

Habitat associations and competition in *Mastomys-Saccostomus-Aethomys* assemblages on coastal dune forests

S. M. FERREIRA* and R. J. VAN AARDE

Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa

Summary

The northern coastal dune forests of KwaZulu-Natal, South Africa, are inhabited by several rodent species. Three of these (*Mastomys natalensis*, *Saccostomus campestris* and *Aethomys chrysophilus*) occur commonly. The hypothesis was investigated that habitat characteristics, and not species interactions, explain most of the variation in species-specific densities of these three species. Existing data were collated and the relationships between species-specific densities determined. In addition, a trapping programme was established between July 1993 and February 1995, during which species-specific densities were estimated and 16 habitat variables measured. Multiple regression analyses were used to investigate the relationship (i.e. not causation) between species-specific densities and a suite of habitat variables. No additional explanation of variation in species-specific densities by densities of other species were evident when habitat variables have been accounted for. It is concluded that most of the variation in species-specific densities of a *Mastomys-Saccostomus-Aethomys* assemblage can be explained by habitat variables rather than species interactions.

Key words: competition, forests, habitat associations, rehabilitation, rodents

Résumé

Les forêts sises sur les dunes de la côte nord du KwaZulu-Natal, en Afrique du Sud, abritent plusieurs espèces de rongeurs. Trois d'entre elles (*Mastomys natalensis*, *Saccostomus campestris* et *Aethomys chrysophilus*) sont communes. On a cherché à vérifier l'hypothèse selon laquelle ce sont les caractéristiques de l'habitat et non les interactions entre espèces qui expliquent la plupart des variations de la densité de chacune de ces trois espèces. On a rassemblé les données existantes et déterminé les relations entre les densités par espèce. De plus, un programme de piégeage a fonctionné de juillet 1993 et février 1995, au cours duquel on a estimé les densités spécifiques et mesuré 16 variables de l'habitat. On a employé des analyses de régression multiple pour étudier la relation (pas la cause) entre les densités spécifiques et une série de variables de l'habitat. Aucune explication supplémentaire de la variation de la densité spécifique n'a pu être apportée par la densité des autres espèces lorsque l'on tenait compte des variables de l'habitat. On en a conclu que la plupart des variations qui touchent les densités spécifiques dans les cohabitations de

Correspondence: Professor R. J. van Aarde. Fax: +27 12 420 2534; e-mail rudi@scientia.up.ac.za

*Current address: Department of Conservation, East Coast/Hawke's Bay Conservancy, PO Box 688, Gisborne, New Zealand.

Mastomys, *Saccostomus* et *Aethomys* pouvaient s'expliquer plus par les variables de l'habitat que par les interactions entre espèces.

Introduction

Habitat selection and inter-specific competition are amongst the most important factors influencing species coexistence (Pimm, 1991; Ricklefs & Schluter, 1993). Laboratory experiments support competition as an explanation for one species causing the local extinction of another (Gause, 1934; van der Meer, 1969), but field evidence is more ambiguous (Connell, 1983; Schoener, 1983). Rosenzweig (1977) argued that habitat selection may have evolved as a result of past competitive effects and that only weak interspecific competition is necessary to maintain habitat selection in the present. The coexistence of species may therefore be explained in terms of the amount of resources available and by the way in which species utilize and influence other species to utilize these resources (Kotler & Brown, 1988).

Three rodent species, the multi-mammate mouse *Mastomys natalensis* (*sensu lato*) (Smith 1834), the pouched mouse *Saccostomus campestris* (Peters 1846) and the red veld rat *Aethomys chrysophilus* (de Winton 1897) coexist in the coastal dune forests of KwaZulu-Natal, South Africa. These species are nocturnal and terrestrial (Skinner & Smithers, 1990), and feed primarily on seed (de Graaff, 1981; Watson, 1987; Kerley, 1989). *Aethomys chrysophilus* is the largest (adult: 71.2 g, range 55–102 g; Gliwicz, 1985), whereas the other two are of similar size (*M. natalensis* adult: 40.1 g, range 30–54 g; Gliwicz, 1985; *S. campestris* adult: 44.4 g, range 30–68 g; Smithers, 1971). All three species are catholic in their habitat requirements, occur in a wide range of habitats (Skinner & Smithers, 1990) and co-occur in grasslands (Meester, Lloyd & Rowe-Rowe, 1979), dry semi-deserts (Kerley, 1989), southern temperate forests (Wirminghaus & Perrin, 1993) and dry savannas (Gliwicz, 1985).

Along the coast of northern KwaZulu-Natal, different patches of dune forests are characteristically dominated by one of the three species. Ferreira & van Aarde (1996) described a directional change in rodent community composition on rehabilitating coastal dune forests representative of dune forest succession (see Mentis & Ellery, 1994; van Aarde, Ferreira & Kritzing, 1996a). Here, *M. natalensis* replaces *S. campestris* during later stages of coastal dune regeneration.

Fox (1982) proposed a habitat accommodation model for mammalian succession following fire in Australia and has applied the same model to ant succession following mining on the east coast of Australia (Fox, 1990). This model suggests that species enter a succession and colonize areas when habitat requirements are satisfied by changes resulting from vegetation succession. These changes may be experienced as change in food resources or refugiums from predators, or both. However, a constraint on colonization potential arises when the changes in vegetation are beyond the range within which a species can remain dominant, resulting in exclusion from the area.

