

DELAYED RESPONSES OF SMALL-MAMMAL ASSEMBLAGES SUBJECT TO AFFORESTATION-INDUCED GRASSLAND FRAGMENTATION

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Twelve Afromontane grassland fragments and 12 control sites were created in a pine-afforested region at Groenvaly in South Africa. Three live-trapping surveys of small mammals were performed, 1 survey a year before planting, 1 immediately after planting, and one 4 years later, yielding 768 small mammals representing 8 species. In 1998, small-mammal assemblages inside the plantations were also monitored. Between 1994 and 1998, similar changes in assemblage structure occurred in control sites and experimental fragments. In small fragments, *Crocidura* was comparatively abundant, apparently attributable to edge effects. Despite extensive habitat disturbance through afforestation by 1998, assemblage structure and movement distances within the plantation were similar to those recorded in undisturbed grassland assemblages. We conclude that, 4 years after afforestation, small mammals do not yet experience afforestation as a major habitat fragmenting force, and that gradual fragmentation at Groenvaly yields trends in small-mammal assemblages that are quite different from those of experiments employing abrupt habitat fragmentation.

Key words: dispersal, forestry, habitat fragmentation, movements, *Pinus patula*, plantation

Natural ecosystems throughout the world are becoming increasingly modified by an array of large-scale human activities (e.g., forestry, mineral extraction, urbanization, and agriculture), often resulting in habitat degradation and fragmentation (Ehrlich 1993). Scientific understanding of these processes is essential for effective conservation and management of natural resources. Microclimate changes inherent to habitat fragmentation (Saunders et al. 1991) can have major structural and behavioral consequences for remnant assemblages (e.g., stochastic extinction, crowding, dispersal, edge effects, and interspecific as well as intraspecific effects: Laurance 1997; Noss and Csuti 1997). Unfortunately, the biotic consequences of habitat fragmentation are often assessed by way of post hoc descrip-

tive studies (Bolger et al. 1997; Soulé et al. 1992). The problems associated with this type of study are multifarious (Margules 1992) but essentially concern their inability to infer fragmentation as the cause of spatial and temporal changes in remnant assemblages because of lack of before-fragmentation documentation, replication of comparable fragments, and explicit use of control sites. Most of these shortcomings are solved in planned habitat fragmentation experiments, e.g., the Amazon basin study (Lovejoy et al. 1983, 1984), the Australian Wog-Wog experiment (Margules 1992), the Kansas agriculture field experiment (Robinson et al. 1992), and the Californian grasslands fragmentation experiment (Quinn and Robinson 1987). The Groenvaly study site in South Africa represents such a planned fragmentation experiment

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(van Jaarsveld et al. 1998). In contrast to other experiments in which fragments were created through clearing of vegetation, the Groenvaly experiment involves gradual fragmentation of preassigned grassland fragments after planting of pine plantation. The aim of this experiment is to determine the effect of forestry-related fragmentation on plant and animal assemblages occupying indigenous montane grasslands.

The Afromontane grasslands on the Drakensberg escarpment of southern Africa are approximately 12,000 years old and are characterized by extensive biodiversity and high levels of plant endemism (Matthews et al. 1993). Industrial afforestation plays a major role in destroying and fragmenting this ecosystem and, as yet, no experimental initiatives have sought to determine how these disturbances impact on remnant assemblages. Late in 1994, South African Paper and Pulp Industries (SAPPI) Forests (Pty) Ltd planted 5,000 ha of pine plantations (*Pinus ellioti* and *P. patula*) at Groenvaly. Prior to planting, grassland fragments, including replicates and controls were demarcated (van Jaarsveld et al. 1998). We explore temporal and treatment effects on mammalian assemblages at Groenvaly that have taken place since afforestation. Our aims are, 1st, to test whether 4 years after afforestation, fragmentation affected small mammals in terms of biodiversity within fragments, assemblage composition, and movement patterns, and 2nd, to compare assemblage structure and movement patterns within plantations with those of grasslands.

MATERIALS AND METHODS

The experiment was initiated on the Drakensberg mountain range at Groenvaly (25°30'S, 30°45'E) in the province of Mpumalanga, South Africa. The experimental setup and prefragmentation information were described by van Jaarsveld et al. (1998) and Bredenkamp et al. (1999). The experiment comprises 2 treatments: 12 grassland fragments (6 of 1.5 ha, 6 of 0.25 ha) within pine plantations (hereafter experimental

fragments; E1–E12 in Fig. 1), and an additional 12 grassland sites (6 of 1.5 ha, 6 of 0.25 ha) within an adjacent conservation area (hereafter control sites; C1–C12 in Fig. 1). In 1998, 12 further sites (6 of 1.5 ha, 6 of 0.25 ha) were surveyed within afforested area (hereafter plantation sites; P1–P12 in Fig. 1). Within each of these treatment groups, first 6 (C1–C6, E1–E6, P1–P6) were large fragments (1.5 ha), remainder being small fragments (0.25 ha). Placement of all the replicates (control, fragment, and plantation) was based on uniform physiographical and botanical considerations (van Jaarsveld et al. 1998). During planting, pine trees were spaced in a grid 2.4 m apart. The level of physical disturbance these trees caused was very noticeable by 1998. Consequently, it was expected that large differences in microhabitat (e.g., in shade and temperature) existed between the plantations and the grasslands (Saunders et al. 1991).

