Genetic variation in *Rhabdomys pumilio* (Sparrman 1784) – an allozyme study

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The striped-mouse, *Rhabdomys pumilio*, is widely distributed throughout southern Africa. It prefers grasslands but is also found in vlei areas and dry river beds and its attraction to cultivated land has resulted in extensive damage to plants. An allozyme study of *R. pumilio* populations in different regions of southern Africa was undertaken to evaluate the genetic structure within and between 23 populations and to draw conclusions about the taxonomic status of populations within this species. Fifteen of the 26 loci examined were polymorphic. The mean heterozygosity (0.073) was high for a mammal, although relatively low heterozygosities (0.036–0.054) were recorded for three localities from the peninsular region of the Western Cape. The high mean value for local genetic differentiation (F_{st}) of 0.459 and the low mean value for the effective number of migrants (Nm) of 0.179 indicated low levels of gene flow between the different localities of *R. pumilio*. The negative, near zero F_{is} value of -0.01 indicated a balance between heterozygotes and homozygotes. Rogers (1972) genetic similarity ranged between 0.796 and 0.988, and Nei's (1978) unbiased genetic distance varied between 0.000 and 0.189 between the samples of *R. pumilio*. The phenogram based on Nei's (1978) unbiased genetic distance showed some degree of geographical subgrouping. The Mantel test indicated a significant relationship between the F_{st} values and the geographical distances between sample pairs, supporting an isolation by distance model for *R. pumilio*. Although the genetic evidence for geographical divergence does suggest the possible existence of subspecies, this remains to be substantiated.

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Introduction

The striped-mouse, *Rhabdomys pumilio*, is widely distributed throughout southern Africa (De Graaff 1981; Skinner & Smithers 1990). It prefers grasslands but is also found in bushy vlei country, dry river beds and the edges of forests (Brooks 1974) although it has also been observed kilometers into forests (P. Taylor pers. obs.). This species is of economic importance because of the extensive damage it causes to cultivated land and crops (Choate 1971; Delany 1972; De Graaff 1981).

Using tail length as a taxonomic feature, Roberts (1951) listed 20 subspecies of *R. pumilio* of which seven were retained by Meester, Rautenbach, Dippenaar & Baker (1986). De Graaff (1981) questioned the validity of some of these described forms. He contended that there may be a valid eastern subspecies and a western subspecies, but concluded 'that very little can be added until the entire species is revisited'. Misonne (1974) considered all these forms to be conspecifics under *R. pumilio*.

A comparative allozyme study of *R. pumilio* populations in different regions of southern Africa was undertaken to describe the population genetic structure of this species. The applicability of the isolation by distance model (Wright 1943) and the niche-width variation hypothesis (Van Valen 1965) and behavioural parameters to the population genetic structure of *R. pumilio* was investigated. The genetic information was also evaluated in terms of shedding some light on the taxonomic status of populations within this species.

Materials and methods

Rhabdomys pumilio specimens were live-trapped from different regions of southern Africa (Table 1) using Sherman-type live traps (Titian Productions, Cape Town) and PVC live-traps (Willan 1979). The Malawi and KwaZulu-Natal specimens were collected during 1992, while the remaining samples were collected between December 1995 and January 1996 and the electrophoretic work was done two months later. The distribution and sampling sites for *R. pumilio* are illustrated in Figure 1. The size of the samples collected in some of the localities were small. In KwaZulu-Natal, three, five and six specimens were collected in Boschoek, Midmar Dam and Good Hope respectively: in the Eastern Cape, seven specimens were collected in King William's Town; in the Western Cape, three, seven and seven specimens were collected in Cape Point, Swartberg and Wellington respectively; in the Free State and Northern Cape, seven specimens were collected in each locality and four specimens in Malawi.

The animals were sacrificed in the field and the standard measurements recorded. The liver, heart and kidneys were removed and stored in liquid nitrogen. Voucher specimens were deposited in the Durban Natural Science Museum and Transvaal Museum (Appendix 1). Starch-gel electrophoresis (Murphy, Sites, Buth & Haufler 1990) was carried out using a discontinuous and two continuous buffers. The continuous

