The influence of food supplementation on a coastal dune rodent community

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Abstract

Studies of the rodent community in regenerating coastal dune forest areas north of Richards Bay, South Africa, have indicated that a number of species occupy newly rehabilitating areas. Unstable environmental conditions result in habitat changes, rather than competitive interactions, being the major determinant of rodent community development. This led to the present study, which investigated the effects of supplementary food on rodent assemblages. We attempted to stabilize food availability in order to elucidate some of the mechanisms responsible for the development of the rodent community. By only increasing an existing portion of the resource spectrum, we reduced species diversity, probably through dominance by competitive superior exploiters of the augmented resource. Thus, species diversity decreased with food supplementation, as a result of an increase in the abundance of *Mastomys natalensis* rather than because of a change in the number of species or the abundance of other species.

Key words: interactions, *Mastomys natalensis*, rodents, supplementary food

Résumé

Des études de la communauté des rongeurs dans les zones forestières des dunes côtières en voie de régénération de Richards Bay, en Afrique du Sud, ont montré que de nombreuses espèces occupent les régions qui commencent à se régénérer. Des conditions environnementales instables aboutissent au fait que des changements d'habitat plutôt que des interactions compétitives sont le facteur déterminant principal du développement de la communauté des rongeurs. Cela a amené la présente étude, qui a investigué les effets de suppléments de nourriture sur les regroupements de rongeurs. Nous avons essayé de stabiliser la disponibilité de la nourriture, pour mettre au clair les mécanismes responsables du développement de la communauté des rongeurs. En augmentant seulement une portion existante du spectre des ressources, nous avons réduit la diversité des espèces, probablement par la dominance des consommateurs, supérieurs dans la compétition, de la ressource accrue. Donc la diversité des espèces a diminué avec l'augmentation de la nourriture, en résultat de l'abondance accrue de *Mastomys natalensis*, plutôt qu'à cause d'un changement du nombre d'espèces, ou de l'abondance des autres espèces.

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Introduction

According to a model developed by MacArthur (1972), species diversity can be increased by a decrease in average width of utilization curves, by an increase in average overlap of resource use between species, or by an increase in the resource spectrum. An increase in the total resource spectrum would increase diversity because resources that were formerly too scarce to form an adequate diet and which were therefore not counted as part of the resource spectrum, now allow species to survive (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, e.g. possible competitive interactions.

Abramsky (1978) was the first to test MacArthur's (1972) theory with a food supplementation experiment. By increasing the resource spectrum he increased diversity, hence supporting MacArthur's (1972) theory. Only a few other experiments have dealt with the effects of food supplementation at the community level for small mammals and/or rodents (Brown & Munger, 1985; Bowers, Thompson & Brown, 1987; Dickman, 1988; Monadjem & Perrin, 1996, 1997), with some of these studies illustrating interspecific interactions (Brown & Munger, 1985; Bowers et al., 1987; Dickman, 1988). Most other food supplementation studies have thus far addressed questions of population regulation and limitation (see Boutin, 1990 and references therein).

The present study was carried out in newly regenerating coastal dune forest areas north of Richards Bay, South Africa (see Van Aarde et al., 1996 for description of the area). Ferreira (1997) studied the rodent community in this area and concluded that a number of species occupy newly rehabilitating areas, but that Mastomys natalensis (Smith 1834) dominates. Other species have no problem colonizing the areas but once they are present struggle to establish themselves permanently. Their colonization appears to be related to source populations and habitat suitability, with interspecific interactions playing no significant role because of unstable environmental conditions (Ferreira, 1997). Furthermore, the densities of potential competitors never reach equilibrium values, resulting in habitat changes, rather than competitive interactions, being the major determinant of rodent communities (Ferreira & Van Aarde, 1999). The present study investigates the effects of supplementary food on the abundance, richness, diversity and interspecific interactions of rodent assemblages. We increased only a small part of the total resource spectrum and attempted to stabilize food availability in order to elucidate the mechanism(s) influencing the development of the rodent community following the

disturbance resulting from sand mining. Based on MacArthur's (1972) model, we expected a decrease in species diversity, as a result of dominance by those species that are competitively superior in exploiting the augmented resource.