Three small-mammal field surveys were carried out, a prefragmentation survey in April–May 1994, followed by surveys in April 1995 (immediately after planting) and March–April 1998, totaling 10,080 trap nights. The rodent population densities in perennial grasslands of the South African highveld are highly seasonal, with reproduction taking place between November and March, reaching peaks in population numbers during March and April (Bronner et al. 1988; Brooks 1982; Davis and Meester 1981). During winter (May–September) vegetation dies down because of frost, and rodent populations decrease substantially (Davis 1973; Smithers 1983). One of the species we trapped, *Mastomys natalensis*, is known to undergo population eruptions in warmer habitats (Withers 1979). However, it formed a small component of the assemblage we encountered. Our surveys were performed at the end of summer season after reproduction had taken place and before cold of winter set in. During each survey, small mammals were live-trapped using Sherman traps so that dispersal, relative densities, and assemblage composition could be assessed. Sampling during each survey consisted of setting 64 traps in each of the large fragments (8 by 8 grid, 15 m between traps) and 16 in the small fragments (4 by 4 grid, 12.5 m between traps). Each trap was uniquely identified in order to document animal movement between and within grids. Traps were placed relative to permanent markers spaced along 2 edges of the grid. Traps were baited with

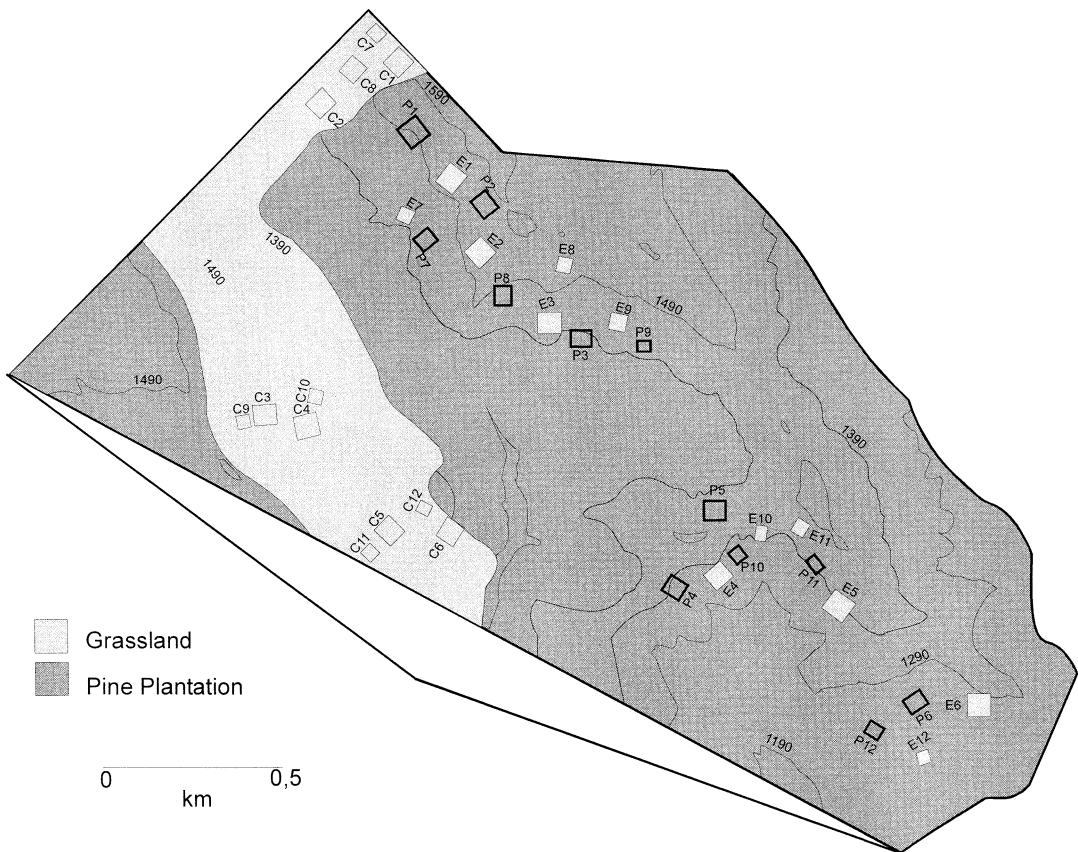


FIG. 1.—Groenvally study site in South Africa. Localities of control sites (C1–C12), experimental sites (E1–E12), and plantation sites (P1–P12) are indicated. Large fragments are numbered 1–6 and small fragments are numbered 7–12. Some of the main contours are shown with values for elevation above sea level (meters).

a mixture of rolled oats, cooking oil, and peanut butter, shaded with vegetation, inspected and baited daily between 0700 and 1000 h. Each grid was trapped for 3 days. Upon 1st capture, each small mammal was identified, sexed, and measured. Because *Aethomys chrysophilus* and *A. namaquensis*, as well as *Crocidura flavescens* and *C. hirta* are not reliably diagnosable without skeletal characteristics (Smithers 1971), they were grouped as species of *Aethomys* and species of *Crocidura*. Animals were marked using the 1–2–4–7 toe-clipping system (DeBlase and Martin 1981).

