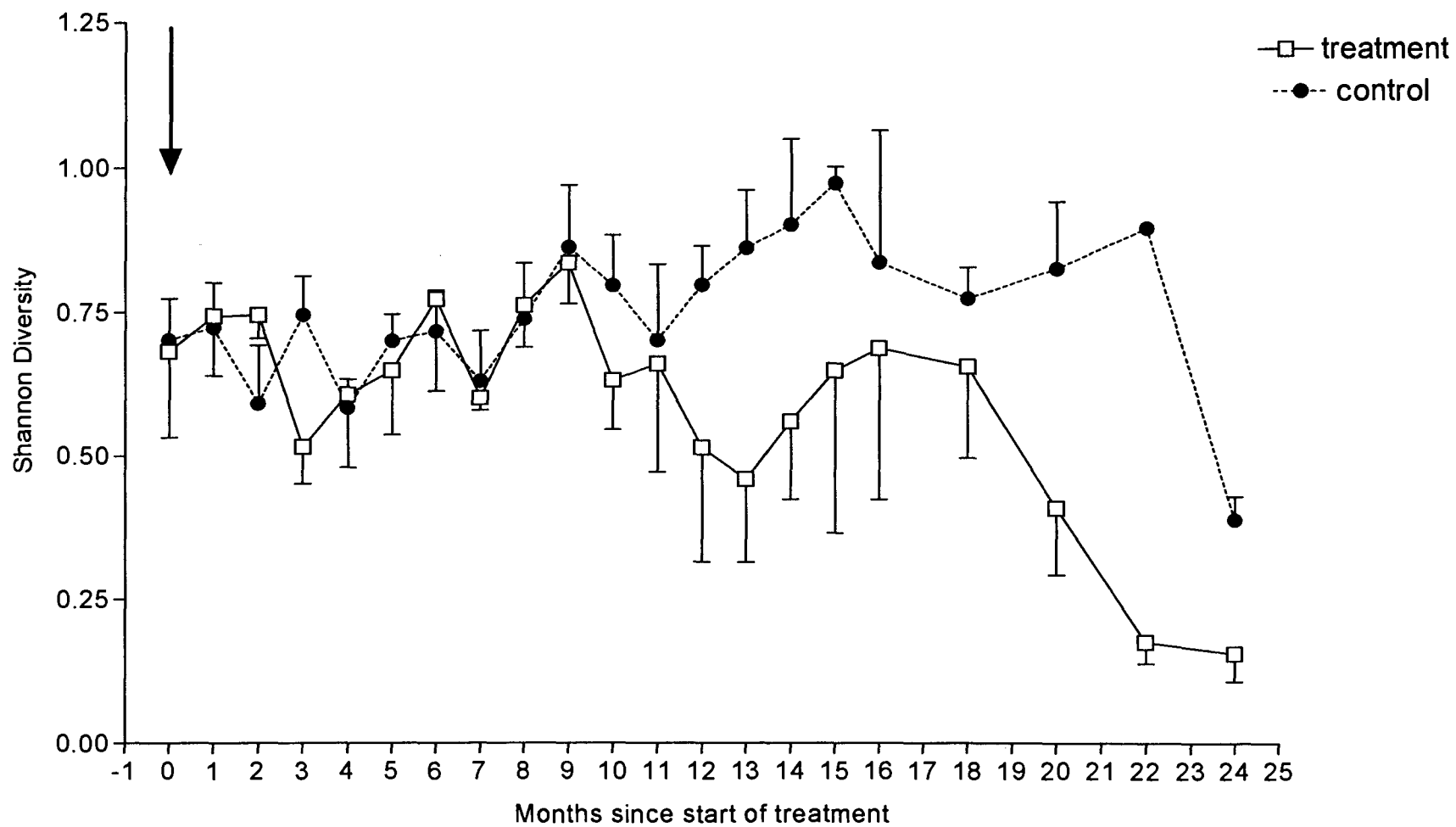


Figure 9. Temporal trends (mean \pm s.e.) in species diversity on four treatment (\square) and four control (\bullet) grids (\downarrow Start of treatment).

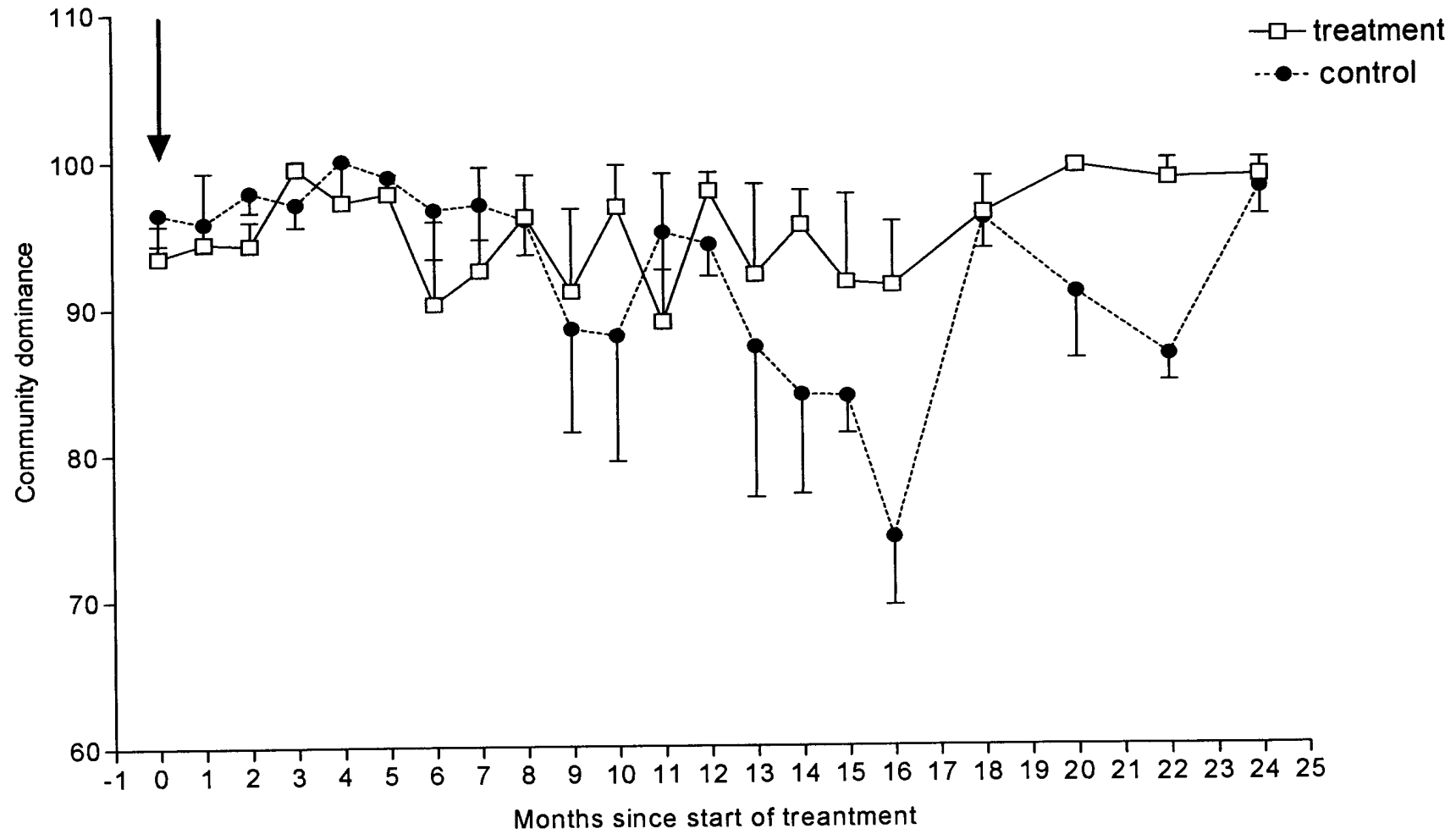


Figure 10. Temporal trends (mean \pm s.e.) in community dominance on four treatment (\square) and four control (\bullet) grids (\downarrow Start of treatment).

Table 2. Results from the repeated measures analysis (ANOVAR) for each of the five species that occurred within the different sampling areas. Mean treatment effect represents the difference between the mean of the treatment and control grids. The time effect represents differences over time of values for treatment and control grids combined. The treatment and time interaction represents the differences between the treatment and control grids over time.

	Mean treatment effect		Time effect		Treatment and Time Interaction	
	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*
<i>Mastomys natalensis</i>	1.95	ns	2.80	0.003	2.65	0.005
<i>Mus minutoides</i>	0.27	ns	5.25	<0.001	0.63	ns
<i>Saccostomus campestris</i>	0.02	ns	2.07	0.031	0.88	ns
<i>Dendromus melanotis</i>	4.93	ns	6.37	0.003	3.13	0.047
<i>Otomys angoniensis</i>	0.07	ns	1.98	0.049	0.88	ns

* Huynh-Feldt adjusted *P* values

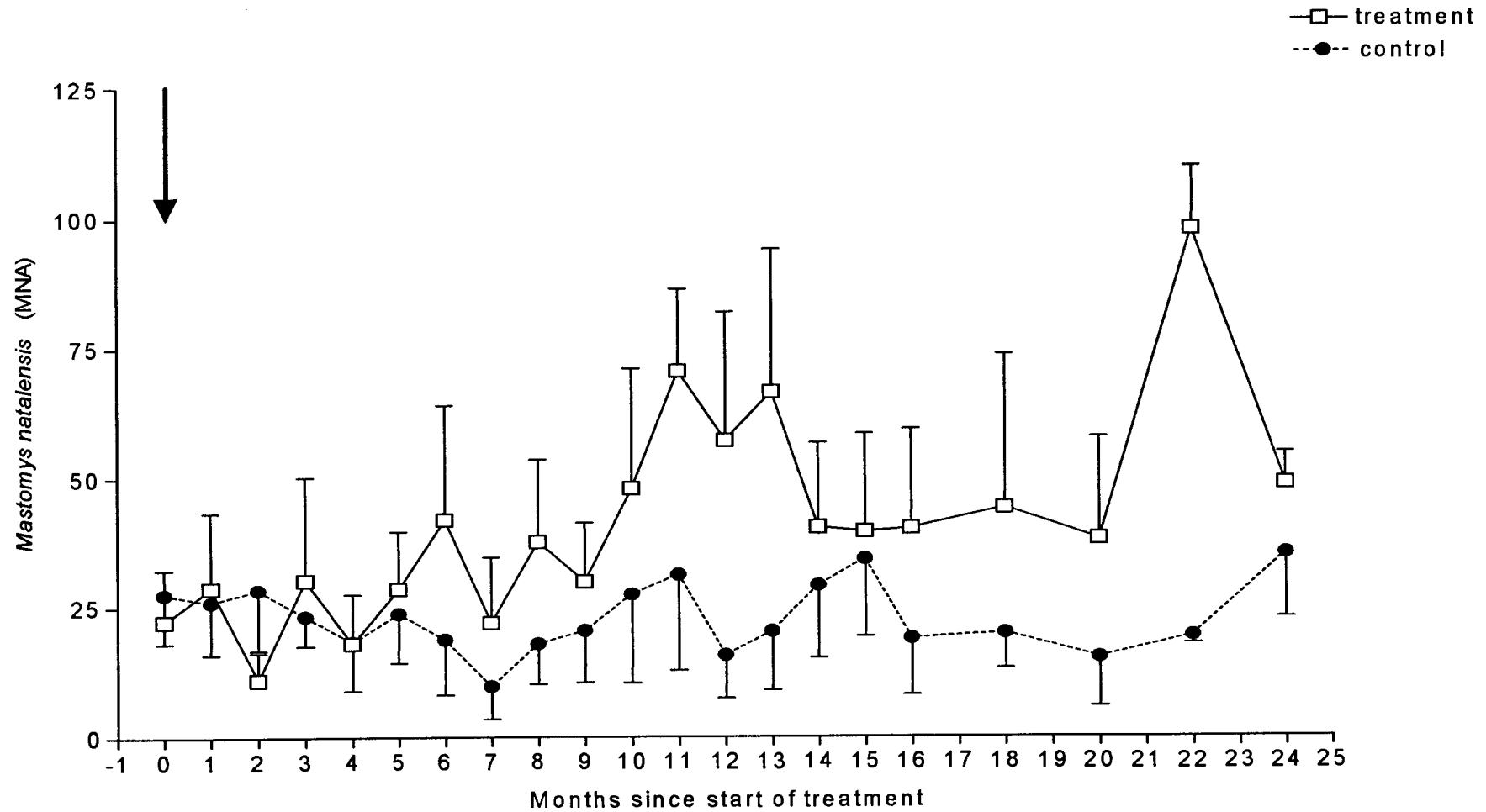


Figure 11. Temporal trends (mean \pm s.e.) in the MNA for *Mastomys natalensis* on the four treatment (□) and four control (●) grids illustrated over a 25 month period (↓ Start of treatment).