Materials and methods

Study area and field procedures

The study area, in northern Kwa-Zulu Natal, South Africa, is located 8.6 km north and 9.3 km east of the coastal town Richards Bay (28°43'S, 32°12'E). The climate is humid and warm to hot, with seasonal differences that are not very pronounced. It rains throughout the year (mean annual rainfall of 1292 mm) (Van Aarde et al., 1996), and the mean daily maximum temperature ranges from 22.6°C in June to 30°C in January. There is no frost and the relative humidity is high, ranging from 59% in August to 72% in April and November (Avis, 1992). The current land use within the region includes mining, forestry, subsistence agriculture, industry and recreation.

Four replicate sites were selected for the present study, on which post-mining dune forest rehabilitation started 2 years prior to the onset of the study. The sites varied between 7 ha and 21 ha in area and were characterized by annual exotic species (Pennisetum americanum, Crotalaria juncea, Sorghum spp. and Helianthus sp.), sowed as part of the rehabilitation programme, being replaced by indigenous grasses such as Eragrostis curvula and Cymbopogon validus (Van Aarde et al., 1996). Towards the end of this study these grasslands had developed into a dense scrub land dominated by 30–80 cm high stands of Acacia karroo shrubs. These early stages of dune vegetation regeneration support relatively dense populations of rodents (Van Aarde et al., 1996), probably as a consequence of the abundant seed crop available in the topsoil spread over the dunes as part of the rehabilitation programme. However, rodent densities fall dramatically after the first year of habitat regeneration (Ferreira & Van Aarde, 1999).

Each of the four study sites selected comprised a treatment and a control trapping grid. These grids were at least 200 m apart and 100 Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, FL, USA) (8 × 9 × 23 cm), arranged in a 10 × 10 configuration with 10 m

intervals between trapping stations, were set on each of the 0.81 ha grids (90 × 90 m).

Monthly trapping (five consecutive nights per session) began 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 (toe-clipped) and released following inspection for previous marks and identification. Trapping began 1 month prior to the experimental supplementation of food on the treatment grids.

Supplementary food (sunflower seed) was placed on the treatment grids at 7-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. The sides of each plant pot had four evenly spaced holes that allowed free access for rodents but limited access for larger granivores, such as vervet monkeys (*Cercopithecus aethiops*). Each feeding station received 200 g of seed per week. The amount taken per feeder was also recorded.

Density was estimated as the minimum number of animals known to be alive (MNA) during a trapping session per grid (Chitty & Phipps, 1966). Species diversity was calculated as species richness (S, the total number of species monthly) and Shannon–Wiener diversity (H′) (Ludwig & Reynolds, 1988). 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). Contributions of each species to the average Bray–Curtis dissimilarity (δ) between the treatment and control groups were calculated for each month using the SIMPER program from PRIMER Version 4.0 (Carr, 1996).

Statistical analysis

The variability of the amount of seed taken over time (recorded by weighing at weekly intervals) was measured following the method described by Pimm & Redfearn (1988). The measure of variability was presented as the standard deviation of the logarithm of the monthly amount of seed taken. An increasing 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. The relationships between species densities were investigated using LSR (Sokal & Rohlf, 1995). The repeated measures analysis of variance (ANOVAR, Potvin, Lechowicz & Tardif, 1990) was used to test for the effect of food supplementation on rodent density, species richness, diversity, dominance and the densities of individual rodent species. All analyses were carried out using the statistical package SAS release 6.12 (SAS Institute Inc., Cary, NC, USA). Huynh–Feldt adjusted probabilities based on the Huynh–Feldt epsilon were 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.