Extending Fox's model (1982) to rodent communities on rehabilitating dunes in KwaZulu-Natal, the present authors suggest that changing habitat characteristics may result in one species replacing another during later stages of succession on regenerating coastal dunes. Should this be the case then the first feature of Kotler & Brown's (1988) classification for coexistence (resource axis of habitat heterogeneity) should play the most important role in the coexistence of species such as *M.*

natalensis, *S. campestris* and *A. chrysophilus* on coastal dune forests. Habitat characteristics should therefore explain variation in species-specific densities, whereas species interactions will play a limited role, if at all. The present study therefore attempts to analyse the relative role of habitat characteristics directly and interspecific competition indirectly in determining the species' distribution and abundance in *Mastomys-Saccostomus-Aethomys* assemblages on coastal dune forests. Here data collected over a period of 4 years on regenerating coastal dune forests are used to establish relationships between the densities of these species, and between their densities and habitat characteristics.

Materials and Methods

The study area is situated on the coast of northern KwaZulu-Natal between Richards Bay (28°43' S, 32°12' E) and Mapelane Nature Reserve (28°25' S, 32°27' E), South Africa. The area comprises stands of mature coastal dune forests, exotic plantations (*Cassuarina equisetifolia* and *Eucalyptus saligna*), areas cleared for forestation, areas cleared for mining, areas being mined, areas in preparation for habitat rehabilitation following mining, and stands of rehabilitating forests of known age. Some of the mature coastal dune forests are of known age and between 30 and 35 years old (van Aarde *et al.*, 1996b). All these habitats and areas are situated within a coastal belt approximately 3 km wide. The present study concentrated on five stands of rehabilitating forests of known age, a stand of mature forest of known age and a stand of mature forest of unknown age (see Table 1).

The first part of this study is based on data collated from Ferreira & van Aarde (1996) and data collected by the present authors between January and May 1991, and between June 1992 and June 1993, using the same methods and trapping grids as described by Ferreira & van Aarde (1996). An analysis of the frequency distribution of rodent densities in this data set indicated a decrease in frequency for densities ≥ 4 individuals ha^{-1} (see Fig. 1). Accordingly, relationships between the species-specific densities of *M. natalensis*, *S. campestris* and *A. chrysophilus* were investigated by including only those samples for which the combined densities of these three species were ≥ 5 individuals ha^{-1} because we expected competition, if present, to be most prevalent at higher densities. The relationships between species densities were investigated using least square regression analyses (Sokal & Rohlf, 1995). This resulted in power relationships ($y = ax^b$) being best suited to describe the relationships between species densities.

In the second part of the study, trapping of these three species commenced during July 1993 and continued until February 1995. Six trapping grids were then established on each of the five rehabilitating stands, with each trapping grid comprising 49 trapping stations arranged in a 7×7 configuration, with 15 m between trapping stations. The trapping grids on each stand were distributed in such a way that the maximum distance was obtained between them (≈ 500 m).

Six trapping grids of similar dimensions were also established on a 30–35-year-old stand of unmined forest where trapping was conducted during June and September 1994. (Access to these trapping grids was difficult as a result of ongoing mining operations resulting in only three of the trapping grids here being trapped during February 1995). Three trapping grids were also established on a stand of unmined forest of unknown age and trapped during September 1994 and February 1995.

Table 1. A description of habitat characteristics of stands on which small mammals were recorded

Stands	Description
Rehabilitating stand established between 1991 and 1993	At the time of the study this stand predominantly comprised cover crop of annual exotic grasses such as <i>Pennisetum americanum</i> , <i>Eragrostis curvula</i> , the legume <i>Crotalaria juncea</i> and a variety of local indigenous species. Towards the end of the study (20 months later), <i>Acacia karroo</i> shrubs increased in abundance. This stand is between 100 and 500 m away from the high water mark. The seaward side of the stand is adjacent to unmined forest, while bare dunes abut the inland side thereof. An older rehabilitating stand adjoins at the southern boundary.
Rehabilitating stand established between 1988 and 1990	Situated 100–200 m from the high water mark and abutted by an unmined forest at the seaward side. Bare sand dunes and <i>Cassuarina equisetifolia</i> plantations comprise the inland border. This stand is in contact with an older stand at the southern end, while a young rehabilitating stand represents the northern boundary. Thick undergrowth dominated by grass species prevails, with <i>Acacia karroo</i> colonizing the area. <i>Acacia karroo</i> and <i>Dodonaea angustifolia</i> are the most prevalent tree species, while herbs such as <i>Chrysanthemoides monilifera</i> and <i>Passerina rigida</i> occur frequently. Ground cover is dominated by dense stands of the grass <i>Dactyloctenium geminatum</i> with <i>Canavalia maritima</i> also present.
Rehabilitating stand established between 1985 and 1987	An <i>Acacia karroo</i> shrubland with sparse undergrowth, mainly comprising grass species. It is situated 100–250 m away from the high water mark adjacent to a strip of unmined forest on the seaward side. Inland, it is bordered by <i>Cassuarina equisetifolia</i> plantations, while an older stand forms the southern boundary and a younger stand the northern boundary. <i>Dodonaea angustifolia</i> also occurs but <i>Brachylaena discolor</i> are scarce. No other indigenous tree species occur here. Ground cover is sparse and consists mainly of the grass <i>Dactyloctenium geminatum</i> .

