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ORIGINAL INVESTIGATION

Genetic structure and dispersal in a small South African rodent. Is dispersal female-biased?

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Abstract

Dispersal greatly determines genetic structure of populations, although it is influenced by landscape heterogeneity, quality of the matrix, resource distribution and local population densities and dynamics. To get insights into some of those processes we analysed the genetic structure of the hairy-footed gerbil *Gerbillurus paeba* (Rodentia, Murinae, Gerbillinae) in the southern Kalahari (South Africa). Samples were taken from 20 populations covering an area of about 2200 km^2. Genetic data were related to landscape characters and population dynamics. We used newly developed microsatellites and found at all loci some indication for the presence of null alleles. However, null alleles seem to have little influence on the general results of our analyses. Altogether we found even nearby populations of *G. paeba* to be significantly differentiated, although assignment tests revealed 24% of individuals as immigrants. Genetic structure was independent of landscape heterogeneities at all spatial scales. Autocorrelation analyses (range 50–90 km) revealed significant genetic structure within populations on distances <3 km. We found some indication for female-biased dispersal. Our study suggests that dispersing individuals have little influence on the long-term genetic structure and that drift is the major cause of genetic diversity. The observed genetic pattern likely derives from strong population fluctuations of *G. paeba*. The landscape structure has little influence on the genetic differentiation between populations.

keywords: *Gerbillurus paeba*; Autocorrelation; Partial Mantel test; Null alleles

Introduction

Dispersal is among the most important determinants of population structure and dynamics (e.g. Boudjemadi et al. 1999; Clobert et al. 2001). On an evolutionary time scale, life history determines both propensity of dispersal and dispersal distance (Greenwood 1980; Cook et al. 2004; Kraaijeveld-Smit et al. 2007). Inbreeding (Pusey 1987; Lawson Handley and Perrin 2007), competition among kin (Greenwood 1980; Perrin and Goudet 2001; Ronce et al. 2001), and mate competition (Solomon 2003) select for dispersal. On an ecological time scale, dispersal is influenced by landscape heterogeneity, matrix quality, resource distribution, and local population density and dynamics (Aars et al. 1998; Lin

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and Batzli 2004; Lin et al. 2006; Solomon et al. 2005; Russell et al. 2007). Taking all factors into account, dispersal is expected to increase with population density as intraspecific competition increases (Perrin and Goudet 2001; Solomon 2003).

In many species of birds and mammals, postnatal dispersal is sex-biased. In mammals, most postnatal dispersal is male-biased (Greenwood 1980), with males moving longer distances than females do (Waser 1985). Dispersal rates and distances have been estimated by mark-recapture, radio tracking, and direct observations (Lawson Handley and Perrin 2007). However, these methods tend to underestimate both the proportion of dispersers and the dispersal distances (Schweizer et al. 2007). Genetic markers provide an alternative way to estimate dispersal parameters (Prugnolle and de Meeus 2002), for applying assignment tests (Guinand et al. 2002; Paetkau et al. 2004) and autocorrelation methods (e.g. Peakall et al. 2003). Of these analyses, autocorrelation analyses can characterise dispersal at fine spatial scales (Smouse and Peakall 1999).

The hairy-footed gerbil *Gerbillurus paeba* (Rodentia, Muridae, Gerbillinae) is found in semiarid to arid areas across southern Africa. It is a nocturnal, omnivorous small rodent whose reproduction depends strongly on rainfall (White et al. 1997; Skinner and Chimimba 2005). As a consequence of the large variation in inter-annual precipitation, *G. paeba* shows considerable fluctuations in population size (Blaum et al. 2007). Although this rodent uses a wide variety of habitats (Nel and Rautenbach 1975; Seely 1977), simulations suggested that small-scale variations in landscape structure (e.g. dune valleys and crests) may influence dispersal in this species (Blaum and Wichmann 2007). As this potentially influences the genetic structure, we conducted a population genetic study with the following four aims: First, with classical population genetics analyses and assignment tests, we estimated gene flow and dispersal at a regional scale. Second, to characterise dispersal at a local scale, we applied autocorrelation analyses. Third, we investigated whether spatial landscape structure influences population structure (Blaum and Wichmann 2007). Finally, we investigated the possibilities of sex-biased dispersal by comparing dispersal and genetic structure of females and males.