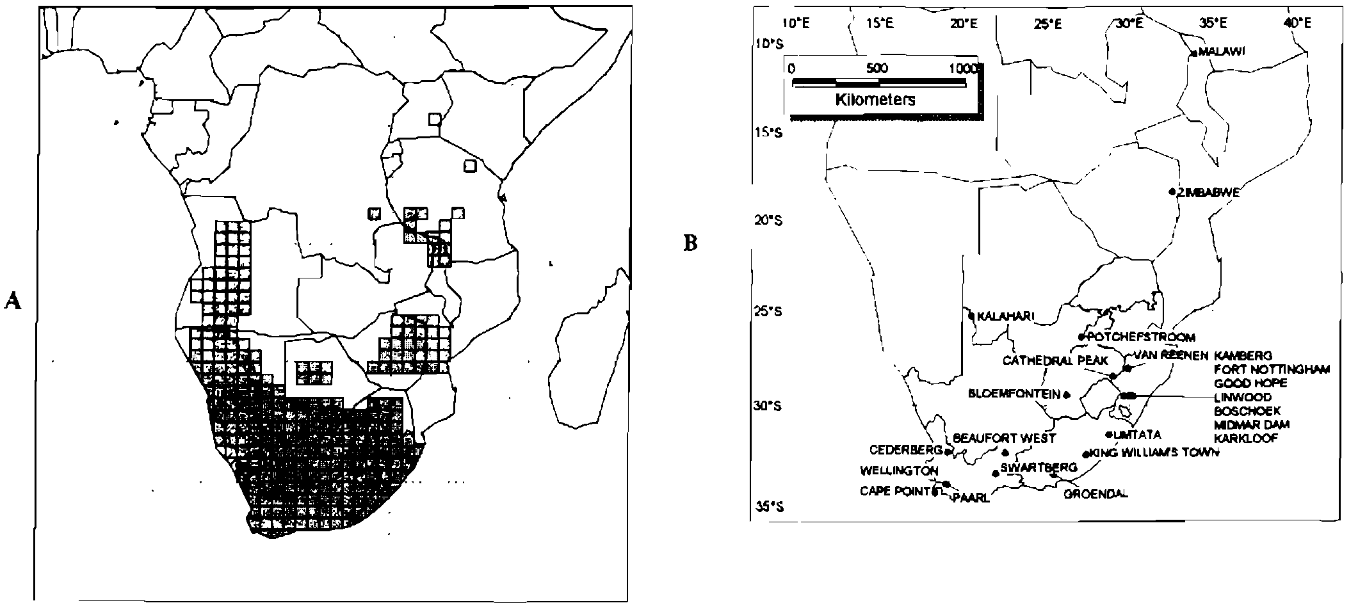

Figure 1 Maps showing (A) the distribution of *Rhabdomys pumilio* (courtesy of Neil Burgess) and (B) the sampling sites

Table 1 Sampling sites and number of specimens (N) of *Rhabdomys pumilio* analysed from each location

Sampling site	Geographical co-ordinates	Number of specimens (N)
Kwazulu-Natal		
1 Kamberg	29°24'S, 29°40'E	15
2. Linwood	29°33'S, 30°05'E	14
3 Boschoek	29°21'S, 30°06'E	3
4 Fort Nottingham	29°25'S, 29°55'E	12
5 Karkloof	29°21'S, 30°13'E	8
6 Midmar Dam	29°30'S, 30°12'E	5
7 Good Hope	29°39'S 29°58'E	6
8 Cathedral Peak	28°55'S, 29°01'E	20
9 Van Reenen	28°22'S, 29°24'E	9
Eastern Cape		
10 Groendal	33°40'S, 25°28'E	10
11 King William's Town	32°53'S, 27°24'E	7
12 Umtata	31°35'S, 28°47'E	13
Western Cape		
13 Beaufort West	32°18'S, 22°36'E	14
14 Cape Point	34°18'S, 18°26'E	3
15 Cedarberg	32°21'S, 19°10'E	6
16 Paarl	33°45'S 18°58'E	13
17 Swartberg	33°13'S, 22°03'E	7
18 Wellington	33°39'S, 19°00'E	7
Free State		
19 Bloemfontein	29°07'S, 26°14'E	7
Northern Cape		
20 Kalahari Gemsbok National Park	35°30'S, 20°30'E	7
Gauteng		
21. Potchefstroom	26°42'S, 27°6'E	9
Zimbabwe		
22 Inyanga	18°12'S, 32°40'E	5
Vumba	18°55'S, 32°40'E	13
Malawi		
23 Nyika National Park, Chelinda	10°34'S, 33°48'E	4

buffers used were those of Whitt (1970) and Markert & Faulhaber (1965), while the discontinuous buffer of Ridgway, Sherburne & Lewis (1970) was used (Table 2).

The BIOSYS-1 computer program (Swofford & Selander 1981) was used to determine the allele frequencies and to calculate the mean heterozygosity for each sample. The Genepop (version 3.1b) computer program (Raymond & Rousset 1995) was used to minimise the errors associated with the small number of animals obtained in some of the localities and the program was used for the exact tests for Hardy-Weinberg proportions, contingency analysis of allelic distribution across populations, the effective number of migrants (Nm) (Slatkin 1985) and the F-statistics (Weir & Cockerham 1984). Rogers (1972) measure of genetic similarity and Nei's (1978) unbiased genetic distance were calculated for each sample pair. Cluster analyses were performed using UPGMA (Sneath & Sokal 1973). The Mantel test (Mantel 1967) was used to determine the relationship between the F_{st} values and the geographical distances between paired samples of *R. pumilio* (Genepop, version 3.1b).

Results

Eleven of the 26 liver tissue loci examined were monomorphic. These were aspartate aminotransferase (*Aat-1*), aminotransferase-2 (*Aat-2*), albumin (*Alb*), lactic dehydrogenase-1 (*Ldh-1*), lactic dehydrogenase-2 (*Ldh-2*), malic enzyme (*Mal*), malate dehydrogenase-1 (*Mdh-1*), malate dehydrogenase-2 (*Mdh-2*), peptidase-1 (*Pep-1*), sorbitol dehydrogenase (*Sdh*) and xanthine oxidase (*Xdh*).

The 'B' allele of the polymorphic *Hb-2* locus was a null allele (Table 3). This locus was only expressed in the four Malawi animals, in a few specimens from Gauteng (0.111) and most of the animals from the Western Cape excluding Beaufort West, Cedarberg and Swartberg. It was not expressed in the Free State, KwaZulu-Natal, Northern Cape and Zimbabwe samples. The *G6pdh* locus was polymorphic only for the Zimbabwe sample and its sex linkage was taken into account

Table 2 Proteins examined and buffers used for the different loci in the *Rhabdomys pumilio* samples