Rehabilitating stand established between 1981 and 1984	Situated between 100 and 600 m from the high water mark and adjacent to unmined forest (seaward side at the central part), rehabilitating older forest (seaward side at the southern part) and <i>Cassuarina equisetifolia</i> plantations (inland side and seaward side at the northern part). A younger stand adjoins in the north. The plant community here also is dominated by <i>Acacia karroo</i> . Other tree species occurring here include <i>Brachylaena discolor</i> and <i>Vepris lanceolata</i> .
Rehabilitating stand established between 1978 and 1980	The oldest rehabilitating stand is abutted by a strip of unmined forest 100–300 m wide on the seaward side and by a younger rehabilitating stand on the inland side. This <i>Acacia karroo</i> woodland is colonized by a variety of secondary dune forest plant species. Several indigenous species are taking root, including tree species such as <i>Trichelia emetica</i> , <i>Trema orientalis</i> , <i>Mimusops caffra</i> , <i>Brachylaena discolor</i> , <i>Celtis africana</i> , <i>Vepris lanceolata</i> , <i>Albizia adianthifolia</i> , <i>Kraussia floribunda</i> and <i>Apodytes dimidiata</i> .
30–35-year-old stand of coastal forest	Three separate and isolated stands ranging from 30 to 35 years in age based on the inspection of aerial photographs taken between 1960 and 1967, illustrating that they were then cleared of all vegetation, presumably for afforestation. However, no afforestation took place and indigenous vegetation recolonized these patches on their own accord. The vegetation here resembles a coastal dune forest dominated by <i>Acacia karroo</i> . Other indigenous trees in the canopy include <i>Trichelia emetica</i> , <i>Trema orientalis</i> , <i>Mimusops caffra</i> , <i>Celtis africana</i> , <i>Vepris lanceolata</i> , <i>Allophylis natalensis</i> , <i>Kraussia floribunda</i> and <i>Apodytes dimidiata</i> . Climbers occurring here include <i>Sarcostemma viminale</i> and <i>Adenia gummifera</i> with <i>Aspistasia gangetica</i> occurring in the woodland ground cover. These stands are surrounded by older unmined coastal forests.
Mature forest	The unmined forests of unknown age comprise relatively undisturbed secondary dune forest. The vegetation here is characteristically dune forest vegetation, with a variety of canopy species. Several vertical strata exist with the forest floor vegetation comprising a variety of grasses and herbs and the herb <i>Issoglossa woodii</i> characteristically occurring frequently here. Fragments of commercial plantations are interspersed throughout the area, with rural agricultural landscapes abutting the area on the inland side.

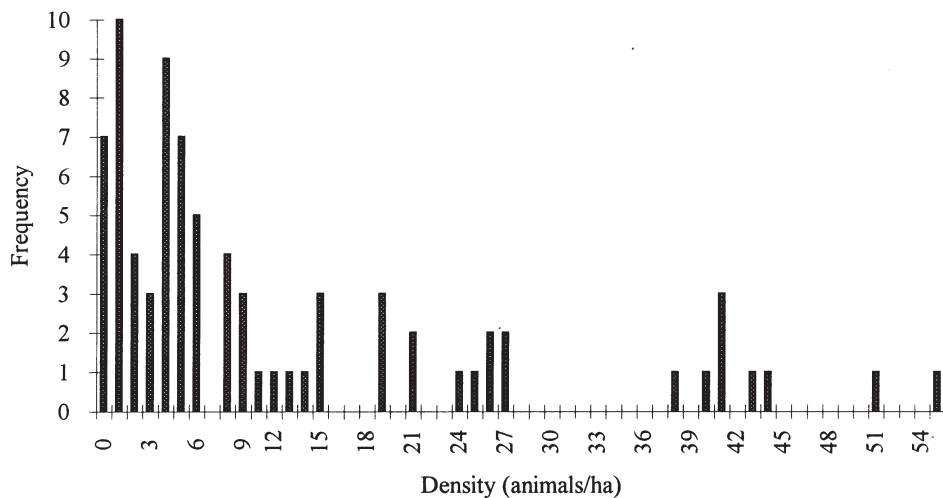


Fig. 1. Frequency distribution of small mammal densities collated from Ferreira & van Aarde (1996) and data collected in this study between January and May 1991, and between June 1992 and June 1993 using the same methods and trapping grids.

Table 2. Summary of trapping on trapping grids from July 1993 to February 1995

Habitats	Number of grids	Months of sampling
Rehabilitating stand established between 1991 and 1993	6	Bimonthly from July 1993 to February 1995
Rehabilitating stand established between 1988 and 1990	6	Bimonthly from July 1993 to February 1995
Rehabilitating stand established between 1985 and 1987	6	Bimonthly from July 1993 to February 1995
Rehabilitating stand established between 1981 and 1984	6	Bimonthly from July 1993 to February 1995
Rehabilitating stand established between 1978 and 1980	6	Bimonthly from July 1993 to February 1995
30–35-year-old stand of coastal forest	6	June 1994 and September 1994
		Three only during February 1995
Mature forest	3	September 1995 and February 1995

During this part of the study the rodent community was therefore sampled on 39 trapping grids throughout the study area from July 1993 until February 1995 (see Table 2 for summary).

Trapping sessions lasted five consecutive days and nights. A Sherman live trap was placed within 1 m of each trapping station, baited with a mixture of peanut butter and oats and checked at dawn. Captured individuals were marked (toe-clipped) and released following inspection for previous marks, identification and the recording of sex and weight. Densities were calculated as the number of individuals

captured per unit area covered by the trapping grid. Effective area covered by a trapping grid was calculated by adding the mean distance moved between captures to the edge of the 7×7 trapping stations.