Material and methods

The study area is situated in the southwest Kalahari Desert in South Africa near the border with Botswana and Namibia (Fig. 1). This area is characterised by parallel longitudinal sand dunes ($\leqslant$20 m high) stretching from northwest to southeast. Inter-dune valleys were

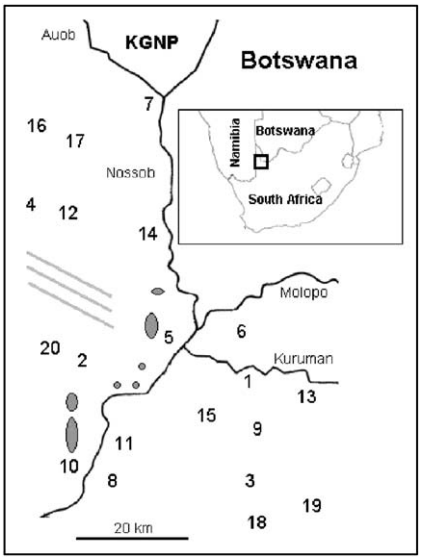

Fig. 1. Study area in southern Africa (insert) and location of study sites. Black lines show the largest dry rivers of the region. Grey ovals indicate pans while the three grey lines (left side) symbolise the stretching of the dunes. KGNP = Kalahari Gemsbok National Park.

100–400 m wide on average, but can reach 2 km (Thomas and Leason 2005).

Tissue samples of the hairy-footed gerbil were collected during a study on habitat features and animal communities in March and April 2005 on 20 farmlands covering an area of about 2200 km^2 (Fig. 1). Two 500 m trap lines were set per farm for one night. Each line had 50 Sherman live traps placed at 10 m intervals. On each farm, the trap lines were 3 km apart and ran perpendicular to the dune stretching. Trap coordinates were recorded by a hand-held GPS. Tissue samples from four or five randomly chosen individuals from each trap line were taken from the ears and stored in 98% ethanol (total $n = 195$, females $n = 121$, males $n = 55$, sex unknown $n = 19$) for genetic analysis. The acquisition of material for genetic analysis has not been the main aim of the field survey. Thus sample size was comparable low and ranged between 8 and 10 individuals per farm, further on labelled as a population.

Microsatellite markers with di-nucleotide repeat motifs were developed on DNA extracted from two specimens sampled in the Molopo Nature Reserve (S 25°50′ and E 22°55′, Meyer 2004) by a commercial company (ECOGENICS, Zurich, Switzerland). From 48 sequences yielding repetitive motifs, primer pairs were designed. Screening revealed 15 primer pairs that produced consistent bands (Table 1).

DNA was extracted with the DNeasy-tissue kit (Qiagen, Hilden, Germany; yield 30–100 ng/µl). PCR protocols started with an initial denaturation at 95 °C for 5 min, followed by 30 cycles of denaturation at 95 °C for 30 s, annealing at 63 °C for 40 s, and extension at

Table 1. Characterisation of 15 microsatellite loci in the southern African hairy-footed gerbil *Gerbillurus paeba* (38 individuals).