Results

Resource use

About 85.2 g (SE = 7.0) of the 200 g of sunflower seeds provided per feeding station was taken per week. The calculated variability increased over time, suggesting a cyclic pattern in the amount of seeds taken. The amount of seed consumed increased significantly with number of rodents (LSR: $F = 7.22$, $P < 0.05$, $r^2 = 0.36$) and with *M. natalensis* numbers (LSR: $F = 13.85$, $P < 0.05$, $r^2 = 0.52$). However, the amount taken did not increase over time (LSR: $F = 3.27$, $P > 0.05$, $r^2 = 0.16$).

Community variables

The mean MNA was higher on treatment than control grids but no significant difference was recorded (ANOVAR: $F = 0.92$, $P > 0.05$). At the onset of the study, the MNA on control and treatment grids was similar, but after 5 months values on the control grids decreased below those on treatment grids (Fig. 1a). MNA on the treatment and control grids increased and decreased simultaneously with similar temporal trends but differed in amplitude. The mean MNA for the treatment and control grids combined increased and changed sig-
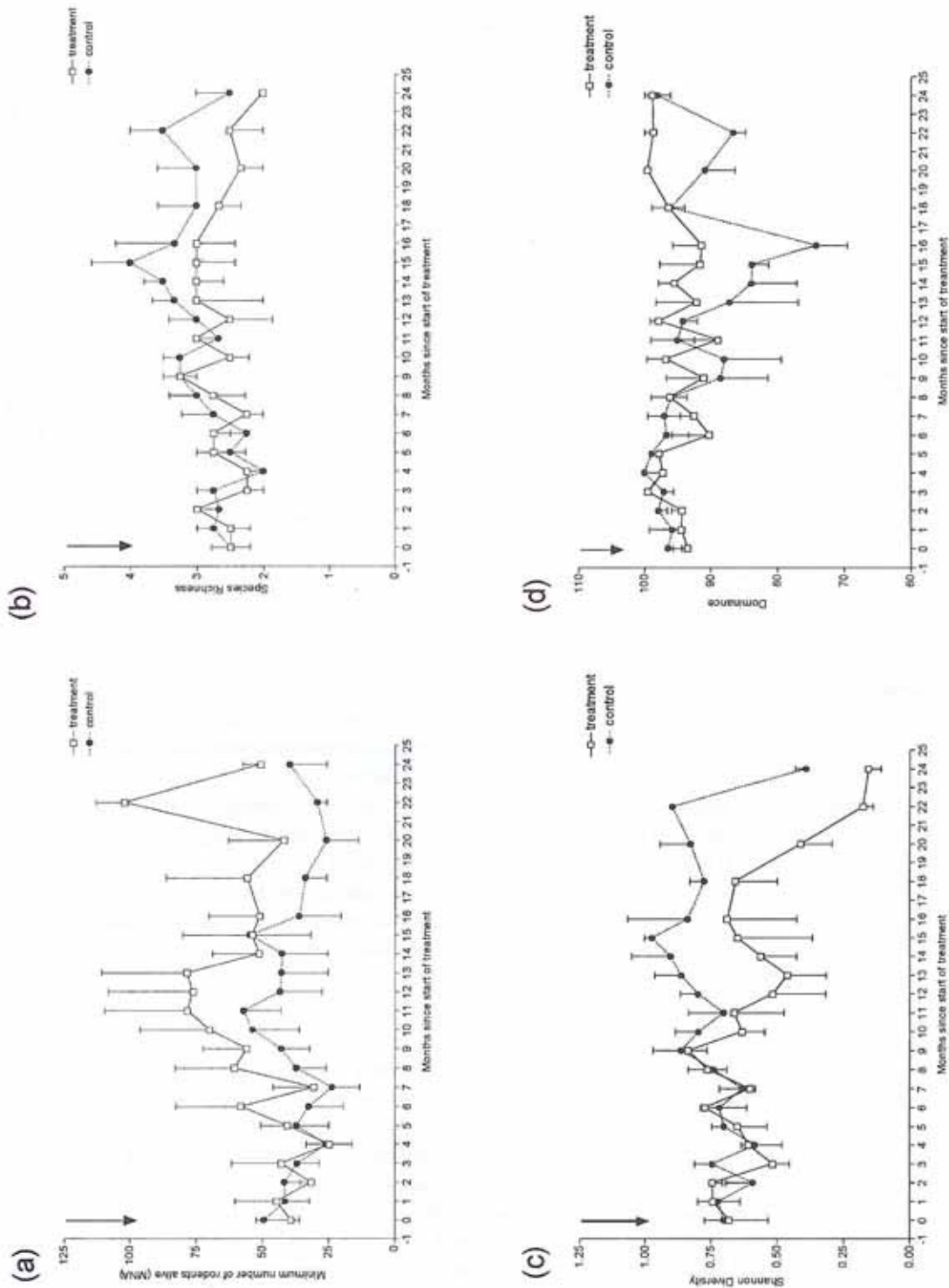
Fig 1 Temporal trends (mean ± SE) for treatment (☐) and the control (●) grids illustrated in (a) the minimum number of rodents alive (MNA), (b) species richness, (c) species diversity and (d) community dominance (↓ start of treatment)