Between June 1993 and February 1995, 16 habitat variables were recorded (see Table 3 for a description) at 1110 trapping stations randomly selected from the 39 trapping grids. The average values on trapping grids were calculated (rodent densities were estimated for each trapping grid) for each of the these habitat variables using habitat characteristics recorded at trapping stations. Rodent densities for which no suite of habitat variables were available were excluded and 85 sets of rodent densities were included in the final analysis. Correlation analyses (Sokal & Rohlf, 1995) suggested no inter-correlation between habitat variables. All habitat variables were characterized by a normal distribution. Correlation analyses (Sokal & Rohlf, 1995) were also used to investigate the association of species-specific densities with each of the habitat variables individually.

Forward stepwise multiple regression analyses (Sokal & Rohlf, 1995) were used to investigate the relationship between species-specific densities and a suite of habitat variables simultaneously. *F*-to-enter was set at 0.0001 to force most variables into the models. To distinguish between the relative role of habitat variables and interaction between species, the method suggested by Crowell & Pimm (1976) was used. Only samples with both rodent species in question present were included in this part of the analyses. The density of one species was used as the dependent variable, and the habitat variables and density of the second species were used as the independent variables. The density of the second species was forced to enter the model only after the habitat variables were included. This resulted in the contribution of the species-interaction in question to the explained variance of the density of the dependent species only being considered after the contribution of habitat variables to the explained variance have been accounted for. The change in r^2 -values was used as an indication of the importance of species interactions.

Results

Inter-specific correlations

The density of *S. campestris* declined as a power function ($y = 6.17x^{-0.50}$, $r^2 = 0.22$) with an increase in the density of *M. natalensis* (Fig. 2). However, this correlation provided relatively little explanation for the observed variation (22%). The densities of *A. chrysophilus* also declined ($y = 12.01x^{-1.03}$, $r^2 = 0.85$) with an increase in the density of *M. natalensis* (Fig. 2), but the densities of *S. campestris* and *A. chrysophilus* were not related (best relationship: $y = 8.60 - 0.15x$, $r^2 = 0.02$; Fig. 2).

Habitat variables

The densities of rodent species were not related to any habitat variable on its own. However, multiple regression analyses resulted in 55% of the variability in the density of *M. natalensis*, 97% of that of *S. campestris* (not significant) and 99% of that of *A. chrysophilus* being explained by a suite of habitat variables (Table 4). All habitat variables measured were included in the model calculated for *M. natalensis*, with vegetation height explaining most of the variation in density. The model established

Table 3. A description of habitat variables measured at 1110 trapping stations distributed on rehabilitating, 30–35-year-old and mature coastal dune forests

Variable	Code	Description
Highest vegetation height	tvh	The highest vegetation above the trapping station measured in centimetres.
Highest shrub height	tsh	The highest shrub-like vegetation within a radius of 2 m from the trapping station measured in centimetres. A shrub was defined as woody vegetation below 200 cm.
Highest herb height	thh	The highest herb-like vegetation within a radius of 2 m from the trapping station measured in centimetres. A herb was defined as non-woody vegetation.
Litter depth	tbd	The greatest depth of dead plant material accumulated on the soil surface within a radius of 2 m from the trapping station measured in centimetres.
Number of shrub stems	nss	The number of shrub stems within a circle with a 2 m radius from the trapping station.
Woody profile index	profile	The index was measured as follows: a horizontal rod, 56 cm in length was horizontally rotated around a vertical rod (200 cm) at 40, 80, 120, 160 and 200 cm heights. During each rotation the number of woody contacts (horizontal rod touching woody parts of plants) by the horizontal rod was recorded. The number of contacts at each level was used to calculate the woody profile index using Simpson's information measure ($S = 1/p$, where p_i represents the relative number of contacts in a height class w . Relative contacts in height class w = number of contacts in w /total number of contacts).
Average shrub height	sh	Four measures of shrub height were recorded within a 2 m radius from the trapping station. These measurements were taken randomly in each quarter of the circle around the trapping station. The observer was standing with his back towards the quarter to be measured and tossed a grid (50 × 50 cm) over his shoulder. Shrub height was subsequently measured in centimetres together with other variables. The four measurements were averaged to get a single estimate of shrub height within the 2 m radius from the trapping station.

Average area covered by shrubs	sar	Four measurements of area covered by shrubs were taken in each quarter within a circle of 2 m radius around the trapping station. The observer tossed a grid (50 × 50 cm) over his shoulder while standing with his back to the quarter to be measured. The grid comprised a 10 × 10 configuration of 100 squares. The number of squares having any part of a shrub covering or overlaying it were counted and expressed as a percentage of the grid. The percentage was converted to cm ² to give an estimate of area covered. The four measurements were averaged to get a single estimate of shrub cover within a 50 × 50 cm area situated within the 2 m radius from the trapping station.
Average volume of shrubs	sv	Four estimates of shrub volume were calculated from shrub heights and shrub cover estimated simultaneously. These four estimates were averaged to give a single estimate of shrub volume (cm ³) within a 50 × 50 cm area of 2 m radius from the trapping station.
Average herb height	hh	Four measurements of herb height were taken and treated in a similar fashion to shrub height.
Average area covered by herbs	har	Four measurements of herb cover were recorded similar to that of shrub cover and averaged in the same way.
Average volume of herbs	hv	Four estimates were calculated similar to shrub volume and a single estimate was obtained by averaging these four values.
Average litter depth	bd	Four measurements of the depth of dead plant material were taken similar to that for shrub and herb height and an average value obtained.
Average area covered by litter	bar	The average area covered by dead plant material was calculated from four measurements taken in a similar fashion to that of shrub and herb area.
Average volume of litter	bv	Four estimates of the volume of dead plant material were calculated by using depth and cover measures. An average value was obtained in a similar fashion to that for shrub and herb volume.