Locus	Primer sequences (5′–3′)	Repeat motif	Size bp (range)	*A*	H_o	H_e	Genbank accession
2	F: AGAAGAGGGGACAGAAGATTGAAG R: TATAGGCCCAGGTTGTTTATTGTG	$(CA)_{18}$	110 (100–128)	9	0.11	0.90	DQ381513
4	F: TCCCTCATAAACCACCCTTC R: TCCTGTCTCCCTATGTTCGTG	(CA)30	156 (140–160)	6	0.50	0.83	DQ381514
7	F: ATGTGTCACACTACACATCCCAAC R: TGCAGCCAAGTCTATGTTATTTTG	$(CA)_{25}$	192 (170–204)	11	0.23	0.90	DQ381515
13	F: AAAAGCATGAGAGCCTGATTTC R: GCTAGCTCTCTGTTTCCCAATG	$(CA)_{23}$	148 (138–162)	11	0.47	0.84	DQ381518
14	F: TTTCGATGGAATGGGGATAG R: AGATGGGGACAGTGACAAGG	$(CT)_{21}+(GT)_{23}$	212 (196–240)	19	0.78	0.93	DQ381519
15	F: AGCAGACTTCCCTGCTGTTC R: TGCTGACCACTCTTGACTCC	$(CA)_{11}$	120 (122–146)	10	0.42	0.87	DQ381520
16	F: CTTCCAGTGTCTTCATCTGAGC R: CCTCCCCATATCTGTAAAGCAG	$(CA)_{18}$	120 (102–128)	12	0.41	0.88	DQ381521
17	F: GTGGGCCTGCATGTAAGGATA R: TCTCAGCAGGTAAAGTCATTGGC	$(CA)_{25}$	157 (141–171)	11	0.42	0.88	DQ381522
18	F: GTGGCTCACAGCAGAAACAG R: CCATAAGAAACCCAAAGATGC	$(CA)_{21}$	256 (244–284)	13	0.26	0.92	DQ381523
21	F: GTTGGGATGCCACTACTTGG R: GACCTTCCTCAAACCGTGAG	$(CT)_{22}+(CA)_{15}$	229 (207–243)	4	0.24	0.60	DQ381524
23	F: CATGATCACAGGTTGGTTTGAC R: GCTTGCTCTTAAGGGAGGACAC	$(CA)_{25}$	184 (154–198)	12	0.42	0.87	DQ381525
34	F: GGTTGACATGACATCCAGAAGG R: CTGTATTTCCATCCACGACTCC	$(GA)_{23}$	165 (155–169)	4	0.39	0.59	DQ381529
41	F: CTCCACGTCATCCCTGTCTC R: TAACGGGTAAGGGGAGATGG	$(GA)_{22}$	235 (211–271)	15	0.63	0.91	DQ381531
50	F: ACCTGGGCATGAAAGAAGC R: GGTTTAAGTGAGGAGGGATGG	$(GA)_{21}$	287 (265–307)	12	0.37	0.78	DQ381532
56	F: AGATGGGGACAGTGACAAGG R: TTCGATGGAACGGGGATAG	$(CA)_{41}$	215 (201–241)	11	0.56	0.87	DQ381533

Locus names, primer sequences, repeat motif, expected size, number of alleles, allele range as well as observed and expected heterozygosity and accession numbers are given.

72 °C for 30 s, followed by 95 °C for 30 s, 60 °C for 1 min, and a final extension at 72 °C for 8 min. Each PCR reaction was carried out with one unit recombinant Taq DNA-polymerase, in 10 mM Tris–HCl-buffer (pH 8.3) and 50 mM KCl (all SIGMA, Taufkirchen, Germany) in a total volume of 20 µl. DNAs were amplified under final concentrations of 1.5 mM $MgCl_2$, 20 µM each dNTP, and 0.5 µM each of the forward and reverse primers. PCR products were run on a 7.5% polyacrylamide gel at 300 V for 3 h, stained with ethidium bromide (2 mg/l, 20 min), and visualised under UV. Based on 100 bp size standard (O'Gene Ruler, Fermentas), each microsatellite locus was scored on high-resolution images.

Descriptive statistics for all 15 microsatellite markers were calculated for 38 individuals collected from four populations (farms 7, 10, 19, 20; Table 1 and Fig. 1). Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium were tested using ARLEQUIN 2.0 (Schneider et al. 2000). For a detailed study on spatial genetic variation across all 20 populations, we selected seven highly polymorphic microsatellites (loci 15–18, 23, 41, and 50; Table 1). Loci were tested for sex-linkage using GENALEX 6 (Peakall and Smouse 2006).