The height, canopy diameter, trunk thickness, and distance to neighboring tree were measured in plantation for 100 trees at each of the sites P3, P8, and P2 (Fig. 1). This allowed the calculation of canopy cover within plantation.

Different sampling intensities on the large and small plots necessitated separate analysis of data from 2 fragment sizes. Abundance represented total number of animals captured during 3 nights, excluding recaptures. Trapping rates among different years were compared using repeated measures analysis of variance (ANOVA). Fragment diversity was calculated using the Shannon–Wiener diversity index (Shannon and Weaver 1949). Changes in diversity between years (1994, 1995, and 1998) and treatments (control, experimental fragments, and plantation) were tested using ANOVA (repeated measures ANOVA among years; 1-way ANOVA among different categories of sites within the same year, with Tukey's post hoc comparisons on results of significant statistics). Assemblage similarity was estimated using the Bray–Curtis

coefficient of similarity (using square-root-transformed abundance data—Bray and Curtis 1957). We used the computer program Primer Version 4.0 for performing 1-way analysis of similarity (ANOSIM—Clarke 1993; Clarke and Gorley 2001) to compare the communities of different treatments during 1998. This is a randomization-based approach using the rank abundances of taxa within sampling plots. We used the RELATE procedure of Primer (Clarke and Gorley 2001), based on a similar approach, to compare communities of different treatments over 3 sampling periods, testing for any temporal trends (seriation) in community structure. A maximum-likelihood ratio test was used to determine whether species of *Crociodura* were trapped more often along edges of large grassland fragments, than in interior of those fragments. Because of small sample sizes, interpretation of recapture data was restricted to individuals recaptured within the same trap grid during a particular survey. As trapping at each grid was performed over 3 nights, recaptures occurred in the 1st and 2nd night after marking an individual. However, a Smirnov 2-sample test indicated that distances traveled by animals recaptured after 1 night did not differ significantly from those recaptured after 2 nights (*Rhabdomys pumilio*: $T = 0.13$, $P > 0.2$; *Crociodura*: $T = 0.19$, $P > 0.2$). Recapture data were therefore combined. Statistical analysis of movement distances per species over treatments and years was performed using a Kruskal–Wallis ANOVA.

RESULTS

During the 3 trapping surveys covering 10,080 trap nights, a total of 768 individuals belonging to 8 small-mammal taxa were captured. Of these, the striped mouse *Rhabdomys pumilio* ($n = 386$), the musk shrews *Crociodura hirta* and *C. flavescens* ($n = 193$), and the forest shrew *Myosorex varius* ($n = 102$) collectively accounted for 89% of all captures. Other species captured included pigmy mouse *Mus minutoides* ($n = 27$), climbing mouse *Dendromus mysticalis* ($n = 21$), rock rats *A. chrysophilus* and *A. namaquensis* ($n = 20$), vlei rat *Otomys irroratus* ($n = 15$), and multimammate mouse *M. natalensis* ($n = 4$). The average trapping success was 7.56% (Table 1).

In 1998, pine trees at Groenvaly were taller than 4.5 m with a mean branch length of 1.45 m and a canopy cover of 86%. This significantly impacted the vegetation under trees (Fig. 2) via dense shade and pine leaves that caused grass tufts to become moribund.

During the 1998 survey, the Shannon–Wiener diversity indexes among the 3 treatments (controls, fragments, and plantations) did not differ significantly for either large or small fragments (Table 2). In addition, no temporal changes in diversity were observed over the 4-year period for either the control sites (large and small) or experimental fragments (large and small; Table 2).

Results from ANOSIM suggested that, during 1998, mammal-assemblage structure in control and experimental large fragments was similar to prefragmentation results (1994; Table 3A). This conclusion was further supported by results indicating that, during the 1998 survey, mammal assemblages of large fragments were also similar among treatments (controls, fragments, and plantations; Table 3B). In contrast, assemblages of small control sites and experimental fragments differed significantly during the 4-year period. However, no systematic temporal effect on the mammal assemblages in small fragments was observed (Table 3A). Data from 1998 suggest that assemblages within small plantation sites and control sites were similar, whereas small experimental fragments differed significantly from both the other treatments (control sites and plantations), mostly because of large numbers of *Crociodura* captured there (Table 3B).