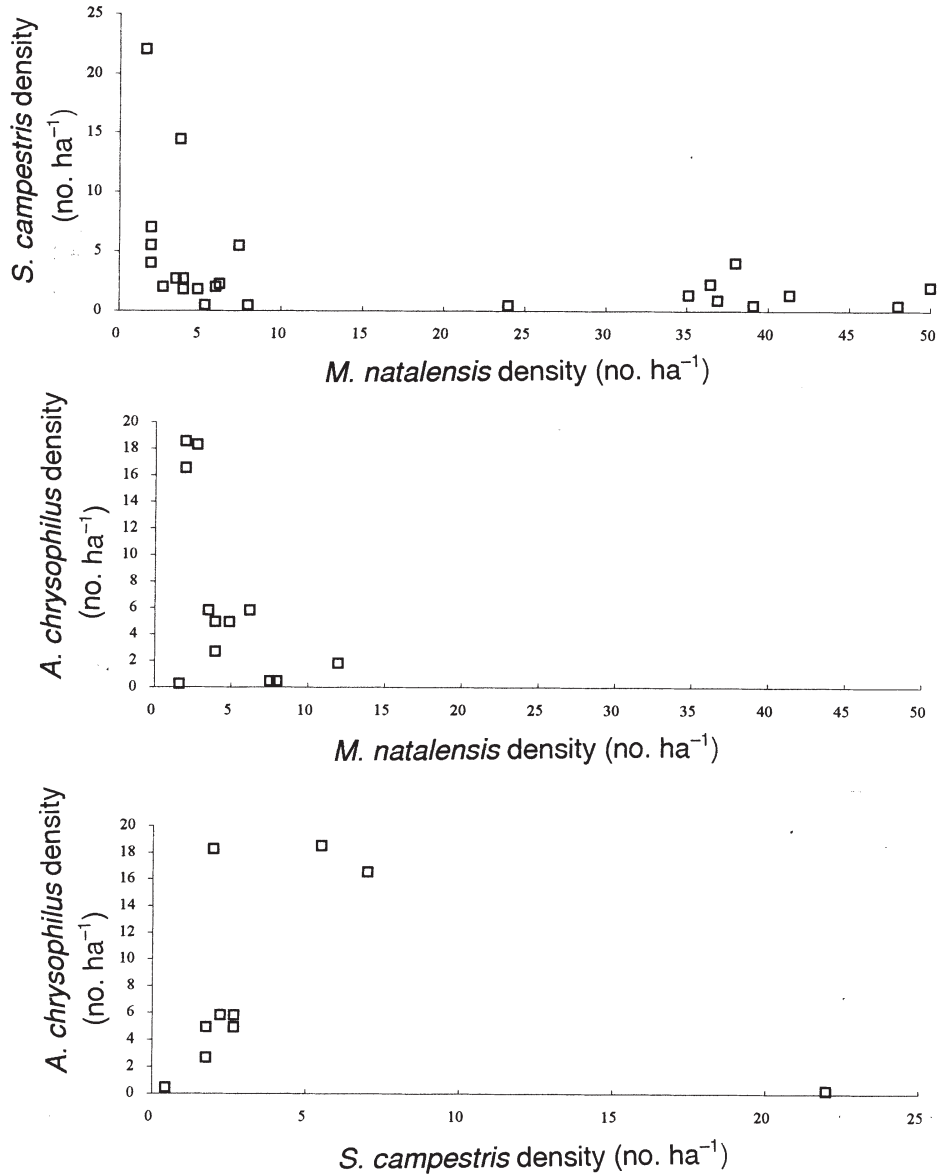


Fig. 2. The scatterplots between species-specific densities of three rodents (*Mastomys natalensis*, *Saccostomus campestris* and *Aethomys chrysophilus*) occurring on stands of rehabilitating and mature coastal dune forests.

for *S. campestris* excluded average shrub height, herb volume, largest biomass depth and shrub volume, but was not significant. All habitat variables were once again included in the model for *A. chrysophilus*, with average shrub height (57%) and area covered by herbs (21%) explaining most of the variation (Table 4).

Table 4. The relationship between species-specific density of three species co-occurring and habitat variables. The results of forward stepwise multiple regression analysis (Limit for F -to-enter set at 0.0001) are also presented. The sequence of variables represent the sequence in which variables entered each model, whereas changes in R^2 -values give an indication of the amount of variation explained by each variable