To investigate the probability of the presence of null alleles, drop-out of large alleles, and scoring errors due to stutter-bands, we used MICRO-CHECKER (van Oosterhout et al. 2004). Null allele frequencies were estimated using the Brookfield 2 estimator (Brookfield 1996). Those analyses showed that null alleles may occur evenly in all our loci and within all populations (Table 2). In the presence of null alleles estimates of genetic differentiation tend to increase (Slatkin 1995; Paetkau et al. 1997). A recent simulation study revealed a bias in F_{ST} values towards larger values in populations, which are significantly differentiated anyway (Chapuis and Estoup 2007). In contrast, autocorrelation procedures on genotypes and tests for genetic differentiation based on permutated genotypes between populations do not rely on allele frequencies. Therefore, these methods are not influenced by the occurrence of

Table 2. Estimated frequencies of null alleles within all 20 populations (seven loci, mean and standard deviation, number of loci supposed to bear null alleles), within the selected seven loci used for large-scale analyses across all 20 populations and within all loci screened on 38 individuals from four populations (see text for details).

Population no.	Within all 20 populations			Within seven loci across all populations		Within all loci	
	Mean	SD	Loci bearing null alleles	Locus	Mean and range	Locus	Brookfield 2
1	0.23	0.14	5	15	0.25 0.00–0.52	2	0.44
2	0.28	0.10	5	16	0.22 0.06–0.33	4	0.37
3	0.28	0.17	6	17	0.19 0.00–0.39	7	0.44
4	0.28	0.12	6	18	0.33 0.09–0.54	13	0.19
5	0.25	0.13	5	23	0.28 0.13–0.44	14	0.08
6	0.28	0.08	7	41	0.28 0.10–0.53	15	0.23
7	0.20	0.09	5	50	0.29 0.16–0.40	16	0.28
8	0.28	0.13	6			17	0.23
9	0.34	0.13	6			18	0.33
10	0.22	0.10	7			21	0.21
11	0.27	0.06	6			23	0.23
12	0.32	0.09	6			34	0.23
13	0.24	0.10	6			41	0.14
14	0.24	0.11	5			50	0.22
15	0.27	0.11	6			56	0.31
16	0.25	0.12	5				
17	0.33	0.20	3				
18	0.31	0.09	6				
19	0.17	0.12	4				
20	0.23	0.08	7				

All null allele frequencies were estimated by applying the Brookfield 2 estimator (Brookfield, 1996).

null alleles. Furthermore, the occurrence of null alleles lowers the correct assignments of individuals to their population of origin by less than 3% (Carlsson 2008). Based on these arguments we decided to use traditional population genetic methods during our analyses despite deviations from HWE.

Partitioning of genetic variation within and among populations (AMOVA) was estimated using Arlequin 2.0 and FSTAT (Goudet 2001). Robustness of results was checked by jackknifing and bootstrapping (15,000 permutations) over all loci. Furthermore, we calculated pairwise F_{ST} values between all populations in FSTAT. The interpretation of F_{ST} values with respect to gene flow, isolation by distance, and number of migrants assumes genetic equilibrium. To test for genetic equilibrium we used the Hutchison and Templeton (1999) protocol. In a balanced situation between gene flow and genetic drift, pairwise F_{ST} values should increase with distance. Because the influence of drift increases with distance, the scatter around the regression plot should also increase with distance. We calculated the absolute residuals from the linear regression of pairwise F_{ST} values versus geographic distance. These residuals were tested against geographic distance by a matrix correlation with 99,999 permutations (R-package *ecodist*; Goslee and Urban 2007).

The number of first-generation migrants was estimated with a frequency-based assignment algorithm provided in GENECLASS 2.0 (Piry et al. 2004). Due to our sampling design, we surely did not collect all potential source populations. The approach suggested by Paetkau et al. (1995) has been found most reliable for such a situation (Piry et al. 2004). We calculated the likelihood that an individual genotype originated from the population where it was collected (model L = L_home in GENECLASS). The probability of an individual being a resident was estimated by the resampling procedure of Paetkau et al. (2004). For a conservative type I error, we set the error probability to 0.01 with the default setting of 1000 simulated individuals (see also Schweizer et al. 2007). Differences in the number of female and male immigrants were tested by a χ^2-test using STATISTICA 6.0 (StatSoft 2002).