Proteins	Enzyme commission number	Locus	Buffer
Adenosine deaminase	3.5.4.4	*Ada*	2
Albumin	–	*Alb*	3
Aspartate aminotransferase-1	2.6.1.1	*Aat-1*	2
Aspartate aminotransferase-2	2.6.1.1	*Aat-2*	2
Creatine kinase	2.7.3.2	*Ck*	1
Esterase-1	3.1.1.1	*Est-1*	2
Esterase-2	3.1.1.1	*Est-2*	2
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6pdh*	2
Glucose phosphate isomerase	5.3.1.9	*Gpi*	2
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3pdh*	2
Haemoglobin-1	–	*Hb-1*	2
Haemoglobin-2	–	*Hb-2*	2
Isocitrate dehydrogenase	1.1.1.42	*Icdh*	1
Lactic dehydrogenase-1	1.1.1.27	*Ldh-1*	1
Lactic dehydrogenase-2	1.1.1.27	*Ldh-2*	2
Malate dehydrogenase-1	1.1.1.37	*Mdh-1*	2
Malate dehydrogenase-2	1.1.1.37	*Mdh-2*	2
Malic enzyme	1.1.1.40	*Mal*	3
Nucleoside phosphorylase	2.4.2.1	*Np*	1
Peptidase-1	3.4.11	*Pep-1*	2
Peptidase-2	3.4.11	*Pep-2*	2
Phosphoglucomutase	2.7.5.1	*Pgm*	1
6-phosphogluconate dehydrogenase	1.1.1.44	*Pgdh*	3
Sorbitol dehydrogenase	1.1.1.14	*Sdh*	1
Superoxide dismutase	1.15.1.1	*Sod*	2
Xanthine oxidase	1.2.1.37	*Xdh*	1

Buffers:
1. Whitt, 1970 (continuous).
2. Markert & Faulhaber, 1965 (continuous).
3. Ridgway *et al.*, 1970 (discontinuous).
(Refer Grant 1989 for continuous buffers.)

when recording the genotype.

Mean heterozygosity per locus (direct count) ranged between 0.022 and 0.145 (Table 4). Values in the peninsular Western Cape were relatively low. The mean heterozygosities (direct count) for the Cape Point, Paarl and Wellington samples were 0.038, 0.036 and 0.022 respectively, while the Cedarberg and Swartberg samples compared favourably with samples from other regions at 0.064 and 0.071 respectively. Potchefstroom and Zimbabwe expressed fairly high mean heterozygosities of 0.145 and 0.118 respectively (Table 4).

With small sample sizes, there is the potential for large errors on the estimation of allele frequencies, thus reducing confidence in the genetic distances and F-statistics. To overcome this problem, the Genepop computer program (version 3.1b) (Raymond & Rousset 1995) was used to minimise these errors. Genepop was also used for the exact tests for Hardy-Weinberg proportions, contingency analysis of allelic distribution across samples, the effective number of migrants (Nm) (Slatkin 1985) and the F-statistics (Weir & Cockerham, 1984).

A mean F_{is} value of -0.010, a mean F_{st} value of 0.459 and a mean F_{it} value of 0.453 for the 15 polymorphic loci was obtained (Table 5). The estimated mean number of migrants per generation was 0.179 (Table 5). Using contingency analysis, the allelic distribution across all the samples was significantly heterogeneous for 13 of the 15 polymorphic loci. Only the *Gpi* and *Icdh* loci were not significant (Genepop version 3.1b).

Significant deviation from Hardy-Weinberg proportions was recorded for *Est-2* in the Karkloof, Potchefstroom, Umtata, Van Reenen and Zimbabwe samples; for *Hb-1* in the Linwood sample; for *Hb-2* in the Paarl and Wellington samples and for *Np* in the Beaufort West sample (Table 6). The problems encountered with accurately scoring the *Est-2* locus probably

Table 3 Allelic frequencies of the polymorphic loci of the different samples of *Rhabdomys pumilio* (A, B, and C are alleles of decreasing mobilities respectively)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Ada																							
A	0.500	0.429	0.333	0.500	0.188	0.625	0.583	0.441	0.444	0.000	0.000	0.192	0.036	0.333	0.000	0.000	0.000	0.000	0.571	0.143	0.222	0.778	0.000
B	0.500	0.571	0.667	0.500	0.813	0.375	0.417	0.559	0.556	1.000	1.000	0.808	0.964	0.667	1.000	1.000	1.000	1.000	0.429	0.857	0.778	0.222	1.000
Ck																							
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.269	0.036	0.000	0.000	0.000	0.000	0.000	0.714	0.000	0.333	0.444	0.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.731	0.964	1.000	1.000	1.000	1.000	1.000	0.286	1.000	0.667	0.556	1.000
Est-1																							
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.667	1.000	1.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000
Est-2																							
A	0.500	0.429	0.500	0.583	0.375	0.125	0.667	0.525	0.444	0.400	0.800	0.417	0.536	1.000	0.250	0.800	0.500	0.929	0.786	0.429	0.500	0.556	0.500
B	0.167	0.429	0.500	0.000	0.375	0.250	0.250	0.125	0.222	0.400	0.200	0.417	0.179	0.000	0.417	0.100	0.071	0.000	0.214	0.429	0.389	0.361	0.500
C	0.333	0.143	0.000	0.417	0.250	0.625	0.083	0.350	0.333	0.200	0.000	0.167	0.286	0.000	0.333	0.100	0.429	0.071	0.000	0.143	0.111	0.083	0.000
G6pdh																							
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.444	1.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.556	0.000
Gpi																							
A	0.967	1.000	1.000	1.000	1.000	1.000	1.000	0.950	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G3pdh																							
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.857	1.000	1.000	1.000	1.000	1.000	1.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000	0.000
Hb-1																							
A	0.967	0.857	1.000	0.875	0.688	0.900	0.917	0.725	0.722	0.400	1.000	1.000	0.000	1.000	1.000	1.000	0.643	1.000	0.000	0.000	0.222	0.111	0.000
B	0.033	0.143	0.000	0.125	0.312	0.100	0.083	0.275	0.278	0.600	0.000	0.000	1.000	0.000	0.000	0.000	0.357	0.000	1.000	1.000	0.778	0.889	1.000
Hb-2																							
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.846	0.000	0.714	0.000	0.000	0.111	0.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.000	1.000	0.154	1.000	0.286	1.000	1.000	0.889	1.000	0.000
Icdh																							
A	0.967	1.000	1.000	1.000	0.938	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	0.033	0.000	0.000	0.000	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Np																							
A	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.475	0.611	0.450	0.571	0.615	0.071	0.000	0.500	0.308	0.571	0.214	0.286	1.000	0.667	0.528	0.625
B	0.967	1.000	1.000	1.000	1.000	1.000	1.000	0.525	0.389	0.000	0.000	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.472	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.550	0.429	0.308	0.929	1.000	0.500	0.692	0.429	0.786	0.714	0.000	0.333	0.000	0.375
Pep-2																							
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.857	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pgdh																							
A	0.733	0.615	0.833	0.727	0.250	0.400	0.750	0.316	0.357	0.600	0.286	0.462	0.679	0.500	0.917	0.808	1.000	1.000	1.000	0.429	0.500	0.444	0.750
B	0.267	0.385	0.167	0.273	0.750	0.600	0.250	0.684	0.643	0.400	0.714	0.538	0.321	0.500	0.083	0.192	0.000	0.000	0.000	0.571	0.500	0.556	0.250
Pgm																							
A	1.000	1.000	1.000	1.000	1.000	1.000	0.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.167	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sod																							
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.000	1.000	1.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	1.000	1.000	0.964	1.000	1.000	1.000	1.000	1.000	0.000	0.000	1.000	1.000	1.000