	<i>Mastomys natalensis</i> $R^2=0.55, F_{15,27}=2.22,$ $P=0.03, n=43$		<i>Saccostomus campestris</i> $R^2=0.97, F_{1,11}=2.74,$ $P=0.44, n=13$		<i>Aethomys chrysophilus</i> $R^2=0.99, F_{15,5}=45.41,$ $P<0.01, n=21$	
	Coefficient	Change in R^2 value	Coefficient	Change in R^2 value	Coefficient	Change in R^2 value
Constant	-0.39	—	-0.23	—	-0.35	—
Highest vegetation height	-0.30	0.18	3.88	0.05	0.38	0.04
Highest shrub height	-0.22	0.01	-1.42	0.06	0.2	<0.01
Highest herb height	0.56	0.03	-0.75	0.04	-0.38	0.01
Litter depth	0.04	0.02	—	—	0.09	<0.01
Number of shrub stems	0.28	0.01	-0.42	0.03	-0.28	0.01
Woody profile index	-0.16	0.03	-1.47	0.02	-0.15	<0.01
Average shrub height	0.26	0.04	—	—	0.51	0.57
Average area covered by shrubs	-0.67	0.01	1.65	0.04	1.45	0.01
Average volume of shrubs	0.59	0.01	—	—	-2.36	0.02
Average herb height	0.52	0.09	2.14	0.01	2.31	0.06
Average area covered by herbs	0.04	0.03	0.88	0.19	0.44	0.21
Average volume of herbs	-1.58	0.07	—	—	-1.50	0.04
Average litter depth	-0.72	0.02	1.56	0.09	-0.63	0.01
Average area covered by litter	-0.63	0.04	-0.22	0.21	-0.16	<0.01
Average volume of litter	0.99	0.01	-3.99	0.25	1.62	0.01

Habitat variables including rodent densities

By using records with density estimates for both *M. natalensis* and *S. campestris* density estimates, 99% of the variation in the density of *M. natalensis* was explained by habitat variables alone (Table 5). The density of *S. campestris* did not enter the model (*F*-to-enter set at 0.0001 to force the density of *S. campestris* as a variable into the model). Records having both *M. natalensis* and *A. chrysophilus* density estimates provided a model explaining 98% of the variation in *M. natalensis* density using habitat variables alone (Table 5). However, this regression was not significant and remained so following the inclusion of the density of *A. chrysophilus* as a variable (although *A. chrysophilus* explained 6.8% of the final model, r^2 increased only from 0.98 to 0.99). Using the densities of *S. campestris* and *A. chrysophilus* as independent variables, respectively, resulted in none of the other species-specific densities being included in models explaining variation in densities of *S. campestris* and *A. chrysophilus*.

Discussion

The densities of *M. natalensis* and *S. campestris* were weakly related to each other, with that of *S. campestris* progressively less affected by the increasing densities of *M. natalensis* densities and *vice versa*. A similar relationship was established between *M. natalensis* and *A. chrysophilus*. This is contradictory to what one would expect from competition theory, which hinges on competitive equilibrium densities being established and maintained (see Volterra, 1926). Any relationship between densities of two competing species should therefore reflect a linear negative relationship. It should be noted that if species populations are below resource equilibrium densities, competition can play no part, in which case habitat variables are likely to be of prime importance. This was one of the prime considerations when distinguishing below 'low' and 'high' densities in the present analysis.

Alternatively, non-linear relationships as recorded here, may reflect on competitive interactions where a slight numerical advantage of one species may result in the apparent exclusion of the other. This would be pertinent if no realized niche differentiation between species exists. One can therefore never have situations of intermediate densities for both species when both species co-occur.

Mastomys natalensis, *S. campestris* and *A. chrysophilus* dominate rodent communities at different stages of coastal dune regeneration (Ferreira & van Aarde, 1996). Thus, it is tempting to conclude that these species' apparent replacement by each other results from competitive interactions leading to competitive exclusion. However, these three species also coexist in mature coastal dune forests (van Aarde *et al.*, 1996b). Based on the present analysis, the associations between *M. natalensis*, *S. campestris* and *A. chrysophilus* appear to be negative for reasons other than species interactions.

Krebs (1978) gave three possible reasons for the absence of a species from a given area. The first is that individuals are not able to disperse to a particular area. However, individuals of *M. natalensis*, *S. campestris* and *A. chrysophilus* occur on all rehabilitating stands and are thus all able to disperse to rehabilitating areas. The second reason given by Krebs (1978) is that the area is unsuitable because habitat requirements are not met, whereas the third reason suggests that individuals cannot

Table 5. The relationships of the densities of *Mastomys natalensis* with a set of habitat variables (habitat variables alone), and a set of habitat variables and species-specific densities of *Saccostomus campestris* and *Aethomys chrysophilus*, (habitat variables and a species' density). *aet* = *Aethomys chrysophilus* density, *sac* = *Saccostomus campestris* density. See also Table 3 for clarification of habitat variable codes

<i>Mastomys natalensis</i>	Set of variables	R ²	Relationship	F-value	P-value
<i>Saccostomus campestris</i> n = 11	Habitat variables alone	0.99	$y = 17.52 - 0.95bar - 0.17profile + 0.57sar - 1.14tsh + 0.40thh - 1.18bv + 1.90/bd + 0.68sv - 0.67tvh$ <i>S. campestris</i> density does not enter the model	$F_{9,1} = 435.95$	0.04
	Habitat variables and <i>S. campestris</i> density	—	—	—	—
<i>Aethomys chrysophilus</i> n = 16	Habitat variables alone	0.98	$y = 63.51 - 2.54thh + 1.57nss + 7.41profile + 36.91sh - 7.66tbd + 10.30bd - 5.90tvh - 26.16sv - 7.61tsh - 1.79sar - 7.85th + 8.62hv + 2.21ba$ $r = 1.27bv$	$F_{14,1} = 2.17$	0.49
	Habitat variables and <i>A. chrysophilus</i> density	0.99	$y = -31.47 + 6.23thh + 1.49nss + 0.82profile + 7.13aet + 6.69hv + 0.90bar - 2.47tvh - 16.69hh + 9.01bd - 8.91sar - 17.01bv + 12.97sv - 2.78tbd - 0.68har$	$F_{14,1} = 18.34$	0.18