To test for gender differences in genetic differentiation, we used two approaches. First, we estimated the confidence limits for male and female F_{ST} values by bootstrapping across loci and looked for an overlap in the confidence interval (CI). Second, we used a Bayesian test statistics implemented in HICKORY 1.1 (Holsinger and Lewis 2001–2007) with the default settings that computed θ^1-values, an analogue to Wright's F_{ST} (Holsinger et al. 2002; Holsinger and Wallace 2004;

see Brändle et al. 2007 for an application). We estimated posterior distributions of θ^1-values for males and females and tested for pairwise differences between these two data sets. To determine if male and female posterior distributions were different, we picked random pairs from each distribution and calculated the difference. If the 95% CI excluded zero, the estimates were considered different. Five populations with only one male sample were excluded from this analysis.

To calculate autocorrelation coefficients (r) among pairwise individual genetic distances from different geographic distance classes, we used GENALEX 6 (Peakall and Smouse 2006). These coefficients are true correlation coefficients ranging from −1 to 1 and measure the genetic similarity between individuals (Smouse and Peakall 1999). Errors and confidence intervals for r when there is no genetic structure were estimated by re-sampling (999 permutations). Distance classes included at least 10 individuals separated by 50 m to 90 km. Distance classes up to 3 km mirror the situation within farms while all distance classes above 3 km reflect genotypic similarity among individuals collected at different populations.

All the methods we applied for analysing our data assume isotropic dispersal which means, that dispersing individuals use all directions with the same probability. However, Blaum and Wichmann (2007) suggested that alternating habitat types like dunes and valleys cause fragmentation of the landscape that might favour non-isotropic dispersal. Consequently, genetic differentiation between populations might be influenced by their relative position to the direction of dunes and valleys. If the connection between two populations has the same orientation as the dunes and valleys (in our case NW–SE), individuals have to cross fewer valleys than individuals from sites for which the connection runs perpendicular to the dunes and valleys. We used the most recent version of Google Earth (www.google.earth.com) to draw lines between all 190 population pairs. We counted the number of dunes to be crossed when moving straight from one population to another. There are a few salt pans in the area, which are unlikely to be crossed by dispersing individuals (Nel and Rautenbach 1975). If the straight line linking two populations crossed such a pan, the number of dunes alongside was counted. The impact of the number of dune frequency on genetic distance was assessed by a partial Mantel test in *R*, controlling for geographic distance (99,999 permutations; Goslee and Urban 2007).

Results

The 15 newly developed microsatellite loci were highly polymorphic (Table 1). We found no linkage disequilibria between loci (sequential Bonferroni correction; Rice 1989). Assignment tests revealed no sex-linked loci. There was a deficiency of heterozygotes within all populations and thus significant deviations from HWE ($p < 0.01$). Null alleles may be one possible cause of such deviations and the application MICRO-CHECKER suggested that null alleles may occur at all loci (Table 2). The mean frequency of null alleles across the seven loci selected to analyse the 20 populations did not differ among populations (ANOVA, $F_{19,0.05} = 0.9$; $p = 0.56$; Table 2). There was no evidence of large-allele drop-out or scoring errors due to stuttering.

Between sites we found an overall genetic differentiation of about 10% (AMOVA: 13%; FSTAT: $F_{ST} = 0.097$, 95% CI from bootstrapping across loci: 0.058–0.141). Pairwise F_{ST} values showed a high proportion of significant comparisons even after sequential Bonferroni correction (36%, 68 out of 190; Fig. 2). We found no correlation between genetic differentiation and geographic distance (matrix correlation, $r = -0.01$; $p = 0.89$). We also found no relationship between absolute residuals and geographic distance ($r = 0.03$; $p = 0.34$). There was also no correlation between pairwise genetic differentiation (x) and the number of dunes (y) between two populations (matrix correlation with permutations: $r_{xy} = 0.02$; $p > 0.3$; controlled for distance (z): $r_{x/yz} = 0.03$; $p > 0.3$).