nificantly over time (ANOVAR: $F = 2.32$, $P < 0.05$). The interaction between the treatment vs. the control grid and time was tested and no significant difference was recorded (ANOVAR: $F = 1.58$, $P > 0.05$). This indicates that the treatment did not cause a significant response in abundance over time.

Species richness increased on the control grids after 11 months and differed significantly from treatment grids (ANOVAR: $F = 8.73$, $P < 0.05$) (Fig. 1b). The mean species richness for the treatment and control grids combined increased and changed significantly over time ($F = 2.29$, $P < 0.05$). However, the interaction between the treatment vs. the control grids was not significantly different (ANOVAR: $F = 0.46$, $P > 0.05$).

No significant difference was recorded between the mean diversities for the treatment and control grids (ANOVAR: $F = 5.39$, $P > 0.05$) (Fig. 1c). However, diversity on treatment grids varied but decreased over time. The decrease in diversity on the treatment grids caused the mean diversity value for the treatment and the control grids combined to decrease rather than to increase over time. This decrease for the combined diversity therefore changes significantly over time (ANOVAR: $F = 3.15$, $P < 0.05$). When the interaction between the

treatment vs. the control grids and time was tested, a significant difference was recorded (ANOVAR: $F = 2.24$, $P < 0.05$). This implies that the supplementary food on the treatment grids caused a significant decline over time in the rodent community diversity. The Bray–Curtis dissimilarity between the treatment and control grids increased significantly with an increase in the treatment duration (LSR: $F = 4.71$, $P < 0.05$, $r^2 = 0.2$) (Fig. 2).

After 12 months of treatment, dominance began to decrease slightly on the control grids. However, mean dominance for the treatment grids did not differ significantly from that of the control grids (ANOVAR: $F = 0.93$, $P > 0.05$). Dominance for treatment and control grids combined decreased significantly over time (ANOVAR: $F = 3.02$, $P < 0.05$). In addition to the time effect, the interaction between treatment and time showed a significant effect (ANOVAR: $F = 1.95$, $P < 0.05$) (Fig. 1d).