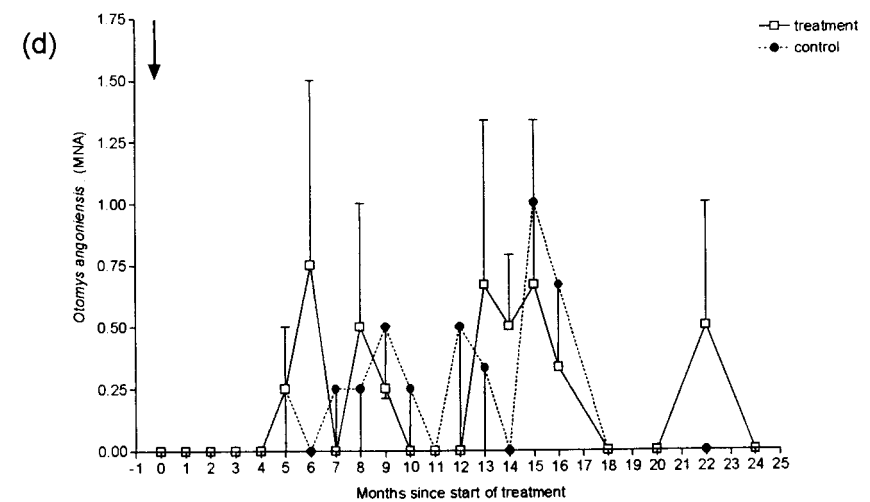
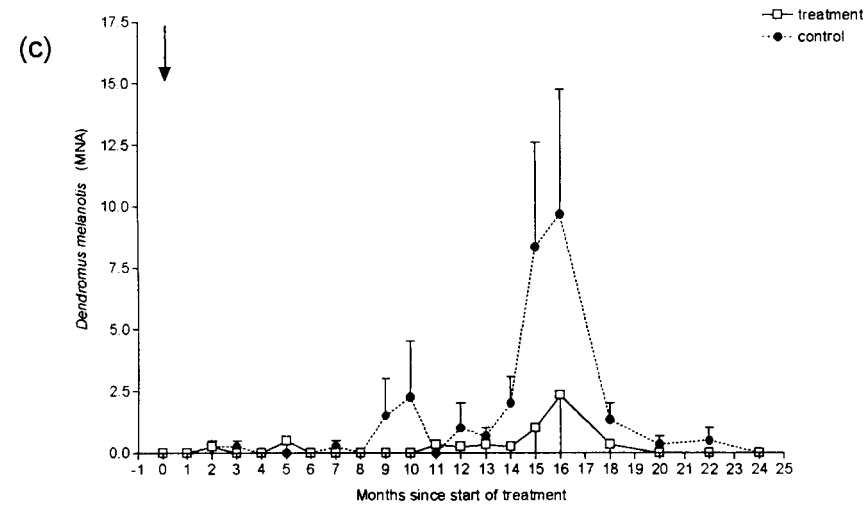
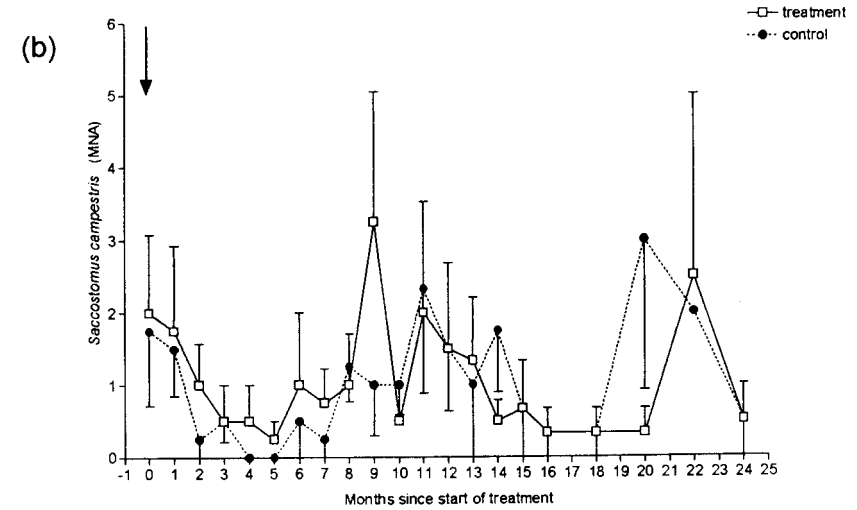
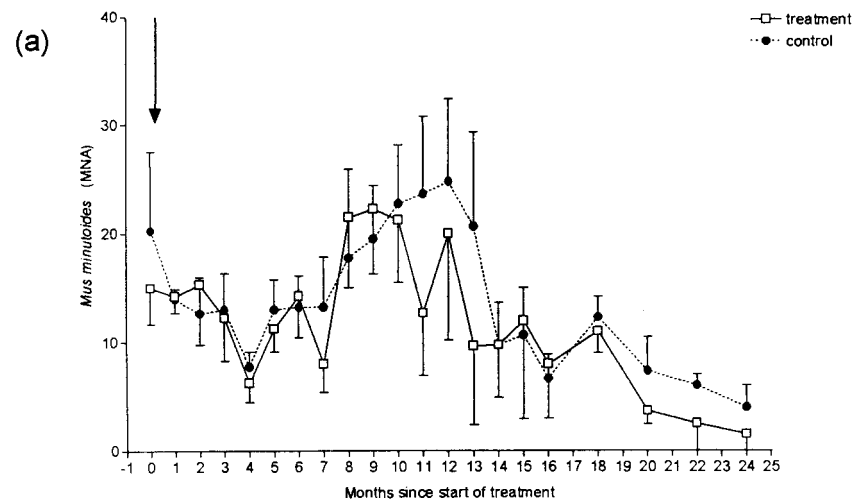


Figure 12. Temporal trends (mean \pm s.e.) in the MNA for (a) *Mus minutoides*, (b) *Saccostomus campestris*, (c) *Dendromus melanotis* and (d) *Otomys angoniensis* on four treatment (□) and four control (●) grids illustrated over a 25 month period (↓ Start of treatment).

and *D. melanotis* (ANOVAR: $F = 3.13$, $P < 0.05$). Supplementary food caused *M. natalensis* numbers to increase on treatment grids over time, while their numbers did not increase on control grids (Fig. 11). After 13 months of treatment *D. melanotis* numbers did show an increase for a period of five months. This increase in numbers on the control grids could not be sustained for a long period. No specific trends, other than the simultaneous change in MNA on the treatment and control grids over time, were recorded for *M. minutoides*, *S. campestris* and *O. angoniensis* (Fig. 12).

Mastomys natalensis and *M. minutoides* were the two most abundant species. There was a significantly positive linear relationship between *M. natalensis* and *M. minutoides* numbers on the control grids (LSR: $F = 30.65$, $r^2 = 0.6$, $P < 0.05$). Although the relationship between the numbers of these two species was negative on the treatment grids, the latter relationship did not deviate significantly from zero. There were no other significant inter-specific correlations between the density of *M. natalensis* and any of the other species present on either the treatment or the control grids. No relationship could be established between *M. natalensis* and *D. melanotis* or *O. angoniensis*, probably due to low densities of the latter two species. *M. minutoides* likewise showed no significant inter-specific correlation with *S. campestris*, *D. melanotis* or *O. angoniensis*.

MONTHLY SURVIVAL RATES

The monthly survival rates for rodents started to increase after five months of treatment and remained higher on the treatment grids than on the control grids for most of the time (Fig. 13). This resulted in the monthly survival rates being higher on treatment grids than control grids, but this difference was not significant (Table 3). The total monthly survival rate decreased, although not significantly, for the treatment and control grids combined over time (Table 3). There was also no significant difference between the treatment and control grids and their interaction over

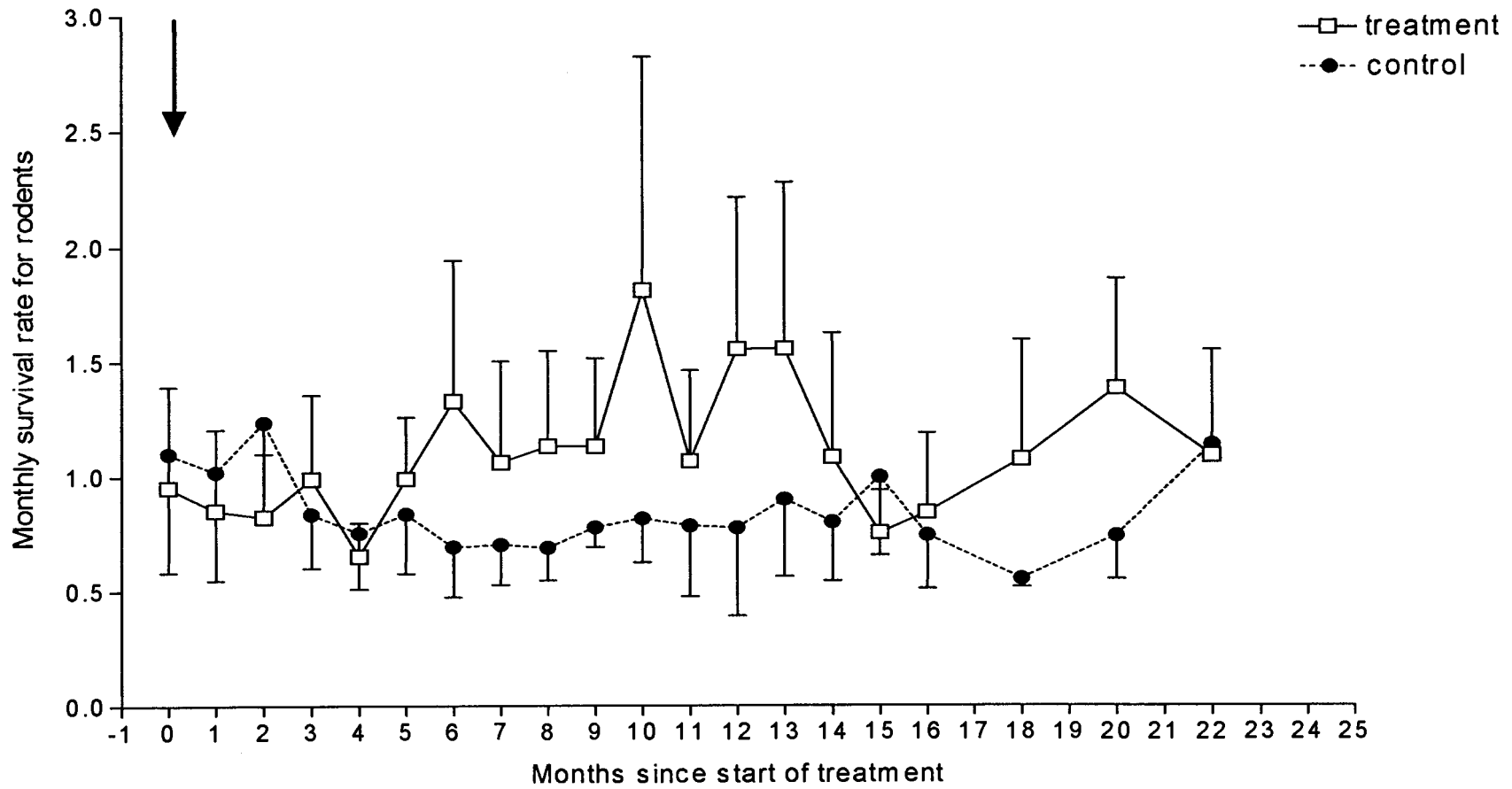


Figure 13. Temporal trends (mean \pm s.e.) in the monthly survival rates for the rodent community on the four treatment (□) and four control (●) grids illustrated over a 25 month period (↓ Start of treatment).