Genetic differentiation among populations was higher for males ($F_{ST} = 0.125$, CI: 0.042–0.217) than for females ($F_{ST} = 0.08$; CI: 0.052–0.116). This trend was also evident when computing pairwise F_{ST} values for each population and sex, and plotting the corresponding values derived from males and females, respectively (Fig. 3). If both sexes were similarly differentiated, data points should be evenly distributed around the bisecting

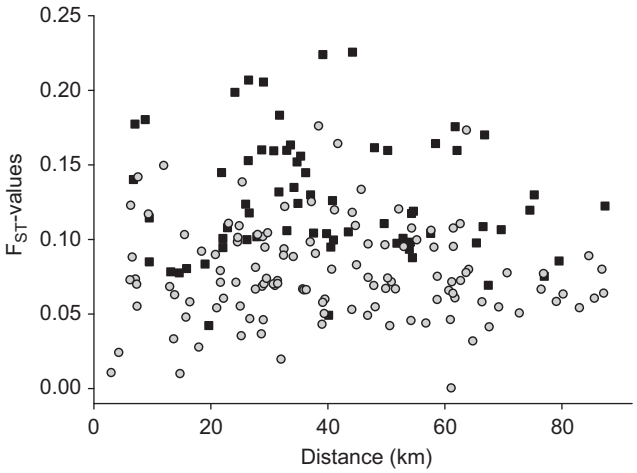

Fig. 2. Pairwise F_{ST} values among 20 populations (seven microsatellites, 195 individuals) of *G. paeba* versus geographic distance. Black squares indicate significant values (test assuming no HWE, with sequential Bonferroni correction).

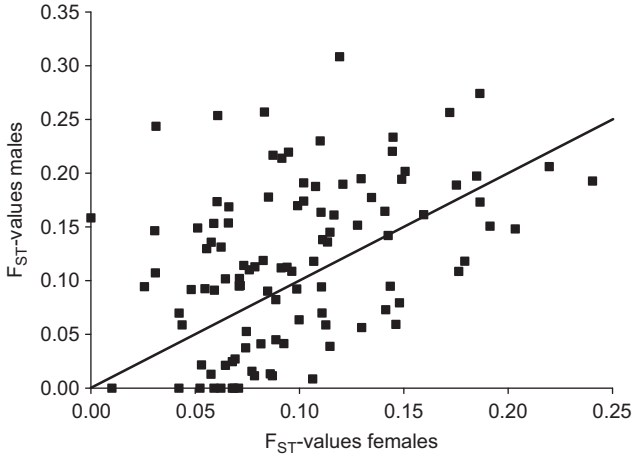

Fig. 3. Comparison of genetic differentiation between sexes. Each point is defined by the respective pairwise F_{ST} values for males and females per population, calculated from microsatellites. Note that for 62 out of 105 comparisons between sites males show a larger differentiation than females (points are above the bisector). This proportion is significant (binomial test, $p = 0.025$). However, this test is suggestive as points are not mutually independent.

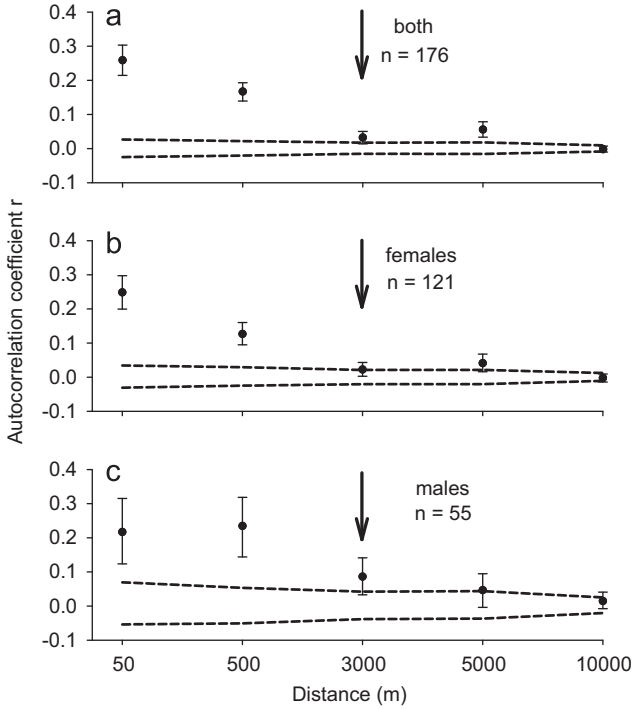

Fig. 4. Mean autocorrelation coefficient r ($\pm$asymmetric SE) for pre-defined distance classes using seven microsatellite loci in *G. paeba*: (a) both sexes, (b) females, and (c) males. The dashed lines indicate the confidence bands of expected autocorrelation coefficients. All data on the left to the arrows (incl. 3000 m class) resemble within-population sampling, all data to the right such of between-population sampling.

line. Estimates from HICKORY ($F_{ST} = 0.024 \pm 0.005$ (mean $\pm$ standard deviation) for males and $F_{ST} = 0.027 \pm 0.005$ for females) were not significantly different ($p > 0.05$).