As expected, several temporal population changes within species (e.g., *R. pumilio*, *M. varius*, and *M. minutoides*) occurred between 1994 and 1998. Multiple comparison confirmed a constant increase in numbers of *M. varius* from 1994 to 1998 in large sites ($F = 5.66$, $d.f. = 2, 33$, $P < 0.01$, Tukey $P < 0.01$; Fig. 3). This result applied to the control as well as experimental sites. Numbers of *R. pumilio* increased significantly

TABLE 1.—Number of animals trapped per site over a 3-day period in control sites and in sites fragmented by pine plantation over a 4-year period. Planting was done in 1995; rightmost column indicates significant differences ($P < 0.05$) between trapping rates for each species over the 3 trapping periods (1994, 1995, and 1998), obtained using a Tukey's post hoc comparison, following a repeated measures ANOVA on combined trapping result for fragments and control plots, excluding plantation plots. Values are given as mean \pm SE.

	1994			1995			1998			Tukey's tests		
	Control	Fragments		Control	Fragments		Control	Fragments	Plantation	Total	$P < 0.05$	
Large fragments												
<i>Rhabdomys pumilio</i>	3.0 ± 1.10	4.3 ± 1.31		10.0 ± 1.73	7.2 ± 2.98		6.5 ± 1.88	9.3 ± 1.38	8.3 ± 1.96	6.9 ± 0.75	94/95 94/98	
<i>Crocidura</i>	2.3 ± 0.42	4.8 ± 0.65		3.5 ± 1.02	2.7 ± 0.71		2.3 ± 0.61	4.8 ± 1.66	2.3 ± 0.67	3.3 ± 0.36		
<i>Myosorex varius</i>	0.5 ± 0.34	0.3 ± 0.33		2.2 ± 0.6	0.8 ± 0.40		2.5 ± 0.67	2.8 ± 1.25	4.8 ± 1.80	2.0 ± 0.40	94/98	
<i>Aethomys</i>	0.3 ± 0.33	0.2 ± 0.17		1.2 ± 0.54	0.2 ± 0.17		0.3 ± 0.33	0.0	0.0	0.3 ± 0.12		
<i>Otomys irroratus</i>	0.00	0.00		1.0 ± 0.45	0.0		0.7 ± 0.33	0.2 ± 0.17	0.3 ± 0.33	0.3 ± 0.10		
<i>Dendromys mysticallis</i>	0.3 ± 0.33	0.5 ± 0.34		0.0	1.5 ± 0.62		0.3 ± 0.33	0.2 ± 0.17	0.0	0.4 ± 0.14		
<i>Mus minutoides</i>	0.7 ± 0.33	0.8 ± 0.48		0.0	0.0		0.0	0.0	0.0	0.4 ± 0.11	94/98	
<i>Mastomys natalensis</i>	0.2 ± 0.17	0.00		0.0	0.0		0.0	0.0	0.0	0.1 ± 0.04		
Mean total	7.3 ± 1.09	11.0 ± 2.10		18.5 ± 2.77	13.3 ± 3.82		12.7 ± 2.35	17.3 ± 2.7	15.8 ± 3.73			
Small fragments												
<i>Rhabdomys pumilio</i>	1.2 ± 0.65	2.2 ± 0.54		2.2 ± 0.60	3.0 ± 0.68		1.5 ± 0.22	2.7 ± 0.67	3.0 ± 1.13	2.2 ± 0.26		
<i>Crocidura</i>	0.2 ± 0.17	2.0 ± 0.73		1.0 ± 0.52	1.7 ± 0.42		0.2 ± 0.17	3.8 ± 1.08	0.5 ± 0.34	1.3 ± 0.28		
<i>Myosorex varius</i>	0.2 ± 0.17	0.2 ± 0.17		0.3 ± 0.21	0.2 ± 0.17		0.7 ± 0.21	0.0	1.5 ± 0.43	0.4 ± 0.11		
<i>Aethomys</i>	0.2 ± 0.17	0.2 ± 0.17		0.8 ± 0.40	0.0		0.0	0.0	0.0	0.2 ± 0.08		
<i>Otomys irroratus</i>	0.0	0.0		0.0	0.0		0.2 ± 0.17	0.2 ± 0.17	0.0	0.1 ± 0.11		
<i>Dendromys mysticallis</i>	0.3 ± 0.21	0.0		0.2 ± 0.17	0.2 ± 0.17		0.0	0.0	0.0	0.1 ± 0.05		
<i>Mus minutoides</i>	0.8 ± 0.54	0.7 ± 0.42		0.0	0.2 ± 0.17		0.0	0.0	0.0	0.2 ± 0.11	95/98	
<i>Mastomys natalensis</i>	0.0	0.0		0.2 ± 0.17	0.0		0.0	0.0	0.0	0.02 ± 0.02		
Mean total	2.8 ± 0.70	5.2 ± 1.54		4.7 ± 1.26	5.2 ± 0.65		2.5 ± 0.50	6.7 ± 1.20	5.0 ± 1.24			