Table 3. Monthly survival rate results from the repeated measures analysis (ANOVAR) for the rodent community and each of the five species that occurred within the different sampling areas. Mean treatment effect represents the difference between the mean of the treatment grids against that of the control grids. The time effect represents differences over time of the treatment and control grids combined. The treatment and time interaction represents the differences between the treatment and control grids over time.

	Mean treatment effect		Time effect		Treatment and Time Interaction	
	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*
Total rodents	0.34	ns	1.08	ns	0.84	ns
<i>Mastomys natalensis</i>	0.87	ns	1.03	ns	1.21	ns
<i>Mus minutoides</i>	0.16	ns	2.57	0.02	0.28	ns
<i>Saccostomus campestris</i>	0.06	ns	0.56	ns	0.06	ns
<i>Dendromus melanotis</i>	0.11	ns	0.59	ns	0.08	ns
<i>Otomys angoniensis</i>	0.00	ns	0.95	ns	1.00	ns

* Huynh-Feldt adjusted *P* values

time (Table 3).

The monthly survival rates for *M. natalensis* on treatment grids increased after five months and remained higher than the monthly survival on the control grids (Fig. 14a). The monthly survival rates on the control grids were more constant, with less variation. The mean monthly survival rate for *M. natalensis* was higher on treatment grids, although not significantly (Table 3). The combined monthly survival rates for treatment and control grids did not increase nor decrease significantly over time (Table 3). The interaction between the treatment versus control grids and time was also not significant (Table 3).

No significance difference was recorded for the mean monthly survival rate for *M. minutoides* between the treatment and control grids (Table 3) (Fig. 14b). The total monthly survival rates for *M. minutoides* on the treatment and control grids combined, did however decrease over time (ANOVAR: $F = 2.87$, $P = < 0.05$). The interaction between treatment versus control grids and time did not show a significant difference suggesting that both treatment and control grids increased over time simultaneously (Table 3).

Monthly survival rates for *S. campestris*, *D. melanotis* and *O. angoniensis* were low (Fig. 14c,d,e). There were no significant differences between the mean treatment and control grids for any of the latter species. Nor were there any significant differences over time or the interaction between treatment versus control grids and time (Table 3).

REPRODUCTIVE RATES

The mean female reproductive rates was higher on the treatment grids than on the control grids (ANOVAR: $F = 6.90$, $P = < 0.05$). However, the female reproductive rates on the treatment grids fluctuated more than those on the control grids (Fig. 15). Female reproductive rates for rodents on treatment and control grids combined increased significantly over time, suggesting that the female reproductive rates increased for both treatment and control grids (ANOVAR: $F = 3.13$,

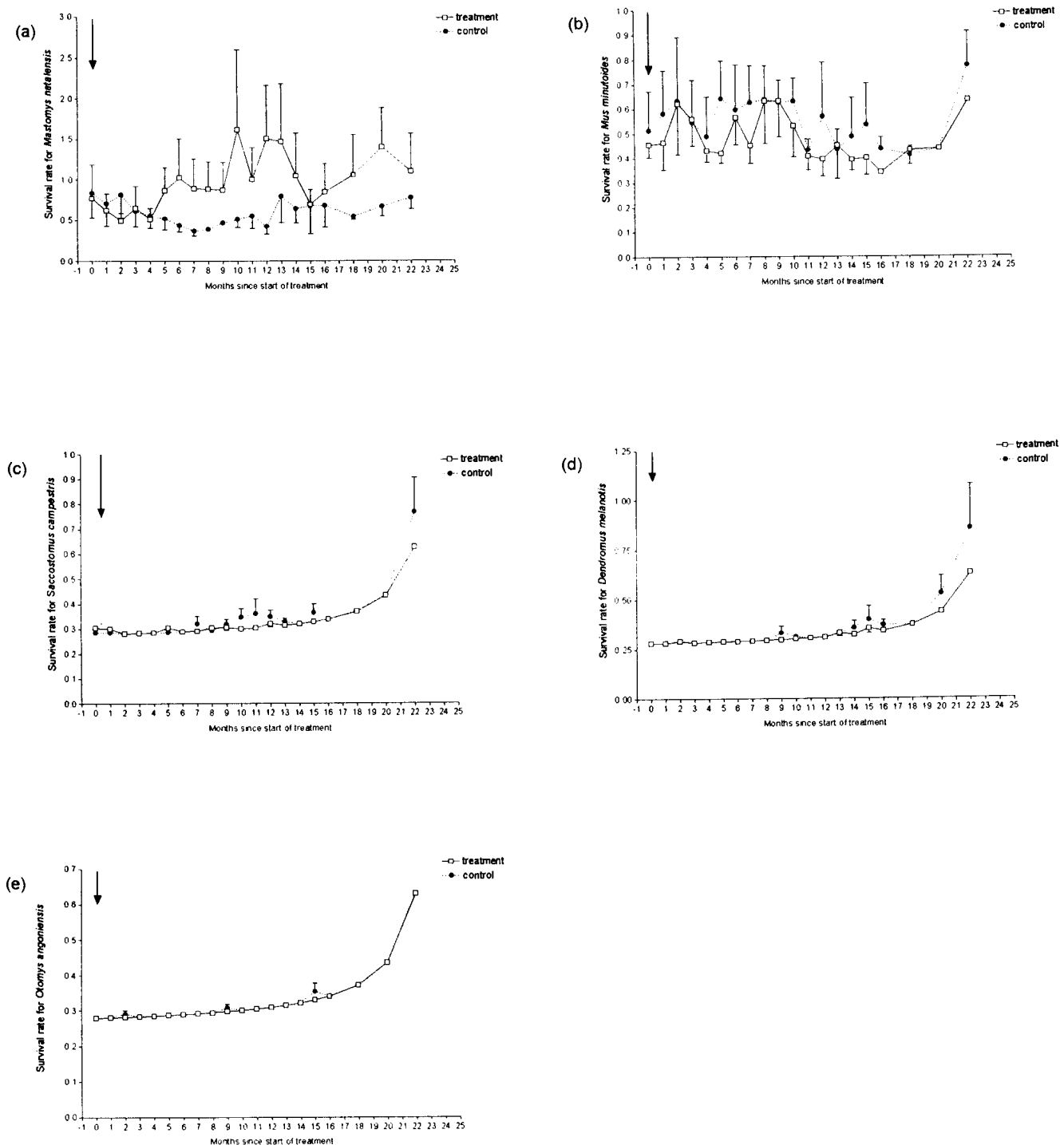


Figure 14. Temporal trends (mean \pm s.e.) in the monthly survival rates for (a) *Mastomys natalensis*, (b) *Mus minutoides*, (c) *Saccostomus campestris*, (d) *Dendromus melanotis* and (e) *Otomys angoniensis* individuals on the four treatment (\square) and four control (\bullet) grids illustrated over a 25 month period (\downarrow Start of treatment).

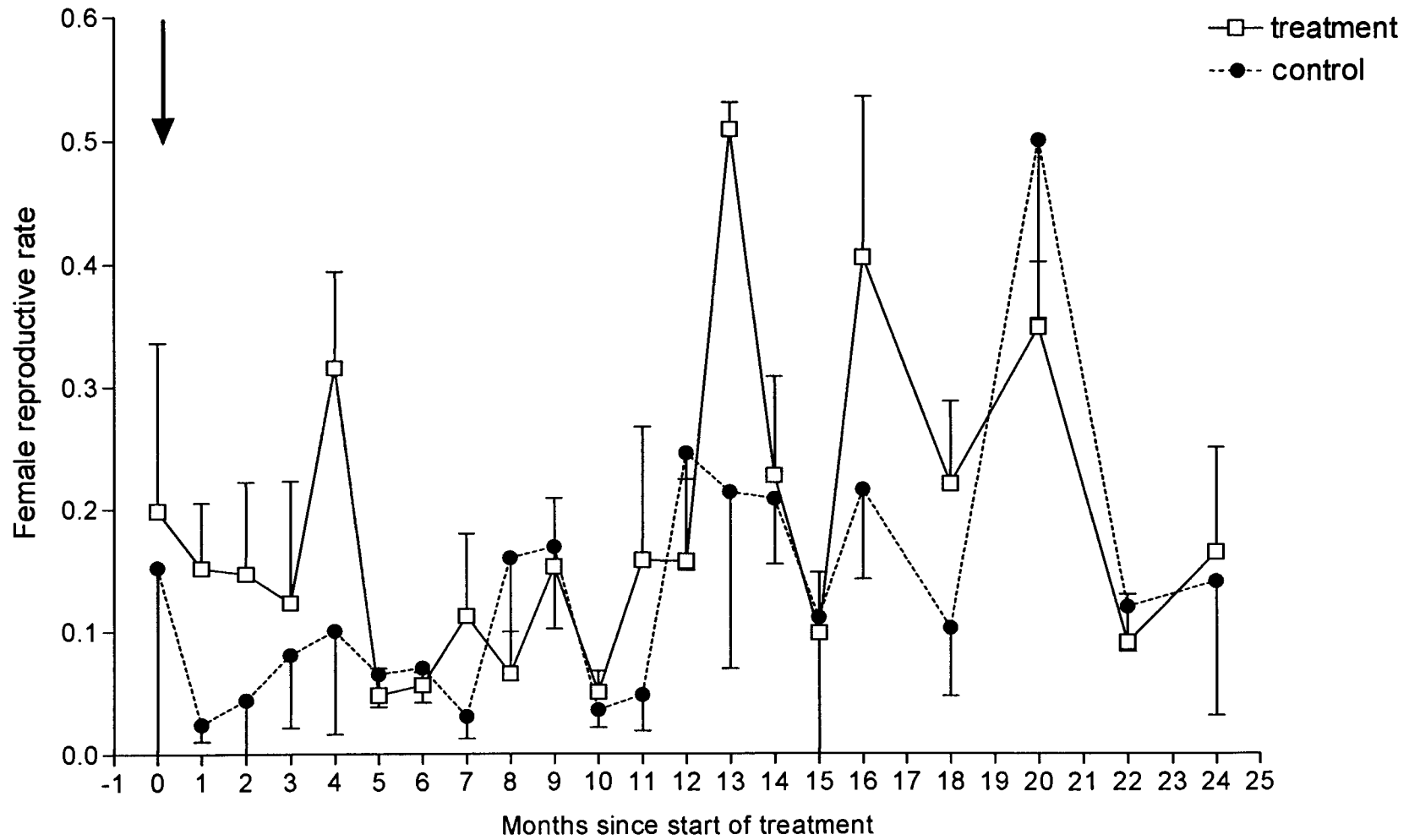


Figure 15. Temporal trends (mean \pm s.e.) in the female reproductive rate for the rodent community on the four treatment (\square) and four control (\bullet) grids illustrated over a 25 month period (\downarrow Start of treatment).

$P < 0.05$). However, values for the treatment and control grids did not differ significantly over time (Table 4). This may be due to values for female reproductive rates on the treatment grids fluctuating above and below those of the control grids. The reproductive rates for *M. natalensis* females did not show any significant trend (Table 4) and varied greatly both on the treatment and control grids (Fig. 16a).

The reproductive rates of *M. minutoides* female were significantly higher on the treatment than control grids (ANOVAR: $F = 5.54$, $P < 0.05$) and values for the treatment and control grids combined (ANOVAR: $F = 2.08$, $P < 0.05$) increased with time. Reproductive rates on treatment and control grids fluctuated in a similar fashion (Fig. 16b). The interaction between treatment versus control and time did show no significant difference (Table 4).

The reproductive rates of *S. campestris*, *D. melanotis* and *O. angoniensis* females did not show any significant differences between the mean treatment and control grids for any of the aforementioned species (Table 4). Overall female reproductive rates were low for all of these species, except for *S. campestris* which showed a higher rates on the treatment grids on a few occasions (Fig. 16c,d,e). There were also no significant differences between treatment and control grids for the interaction between treatment versus control grids and time (Table 4).

The mean male reproductive rate for rodents was lower on the treatment grids than on the control grids (Fig. 17). However, this was not significant (Table 5). The male reproductive rates of the treatment and control grids combined increased significantly over time (ANOVAR: $F = 2.47$, $P < 0.05$). The male reproductive rates on the treatment grids tended to be lower than those on control grids but the interaction between treatment versus control and time was not significantly different (Table 5).