Assignment tests suggested that 47 individuals (24% of the total sample of 195 individuals) were first-generation migrants. The majority ($n = 31$, 66%) of these migrants were females, while just 24% ($n = 11$) were males. Five migrants were of unknown sex. This female-bias among immigrants was significant (Yates corrected $\chi^2 = 5.05$; $p = 0.04$). Despite individuals being genetically most similar to the population where they were sampled, they might be erroneously assigned as migrants by the algorithm (“home-assigned migrants”; see also Schweizer et al. 2007). However, likelihood of origin in all individuals assigned as immigrants were always highest for populations others than the sampling population. Therefore, “home-assigned migrants” should be rare in our analysis.

When the data from both sexes were pooled, genetic autocorrelation analysis revealed significant positive values up to distances of 3 km (Fig. 4a, distance classes presented were restricted to 10,000 m for convenience). The numeric results, however, depend on the chosen distance classes. We varied distance classes, but all experiments generated significant positive autocorrelation coefficients up to several kilometres (data not shown). To test for sex-specific patterns in the autocorrelation, we split the data into males and females (Figs. 4b and c). In females, genotypic similarity decreased significantly between the 50 m distance class and the 3000 m distance class (no overlap of CIs). In contrast, male autocorrelation coefficients did not differ significantly in these three distances classes.

Discussion

Here we investigated dispersal pattern and genetic variation in 20 *G. paeba* populations with seven highly polymorphic microsatellite loci. Heterozygote deficiency resulted in the rejection of HWE at all loci. The most likely cause for this deviation from HWE is the presence of null alleles, which occur in many if not all microsatellite studies (Dakin and Avise 2004). However, most studies inclusive of ours infer the occurrence of null alleles on the basis of deviations from the Hardy–Weinberg equilibrium caused by the deficiency of heterozygotes. Other sources of homozygote excess are Wahlund-effects or sampling of closely related individuals. Null alleles typically result from either technical problems during PCR or scoring or due to mutations in the microsatellite flanking regions. Microsatellites have high mutation rates (e.g. Callen et al. 1993) that can alter flanking sequences between distant populations. We developed primers from individuals sampled on a

site about 300 km distant from our study area. Nevertheless, the observed null allele frequencies (0.2–0.3) were comparable to null allele frequencies in other mammalian studies (0.06–0.35; Ishibashi et al. 1995; Becher and Griffiths 1998; Nievergelt et al. 1998; Ohnishi et al. 1998; Dakin and Avise 2004).

Our analyses revealed conflicting results about the relative importance of genetic drift and gene flow for the spatial genetic structure of *G. paeba*. While significant genetic differentiation between neighbouring populations suggested restricted dispersal, assignment tests revealed that about 24% of the sampled individuals were migrants, suggesting considerable gene flow. This contradiction may be affected by null alleles. Chapuis and Estoup (2007) simulated the influence of null alleles on the estimation of F_{ST} values. When null alleles occur at high frequencies, F_{ST} values were tendentiously overestimated. However, this bias was found only at low levels of gene flow, and if populations were significantly differentiated anyway. Null alleles seem also widely negligible when estimating likelihoods of individuals being migrants by assignments tests. Null alleles have little (below 3%) or no effect on the general outcome (Carlsson 2008). The conflict between the F_{ST} values and assignment test results is thus not likely due to null alleles.

Another measure of the importance of gene flow compared to drift in genetic differentiation is the standard deviation of the pairwise F_{ST} values (Hutchison and Templeton 1999). In the eastern collared lizard *Crotaphytus collaris*, the standard deviation of mean pairwise F_{ST} values in a situation with considerable gene flow (mean $F_{ST} = 0.20$; $n = 36$) was 0.08. In another study area, where drift played a larger role than gene flow (mean $F_{ST} = 0.36$; $n = 120$), the standard deviation was 0.22. In our data (mean $F_{ST} = 0.12$; $n = 190$), the standard deviation was 0.04, suggesting that gene flow is more important than drift. Three other related factors can explain the contradiction between gene flow and genetic differentiation in these populations: (1) population density fluctuations, (2) low reproductive success of dispersers, and (3) non-isotropic dispersal. Based on the proposed suitability and spatial structure of the matrix, we found no evidence for non-isotropic dispersal.