FIG. 2.—Pine plantation surrounding fragment E3, indicating the dense stand of *Pinus patula* trees around fragments and in plantation.

between 1994 and 1995 in large sites ($F = 4.26$, $d.f. = 2, 33$, $P < 0.03$, Tukey $P < 0.03$), with increases in control sites ($F = 4.76$, $d.f. = 2, 15$, $P < 0.03$, Tukey $P < 0.02$) as well as experimental fragments ($P = \text{n.s.}$). Finally, a general decrease in abundance of *M. minutoides* from 1994 to 1998 was recorded in both large ($F = 3.96$, $d.f. = 2, 33$, $P < 0.03$, Tukey $P < 0.04$) and small ($F = 4.41$, $d.f. = 2, 33$, $P < 0.025$, Tukey $P < 0.03$) fragments among all treatments (Fig. 3).

The temporal increase of *Crocidura* in small experimental fragments (Fig. 3) resulted in the 1998 populations being signif-

icantly more abundant than populations of small plantation sites ($F = 9.44$, $d.f. = 2, 15$, $P < 0.01$, Tukey $P < 0.01$) and the small control sites (Tukey $P < 0.01$; Fig. 4). These results are consistent with assemblage-level differences observed (Table 3). The density of *M. varius* was higher in small plantation sites than in experimental fragments ($F = 7.43$, $d.f. = 2, 15$, $P < 0.01$, Tukey $P < 0.01$). Despite lack of statistical significance, changing dominance trend between 2 abundant insectivores was also observed in the large plots (Table 1).

The high abundance of *Crocidura* in small experimental sites (Table 1) could either result from a type-II error associated with a small sample size or *Crocidura* preferred-edge habitat. A trend suggesting such an edge effect was evident in large fragments (1.42 times the expected trap rate < 15 m from edge; 0.24 times expected trap rate > 45 m from edge). However, a maximum-likelihood ratio test failed ($G = 4.70$, $d.f. = 4$, $P < 0.2$) to confirm this trend. The geographic distribution of *Crocidura* captured in large control ($G = 9.20$, $d.f. = 4$, $P > 0.05$) and plantation ($G = 0.98$, $d.f. = 4$, $P > 0.9$) sites was uniform throughout the grids.

Except for *R. pumilio* and *Crocidura*,

TABLE 2.—Shannon–Wiener diversity and statistical difference in diversity between 3 treatments (control sites, experimental fragments, and plantation sites) in 1998 and between 3 trapping surveys. Significance levels result from repeated measures ANOVA (A) and 1-way ANOVA (B).

	1994	1995	1998	F-statistic ($d.f. = 2, 15$)	P
A. Between the 3 survey years (1994, 1995, and 1998)					
Experimental large	0.96	0.99	0.89	0.19	0.82
Experimental small	0.66	0.73	0.52	0.40	0.68
Control large	0.96	1.23	1.06	2.41	0.14
Control small	0.39	0.78	0.57	0.90	0.44
	Control	Fragments	Plantation		
B. Between treatments in 1998 (control, fragment, plantation)					
Large sites	1.06	0.89	0.89	1.47	0.26
Small sites	0.57	0.52	0.48	0.08	0.93

TABLE 3.—A) Changes in small-mammal community structure over 3 survey years (tested using RELATE) and ANOSIM results testing differences between control and experimental sites over a 4-year period. Large and small fragments were analyzed separately; and B) results of 1-way ANOSIM testing for differences in community structure of small mammals inhabiting the 3 different treatments (control sites, experimental fragments, and plantation sites) in 1998.

Groups compared		ρ	Permutations	Significant statistics	P
A. Between the 3 survey years (1994, 1995, and 1998)					
Large sites (1.5 ha)					
Global test	Control and Fragments	0.05	5,000	732	0.140
	1994, 1995, and 1998	0.41	999	319	0.32
Small sites (0.25 ha)					
Global test	Control and Fragments	0.26	5,000	7	0.002
	1994, 1995, and 1998	0.1	999	151	0.15
B. Between treatments in 1998 (control, fragment, plantation)					
Large sites (1.5 ha)					
Global	All	-0.07	5,000	4,201	0.840
Small sites (0.25 ha)					
Global test	All	0.39	2,500	2	0.001
Pairwise test	Fragments and Control	0.69	462	2	0.004
	Fragments and Plantations	0.47	462	2	0.004
	Plantations and Control	0.03	462	117	0.250