The mean reproductive rate of *M. natalensis* males was lower and more variable on treatment than control grids but the differences was not significant (Table 5) (Figure 18a). The male reproductive rates on treatment and control grids decreased significantly (ANOVAR: $F =$

Table 4. Results of the repeated measures analysis (ANOVAR) for female reproductive rates for all rodents and each of the five species that occurred within the different sampling areas. Mean treatment effect represents the difference between the mean of the treatment grids against that of the control grids. The time effect represents differences over time of the treatment and control grids combined. The treatment and time interaction represents the differences between the treatment and control grids over time.

	Mean treatment effect		Time effect		Treatment and Time Interaction	
	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*
Total rodents	6.90	0.04	3.13	0.0006	0.93	ns
<i>Mastomys natalensis</i>	0.83	ns	1.23	ns	0.63	ns
<i>Mus minutoides</i>	5.54	0.08	2.08	0.05	1.32	ns
<i>Saccostomus campestris</i>	1.92	ns	1.19	ns	1.01	ns
<i>Dendromus melanotis</i>	0.28	ns	1.83	ns	0.62	ns
<i>Otomys angoniensis</i>	0.20	ns	0.96	ns	1.04	ns

* Huynh-Feldt adjusted *P* values

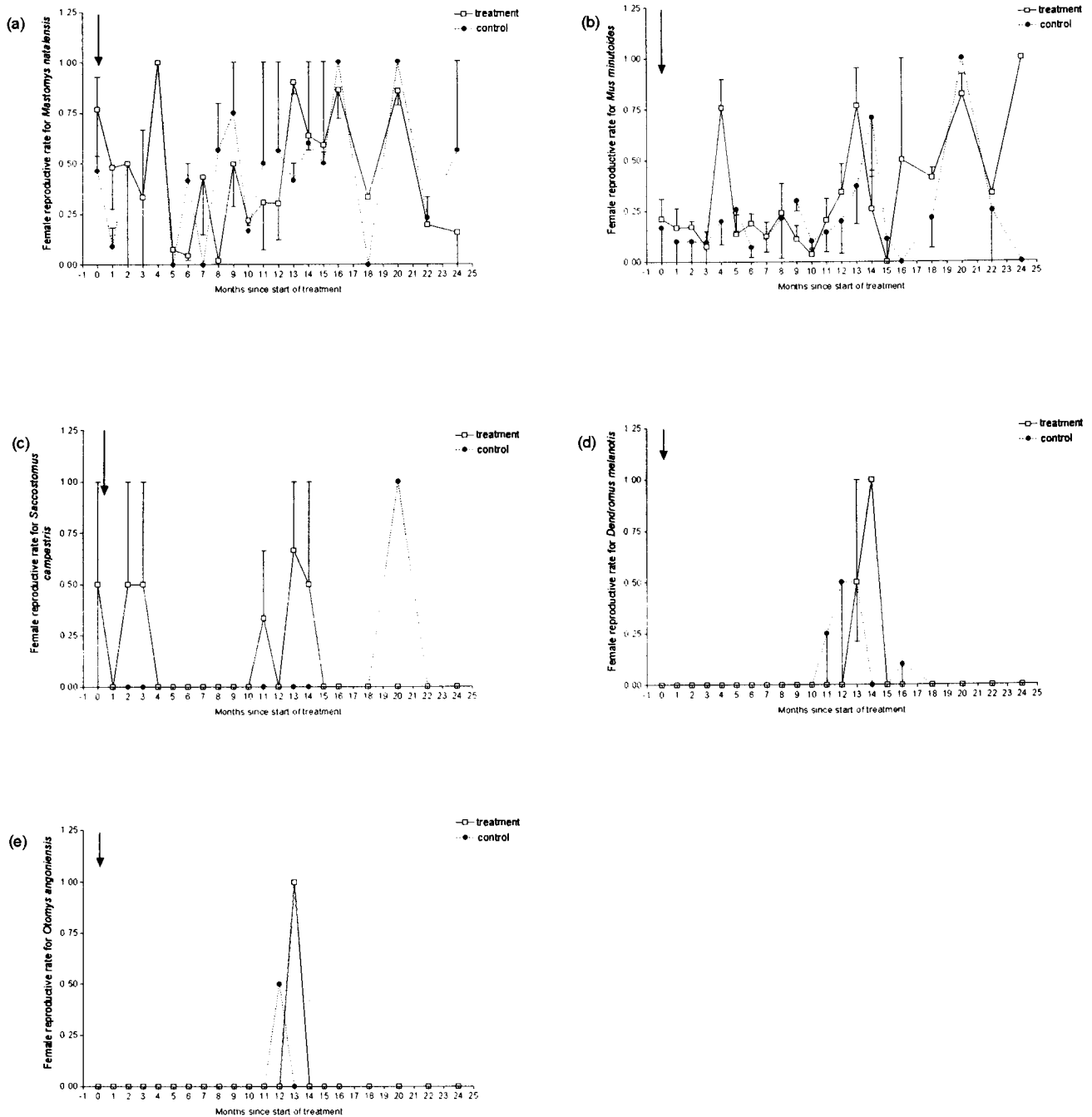


Figure 16. Temporal trends in the female reproductive rates (mean \pm s.e.) for (a) *Mastomys natalensis*, (b) *Mus minutoides*, (c) *Saccostomus campestris*, (d) *Dendromus melanotis* and (e) *Otomys angoniensis* on the four treatment (\square) and four control (\bullet) grids illustrated over a 25 month period (\downarrow Start of treatment).

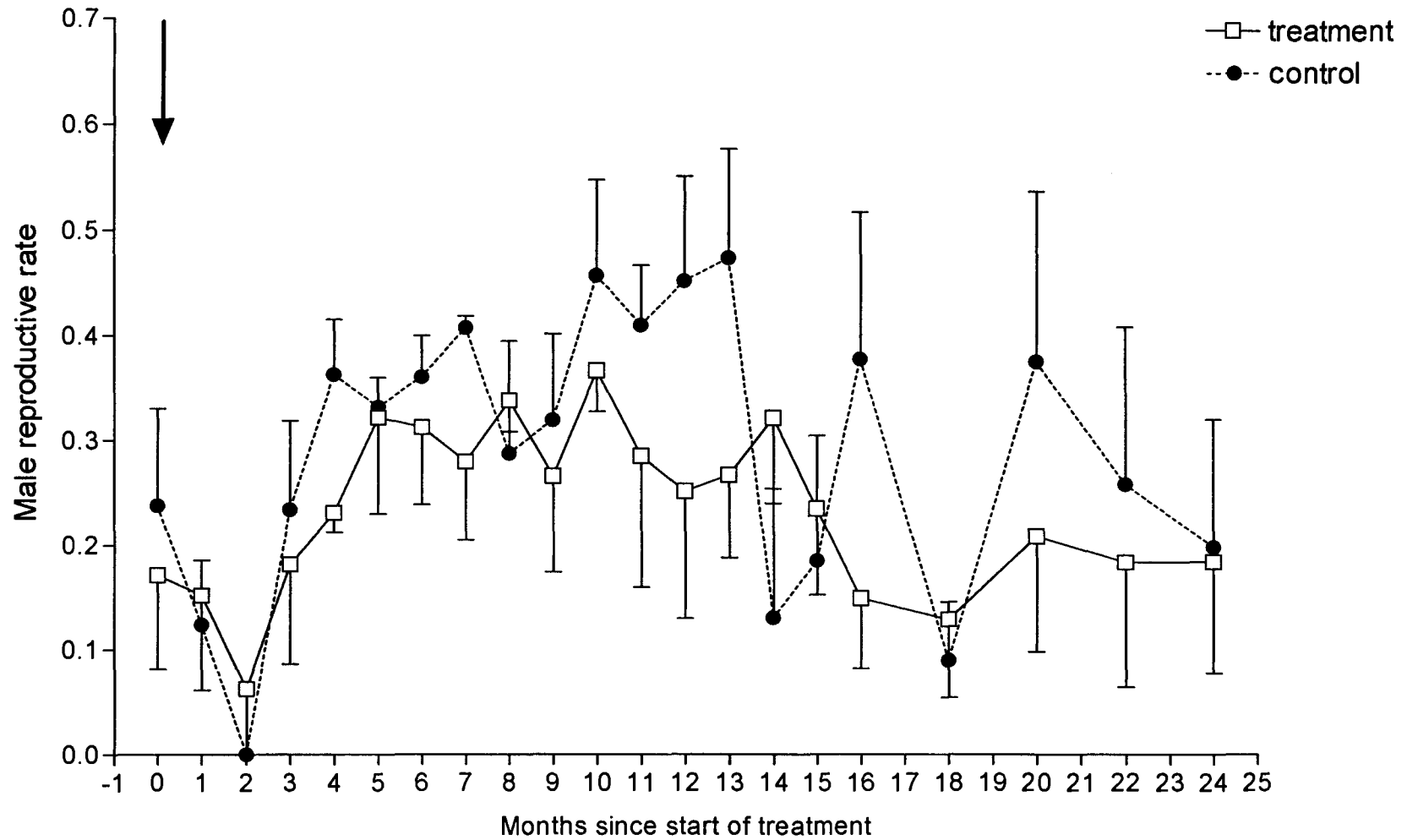


Figure 17. Temporal trends (mean \pm s.e.) in the male reproductive rates for rodents on the four treatment (\square) and four control (\bullet) grids illustrating changes over a 25 month period (\downarrow Start of treatment).

Table 5. Repeated measures analysis (ANOVAR) for male reproductive rates for rodents and each of the five species that occurred within the different sampling areas. Mean treatment effect represents the difference between the mean of the treatment and the control grids. The time effect represents differences over time of the treatment and control grids combined. The treatment and time interaction represents the differences between the treatment and control grids over time.

	Mean treatment effect		Time effect		Treatment and Time Interaction	
	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*
Total rodents	1.16	ns	2.47	0.01	0.76	ns
<i>Mastomys natalensis</i>	0.00	ns	2.58	0.02	0.80	ns
<i>Mus minutoides</i>	0.11	ns	3.34	0.03	0.46	ns
<i>Saccostomus campestris</i>	0.68	ns	0.73	ns	0.87	ns
<i>Dendromus melanotis</i>	1.73	ns	0.96	ns	0.74	ns
<i>Otomys angoniensis</i>	0.09	ns	1.50	ns	1.20	ns