accounted for the deviation from Hardy-Weinberg proportions. The high F_{st} values obtained for the *Hb-1* (0.60), *Hb-2* (0.80), and *Np* (0.54) indicated localized differentiation at these loci.

Rogers (1972) genetic similarity ranged between 0.796 and 0.988, and Nei's (1978) unbiased genetic distances ranged between 0.000 and 0.189 between the different samples of *Rhabdomys pumilio* (Table 7). The clustering of the various samples of *R. pumilio* using the UPGMA method is shown in the phenogram (Figure 2). A cophenetic correlation coefficient of 0.852 was obtained using Nei's (1978) unbiased genetic distance. A correlation coefficient of 0.54 ($p < 0.001$)

Table 4 Comparison of the mean (± se) heterozygosity (het), mean number (± se) of alleles per locus and percent polymorphism in the different samples of *Rhabdomys pumilio*

	Locality	Mean het. per locus (unbiased estimate)	Mean het per locus (direct count)	Mean number of alleles per locus	% Locus polymorphic (0.95)
KwaZulu-Natal	Kamberg	0.070	0.077	1.31	11.54
		(0.033)	(0.039	(0.11)	-
	Linwood	0.073	0.068	1.19	15.38
		(0.036)	(0.039)	(0.10)	-
	Boschoek	0.056	0.077	1.12	11.54
		(0.032)	(0.046)	(0.06)	-
	Fort Nottingham	0.064	0.088	1.15	15.38
		(0.032)	(0.045)	(0.07)	-
	Karkloof	0.077	0.072	1.23	19.23
		(0.036)	(0.033)	(0.10)	
	Midmar Dam	0.072	0.042	1.19	15.38
		(0.036)	(0.021)	(0.10)	
	Good Hope	0.075	0.058	1.23	19.23
		(0.033)	(0.029)	(0.10)	
	Cathedral Peak	0.099	0.098	1.27	23.08
		(0.039)	(0.041)	(0.10)	
	Van Reenen	0.104	0.113	1.23	19.23
		(0.042)	(0.052)	(0.10)	
Eastern Cape	Groendal	0.085	0.073	1.19	15.38
		(0.040)	(0.038)	(0.10)	-
	King William's Town	0.061	0.070	1.15	15.38
		(0.030)	(0.034)	(0.07)	-
	Umatata	0.094	0.093	1.27	19.23
		(0.040)	(0.042)	(0.12)	
Western Cape	Beaufort-West	0.055	0.058	1.27	11.54
		(0.029)	(0.035)	(0.10)	
	Cape Point	0.044	0.038	1.08	7.69
		(0.030)	(0.028)	(0.05)	
	Cedarberg	0.055	0.064	1.15	11.54
		(0.034)	(0.040)	(0.09)	
	Paarl	0.054	0.036	1.19	15.38
		(0.026)	(0.021)	(0.10)	-
	Swartberg	0.073	0.071	1.19	15.38
		(0.036)	(0.035	(0.10)	
	Wellington	0.036	0.022	1.12	11.54
		(0.022)	(0.017)	(0.06)	-
	Bloemfontein	0.068	0.071	1.15	15.38
		(0.032)	(0.035)	(0.07)	-
	Kalahari	0.056	0.055	1.15	11.54
		(0.033)	(0.032)	(0.09)	-
	Potchefstroom	0.135	0.145	1.31	30.77
		(0.042)	(0.055)	(0.11)	
	Zimbabwe	0.122	0.118	1.31	26.92
		(0.042)	(0.044)	(0.11)	
	Malawi	0.059	0.087	1.12	11.54
		(0.033)	(0.050)	(0.06)	-
	Mean	0.073	0.074	1.20	16.05
	(± se)	(0.005)	(0.006)	(0.014)	(1.13)

was obtained between the genetic distance (Nei 1978) and geographical distance of the different samples of the striped-mouse. The Mantel test indicated a significant ($p < 0.001$) relationship between the F_{st} values and the geographical distances between samples of *R. pumilio*.