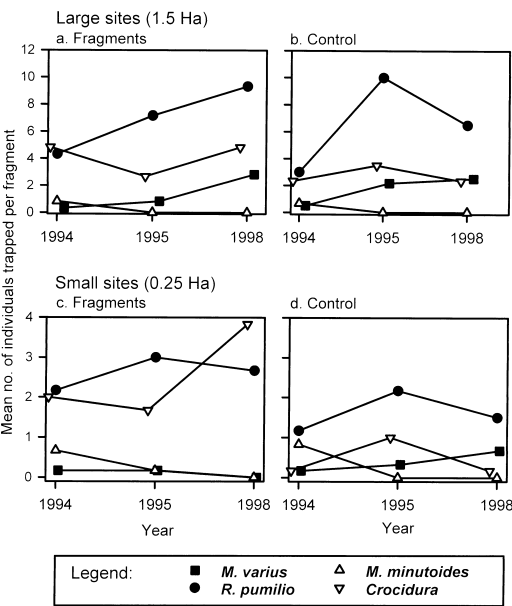


FIG. 3.—Mean number of small mammals captured per plot for each of 3 surveys (1994, 1995, and 1998) within different treatment areas. Data are presented for 4 most common species for which statistics could be performed and for each of the treatments.

small numbers of recaptures were not sufficient for statistical analysis. Movement patterns for the above 2 species have not been modified by fragmentation in any respect. There was no change in movement distances for either *R. pumilio* (Kruskal-Wallis $H = 4.27$, $P > 0.1$) or *Crocidura* ($H = 4.35$, $P > 0.1$) during the 3 surveys (Fig. 4). Likewise, during the 1998 movement

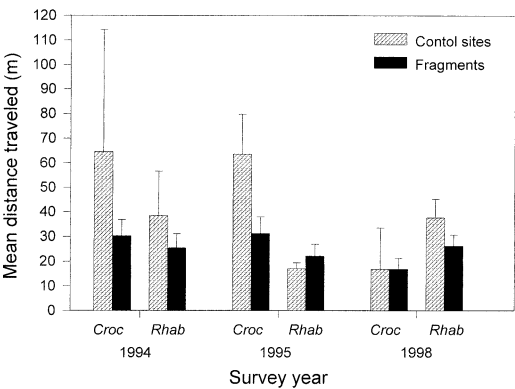


FIG. 4.—Mean distance moved by recaptured *Crocidura* and *Rhabdomys pumilio*. Vertical lines represent 1 SD.

distances for same species were similar for all 3 categories of sampling plots (*Crocidura*: $H = 3.75$, $P > 0.2$; *R. pumilio*: $H = 3.34$, $P > 0.3$).

DISCUSSION

Interpretation of trapping results of small mammals in grassland fragments and in control plots is complicated by the fact that many rodents could potentially be trapped even if only part of their home ranges fell into a control plot. This possibility does not exist in grassland fragments surrounded by plantation and could give rise to biases in population estimates based on trapping rates (Bowers et al. 1996). Although this effect may become evident in future work in these fragments, it was not important during the present study, as discussed subsequently.

Small-mammal populations in the study area have changed between 1994 and 1998. *R. pumilio* increased noticeably from 1994 to 1995 in control sites and in experimental fragments. These findings, together with the trend toward shorter movement distances of *R. pumilio* in control sites during 1995, suggest that fragmentation-induced crowding was not responsible and that factors other than fragmentation such as resource availability and modified home range size could explain high trap success during 1995. The strengths of planned fragmentation experiments are evident with data such as those for *R. pumilio* presented here, as it is possible to determine whether changes in population densities were attributable to fragmentation effects or to other broad-scale population changes (Margules 1992). *M. varius* has become increasingly common in our entire study area, with most abundant populations occurring inside pine plantations. As the preferred habitat of *M. varius* is within natural forests (Meester 1963), this finding during 1998 is perhaps not surprising. The pigmy mouse (*M. minutoides*) has decreased in abundance from 1994 to 1998 at Groenvaly. However, because it was originally a rare species, it is impossi-

ble to determine statistically whether its decline was restricted to either experimental or control sites. *Crocidura* populations were abnormally abundant in small fragments during 1998 and constitute major source of observed assemblage differences for small fragments (Table 1). An explanation for this may be that the ecotone between plantation and grassland is proportionally larger in small fragments because of an increased edge-to-interior ratio, resulting in a unique environment, different from both grasslands and plantations and favoring *Crocidura*. Although this trend was not statistically significant, larger numbers of *Crocidura* were captured near edges of large fragments, and we expect that this phenomenon is biologically significant, as has been found for several other taxa (Bayne and Hobson 1998; Laurance 1997). Because several mammalian species are analyzed simultaneously, it is possible that some statistical results are significant because of the fact that several species are analyzed separately. However, the congruence of trends in control plots with those of fragments and trends in large fragments with those of the small fragments strongly indicate that the trends discussed above are general over the whole study area. In addition, a Bonferroni adjustment of statistical results indicate that 3 of the 4 statistically significant results in Table 1 reflect differences in trapping rates among years.

If plantation-related fragmentation of the small-mammal assemblage had occurred at Groenvaly, a number of outcomes would be predicted (Noss and Csuti 1997), as has been observed with other small-mammal assemblages in fragmented environments (Andren 1994; Bayne and Hobson 1998; Bolger et al. 1997; Laurance 1997). These include a drop in species diversity within fragments and plantations relative to control sites, changes in small-mammal assemblage structure, and significant changes in movement behavior of small mammals.