* Huynh-Feldt adjusted *P* values

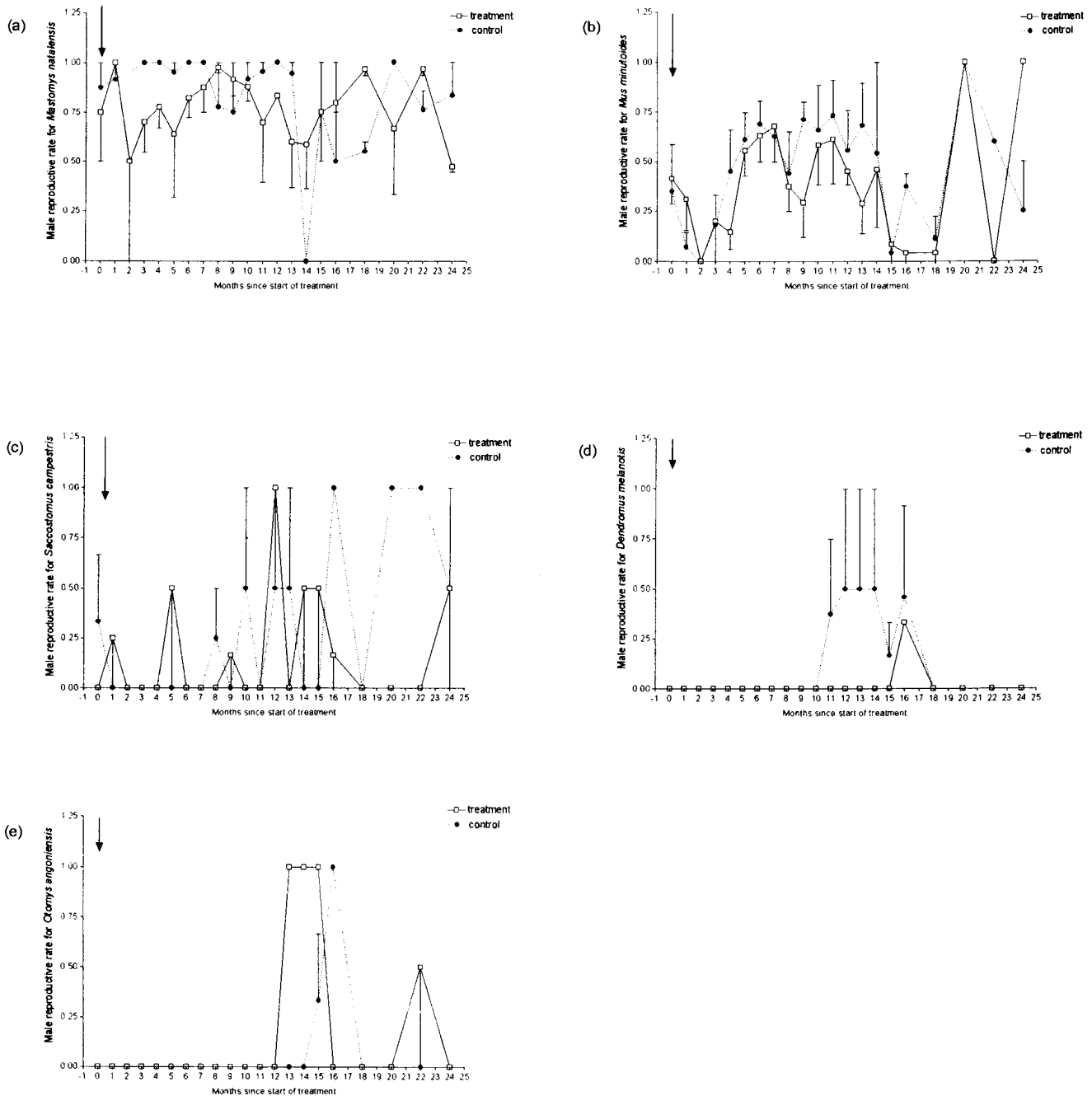


Figure 18. Temporal trends (mean \pm s.e.) in the male reproductive rates for (a) *Mastomys natalensis*, (b) *Mus minutoides*, (c) *Saccostomus campestris*, (d) *Dendromus melanotis* and (e) *Otomys angoniensis* on the four treatment (\square) and four control (\bullet) grids illustrated over a 25 month period (\downarrow Start of treatment).

2.58, $P < 0.05$). However when the interaction between treatment versus control and time was tested, no significant difference was recorded (Table 5).

The reproductive rates of *M. minutoides* males on treatment grids fluctuated simultaneously with those of the control grids but were slightly lower than the control grids (Fig. 18b). This difference was nevertheless not significant (Table 5) but the mean of the treatment and control grids combined did increase significantly over time (ANOVAR: $F = 2.58$, $P < 0.05$). The interaction between the reproductive rates of *M. minutoides* males and time was not significantly different (Table 5).

The reproductive rates for *S. campestris*, *D. melanotis* and *O. angoniensis* males on the treatment and control grids were not significantly different (Table 5). The male reproductive rates did not show any specific trends and did not differ significantly over time or between the treatment and control grids and time (Table 5) (Fig. 18c,d,e).

A significant decrease in the juvenile ratio of rodents was recorded over time for the treatment and control grids combined (ANOVAR: $F = 3.24$, $P < 0.05$). Apart from this difference no other trends were recorded for juvenile ratios of the rodents or any of the individual species (Table 6) (Figure 19). This suggests that juvenile ratios tended to remain constant over time and was similar for treatment and control grids.

Table 6. Repeated measures analysis (ANOVAR) for juvenile ratio results for rodents and each of the five species that occurred within the different sampling areas. Mean treatment effect represents the difference between the mean of the treatment and the control grids. The time effect represents differences over time of the treatment and control grids combined. The treatment and time interaction represents the differences between the treatment and control grids over time.

	Mean treatment effect		Time effect		Treatment and Time Interaction	
	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*	<i>F</i>	<i>P</i> (H-F adj)*
Total rodents	1.71	ns	3.24	0.0001	0.77	ns
<i>Mastomys natalensis</i>	1.51	ns	2.36	ns	0.50	ns
<i>Mus minutoides</i>	0.68	ns	2.8	ns	0.59	ns
<i>Saccostomus campestris</i>	2.33	ns	1.29	ns	0.64	ns
<i>Dendromus melanotis</i>	1.00	ns	1.00	ns	1.00	ns
<i>Otomys angoniensis</i>	0.02	ns	1.14	ns	0.69	ns

* Huynh-Feldt adjusted *P* values

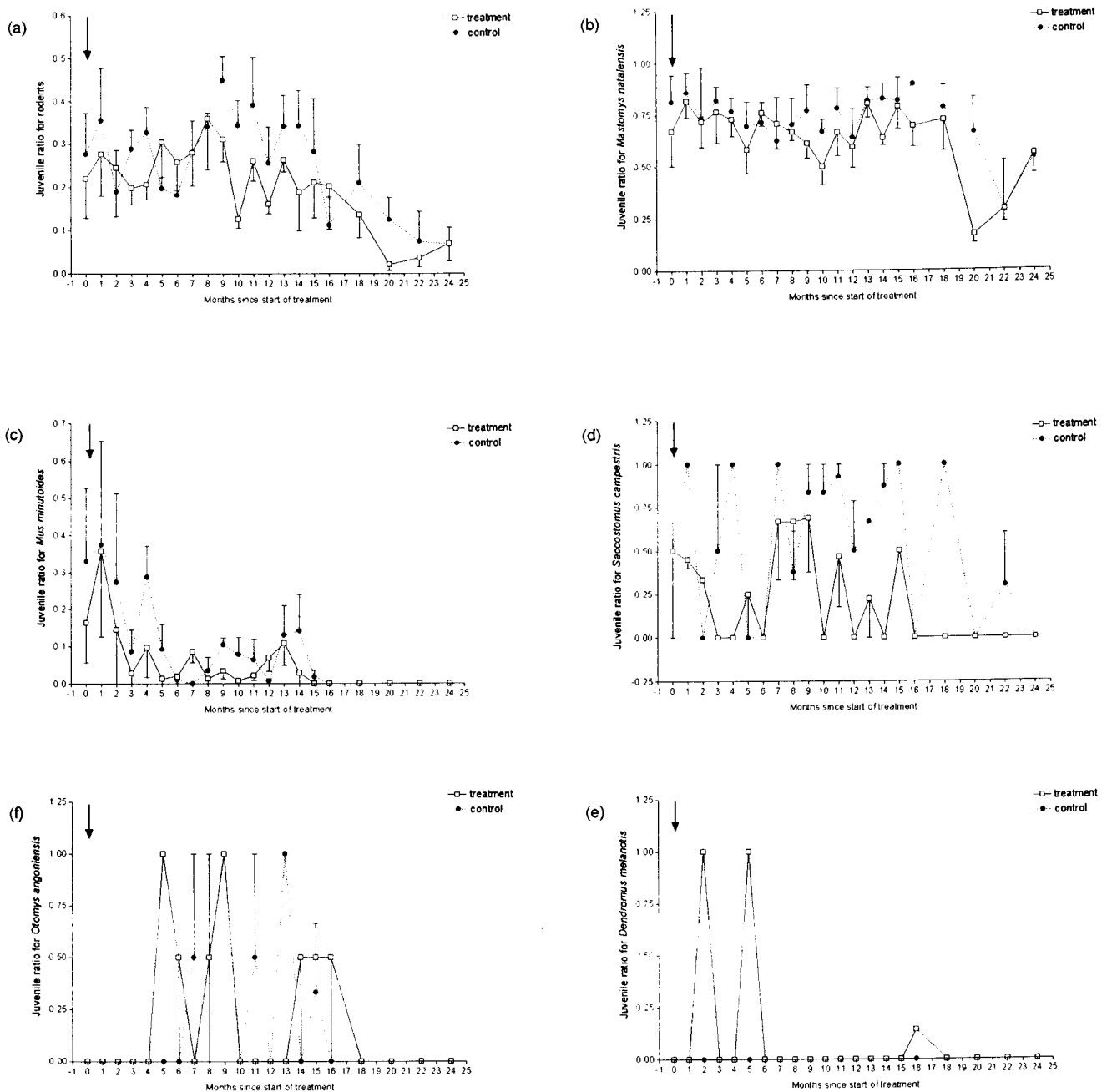


Figure 19. Temporal trends (mean \pm s.e.) in the proportion of juveniles to the total MNA of the rodent community or individuals species in (a) rodent community (b) *Mastomys natalensis*, (c) *Mus minutoides*, (d) *Saccostomus campestris*, (e) *Dendromus melanotis* and (f) *Otomys angoniensis* respectively on the four treatment (\square) and four control (\bullet) grids illustrating changes over a 25 month period (\downarrow Start of treatment).

CHAPTER 5

DISCUSSION

DIET PREFERENCES

Abramsky (1978) reported an increase in species diversity when he supplemented the rodent community with a scarce or new resource. This increase in diversity resulted from the invasion of a new seed eating species. Other species already present in the community were mostly insectivores and did therefore not respond to the supplementary food supplied. Since none of the species were granivore, they were not affected by the amount of seeds available.

Rodents preferred seeds with a high energy content (Kerley & Erasmus, 1991) and sunflower seed, used in the present study to supplement diet, is a high in protein (22.2%) and is attractive to rodents (Bomford & Redhead, 1987). Hence, it may be assumed that most of the rodents of the newly rehabilitated area may use this food resource.

It is also evident from the results that most of the additional sunflower seeds were consumed. This indicates that rodents utilise this resource. The consumption rate also coincides with the numerical abundance of *M. natalensis*.

COMMUNITY RESPONSE

The preponderance of *M. natalensis* on my study sites confirms that the rodent assemblages here were in the early phase of ecological succession in the response to the disturbances evoked by sand mining (see Ferreira, 1997). However, densities were low and varied substantially between trapping grids. Further habitat development will most probably give rise to *M. natalensis* being replaced in dominance by *S. campestris* and *A. chrysophylis* (Ferreira & Van Aarde, 1996; Ferreira & Van Aarde, 1999). Early seral stages of coastal dune succession are associated with

high production and a lack of structural complexity (Ferreira & Van Aarde, 1996). However, this stage is followed by the development of a scrubland with limited seed production associated with a dramatic decline in rodent numbers (Ferreira, 1997) and a change in the characteristics of rodent assemblages (Ferreira & Van Aarde, 1999). Accordingly food supplementation on the study sites may have had some predictable consequences for the development of rodent assemblages. On the one hand it may have benefited the early colonisers (see MacArthur, 1972), such as *M. natalensis*, giving rise to reduced rates of colonisation of such areas by potential competitors (*i.e.* *S. campestris* and *A. chrysophylis*). On the other hand food supplementation may have negated competitive interactions for food as a resource, thus giving rise to an increased rate in the development of rodent assemblages. Should food not be a limiting factor in the development of these assemblages, supplementation is expected not to have any influence on them.

The increase in *M. natalensis* numbers on the treatment grids in contrast to control grids may be ascribed to supplementation representing a secondary disturbance, giving rise to *M. natalensis* benefiting as a pioneer. However, food supplementation may have merely increased the period of abundant food supply, thereby providing early colonisers, such as *M. natalensis*, the time to increase locally through breeding on the sites rather than increasing in abundance through immigration (dispersal from other sites).

Given that intraspecific competition may limit the abundance of *M. natalensis* during early stages of habitat development (see Ferreira, 1997), food supplementation during my study also may have given rise to an increase in this species' numbers by relaxing the consequences of intraspecific competition. The amount of seed taken increased with an increase in rodent numbers, and more specifically the numbers of *M. natalensis*, supporting the suggestion that supplementary food enables *M. natalensis* to increase in numbers. This is in agreement with studies elsewhere where *M. natalensis* (Monadjem & Perrin, 1998) and other rodents (*e.g.* Akbar & Gorman, 1993; Doonan & Slade, 1995; Perrin & Johnson, 1999) tend to increase in numbers with food

supplementation. There is strong evidence that food supply frequently limits population density (see Boutin, 1990). However, different to these studies and to the situation with *M. natalensis*, the numbers of other species typically occurring at low numbers during early successional seres (*M. minutoides*, *D. melanotis*, *S. campestris* and *O. angoniensis*) did not increase with food supplementation. This is in accordance with the results of Monadjem and Perrin (1998) where only *M. natalensis* increased while other species did not respond to the supplementary food.

The presence of species seem to be affected by habitat requirements and suitability (Ferreira, 1997). However, rodent communities on areas supplemented with sunflower seed became more dissimilar over time compared to those with no supplementary food, suggesting that rodent community development may also be related to factors such as food availability. Ferreira (1997) concluded that seedbank composition had a greater explanation value for rodent community composition than habitat structure. Limitations imposed by food availability thus seem to be relevant to the development of these rodent assemblages in a relative unstable environment.