Discussion

Allelic variation

Haemoglobin (*Hb*), nucleoside phosphorylase (*Np*) and superoxide dismutase (*Sod*) were the only loci to provide a geographic pattern of allelic variation The localities in which the

Table 5 Summary of F-statistics (Weir & Cockerham 1984) and the mean number of migrants (Nm) for the different samples of *Rhabdomys pumilio*

Locus	F(is)	F(it)	F(st)	Nm
Ada	–0.046	0.245	0.279	–
Ck	0.229	0.515	0.371	–
Est-1	0.056	0.336	0.297	–
Est-2	–0.140	–0.055	0.075	–
Hb-1	0.325	0.731	0.601	–
G3pdh	–0.112	0.003	0.103	–
G6phd	–0.778	0.204	0.553	–
Gpi	–0.010	–0.005	–0.015	–
Hb-2	1.000	1.000	0.799	–
Icdh	0.006	–0.003	–0.008	–
Np	–0.049	0.518	0.541	–
Pep-2	–0.112	0.003	0.103	–
Pgdh	–0.075	0.106	0.169	–
Pgm	1.000	1.000	0.071	–
Sod	0.019	0.991	0.991	–
Mean	–0.010	0.453	0.459	0.179

'A' allele of *Hb-1* locus was fixed, were King William's Town and Umtata in the Eastern Cape, and Cape Point, Cedarberg, Paarl and Wellington in the Western Cape. The localities in which the 'B' allele of the *Hb-1* locus was fixed, were Beaufort West in the Western Cape, Bloemfontein in the Free State, Kalahari in the Northern Cape and Chelinda in Malawi. The 'A' allele for the *Hb-2* locus appeared only in the peninsular region of the Western Cape, Gauteng and Malawi. The *Np* locus was fixed for the 'A' allele in the Kalahari and the 'C' allele in Cape Point. The 'A' allele for *Sod* was fixed in Bloemfontein, Kalahari and KwaZulu-Natal while the Eastern and Western Cape localities were fixed for the 'B' allele. Potchefstroom, Zimbabwe and Malawi were also fixed for the 'B' allele for *Sod*.

Heterozygosity and polymorphism

The mean heterozygosity (0.073) for *Rhabdomys pumilio* was high compared to the mammalian mean (0.036) and vertebrate mean (0.049) obtained by Nevo (1978) and Wooten & Smith (1985) respectively. The high heterozygosities of the Cathedral Peak ($H = 0.099$) sample suggested some genetic exchange across the Drakensberg mountains between the Free State and KwaZulu-Natal populations. The mean percent polymorphism (16.1%) obtained for *R. pumilio* was only slightly higher than the mean polymorphism for mammals (14.7%) and lower than that for vertebrates (17.3%) (Nevo 1978). However the Potchefstroom and Zimbabwe samples produced polymorphisms of 30.8% and 26.9% respectively. *R. pumilio* is a generalist, occupying a variety of habitat types, temperature and rainfall regimes. A high polymorphism and heterozygosity could be expected.

Table 6 Chi-square test for deviation from Hardy-Weinberg proportions in the samples *Rhabdomys pumilio* from different localities

Locality	Locus	P
Linwood	*Hb-1*	0.004
Karkloof	*Est-2*	0.007
Umtata	*Est-2*	0.014
Van Reenen	*Est-2*	0.026
Beaufort-West	*Np*	0.037
Paarl	*Hb-2*	0.005
Wellington	*Hb-2*	0.021
Potchefstroom	*Est-2*	0.024
Zimbabwe	*Est-2*	0.005

F-statistics

Support for geographic differentiation was provided by the high F_{st} (0.459) value which according to Hartl (1988); Hogan, Hedin, Koh, Davis & Greenbaum (1993); McCracken, McCracken & Vawter (1994); Peppers, Kennedy & Kennedy (1996) and Loxterman, Moncrief, Dueser, Carlson & Pagels (1998) indicated a high level of genetic differentiation between samples. This was further supported by the value obtained for the effective number of migrants ($Nm = 0.179$) which is indicative of a low level of gene flow (Loxterman *et al.* 1998). However, the mean F_{is} of -0.01 indicated that *R. pumilio* remained essentially an outbreeding species.

Population genetic structure

The extremes in population structure are the panmictic (outcrossed) and Wrightian (sub-divided) (Templeton 1980). Panmictic populations are characterised by high heterozygosities, low F_{st}, low F_{is} and low F_{it} values, while Wrightian populations are characterised by low heterozygosities, high F_{st}, high negative F_{is} and high F_{it} values. *R. pumilio* seems to fit somewhere in between these two extremes in population structure because it has a high F_{st} (0.459), a negative F_{is} (-0.01) and a high F_{it} (0.453) value.

Demastes, Hafner & Hafner (1996) and Patton, Da Silva & Malcolm (1996) were of the opinion that in the absence of physical barriers to gene flow, geographical differentiation is expected to exhibit an isolation by distance relationship. The correlation coefficient of 0.54 ($p < 0.001$) between the genetic and geographical distances between the different sample pairs and the significant Mantel test ($p < 0.001$) between the F_{st} values and the geographical distances between the different sample pairs supports an isolation by distance relationship in *R pumilio*.

The data obtained with *R. pumilio* provides less support for a niche-width variation hypothesis. Nevo (1978), Lavie, Achituv & Nevo (1993) and Wójcik, Wójcik, Zalewska & Rychlik (1996) showed that among the vertebrates, habitat specialists have a mean heterozygosity of 0.037, while habitat generalists have a mean value of 0.071. The increased genetic variation ($H = 0.074$) of *R. pumilio* may be regarded as an adaptive strategy for greater population fitness in a variety of environments but the problem is that the KwaZulu-Natal (Drakensberg and midlands) sample of *R. pumilio* which experiences the most stable climate that is a narrow niche, should have a low heterozygosity. This in not the case ($H =$

Table 7 Matrix of similarity and distance coefficients between the samples of *Rhabdomys pumilio* from different localities. Above diagonal: Rogers (1972) genetic similarity. Below diagonal: Nei's (1978) unbiased genetic distance

Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1 Kamberg	****	0.976	0.972	0.987	0.948	0.963	0.975	0.952	0.947	0.873	0.871	0.886	0.864	0.849	0.890	0.859	0.876	0.852	0.874	0.889	0.844	0.838	0.818
2 Linwood	0.001	****	0.978	0.978	0.964	0.966	0.972	0.952	0.953	0.892	0.875	0.899	0.866	0.851	0.888	0.952	0.871	0.844	0.873	0.910	0.863	0.850	0.830
3 Boschnek	0.000	0.000	****	0.967	0.949	0.947	0.969	0.931	0.931	0.877	0.877	0.895	0.857	0.853	0.901	0.867	0.873	0.862	0.873	0.895	0.851	0.832	0.835
4 Fort Nottingham	0.000	0.004	0.005	****	0.947	0.966	0.976	0.952	0.947	0.872	0.868	0.879	0.865	0.849	0.882	0.857	0.881	0.853	0.877	0.888	0.844	0.838	0.818
5 Karkloof	0.015	0.006	0.013	0.015	****	0.954	0.938	0.955	0.954	0.892	0.885	0.894	0.866	0.834	0.877	0.837	0.872	0.830	0.852	0.921	0.866	0.841	0.826
6 Midmar Dam	0.005	0.005	0.014	0.006	0.008	****	0.957	0.949	0.949	0.863	0.865	0.882	0.842	0.836	0.871	0.828	0.853	0.821	0.854	0.891	0.839	0.846	0.796
7 Good Hope	0.000	0.000	0.000	0.000	0.017	0.011	****	0.935	0.933	0.865	0.868	0.876	0.852	0.844	0.876	0.855	0.862	0.847	0.882	0.882	0.839	0.842	0.817
8 Cathedral Peak	0.016	0.014	0.023	0.015	0.011	0.012	0.019	****	0.988	0.889	0.895	0.898	0.869	0.850	0.878	0.846	0.886	0.838	0.875	0.924	0.872	0.868	0.828
9 Van Reenen	0.018	0.016	0.024	0.019	0.014	0.015	0.022	0.000	****	0.898	0.896	0.908	0.872	0.850	0.887	0.849	0.890	0.839	0.878	0.915	0.881	0.872	0.847
10 Groendal	0.099	0.090	0.092	0.099	0.082	0.106	0.102	0.072	0.065	****	0.941	0.944	0.955	0.884	0.957	0.917	0.954	0.907	0.862	0.931	0.943	0.889	0.927
11 King William's Town	0.094	0.090	0.089	0.098	0.083	0.106	0.097	0.066	0.062	0.021	****	0.953	0.907	0.905	0.949	0.928	0.933	0.919	0.829	0.878	0.908	0.860	0.886
12 Umtata	0.080	0.076	0.075	0.085	0.078	0.085	0.084	0.060	0.054	0.018	0.007	****	0.906	0.899	0.952	0.909	0.926	0.899	0.844	0.805	0.947	0.896	0.886
13 Beaufort West	0.128	0.120	0.127	0.122	0.108	0.137	0.130	0.103	0.100	0.011	0.060	0.061	****	0.884	0.922	0.902	0.929	0.896	0.885	0.904	0.921	0.881	0.922
14 Cape Point	0.136	0.139	0.136	0.136	0.146	0.155	0.134	0.129	0.129	0.077	0.058	0.070	0.092	****	0.888	0.951	0.870	0.946	0.810	0.816	0.859	0.821	0.896
15 Cederberg	0.084	0.085	0.075	0.090	0.096	0.100	0.092	0.081	0.073	0.015	0.022	0.011	0.051	0.076	****	0.937	0.963	0.936	0.844	0.872	0.904	0.850	0.900
16 Paarl	0.119	0.122	0.112	0.121	0.132	0.146	0.122	0.116	0.112	0.050	0.042	0.047	0.076	0.009	0.038	****	0.910	0.970	0.829	0.830	0.866	0.818	0.927
17 Swartberg	0.089	0.094	0.087	0.089	0.101	0.110	0.097	0.083	0.073	0.009	0.029	0.023	0.030	0.008	0.005	0.041	****	0.924	0.856	0.875	0.909	0.855	0.903
18 Wellington	0.116	0.123	0.108	0.117	0.139	0.152	0.118	0.122	0.119	0.051	0.046	0.052	0.071	0.015	0.035	0.001	0.035	****	0.836	0.820	0.856	0.808	0.907
19 Bloemfontein	0.099	0.096	0.098	0.094	0.109	0.119	0.091	0.085	0.079	0.095	0.147	0.123	0.077	0.167	0.131	0.155	0.103	0.143	****	0.895	0.869	0.864	0.849
20 Kalahari	0.089	0.075	0.087	0.087	0.060	0.088	0.089	0.038	0.028	0.060	0.096	0.091	0.078	0.184	0.104	0.149	0.084	0.157	0.064	****	0.902	0.871	0.886
21 Potchefstroom	0.115	0.105	0.112	0.114	0.097	0.119	0.115	0.077	0.069	0.009	0.037	0.026	0.025	0.101	0.042	0.078	0.029	0.081	0.076	0.054	****	0.916	0.903
22 Zimbabwe	0.118	0.109	0.124	0.115	0.109	0.113	0.111	0.091	0.087	0.062	0.092	0.068	0.074	0.147	0.103	0.140	0.085	0.145	0.097	0.090	0.036	****	0.856
23 Malawi	0.174	0.160	0.162	0.173	0.152	0.189	0.173	0.140	0.131	0.046	0.093	0.090	0.054	0.068	0.084	0.047	0.065	0.058	0.129	0.091	0.052	0.101	****

0.074). Furthermore, Nevo, Filippucci, Redi, Simson, Heth & Beiles (1995) noted that when subterranean mammals ranged towards stressful environments, genetic diversity increased. But this was not applicable to samples from arid regions such as the Kalahari, Bloemfontein and Beaufort West.