Species and their interactions

Five rodent species (*M. natalensis*, *Mus minutoides* (Smith 1834), *Dendromus melanotis* (Smith 1834), *Saccostomus campestris* (Peters 1846) and *Otomys ango-*
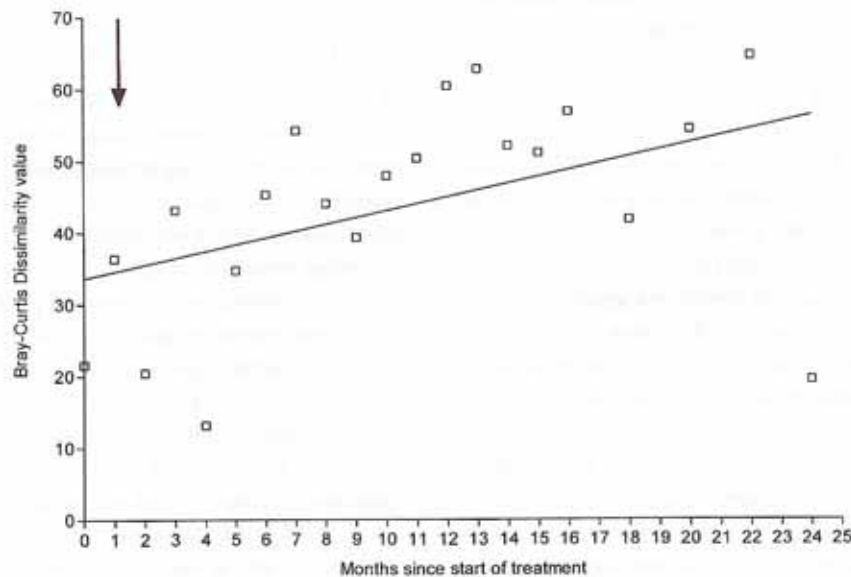

Fig 2 The least square regression line illustrating temporal trends in the Bray–Curtis dissimilarity values calculated to show differences in the community variables of the treatment and the control grids (↓ start of treatment)

Table 1 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 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	
	F	P (H–Fadj)*	F	P (H–Fadj)*	F	P (H–Fadj)*
Mastomys natalensis	1.95	NS	2.80	0.003	2.65	0.005
Mus minutoides	0.27	NS	5.25	< 0.001	0.63	NS
Saccostomus campestris	0.02	NS	2.07	0.031	0.88	NS
Dendromus melanotis	4.93	NS	6.37	0.003	3.13	0.047
Otomys angoniensis	0.07	NS	1.98	0.049	0.88	NS

*Huynh–Feldt adjusted P-values.

niensis (Wroughton 1906)) were present on the different sampling grids. Their MNA values for treatment and control grids did not differ significantly (Table 1). However, all of them did show a significant difference when the MNA of treatment and control grids were combined and tested for significant differences over time (Table 1). The MNA of all the species fluctuated over time, with, for example, *M. natalensis* increasing in numbers, while others (e.g. *M. minutoides*) decreased in numbers. *Saccostomus campestris* numbers fluctuated, with a slow increase in numbers over time. *Otomys angoniensis* occurred in low numbers, which fluctuated over the period with no specific patterns. After a 12-month period, *D. melanotis* had a short period (5 months) of increase in numbers that was followed by a decrease.

The interaction between treatment and time was only significant for two species, *M. natalensis* (ANOVAR: $F = 2.65$, $P < 0.05$) and *D. melanotis* (ANOVAR: $F = 3.13$, $P < 0.05$). Supplementary food caused *M. natalensis* numbers to increase on treatment grids over time, but not on control grids (Fig. 3). After 12 months of treatment *D. melanotis* did show an increase in numbers for a short period of 5 months. No specific trends, other than the simultaneous changes on treatment and control grids over time, were recorded for *M. minutoides*, *S. campestris* or *O. angoniensis*.