The population sizes of rodents, like *G. paeba*, that live in semiarid and arid environments fluctuate with annual rainfall (White et al. 1997). Rain increases seed production and leads to peaks in the population dynamics of rodents. The resulting high population sizes are favourable dispersal conditions. Effective population size (N_e) in fluctuating populations is the harmonic mean of population sizes across time (Hartl and Clark 1997) and is strongly affected by the minimum population size (Hartl and Clark 1997; Chiappero et al. 2006). In these populations with small N_e, drift can cause considerable genetic differentiation between populations irrespective of geographic distance (Bowen 1982; Plante et al. 1989; Stacy et al. 1997; Berthier et al. 2005 2006; Redeker et al. 2006).

Regional F_{ST} values estimate an average across larger time scales, reflecting the average situation. The transport of genetic information (gene dispersal) does not ensure the successful implementation of alleles into the gene pool of the recipient population (gene flow). Collecting genetic samples during a wave of dispersal and detecting such dispersal events by assignment test may lead to an overestimation of gene flow (Schweizer et al. 2007). The assigned "migrants" might be dispersers with little impact on average genetic structure. Inclusion of a large number of dispersers is also capable to explain departure from HWE within populations.

Autocorrelation coefficients indicate significant genotypic similarity at distances up to 3 km, consistent with the range of genotypic similarity from other studies (Peakall et al 2003; Kraaijeveld-Smit et al. 2007; Piggott et al. 2006). The mean home range size in *G. paeba* is 1.5 ha and regular movements between 130 and 500 m have been documented (Skinner and Chimimba 2005; White et al. 1997). These field observations are consistent with our genetic data and suggest limited gene flow within populations. The spatial scale of significant genotype similarity found during our study is not unusual. Some available studies report significant similarities below 1 km (Peakall et al 2003; Kraaijeveld-Smit et al. 2007; Piggott et al. 2006).

Female-biased dispersal was suggested from genetic differentiation, patterns of genotype similarity with distance, and the assignment tests. In mammals, dispersal is usually male-biased (Greenwood 1980). For example, male deer mice *Peromyscus maniculatus* made more long-distance movements than females (Rehmeier et al. 2004). While our results that dispersal might be female-biased indicate the opposite, the significance of the difference in dispersal between males and females depends on statistical test. The observed sex-biased dispersal may arise from skewed sex ratios. Although little is known about the demographics and population dynamics of *G. paeba*, the sex ratio in our sample was female-biased (2.2:1), which can cause higher drift in males (Hedrik 2007). Female-biased sex ratios are common in rodents, such as *Peromyscus leucopus* (Fahrig and Merriam, 1985), *Clethrionomys glareolus*, and *Apodemus flavicollis* (Glitzner and Gossow, 2001; Rajska-Jurgiel, 1992). Sex-biased dispersal is influenced by the relative costs and benefits in males and females. In most mammals, females invest most energy to rearing offspring and benefit most from familiarity of the resources (Greenwood 1980). The few reports on female-biased dispersal suggest that competition for key resources, such as mates, drives the dispersal (e.g. Favre et al. 1997; Banks et al. 2002; Hammond

et al. 2006; Zhan et al. 2007). The cause of female-biased dispersal in *G. paeba* remains unknown.

Altogether we found genetic differentiation between *G. paeba* populations despite hints for high gene dispersal. The migrants appear to have little effect on the long-term genetic structure. Furthermore, genetic structure was not correlated with geographic distance, suggesting that population sizes become sometimes such small that drift is the major driver of genetic diversity. Therefore, the landscape structure had little influence on *G. paeba* genetic differentiation. Interestingly, our data suggest that unlike most mammals, *G. paeba* dispersal was female-biased. This finding, however, requires further investigations.

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