First, local extinctions because of stochastic events are expected to decrease spe-

cies diversity within habitat remnants (Noss and Csuti 1997). However, we found that species diversity has remained constant within fragments since afforestation, and that species diversity in the control sites, experimental fragments, and pine plantations were still comparable by 1998 (Table 2).

Second, assemblage structure is expected to change resulting in differences between control sites and fragments. Although significant temporal changes have occurred in small-mammal assemblages since 1994, none of these changes have been restricted to either control or experimental treatments. Similarly, with the exception of *Crocidura* populations in small fragments, similarity of mammal assemblage structure among 3 habitat classes during 1998 (grassland, fragments, and plantation) is remarkable (Table 3).

Third, Diffendorfer et al. (1995) found that as fragmentation increases, distance moved by 3 species of small mammals increased, whereas proportion of animals moving decreased. It is possible that increased movement was a result of decreased resource availability. If fragmentation had an effect, movement distances within fragments would be expected to be largest in 1998. Similarly, if plantation area was acting as a habitat used for dispersal, an increase in magnitude of movement in that habitat would be expected. Results obtained in 1998 show that movement behavior of *Crocidura* and *R. pumilio* was similar among all three treatments, suggesting that such effects were absent.

Four years into the Groenvaly project, level of physical disturbance to environment is structurally significant (Fig. 2). Yet, the most prominent feature of our study is that small-mammal assemblage at Groenvaly is very robust and has not responded noticeably to this disturbance. It appeared that small mammals do not recognize plantations as uninhabitable because the microhabitats underneath pine trees still contain sufficient resources for survival. The mam-

mals do not only move through plantations but inhabit pine plantations in the same way as they do in grassland. The remarkable fact is that fragmentation of small-mammal populations has not taken place, despite extensive habitat alteration inside plantations. Grassland vegetation under pine trees had died by 1998 and there was no greenery available. In addition, there were no stems with grass seeds. However, physical structure of dead grassland within plantation was similar to that of control plots (Bredenkamp et al. 1999). We speculate that enough grass seeds (on the ground) and other plant material could still be found by rodents in plantations. However, large numbers of insectivores (shrews) in plantations (Table 1) are remarkable.

The forestry industry in southern Africa frequently experiences rodent-induced damage to pine trees (Willan 1984). This damage is often observed when trees are taller than 6 m and when plantations are some 6 years old, suggesting that these animals survive in plantations for long periods after afforestation. Significance of our study is that the small-mammal assemblage within plantation has not been affected in any clear way since preplanting in 1994. This knowledge is important for understanding the damage incurred by the forestry industry. Within the context of fragmentation experiments, our results differ from those observed in similar experiments elsewhere (Lovejoy et al. 1984; Margules et al. 1995), in that the reactions of small-mammal assemblages to fragmentation were not measurable. We believe that the main reason for this is that fragmentation process at Groenvaly has been gradual, as opposed to other fragmentation experiments involving abrupt removal of between-fragment vegetation. Gradual fragmentation allows small mammals to use the maturing plantation between fragments and to interact with those in the grassland fragments for some time. We therefore expect our fragmented mammal assemblages to survive for much longer periods compared with those in abruptly cre-

ated fragments. Ultimately, we expect habitat fragmentation to have strong effects on small-mammal communities in remaining grasslands among plantations, but these effects have not been observed yet. It is, therefore, highly desirable to perform a longer-term study on the changes in small mammal community structure within grassland fragments as plantation matures and as grass cover inside plantation disappears.

ACKNOWLEDGMENTS

We thank SAPPI Forests, and especially H. de Villiers (Regional Forester), S. Meikle (Environmental Officer), and M. Britz (Senior Forester) who supplied invaluable infrastructure without which the work would not be viable. We thank people who volunteered to help during trapping survey; these include J. Sesane and J. Kone (Transvaal Museum) and W. Delpont, A. Grobler, B. Reyers, S. Koch, D. Kamffeer, K. Kuc, M. Oosthuizen, M. Herbst, V. Linga, B. Erasmus, and K. Wilson (Pretoria University). This work was supported by funding from the National Research Foundation.