A number of studies have shown that despite the potential for individual movement of animals over large areas, behavioural factors can result in localized variation between the different populations of a species (Chesser 1983; Pope 1992; White & Svendsen 1992; Van Staaden, Michener & Chesser 1996). Van Staaden *et al.* (1996) working with Richardson's ground squirrels and Lidicker & Patton's (1987) review of four rodent taxa concluded that breeding tactics were more important in the development of genetic structure than dispersal characteristics and that the isolation by distance model was insufficient to explain local genetic structure. This is supported by Chesser's (1991a & b) theoretical studies. In Chesser (1991a) the evolutionary importance of polygynous breeding tactics for maintaining intra-group variation rather than a reduction in migration rates is emphasized and in Chesser (1991b) it was shown that F_{is} is a robust indicator of breeding tactics. Mathematical (Chesser 1991a) and simulation models (De Jong, De Ruiter & Haring 1994) indicated that for socially structured populations, F_{IS} was always negative and indicated a complicated sub-structure rather than simply avoiding inbreeding. A negative F_{IS} value was obtained for *R. pumilio*.

R. pumilio is a highly social animal. The males of this species form a structured hierarchy, with many of the subadults or nearly mature males emigrating while females form the breeding nucleus of the group (Johnson 1980). Only the dominant male is territorial while females are territorial only during the breeding season. This social structure within *R. pumilio* could account for the high F_{st} (0.469) value without contradicting the general validity of an isolation by distance model. This emphasizes the importance of intergrating behavioural and genetic data in the study of population genetics.

Comparisons of genetic similarities and distances

Rogers (1972) genetic similarity values for *R. pumilio* (0.796–0.988) represents a much wider range and a lower mean value compared to other rodents. Work done by Johnson & Selander (1971), Patton, Selander & Smith (1972), Rogers (1972), Hunt & Selander (1973) and Calhoun, Greenbaum & Fuxa (1988) on local populations of the same species or subspecies within species obtained a genetic similarity range (Rogers 1972) of 0.933–0.990. Using Nei's (1978) unbiased genetic distance for the different samples of *R. pumilio*, the values of 0.000–0.189 also represented a wider range compared to the range (0.01–0.08) obtained by Sage, Contreras, Roig & Patton (1986), Gill, Petrov, Zivkovic & Rimsa (1987) and Taylor, Campbell, Van Dyk, Meester & Willan (1992) for a range of species. The above cases substantiates the argument for the genetic diversification of *R. pumilio* populations.

Cluster analysis

The phenogram (Figure 2) shows a KwaZulu-Natal subgroup, a peninsular Western Cape and an Eastern Cape subgroup. The Zimbabwe sample was an outlier to the Eastern and Western Cape subgroups. Further sampling is required in the Northern Cape Province and Gauteng areas to establish the

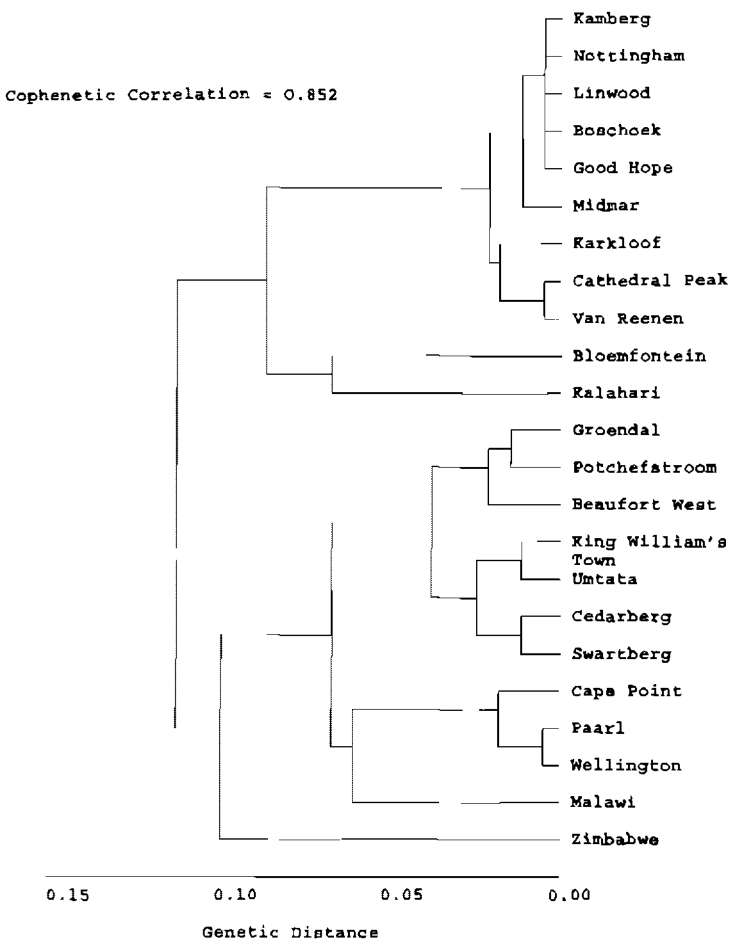

Figure 2 Unweighted pair group method with arithmetic averages (UPGMA) phenogram using Nei's (1978) unbiased genetic distance between the samples of *Rhabdomys pumilio* from different localities

genetic relationships of the Cedarberg and Potchefstroom populations. Further sampling is also required in the central Cape region to determine the boundaries of the Eastern Cape population.