SPECIES DIVERSITY

In addition to the increased densities of *M. natalensis* numbers, total rodent densities increased on treatment grids and species richness was lower on control grids. Although these differences were not significant, the combined effect of total rodent densities and species richness caused species diversity to be significantly lower on treatment grids than on control grids. Species diversity decreased with food supplementation due to an increase in the abundance of *M. natalensis*, rather than a change in the number of species. Food supplementation also reduced species diversity in a rodent community in Swaziland, South Africa (Monadjem & Perrin, 1998) due to an increase in the proportional representation of one species, namely *M. natalensis*.

The decrease in species diversity in the present study is in accordance with the findings of Abramsky (1978), who illustrated an increase in diversity through the increase of a scarce

resource. However, the increase in diversity recorded by Abramsky (1978) could be explained by an increase in species richness and is at variance with my study where the decrease in diversity could not be explained by a change in the number of species. By only increasing an existing portion of the resource spectrum, thereby benefiting *M. natalensis* as an opportunistic coloniser (Meester, Lloyd & Rowe-Rowe, 1979), I reduced species diversity, probably through dominance by competitively superior exploiters of the augmented resource.

Pimm and Pimm (1982) tested and supported a model where the subordinate species is forced to specialise on clearly inferior resources because the dominant species controls the better or more prevalent resources. *Mastomys natalensis* thus may force the second most dominant species, in our case *M. minutoides*, from the superior resource. The inferior resource still may have been sufficient to support and maintain the numbers of subordinate species on the treatment and control grids.

Ferreira (1997) suggested that the only period during which rodent communities may be shaped by interspecific interactions is during the early stages of succession. However, least square regression analysis that investigated the relationships between species in the present study gave no indication of negative interspecific interactions between specific species. Ferreira (1997) came to the conclusion that Rosenzweig's (1979) argument hold for the rodent community. Both the present study and the removal experiment conducted by Ferreira (1997), could not illustrate interspecific interaction, possible because all species comprising the rodent community are native species which may have been shaped by past competitive interactions. This may minimize present competition. The increase in *M. natalensis* numbers therefore affected only the species diversity with no influence on interspecific interactions. This rather illustrates and confirms the results of the removal experiment by Ferreira (1997) that intraspecific interactions could be inferred for the pioneer and dominant species *M. natalensis*.

SURVIVAL OF RODENTS

One would expect that the survival of individuals on the treatment grids would increase because of the abundance of food. In contrast, food on the control grids may become relatively scarce in comparison with the treatment grids possibly due to successional changes in habitat characteristics. Habitat characteristics are not as favourable for rodents in the later successional stages compared to the onset of the newly rehabilitating stage (see Ferreira, 1997). However, from the literature it is clear that supplementary food can have one of three possible effects on the survival of animal populations. The first effect can be a positive one where the survival probability increases as a result of the food provided (*e.g.* Sullivan & Sullivan, 1982; Sullivan, Sullivan & Krebs, 1983; Cole & Batzli, 1978; Klenner & Krebs, 1991). Supplementary food can also have no effect on the survival probability of a population or community (*e.g.* Taitt, 1981; Taitt & Krebs, 1981; Sullivan, 1990; Adler, 1998; Desy & Batzli, 1989; Akbar & Gorman, 1993). The third response can be negative with survival decreasing with the provisioning of food (*e.g.* Klenner & Krebs, 1991; Doonan & Slade, 1995).

Supplementary food in the present study had no effect on the survival of the total rodent community or on one of the species, with the exception of *M. minutoides*. *Mus minutoides* survival decreased over time on the treatment and control grids combined. This suggests that the successional change in the newly rehabilitated areas result in unfavourable conditions for the survival of *M. minutoides* individuals. This decrease in the survival probability of *M. minutoides* individuals coincides with the decrease in the minimum number of individuals alive on both treatment and control grids. These areas therefore become less suitable for their survival because of factors other than the availability of supplemented sunflower seeds. However, the survival of *M. natalensis* individuals did not increase with supplementary food and can therefore not explain the maintaining of high numbers of this species on the treatment grids.

REPRODUCTIVE RATES

Breeding intensity of adult females increased in response to food supplementation in 18 of the 25 studies Boutin (1990) reviewed. In my study sites female and male breeding rates of rodents and all the individual species did not increase in response to food supplementation. *Mus minutoides* is a solitary species (Skinner & Smithers, 1990) and may therefore exclude conspecifics from their territories and thus prevent an increase in numbers from occurring (Monadjem & Perrin, 1996). Although it seems as if female reproductive rates are higher on the treatment grids than on the control grids for *M. minutoides* and rodent females, this was not necessarily due to the supplementary food. When the influence of supplementary food on the treatment grids was investigated over time for *M. minutoides* and rodent females, there were no significant differences implying that reproductive rates were variable for both treatment and control grids and differences for their means was not the result of supplementary food (see Fig. 16b).

Although *M. natalensis* is a social species (Skinner & Smithers, 1990) and tolerate other individuals in close proximity, their female and male reproductive rates on the treatment grids did not differ from that of the control grids over time. *Mastomys natalensis* individuals must therefore be able to increase and maintain a high density possibly through immigration.

The proportional contribution of juveniles to the MNA for the treatment and control grids combined declined over the study period, suggesting that food supplementation either did not enhance reproductive output or juvenile survival to the age where juveniles became trapable. Lack of temporal trends in the breeding rates for both adult males and adult females in response to food supplementation support the notion that breeding rate amongst rodents was not affected by food supplementation. The tendency for *M. natalensis* numbers to increase with food supplementation may thus be ascribed to immigration rather than survival or dispersal.

CONCLUSION

Most of the species in the rodent community on the newly rehabilitated areas were granivores. The provision of sunflower seeds in an effort to increase only a small part of the resource spectrum thus had the likelihood of affecting this rodent community. Food supplementation resulted in a decrease in diversity as MacArthur's (1972) model predicted. However, the decrease in diversity was not as a result of a decrease in species richness, but rather the result of the increase and maintained dominance of the pioneer species *M. natalensis*. No interspecific interactions could be demonstrated but rather the existence of intraspecific interactions for *M. natalensis*. The proportion contribution of juveniles to the MNA for the treatment and control grids combined declined over the study period, suggesting that food supplementation either did not enhance reproductive output or juvenile survival to the age where juveniles became trapable. Lack of temporal trends in the breeding rates for both adult males and adult females in response to food supplementation support the notion that breeding rate amongst rodents was not affected by food supplementation. The tendency for *M. natalensis* numbers to increase with food supplementation may thus be ascribed to immigration rather than survival or dispersal. The rodent community is therefore shaped by factors other than interspecific interactions, with supplementary food having no effect on species other than *M. natalensis*.

CHAPTER 6

SYNTHESIS

Theory predicts that species diversity of rodent communities is positively correlated with the breadth of the resource spectrum. According to a model by MacArthur (1972), species diversity can be increased by a decrease in average width of the utilization curves, by an increase in average overlap between species, or by an increase in the resource spectrum. Different responses to increased production were suggested to be dependent on the pattern of increase in production. An increase in the total resource spectrum would result in increased diversity because resources that were formerly too scarce to form an adequate diet, and therefore not counted as part of the resource spectrum, are now sufficient to support species survival. However, diversity may also be decreased through dominance by those species that are competitively superior in exploiting an augmented resource when only a small part of the total resource spectrum is increased. This implies that species in the community will only coexist if the overlap of resource use between these species is relatively small. Different responses to increased production of resources are therefore dependent on the pattern of the increase in production and can shed light on mechanisms responsible for community structure, like possible competitive interactions.

In the present study, only a small part of the existing resource spectrum was increased. I expected that species diversity would decrease as a result of the supplementary, since MacArthur (1972) predicted such a decrease if only a small part of the total resource spectrum was increased. The addition of sunflower seeds to treatment grids indeed resulted in a decrease in diversity as MacArthur's (1972) model predicted. However, this decrease was not as a result of a decrease in species richness, but rather the result of the increase and maintained dominance of the pioneer species, *Mastomys natalensis*. The rodent community is therefore shaped by factors other than interspecific interactions, with supplementary food having no effect on species other than *M.*

natalensis. To come to these results the following hypotheses were investigated.

Hypothesis 1: *The diets of rodent species that occur on the newly established rehabilitating coastal dune forests do not differ from each other.*

Most of the species, with the exception of *Otomys angoniensis* take seeds as part of their diet. Other species that occurred in the newly rehabilitated areas included *M. natalensis*, *Mus mimutoides*, *Saccostomus campestris* and *Dendromus melanotis* and they all take seeds as part of their diet. The provision of sunflower seeds was therefore relevant to all the species contained within the rodent community. Most of the seed provided were removed by rodents. However, *M. natalensis* was the only species that responded numerically to the additional food provided on the treatment grids. Their numbers were also correlated with the amount of sunflower seed taken. It can therefore be deduced from that although other species may take sunflower seed, they did not use it in such a manner or proportion which may have had consequences for their population demography. This hypothesis was rejected since *O. angoniensis* did not take seed, while other species recorded in the present study did consume seeds.

Hypothesis 2: *Species composition, species richness and species diversity of rodent assemblages on newly established rehabilitating stands is not influenced by an increase in food availability.*

The increase in food availability did not influence the species richness and rodent community densities. However, it did result in a decrease in species diversity on those areas that were supplemented with sunflower seeds. This decrease in species diversity resulted from the proportional increase in the number of *M. natalensis* individuals and no interspecific interactions could be demonstrated. This hypothesis was partially rejected since only species diversity was influenced by supplementary feeding.

Hypothesis 3: *Species specific survival for rodents on the rehabilitating stands is not affected by food availability.*

The species specific survival rate of only one of the species, *M. minutoides*, decreased with time since the onset of the study. This may be the result of the successional changes on both the control and treatment grids in habitat characteristics. The presence of *M. minutoides* on the newly rehabilitating areas must be influenced by factors other than the availability of sunflower seeds that was not only provided as supplementary food but also forms part of the existing resource spectrum since it is sown as part of the rehabilitation program.

The survival probability of *M. natalensis* individuals were not influenced by the supplementary food. Demographic variables other than survival are responsible for their increase in numbers on treatment grids with time since the onset of the study. Therefore, this hypothesis could not be rejected.

Hypothesis 4: *The species specific reproductive rate for rodents in the rehabilitating stands is not affected by food availability.*

Temporal trends in the reproductive rates of adults and the proportion of juveniles on both the treatment and control grids imply that supplementary did not affected population output.

This hypothesis could therefore not be rejected since there was no significant indication that supplementary food influenced the reproductive output of rodents in this study over time.

Resilience of a developing rodent community

From the studies conducted on the rodent communities of newly rehabilitated areas north of Richards Bay, South Africa, it is clear that these communities are not shaped by interspecific interactions. Past competitive interactions may have shaped species so that those that co-occur at present, are occupying distinct niches. This is possible since all the species that occur in the

rodent community are native to the area and co-occurred before the disturbance of the area if areas were equal to the unmined forests as is assumed. These species also co-occur in adjoining areas which serve as the source populations for the newly rehabilitating areas.

Pimm (1991) discussed resilience of communities at great length in his book “ The Balance of Nature”. Resilience is defined as the rate at which disrupted population density returns to equilibrium. Resilience depends on many factors and at different levels of ecological organization. There are three different kinds or levels of factors that affect resilience: population, community and ecosystem. How fast a population take to recover from a severe decline in density could depend on it’s reproductive rate: the more young produced, the faster the population can recover to it’s former level. Population densities of small-bodied species may increase or decrease more rapidly from year-to-year than do large-bodied species. How fast a population will increase may also depend on the species’ interactions with other species in the community. If an area is disturbed, the densities of a set of interacting species will depend on the least resilient species since no species density can return to equilibrium until all the others have done so. This suggest that food-chain length may have a strong effect on resilience. Finally, resilience will depend on how quickly the nutrients necessary for a species’ growth become available. The nutrient availability partly depends on food-web structure but also on abiotic processes.

How fast a community recovers will therefore depends on the nutrient cycle, interactions between species and on population characteristics. The recovery of the rodent community therefore depends on various factors of which this study only investigated a small part. It is clear from the present study that species diversity and the *M. natalensis* population is influenced by supplementary food. No interspecific interaction could be identified indicating that the development of this community is likely to be dependent on other factors and most probably on the level of the nutrient cycle. It can therefore be concluded that there is no single answer to what determines resilience and there is a recognition that many factors operate on the spacial and

temporal scale (Pimm, 1991).