LITERATURE CITED

- ANDREN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: review. *Oikos* 71:355–366.
- BAYNE, E. M., AND K. A. HOBSON. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed wood forest. *Canadian Journal of Zoology* 76:62–69.
- BOLGER, D. T., ET AL. 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7:552–563.
- BOWERS, M. A., S. F. MATTER, J. L. DOOLEY, J. L. DAUTEN, AND J. A. SIMKINS. 1996. Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. *Oecologia* 108:182–191.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- BREDENKAMP, G. J., J. W. H. FERGUSON, S. H. FOORD, AND W. H. DE FREY. 1999. Floristic assessment of an Afromontane grassland fragmentation experiment in a pine plantation. *African Journal of Ecology* 37:49–60.
- BRONNER, G., I. L. RAUTENBACH, AND J. MEESTER. 1988. Environmental influence on reproduction in the Natal multimammate mouse *Mastomys natalensis*. *South African Journal of Wildlife Research* 18:142–148.
- BROOKS, P. M. 1982. Aspects of reproduction, growth and development of the four-striped fieldmouse *Rhabdomys pumilio* (Sparrman, 1784). *Mammalia* 46:53–64.
- CLARKE, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- CLARKE, K. R., AND R. N. GORLEY. 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E, Plymouth, United Kingdom.
- DAVIS, R. M. 1973. The ecology and life history of the vlei rat *Otomys irroratus* (Brants 1872) on the Van Riebeeck Nature Reserve, Pretoria. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.
- DAVIS, R. M., AND J. MEESTER. 1981. Reproduction and postnatal development in the vlei rat *Otomys irroratus* on the Van Riebeeck Nature Reserve, Pretoria. *Mammalia* 45:99–116.
- DEBLASE, A. F., AND R. E. MARTIN. 1981. A manual of mammalogy: with keys to the families of the world. Wm. C. Brown, Dubuque, Iowa.
- DIFFENDORFER, J. E., M. S. GAINES, AND R. D. HOLT. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76:827–839.
- EHRlich, P. R. 1993. The scale of human enterprise. Pp. 3–8 in *Reconstruction of fragmented ecosystems: global and regional perspectives* (D. A. Saunders, R. J. Hobbs, and P. R. Ehrlich, eds.). Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- LAURANCE, W. F. 1997. Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. *Wildlife Research* 24:603–612.
- LOVEJOY, T. E., R. O. BIERREGAARD, J. M. RANKIN, AND H. O. R. SCHUBART. 1983. Ecological dynamics of tropical forest fragments. Pp. 377–384 in *Tropical rainforests: ecology and management* (S. L. Sutton, T. C. Whitmore, and A. C. Whitmore, eds.). Blackwell Scientific Publications, Oxford, United Kingdom.
- LOVEJOY, T. E., J. M. RANKIN, R. O. BIERREGAARD, K. S. BROWN, L. H. EMMONS, AND M. E. VAN DER VOORT. 1984. Ecosystem decay in Amazon rain forest remnants. Pp. 295–325 in *Extinctions* (H. H. Nitecki, ed.). University of Chicago Press, Chicago, Illinois.
- MARGULES, C. R. 1992. The Wog-Wog habitat fragmentation experiment. *Environmental Conservation* 19:316–325.
- MARGULES, C. R., K. F. DAVIES, J. A. MEYERS, AND G. MILKOVITS. 1995. The responses of some selected arthropods and the frog *Crinia signifera* to habitat fragmentation. Pp. 94–103 in *Conserving biodiversity: treats and solutions* (R. Bradstock, T. Auld, D. Keith, R. Kingsford, D. Lunney, and D. P. Sivertsen, eds.). Surrey Beatty & Sons, Sydney, New South Wales, Australia.
- MATTHEWS, W. S., A. E. VAN WYK, AND G. J. BREDENKAMP. 1993. Endemic flora of the north-eastern Transvaal, South Africa. *Biological Conservation* 63:83–94.
- MEESTER, J. 1963. The genera of African shrews. *Annals of the Transvaal Museum* 13:4.
- NOSS, R. F., AND B. CSUTI. 1997. Habitat fragmentation. Pp. 269–304 in *Principles of conservation bi-*

- ology (G. K. Meffe and C. R. Carroll, eds.). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- QUINN, J. F., AND G. R. ROBINSON. 1987. The effects of experimental subdivision on flowering plant diversity in a California annual grassland. *Journal of Ecology* 75:873–876.
- ROBINSON, G. R., ET AL. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524–526.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–33.
- SHANNON, C. E., AND W. WEAVER. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.
- SMITHERS, R. H. N. 1971. The mammals of Botswana. *Memoirs of the National Museums of Rhodesia* 4: 1–340.
- SMITHERS, R. H. N. 1983. The mammals of the southern African subregion. 1st ed. University of Pretoria, Pretoria, South Africa.
- SOULÉ, M. E., A. C. ALBERTS, AND D. T. BOLGER. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. *Oikos* 63:39–47.
- VAN JAARSVELD, A. S., J. W. H. FERGUSON, AND G. J. BREDENKAMP. 1998. The Groenvaly grassland fragmentation experiment: design and initiation. *Agriculture, Ecosystems, and Environment* 68:139–150.
- WILLAN, K. 1984. Rodent damage in southern African plantations: a review. *South African Forestry Journal* 128:1–7.
- WITHERS, P. C. 1979. Seasonal reproduction by small mammals of the Namib Desert. *Mammalia* 47:195–204.
- Submitted 9 October 2000. Accepted 28 June 2001.*
- Associate Editor was Brett R. Riddle.*