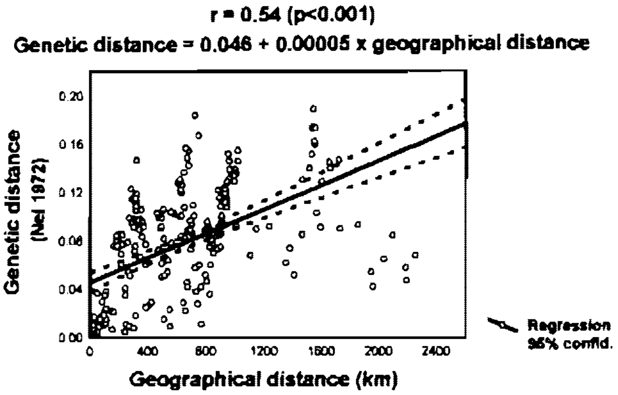

Figure 3 Relationship between the geographical distance (km) and Nei's (1978) unbiased genetic distance between the different samples of *Rhabdomys pumilio*

Taxonomic status

The average Rogers (1972) genetic similarity between populations of the subspecies of the house mouse *Mus musculus musculus* and *M. m. domesticus* was 0.769 ± 0.001 (Hunt & Selander 1973). Avise, Smith & Selander (1974) obtained Rogers (1972) similarity values of 0.793 ± 0.026 between subspecies of the *Peromyscus boylii* group. But in these cases the subspecies status of these animals was supported by other evidence, such as morphology and chromosomal rearrangements. Rogers (1972) genetic similarity for *R. pumilio* ranged between 0.796–0.988 ($\bar{x}$ 0.883 ± s.d. 0.04) between the different samples of *R. pumilio* and can be considered sufficiently genetically divergent for subspecies status, if it is supported by other evidence. To this end, further work involving randomly amplified polymorphic deoxyribonucleic acid (RAPD) involving the polymerase chain reaction (PCR) and cytogenetic studies will be undertaken.

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Appendix 1 Specimen number for the tissues of *Rhabdomys pumilio* used in the allozyme study

1. Kamberg	DM 6025	DM 6093
	DM 6026	DM 6094
	DM 6027	DM 6095
	DM 6028	DM 1096
	DM 6089	UN 1
	DM 6090	UN 2
	DM 6091	
2. Linwood	DM 3375	DM 3400
	DM 3376	DM 3401
	DM 3377	DM 3402
	DM 3378	DM 3403
	DM 3380	DM 3409
	DM 3397	DM 3401
	DM 3398	DM 2734
3. Boschoek	DM 6034	DM 6036
	DM 6035	
4. Fort Nottingham	DM 3385	DM 3405
	DM 3386	DM 6029
	DM 3387	DM 6030
	DM 3388	DM 6031
	DM 3389	DM 6032
	DM 3390	DM 6033
5. Karkloof	UN 4-11	
6. Midmar Dam	DM 6037	DM 6040
	DM 6038	UN 12
	DM 6039	
7. Good Hope	DM 3372	DM 3414
	DM 3373	DM 3415
	DM 3374	DM 3423
8. Cathedral Peak	DM 1604	DM 2734
	DM 1605	DM 2735
	DM 2726	DM 2736
	DM 2727	DM 2737
	DM 2728	DM 2738
	DM 2729	DM 2739
	DM 2730	DM 2740
	DM 2731	DM 2741
	DM 2732	DM 2742
	DM 2732	DM 2743
9. Van Reenen	DM 6083	DM 6061
	DM 6084	DM 6062
	DM 6085	DM 6063
	DM 6059	DM 6064
10. Groendal	DM 4225	DM 4230
	DM 4226	DM 4231
	DM 4227	DM 4237
	DM 4228	DM 4242
	DM 4229	DM 4243
11. King William's Town	DM 4249	DM 4253
	DM 4250	DM 4254
	DM 4251	DM 4255
	DM 4252	
12. Umtata	DM 6041	DM 6048
	DM 6042	DM 6049
	DM 6043	DM 6050
	DM 6044	DM 6051
	DM 6045	DM 6052
	DM 6046	DM 6053
	DM 6047	
13. Beaufort-West	DM 4083	DM 4101
	DM 4084	DM 4102
	DM 4085	DM 4103
	DM 4086	DM 4110
	DM 4087	DM 4111
	DM 4099	DM 4112
	DM 4100	DM 4113
14. Cape Point	DM 4175	DM 4178
	DM 4177	
15. Cedarberg	DM 4184	DM 4188
	DM 4185	DM 4189
	DM 4186	DM 4192
16. Paarl	DM 4120	DM 4129
	DM 4121	DM 4130
	DM 4122	DM 4140
	DM 4124	DM 4143
	DM 4125	DM 4144
	DM 4126	DM 4145
	DM 4128	
17. Swartberg	DM 4199	DM 4206
	DM 4200	DM 4207

	DM 4203	DM 4208
	DM 4205	
18. Wellington	DM 4166	DM 6069
	DM 4168	DM 6070
	DM 6067	DM 6071
	DM 6068	
19. Bloemfontein	DM 4088	DM 4115
	DM 4089	DM 4116
	DM 4090	DM 4117
	DM 4114	
20. Kalahari	UN 13-18	
	DM 6100	
21. Potchefstroom	TM 44953	TM 44966
	TM 44954	TM 49967
	TM 44955	TM 49968
	TM 44956	TM 49969
	TM 44960	TM 49969
22. Zimbabwe		
Inyanga	DM 4649	DM 5007
	DM 4690	DM 5008
	DM 5006	
Vumba	DM 4625	DM 4635
	DM 4626	DM 4636
	DM 4627	DM 4637
	DM 4628	DM 4638
	DM 4629	DM 4639
	DM 4632	DM 4640
	DM 4633	
23. Malawi		
Chelinda	CC 751	CC 753
	CC 752	CC 757

UN = Biology Department, University of Natal, Durban (uncatalogued).

DM = Durban Natural Science Museum.

CC = Transvaal Museum, Pretoria.