Further ideas that could be investigated

The use of habitat space seem to play an important role in the different social structures of different species. It would therefore make good sense to investigate the habitat ranges and uses of the different species so as to find an explanation for the increase in rodent numbers.

The present experiment was conducted in the newly rehabilitating areas and showed that *M. natalensis* responded positively to the provision of supplementary food. *Mastomys natalensis*, considered to be an opportunistic and pioneer species, remained dominant on the treatment grids. It was speculated that the increase in their numbers could have been as a result of the supplementary food acting as an additional disturbance to the area. It would be interesting to investigate the effect of supplementary food on rodent communities inhabiting areas in the older stages of rehabilitation. However, it is important to note that this was designed as a long term study since some influences of supplementary food on rodent communities are only evident after a long period.

REFERENCE

- ABRAMSKY, Z. (1978) Small mammal community ecology: Changes in species diversity in response to manipulated productivity. *Oecologia*, **34**, 113-123.
- ADLER, G.H. (1998) Impacts of resource abundance on populations of a tropical forest rodent. *Ecology*, **79**, 242-254.
- AKBAR, Z. & GORMAN, M.L. (1993) The effect of supplementary feeding upon the demography of a population of woodmice *Apodemus sylvaticus*, living on a system of maritime sand dunes. *Journal of Zoology, London*, **230**, 609-617.
- ANDERSON, D.C. & MACMAHON, J.A.. (1985) The effects of catastrophic ecosystem disturbance: The residual mammals at Mount St. Helens. *Journal of Mammalogy*, **66**, 581-589.
- AVIS, M.A. (1992) Climate, soils and land use potential. *Environmental impact assessment. Eastern shores of lake St Lucia. (Kingsa / Tojan lease area) Specialist report* (eds. Coastal and Environmental Services, Vol. I.) pp 172-176. CSIR, Pretoria.
- BEGON, M., HARPER, J.L. & TOWNSEND, C.R. (1990) *Ecology. Individuals, populations and communities*. Blackwell Scientific Publications, Oxford.
- BENDER, E.A., CASE, T.J. & GILPIN, M.E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology*, **65**, 1-13.
- BOMFORD, M. & REDHEAD, T. (1987) A field experiment to examine the effects of food quality and population density on reproduction of wild house mice. *Oikos*, **48**, 304-311.
- BOWERS, M.A., THOMPSON, D.B. & BROWN, J.H. (1987) Spatial organization of a desert rodent community: food addition and species removal. *Oecologia*, **72**, 77-82.
- BOUTIN, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, **68**, 203-220.
- BROWN, J.H. & DAVIDSON, D.W. (1977) Competition between seed-eating rodents and ants in

- the desert ecosystems. *Science*, **196**, 880-882.
- BROWN, J.H. & MUNGER, J.C. (1985) Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, **66**, 1545-1563.
- CARR, M.R. (1996) *Primer User Manual (Plymouth Routines in Multivariate Ecological Research)*, Plymsolve, Plymouth, UK.
- CAUGHLY, G. (1977) *Analysis of Vertebrate populations*, John Wiley & Sons, New York.
- CHARNOV, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.
- CHEAL, P.D. (1979) Vegetation analysis - an essential part of (small) mammal studies. *Bulletin for the Australian Mammalogy Society*, **6**, 46-47.
- CHITTY, D. & PHIPPS, E. (1966) Seasonal changes in survival in mixed populations of two species of voles. *Journal of Animal Ecology*, **35**, 313-331.
- CLARK, B.K. & KAUFMAN, D.W. (1990) Short-term responses of small mammal to experimental fire in tallgrass prairie. *Canadian Journal of Zoology*, **68**, 2450-2454.
- CODY, M.L. (1975) Towards a theory of continental species diversities. *Ecology and Evolution of Communities* (eds. M.L. Cody & J.M. Diamond), pp 214-257. Belknap, Cambridge, MA.
- COLE, F.R. & BATZLI, G.O. (1978) Influence of supplemental feeding on a vole population. *Journal of Mammalogy*, **59**, 809-819.
- COLWELL, R.K. & WINKLER, D.W. (1984) A null model for null models in biogeography. *Ecological Communities: Conceptual Issues and the Evidence* (eds. D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle), pp 344-359. Princeton University Press, Princeton, NJ.
- CONNELL, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition

- past. *Oikos*, **35**, 131-138.
- CONNELL, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist*, **122**, 661-696.
- DESY, E.A. & BATZLI, G.O. (1989) Effects of food availability and predation on Prairie Vole demography: a field experiment. *Ecology*, **70**, 411-421 .
- DIAMOND, J. & CASE, T.J. (1986) *Community Ecology*. Harper & Row, New York.
- DOONAN, T.J & SLADE, N.A. (1995) Effects of supplemented food on population dynamics of cotton rats, *Sigmodon hispidus*. *Ecology*, **76**, 814-826.
- DICKMAN, C. (1988) Sex-ratio variation in response to interspecific competition. *The American Naturalist*, **132**, 289-297.
- FERREIRA, S.M. (1993) *The effect(s) of habitat rehabilitation at Richard's Bay on small mammal community structure*. MSc thesis, University of Pretoria, Pretoria.
- FERREIRA, S.M. (1997) *Determinants of small mammal community structure on rehabilitating dune forests in northern KwaZulu/Natal, South Africa*. PhD thesis, University of Pretoria, Pretoria.
- FERREIRA, S.M. & VAN AARDE, R.J. (1996) Changes in community characteristics of small mammals in rehabilitating coastal dune forests in northern KwaZulu/Natal, South Africa. *African Journal of Ecology*, **34**, 113-130.
- FERREIRA, S.M. & VAN AARDE, R.J. (1997) The chronosequence of rehabilitating stands of coastal dune forests: do small mammals confirm it? *South African Journal of Science*, **93**, 211-214.
- FERREIRA, S.M. & VAN AARDE, R.J. (1999) Habitat association and competition in *Mastomys-Saccostomus-Aethomys* assemblages in coastal dune forests. *African Journal of Ecology*, **37**, 121-136.

- FORD, R.G. & PITELKA, F.A. (1984) Resource limitation in populations of the California vole. *Ecology*, **65**, 122-136.
- FOX, B.J. (1990) Changes in the structure of small mammal communities over successional time scales. *Oikos*, **59**, 321-329.
- FOX, B.J. & FOX, M.D. (1978) Recolonisation of coastal heath by *Pseudomys novaehollandiae* (Muridae) following sand mining. *Australian Journal of Ecology*, **3**, 447-465.
- FOX, B.J. & FOX, M.D. (1981) A comparison of vegetation classification as descriptors of small mammal habitat preferences. *Vegetation Classification in the Australian Region* (eds. A.N. Gillison & D.J. Anderson). The Commonwealth Scientific and industrial Research Organization with Australian National University Press, Canberra.
- FOX, B.J. & FOX, M.D. (1984) Small mammal recolonisation of open forest following sand mining. *Australian Journal of Ecology*, **9**, 241-252.
- FOX, B.J. & MCKAY, G.M. (1981) Small mammal responses to pyric successional changes in eucalypt forest. *Australian Journal of Ecology*, **6**, 29-41.
- FOX, B.J., QUINN, R.D. & BREYTENBACH, G.J. (1983) A comparison of small mammal succession following fire in shrub lands in Australia, California and South Africa. *Proceedings of the Ecological Society of Australia*, **14**, 179-197.
- FRETWELL, S.D. & LUCAS, H.L. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *I. Theoretical development. Acta Biotheoretica*, **19**, 16-36.
- GEE, J.H.R. & GILLER, P.S. (1987) *Organization of Communities: Past and Present*. Blackwell Scientific Publications, Oxford.
- GILL, A.M. (1975) Fire and the Australian Flora: a review. *Australian Forum*, **38**, 4-25.
- HULME, P.E (1998) Post-dispersal seed predation and seed bank persistence. *Seed Science Research*, **8**, 513-519.

- KEDDY, P.A. (1989) *Competition*. Chapman & Hall, London.
- KERLEY, G.H.I. & ERASMUS, T. (1991) What do mice select for in seeds? *Oecologia*, **86**, 261-267.
- KIRKLAND, G.L. (1990) Patterns of initial small mammal community change after clearcutting of temperate North American forests. *Oikos*, **59**, 313-320.
- KLEINBAUM, D.G., KUPPER, L.L., MULLER, K.E. & NIZAM, A. (1998) *Applied regression analysis and other multivariable methods*. Duxbury Press, Pacific Grove, CA.
- KLENNER, W. & KREBS, C.J. (1991) Red Squirrel population dynamics. I. The effect of supplementary food on demography. *Journal of Animal Ecology*, **60**, 961-978.
- KREBS, C.J. (1994) *Ecology. The Experimental Analysis of Distribution and Abundance*. HarperCollins, New York.
- KREINER, A. (1993) *Dietary and temporal separation of three coexisting rodents at Richards Bay*. BSc (Hons) thesis, University of Pretoria, Pretoria.
- LAWLOR, L.R. & MAYNARD SMITH, J. (1976) The coevolution and stability of competing species. *The American Naturalist*, **110**, 79-99.
- LEWIN, R. (1983a) Santa Rosalia was a goat. *Science*, **221**, 213-239.
- LEWIN, R. (1983b) Predators and hurricanes change ecology. *Science*, **221**, 737-740.
- MACARTHUR, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.
- MACARTHUR, R.H. & PIANKA, E.R. (1966) On the optimal use of a patchy environment. *The American Naturalist*, **100**, 603-609.
- MAYNARD SMITH, J. (1980) A new theory of sexual investment. *Behaviour Ecology and Sociobiology*, **7**, 247-251.
- MCNAUGHTON, S.J. (1968) Structure and function in California grasslands. *Ecology*, **49**, 962-972.
- MEESTER, J., LLOYD, C.V.N. & ROWE-ROWE, D.T. (1979) A note on the ecological role of

- Praomys natalensis*. *South African Journal of Science*, **75**, 183-184.
- MELTON, D.A. (1987) Habitat selection and resource scarcity. *South African Journal Science*, **83**, 646-650.
- MONADJEM, A. & PERRIN, M.R. (1996) The effect of additional food on the demography of rodents in a subtropical grassland in Swaziland. *Mammalia*, **60**, 785-789.
- MONADJEM, A. & PERRIN, M.R. (1998) Effect of food supplementation on the habitat selected by *Mastomys natalensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *South African Journal of Zoology*, **33**, 172-177.
- MOUNT, A.B. (1964) The interdependence of the eucalypts and forest fires in southern Australia. *Australian Forum*, **28**, 166-172.
- PATRICK, R., HOHN, M. & WALLACE, J. (1954) A new method of determining the pattern of the diatom flora. *Notulea Natura*, **259**. Academic for Natural Science, Philadelphia, Pa.
- PERRIN, M.R. & JOHNSON, S. J. (1999) The effect of supplementary food and cover availability on a population of the striped mouse. *South African Journal of Wildlife Research*, **29**, 15-18.
- PIMM, S.L. (1991) *The balance of nature*. The University of Chicago Press, Chicago & London.
- PIMM, S.L. & PIMM, J.W. (1982) Resource use, competition and resource availability in Hawaiian Honeycreepers. *Ecology*, **63**, 1468-1480.
- PIMM, S.L. & REDFEARN, A. (1988) The variability of population densities. *Nature*, **334**, 613-614.
- POTVIN, C., LECHOWICZ, M.J & TARDIF, S. (1990) The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, **7**, 1389-1400.
- ROSENZWEIG, M.L. (1974) On the evolution of habitat selection. *Proceedings of the First International Congress of Ecology*. Centre for Agricultural Publishing and

Documentation, Wageningen, Netherlands.