persist in an area in the presence of another species. Biologically, this sequence of criteria suggests that species interactions can only be considered once species have established themselves and habitat characteristics have been accounted for. The analyses in this study illustrate that the majority of variation in species-specific densities of *Mastomys-Saccostomus-Aethomys* assemblages can be explained by habitat characteristics. Variation in the density of *S. campestris* is primarily accounted for by the area covered by herbs, the area covered in litter, and the total amount of litter. The density of *A. chrysophilus* density can be explained by shrub height and the area covered by herbs. However, for both of these species numerous other habitat variables are required to produce satisfactory explanation of their densities.

Variation in the density of *M. natalensis* is not well accounted for by habitat variables, with only 55% of the variation in densities explained by the recorded habitat variables. As such, the contribution of any particular habitat feature was not outstanding. This most likely reflects on the opportunistic nature of *M. natalensis* (see Meester *et al.*, 1979). The present results suggest that *M. natalensis* is the most likely candidate for species interactions playing a potential role in determining density of this species. Although data were limited, this analysis illustrates that accounting for habitat variables first and subsequently for the density of *S. campestris* resulted in no additional variance of the density of *M. natalensis* being explained. The present analysis also illustrates that the density of *A. chrysophilus* contributed little to explaining variability in the density of *M. natalensis*—it entered the model after the inclusion of habitat variables first and explained only an additional 1% of the variance.

The influence of age-related change in habitat on densities of these species suggests that their low densities on older rehabilitating stands may be due to changes in vegetational characteristics and habitat structure with the regeneration of coastal dune forests (see Ferreira & van Aarde, 1996; van Aarde *et al.*, 1996b). Here, densities of potential competitors probably never reach equilibrium values, resulting in habitat changes, rather than competition, being the major determinant of rodent communities in coastal dune forests.

Based on the decrease in rodent densities with an increase in habitat regeneration age (Ferreira & van Aarde, 1996), it seems that environmental conditions become progressively more unsuitable for rodents. On older regenerating stands, rodents occur at such low densities that intra-specific competition is unlikely to occur. On the other hand, older, mature forests will be much more suitable for rodents, possibly as a result of greater diversity of habitats in patches within these forests.

Abramsky (1981) based his illustration of interspecific competition between the congeneric species *Apodemus mystacinus* and *A. sylvaticus* on the same methods as used by us in the present study. Kincaid & Cameron (1982) illustrated that *Mus* sp. and *Peromyscus* sp. did not exhibit a habitat shift in the absence of each other, and Scott & Dueser (1992) reported similar results. In addition, Ellenbroek & Hamburger (1991) reported no inter-specific interactions between two shrew species. Rosenzweig (1979) furthermore argued that habitat specialization of species has been moulded by past competitive interactions. This is quite likely as all three species in question in the present study are native to Africa, suggesting that past competitive interactions cannot be discounted.

In contrast, Fox & Pople (1984) reported interspecific competition between native and introduced mice, which were not congeneric, in the successional development

of rodent communities following mining in Australia. The present study is in agreement with that of Rosenzweig (1979) in illustrating no interspecific competition, probably because all species in the community in this study are native species. Past competitive interactions may have minimized present competition. However, Abramsky *et al.* (1990) as well as Ziv *et al.* (1993) reported interspecific competition between two native congeneric gerbil species *Gerbillus allenbyi* and *G. pyramidum*, and Higgs & Fox (1993) and Thompson & Fox (1993) documented interspecific competition between *Pseudomys gracilicaudatus* and *Rattus lutreolus*, two non-congeneric native species occurring in Australian heathlands. In southern Africa, Hughes, Ward & Perrin (1994) reported competition between *Gerbillurus tytonis* and *Rhabdomys pumilio*. It is more likely that competition amongst native rodents will occur when environmental conditions have been stable for a long enough period for equilibrium densities to be reached (see Keddy, 1989).

Although the apparent significance of competition in playing a role in the species replacement reported by Ferreira & van Aarde (1996) is not supported by the results presented here, interspecific competition may have been recorded had species occurred at higher densities. Furthermore, the combination of other factors such as meta-population dynamics (see Valone & Brown, 1995) with habitat characteristics and species interactions may hide competitive interactions amongst species. Nevertheless, the present approach illustrated that most variation in species-specific density of *Mastomys-Saccostomus-Aethomys* assemblages could be explained by habitat variables without giving rise to species interactions.

Acknowledgements

We would like to thank the Foundation for Research Development, Department of Trade and Industry, and Richards Bay Minerals for logistical and financial support. We appreciate field-assistance provided by Zamani Tembi, D. J. Matagne, Faure Goedhals, Andre la Cock, Phiwa Mtembu, Bheki Mpanza, Bheki Mbonazi and Jaco Delpont.