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

Discussion

The preponderance of *M. natalensis* on our study site confirms that the rodent assemblages here were in the early phase of ecological succession, in response to the disturbances evoked by sand mining. Further habitat development will most probably give rise to *M. natalensis* being replaced in dominance by *S. campestris* and *Aethomys chrysophylis* (Ferreira & Van Aarde, 1996, 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 scrub land 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 these sites may have had some predictable consequences for the development of rodent assemblages. On the one hand it may have benefited the
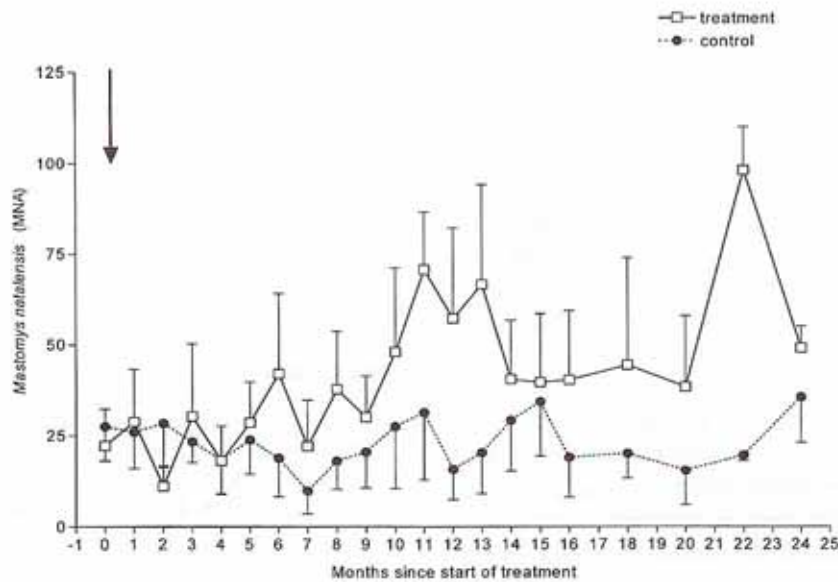
Fig 3 The MNA for *M. natalensis* on the treatment (□) and the control (●) grids illustrating changes over a 24-month period (mean ± SE) (↓ start of treatment)

early colonisers (see MacArthur, 1972), such as *M. natalensis*, giving rise to reduced rates of colonization 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 of development of rodent assemblages. Should food not be a limiting factor in the development of these assemblages, supplementation is not expected 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 (Ferreira, 1997), food supplementation during our study may also 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 latter statement that supplementary food enables *M. natalensis* to increase in numbers. This is in agreement with other studies, where rodent numbers tend to increase with food supplementation (Akbar & Gorman, 1993; Doonan & Slade, 1995; Monadjem & Perrin, 1998; Perrin & Johnson, 1999). However, in contrast to these studies and to the situation with *M. natalensis*, the numbers of other species typically occurring at low numbers during early succession series (*M. minutoides*, *D. melanotis*, *S. campestris* and *O. angoniensis*) did not increase with food supplementation. The presence of species seems 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 seed bank composition had a greater explanation value for rodent community com-

position than habitat structure. Limitations imposed by food availability thus seem to be relevant to the development of these rodent assemblages within an unstable environment.

In our study species diversity decreased with food supplementation as a result of an increase in the abundance of M. natalensis, rather than a change in the number of species. Rodent densities did not increase and species richness did not decrease with food supplementation. However, the decrease in diversity 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 our 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), we reduced species diversity, probably through dominance by competitively superior exploiters of the augmented resource.

Pimm & Pimm (1982) tested and supported a model in which the subordinate species is forced to specialize on clearly inferior resources because the dominant species controls the better or more prevalent resources. M. natalensis may therefore force the second most dominant species, in our case M. minutoides, from the superior resource. The inferior resource may still have been sufficient to support and maintain the numbers of subordinate species on the treatment and control grids. Least squares regression analysis to investigate the relationships between species gave no indication of a negative interspecific interaction between specific species. The increase in M. natalensis numbers therefore affected only the species diversity, with no influence on interspecific interactions.

In conclusion, food supplementation for a 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. The rodent community is therefore shaped by factors other than interspecific interactions, with supplementary food having no effect on species other than M. natalensis.

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