- ROSENZWEIG, M.L. (1979) Optimal habitat selection in two species competitive system. *Fortsch. Zoology*, **25**, 283-293.
- ROSENZWEIG, M.L. (1981) A theory of habitat selection. *Ecology*, **62**, 327-335.
- ROWE-ROWE, D.T. & LOWRY, P.B. (1982) Influence of fire on small-mammal populations in the Natal Drakensberg. *South African Journal of Wildlife and Research*, **12**, 130-139.
- SCHOENER, T.W. (1974) Some methods for calculating competition coefficients from resource-utilization spectra. *The American Naturalist*, **108**, 332-340.
- SCHOENER, T.W. (1983) Field experiments on interspecific competition. *The American Naturalist*, **122**, 240-285.
- SKINNER, J.D. & SMITHERS, R.H.N. (1990) *The mammals of the southern African subregion*. University of Pretoria, Pretoria.
- SOKAL, R.R. & ROHLF, F.J. (1995) *Biometry. The Principles and Practices of Statistics in Biological Research*. W.H. Freeman & Co., San Francisco.
- SULLIVAN, T.P. (1990) Responses of Red Squirrel (*Tamiasciurus hudsonicus*) population to supplementary food. *Journal of Mammalogy*, **71**, 579-590.
- SULLIVAN, T.P. & SULLIVAN, D.S. (1982) Population Dynamics and Regulation of the Douglas Squirrel (*Tamiasciurus douglasii*) with Supplemental Food. *Oecologia*, **53**, 264-270.
- SULLIVAN, T.P., SULLIVAN, D.S. & KREBS, C.J. (1983) Demographic response of a chipmunk (*Eutamias Townsendii*) population with supplemental food. *Journal of Animal Ecology*, **52**, 743-755.
- SWANEPOEL, C.M. (1981) The effects of fire on a small mammal community. *South African Journal of Mammalogy*, **16**, 232-236.
- TAITT, M.J. (1981) The effects of extra food on small rodent populations: I Deermice

- (*Peromyscus maniculatus*). *Journal of Animal Ecology*, **50**, 111-124.
- TAITT, M.J. & KREBS, C.J (1981) The effects of extra food on small rodent populations: II Voles (*Microtus Townsendii*). *Journal of Animal Ecology*, **50**, 125-137.
- TINLEY, K.L. (1985) *Coastal dunes of South Africa*. South African National Scientific Programmes Report No 109.
- VAN AARDE, R.J., FERREIRA, S.M. & KRITZINGER, J.J. (1996a) Successional changes in rehabilitating coastal dune communities in northern KwaZulu/Natal, South Africa. *Landscape and Urban Planning*, **4**, 334-345.
- VAN AARDE, R.J., FERREIRA, S.M., KRITZINGER, J.J., VAN DYK, P.J., VOGT, M. & WASSENAAR, T.D. (1996b) An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu/Natal, South Africa. *Journal of Restoration Ecology*, **4**, 334-345.
- VAN AARDE, R.J., COE, M. & NIERING, W.A. (1996c) On the rehabilitation of coastal dunes in KwaZulu-Natal. *South African Journal of Science*, **92**, 151-163.
- VAN DYK, P.J. (1996) *The population biology of the sweetthorn Acacia karoo in the rehabilitating coastal dune forests in northern KwaZulu - Natal, South Africa*. MSc thesis, University of Pretoria, Pretoria
- VON ENDE, C.N. (1993) Repeated-measures analysis: Growth and other time-dependent measures. *Design and analysis of ecological experiments* (eds. Scheiner, S.J. & Gurevitch, J.), pp 113-137. Chapman & Hall, New York.
- WATSON, C.R.B. (1987) *The comparative ecology of two small mammal communities in the Kruger National Park*. MSc Thesis, University of Pretoria, Pretoria.
- WHITE, T.C.R. (1978) The importance of a relative shortage of food in animal ecology. *Oecologia*, **33**, 71-86
- WILLIAMS, O. (1962) A technique for studying microtine food habits. *Journal of Mammalogy*, **43**,

SUMMARY

The present study arrived at investigating the influence of supplementary food on a developing rodent community on the coastal dune forests north of Richards Bay, South Africa. Four sites were selected for the field experiment. Each of these study sites comprised a treatment and control grid. Sunflower seeds were provided on the treatment grids and the response thereof on rodent population and community variables were measured.

Each of the grids were trapped on a monthly bases as to follow the cumulative effects that supplementary food may have had on the rodent populations and the community. The amount of seed taken was measured. The minimum number of animals alive, as well as the survival and reproductive rates were calculated for the rodent community and each species on all the grids. Various community variables (richness, diversity and Bray-Curtis dissimilarities) were calculated. The diet of each species was investigated as to confirm that the species present take seeds as a food item.

Five rodent species were recorded on the newly rehabilitating areas. They include *Otomys angoniensis*, *Mastomys natalensis*, *Mus minutoides*, *Saccostomus campestris* and *Dendromus melanotis*. Most of these species are granivores and consume seeds as part of their diet with the exception of *O. angoniensis* that is a herbivore. Seeds form the main part of the diet of *M. natalensis*, *M. minutoides* and *S. campestris* and it could be assumed that sunflower seeds can form part of their diet.

Bray-Curtis dissimilarity values indicated that treatment and control grids became more dissimilar as time progressed. Supplementary food had no significant effect on the species richness and rodent community densities. However, the supplementary food on treatment grids resulted in the significant decrease in species diversity in contrast with control grids. This decrease in species diversity was not as a result in the change in species richness, but was rather the result of

the proportional increase in the number of individuals of *M. natalensis* on the treatment grids. *Mastomys natalensis* were the most dominant species. Their numbers increased on the treatment grids where they continued to dominate the rodent community. *Mus minutoides* was the second most abundant on the study grids. This species, however, did not responded to the food supplied and decreased in numbers on both the treatment and control grids. No relationship could be demonstrated between any pair of species for treatment or control grids. Interspecific interactions between species could therefore not be illustrated. The possible existence of intraspecific interactions for *M. natalensis* is a more plausible explanation as to why their numbers increase on treatment grids were food was no more limiting than on control grids.

Species specific survival rate of *M. minutoides* decreased with time for the treatment and control grids combined. This coincide with the decrease in the minimum number of *M. minutoides* alive and may be explained by the successional changes in habitat characteristics. Factors other than the availability of sunflower seeds must therefore influence *M. minutoides* numbers on the newly rehabilitating areas. The survival probability of *M. natalensis* individuals were not influenced by the supplementary food. Factors other than supposedly increased survival are responsible for their high numbers that were maintained on treatment grids.

Supplementary food had no influence on the reproductive rates of adults and the proportion of juveniles present in each of the species present. This imply that the effects that supplementary food had on the rodent community and the species it contain, were not established through the reproductive effort and output. This suggests that immigration may be the reason for increased numbers of *M. natalensis* individuals rather than their survival probability or reproductive performance.

Sunflower seeds were provided as supplementary food to increase only a small part of the resource spectrum. Food supplementation for this developing rodent community resulted in a decrease in diversity as MacArthur's (1972) model predicted. However, the decrease in diversity

was not as a result of a decrease in species richness, but rather the result of the increase and maintained dominance of the pioneer species *M. natalensis*. No interspecific interactions could be demonstrated, and it is speculated that intraspecific interactions play an important role in the *M. natalensis* population. The rodent community is therefore shaped by factors other than interspecific interactions, with supplementary food having no effect on species other than *M. natalensis*.

OPSOMMING

Die doelstelling van die huidige studie was om die invloed van addisionele voedsel op die ontwikkeling van 'n knaagdiergemeenskap op die kusduinwoude noord van Richardsbaai, Suid-Afrika, te ondersoek. Vier studiegebiede is gekies vir die veldeksperiment. Elk van die studiegebiede het bestaan uit 'n benadelings- en kontrole-eenheid. Sonneblomsaad is op die behandelingseenheid verskaf en die invloed daarvan op veranderlikes van die knaagdierbevolkings- en -gemeenskap is gemeet.

Elk van die eenhede is op 'n maandelikse basis gemonster. Die minimum aantal diere lewendig, sowel as die oorlewings- en voortplantingstempos is bereken vir die knaagdiergemeenskap en elk van die spesies op al die eenhede. Verskeie gemeenskapsveranderlikes (rykheid, diversiteit en Bray-Curtis dissimilariteit) is bereken. Die dieet van elk van die spesies is ondersoek om te bevestig dat die spesies wat teenwoordig is, afhanklik is van saad as 'n voedselbron.

Vyf knaagdierspesies is waargeneem in die nuwe rehabiliterende gebiede. Hulle sluit *Otomys angoniensis*, *Mastomys natalensis*, *Mus minutoides*, *Saccostomus campestris* en *Dendromus melanotis* in. Die meeste, met die uitsondering van *O. angoniensis* wat 'n herbivoor is, van hierdie spesies is saadvreters. Sade vorm die hoofdeel van *M. natalensis*, *M. minutoides* en *S. campestris* se dieet en dit kan dus veronderstel word dat sonneblomsaad deel sal vorm van hulle dieet.

Bray-Curtis dissimilariteit waardes het aangedui dat behandelings- en kontrole-eenhede meer van mekaar begin verskil het oor verloop van tyd. Addisionele voedsel op die behandelingseenhede het geen invloed op die spesierykheid en knaagdiergemeenskap se digtheid gehad nie. Die addisionele voedsel op die behandelingseenhede het egter daartoe gelei dat die spesiesdiversiteit betekenisvol gedaal het in teenstelling met die kontrole-eenhede. Hierdie daling

in spesiesdiversiteit was nie die gevolg van 'n verandering in spesierykheid nie, maar dit was eerder die gevolg van die proporsionele toename in die aantal *M. natalensis* individue. *Mastomys natalensis* was die mees dominante spesie. Hulle getalle op die behandelingseenhede het toegeneem terwyl hulle steeds dominant oor die ander spesies gebly het. *Mus minutoides* was die tweede mees algemene spesie op die studie-eenhede. Hierdie spesie het egter nie gereageer op die addisionele voedsel nie en getalle op beide die behandelings- en kontrole-eenhede het afgeneem met die verloop van die behandeling. Geen verwantskappe kon gedemonstreer word tussen enige van die pare spesies vir die behandelings- en kontrole-eenhede nie. Verandering in getalle as gevolg van interspesifiek interaksies tussen spesies kon derhalwe nie afgelei word nie. Die moontlike bestaan van intraspesifieke interaksies tussen *M. natalensis* individue is 'n meer aanvaarbare verduideliking waarom hulle getalle toeneem op die behandelingseenhede waar voedsel nie meer beperkend is soos op die kontrole-eenhede nie.

Die spesie spesifieke oorlewingstempo vir *M. minutoides* het afgeneem oor tyd op die behandelings-en kontrole-eenhede gekombineerd. Dit was met 'n afname in die minimum aantal *M. minutoides* individue lewendig geassosieer en kan dalk verduidelik word aan die hand van suksessionele veranderinge in die habitatseienskappe. Ander faktore, die beskikbaarheid van sonneblomsaad uitgesluit, kon derhalwe die getalle van *M. minutoides* beïnvloed. Die oorlewingswaarskynlikheid van *M. natalensis* individue is nie deur die addisionele voedsel beïnvloed nie. Ander faktore, uitgesluit die veronderstelde verhoging in oorlewingtempos, is derhalwe verantwoordelik vir die toename in getalle op die behandelingseenhede en die volhouing daarvan. Immigrasie mag moontlik een van hierdie faktore wees.

Addisionele voedsel het geen invloed gehad op die voortplantingstempos van volwasse individue of die proporsie van kleintjies teenwoordig in elk van die spesies teenwoordig nie. Addisionele voedsel het dus nie die voortplantingstempos of oorlewings van jongelinge beïnvloed nie. Die toename in getalle van *M. natalensis* individue kan dus eerder aan immigrasie as aan hul

oorlewings- of voortplantingsvermoë toegeskryf word.

Sonneblomsaad is verskaf as die addisionele voedsel om slegs 'n klein gedeelte van die voedselbronspektrum te vermeerder. Die verskaffing van addisionele voedsel vir hierdie ontwikkelende knaagdiergemeenskap het tot 'n afname in diversiteit gelei, soos MacArthur (1972) se model voorspel het. Die afname in diversiteit is egter nie die gevolg van 'n verlaging in spesierykheid nie maar eerder die gevolg van 'n toename in getalle en volgehoue dominansie van die pionierspesie, *M. natalensis*. Geen interspesifieke interaksies kon gedemonstreer word nie en daar word gespekuleer dat intraspesifieke interaksies 'n belangrike rol speel in die *M. natalensis* bevolking. Die knaagdiergemeenskap word derhalwe gevorm deur deur ander faktore, interspesifieke interaksie uitgesluit, met die addisionele voedsel wat geen invloed op die verskillende spesie, behalwe *M. natalensis* het.