References

- ABRAMSKY, Z. (1981) Habitat relationships and competition in two Mediterranean *Apodemus* spp. *Oikos* **36**, 219–225.
- ABRAMSKY, Z., ROSENZWEIG, M.L., PINSHOW, B., BROWN, J.S., KOTLER, B. & MITCHELL, W.A. (1990) Habitat selection: an experimental field test with two gerbil species. *Ecology* **71**, 2358–2369.
- CONNELL, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**, 661–696.
- CROWELL, K.L. & PIMM, S.L. (1976) Competition and niche shifts of mice introduced onto small islands. *Oikos* **27**, 251–258.
- DE GRAAFF, G. (1981) *The Rodents of Southern Africa*. Butterworth, Pretoria.
- ELLENBROEK, F.J.M. & HAMBURGER, J. (1991) Interspecific interactions between the shrews *Sorex araneus* L. and *S. minutus* L. (Soricidae, Insectivora) and the use of habitat: a laboratory study. *Neth. J. Zool.* **41**, 32–62.
- 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. *Afr. J. Ecol.* **34**, 113–130.
- FOX, B.J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* **63**, 1332–1341.
- FOX, B.J. (1990) Changes in the structure of mammal communities over successional time scales. *Oikos* **59**, 321–329.

- FOX, B.J. & POPLE, A.R. (1984) Experimental confirmation of interspecific competition between native and introduced mice. *Aust. J. Ecol.* **9**, 323–334.
- GAUSE, G.F. (1934) *The Struggle for Existence*. Williams & Wilkins, Baltimore.
- GLIWICZ, J. (1985) Rodent community of dry African savanna: population study. *Mammalia* **49**, 509–516.
- HIGGS, P. & FOX, B.J. (1993) Interspecific competition—a mechanism for rodent succession after fire in wet heathland. *Aust. J. Ecol.* **18**, 193–201.
- HUGHES, J.J., WARD, D. & PERRIN, M.R. (1994) Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology* **75**, 1397–1405.
- KEDDY, P.A. (1989) *Competition*. Chapman & Hall, London.
- KERLEY, G.I.H. (1989) Diet of small mammals from the Karoo, South Africa. *S. Afr. J. Wildl. Res.* **19**, 67–72.
- KINCAID, W.B. & CAMERON, G.N. (1982) Effects of species removal on resource utilization in a Texas rodent community. *J. Mammal.* **63**, 229–235.
- KOTLER, B.P. & BROWN, J.S. (1988) Environmental heterogeneity and the coexistence of desert rodents. *Ann. Rev. Ecol. Syst.* **19**, 281–307.
- KREBS, C.J. (1978) A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* **56**, 2463–2480.
- MEESTER, J., LLOYD, C.N.V. & ROWE-ROWE, D.T. (1979) A note on the ecological role of *Praomys natalensis*. *S. Afr. J. Sci.* **75**, 183–184.
- MENTIS, M.T. & ELLERY, W.N. (1994) Post-mining rehabilitation of dunes on the north-east coast of South Africa. *S. Afr. J. Sci.* **90**, 69–74.
- PIMM, S.L. (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago.
- RICKLEFS, R.E. & SCHLUTER, D. (1993) *Diversity in Ecological Communities*. University of Chicago Press, Chicago.
- ROSENZWEIG, M.L. (1977) Coexistence and diversity in heteromyid rodents. In: *Evolutionary Biology* (Eds B. Stonehouse and C. Perrins). MacMillan, London.
- ROSENZWEIG, M.L. (1979) Optimal habitat selection in two species competitive systems. *Fortsch. Zool.* **25**, 283–293.
- SCHOENER, T.W. (1983) Field experiments on interspecific competition. *Am. Nat.* **122**, 240–285.
- SCOTT, D.E. & DUESER, R.D. (1992) Habitat use by insular populations of *Mus* and *Peromyscus*: what is the role of competition? *J. Anim. Ecol.* **61**, 329–338.
- SKINNER, J.D. & SMITHERS, R.H.N. (1990) *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.
- SMITHERS, R.H.N. (1971) The mammals of Botswana. *Mus. Mem. Natl. Mus. Monum. Rhod.* **4**, 1–340.
- SOKAL, R.R. & ROHLF, F.J. (1995) *Biometry. The Principles and Practice of Statistics in Biological Research*. W.H. Freeman & Co., San Francisco.
- THOMPSON, P. & FOX, B.J. (1993) Asymmetric competition in Australian heathland rodents—a reciprocal removal experiment demonstrating the influence of size-class structure. *Oikos* **67**, 264–278.
- VALONE, T.J. & BROWN, J.H. (1995) Effects of competition, colonization and extinction on rodent species diversity. *Science* **267**, 880–883.
- VAN AARDE, R.J., FERREIRA, S.M. & KRITZINGER, J.J. (1996a) Successional changes in rehabilitating coastal dune communities in northern KwaZulu/Natal, South Africa. *Land. Urb. Plan.* **34**, 277–286.
- 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. *Rest. Ecol.* **4**, 334–345.
- VAN DER MEER, J.H. (1969) The competitive structure of communities: an experimental approach with protozoa. *Ecology* **50**, 362–367.
- VOLTERRA, V. (1926) Variations and fluctuations of the numbers of individuals in animal species living together. Reprinted 1991. In: *Animal Ecology* (Ed. R.N. Chapman). McGraw-Hill, 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, South Africa.
- WIRMINGHAUS, J.O. & PERRIN, M.R. (1993) Seasonal changes in density, demography and body composition of small mammals in a southern temperate forest. *J. Zool., Lond.* **229**, 303–318.
- ZIV, Y., ABRAMSKY, Z., KOTLER, B.P. & SUBACH, A. (1993) Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* **66**, 237–246.

(Manuscript accepted 16 June 1998)