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Highly asymmetric fine-scale genetic structure between sexes of African striped mice and indication for condition dependent alternative male dispersal tactics

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Abstract

Sex-biased dispersal is observed in many taxa, but few studies have compared sex-biased dispersal among and within populations. We addressed the magnitude and habitat dependency of sex-biased dispersal in social African striped mice by separating group-related from population-related genetic variance to understand the contribution of each sex to deme structure. As dispersal over unoccupied habitat is likely to be more costly than dispersal within a population, we predicted that individuals leaving the natal population have a lower body condition, being inferior to heavier territorial individuals. Fine-scale genetic structure was detected in both sexes. Female relatedness decreased continuously from R = 0.21 at 25 m to zero at 500 m. Maximum male relatedness R = 0.05 was constant at distances between 25 and 75 m, becoming zero at 100 m. Genetic variance (F_{ST}) among seven locations was significantly higher in females than in males, while inbreeding estimates (F_{IS}) were significantly higher in males than in females. Assignment tests estimated significantly more migrants among males, while Bayesian clustering estimated only a single genetic unit cluster for males among the seven locations. The mean body mass of migrant males (44 g) was significantly lower than for males that remained resident and thus dispersed within their sub-population (48 g). Combined, the results showed habitat-independent male-biased dispersal and high female philopatry, and suggested that body condition was more important than kinship in male dispersal decisions. We suggest that locally inferior males are important for gene flow between sub-populations. Thus, males might follow alternative dispersal tactics.

Keywords: body mass, female philopatry, habitat-independent dispersal, reproductive tactics, *Rhabdomys pumilio*

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Introduction

Effective dispersal leading to successful breeding (gene flow) is fundamental in determining the genetic relatedness of individuals and populations and in shaping the genetic variance on which selection can act (Falconer 1989). The decision to disperse is influenced by a complex combination of social interactions, competitive ability, distribution and availability of resources and habitat heterogeneity (Perrin & Goudet 2001; Wiens 2001; Lawson Handley & Perrin 2007). The social system influences dispersal by affecting the reproductive success through local mate competition, local resource competition and/or inbreeding avoidance (Greenwood 1980; Pusey 1987; Perrin & Mazalov 2000). Male-biased dispersal is predicted to evolve when local mate competition exceeds local resource competition (Perrin & Mazalov 2000). This is confirmed for mammalian

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species where polygynous and promiscuous mating systems generally have male-biased dispersal (Greenwood 1980; Dobson 1982).

The level of sex-biased dispersal is resource dependent and may depend on environmental as well as demographic parameters (Nutt 2008; Busch *et al.* 2009). However, describing the pattern of sex specific dispersal tells little about individual dispersal tactics, which might significantly influence the degree of gene flow and individual fitness consequences: for example in small mammals with male biased dispersal not all males might disperse the same distance, and individual females might disperse as well. Many species show alternative reproductive tactics within a single sex, for example when males differing in competitive ability follow different ways to maximise their reproductive success, with some males following a sub-optimal tactic that yields the maximum reproductive success for their own status (Gross 1996). Similarly, it can be expected that males might choose different dispersal tactics, depending on their individual abilities. Males of low competitive ability might be forced to remain philopatric and withhold dispersal until getting older and stronger (see e.g. Schradin *et al.* 2009), while very competitive males might be able to reduce costs of dispersal by becoming the breeding males of relatively closely situated groups or demes, reducing distance and costs of dispersal. Males of intermediate competitive ability might then be forced to migrate over longer distances, facing higher dispersal costs before being able to settle successfully. To our knowledge, few previous studies tried to differentiate between such potential dispersal tactics, which would help us to obtain a deeper understanding of gene flow within and between populations.

In African striped mice (*Rhabdomys pumilio*; Sparrman 1784) from the Succulent Karroo of South Africa, high population density favours group-living and philopatry (Schradin *et al.* 2010a). Groups consist of one breeding male, 2–4 communally breeding females and non-breeding male and female offspring that help in territorial defence and nest building (Schradin & Pillay 2004; Schradin *et al.* 2010b). Females are territorial aggressive (Schradin 2004) and increase their home ranges during the breeding season (Schradin *et al.* 2006), indicating high nutritional demands. There is strong competition between males for the access to groups of communally breeding females (Schradin *et al.* 2009), leading to local mate competition. Thus, high population density resulting in habitat saturation, local competition for mates and resources as well as kin cooperation should affect individual decision making on dispersal in striped mice. This predicts males to be the dispersing sex, as there is cooperation between communally breeding females but strong local mate competition between males (Perrin & Mazalov 2000). While male-biased dispersal is predicted for striped mice, we also need to know the relative level of female versus male gene flow to understand the scale of genetic cohesion of the population. This defines the scale (number of individuals per population) at which selection may act differentially on each sex through resource and/or mate competition. Thus the question is what is the combined magnitude of gene flow of each sex and their dispersal tactics?

Body mass determines reproductive tactics in male striped mice and upon gaining mass, philopatric individuals can change into roamers or territorial breeders, and roamers can become territorial breeders (Schradin *et al.* 2009). Further, heavier males are more likely to win male-male competitions (Schradin 2004) and male body mass is known to be important in other polygynous mammals (Heske & Ostfeld 1990; Martin *et al.* 1994; Roberts *et al.* 1998). Dispersal over unsuitable habitat might be risky and thus a tactic followed by males with low competitive ability doing the best of a bad job (Dawkins 1980) with little chance of reproductive success in their natal habitat. Hence, we predicted that migrants between sub-populations are of lower than average body mass than males dispersing within their natal sub-population. This would, to our knowledge, be one of the first studies to indicate alternative dispersal tactics.

In social species with family groups, territoriality and breeding tactics limit individual interactions in the random-mating sense within populations, while allowing genetic cohesion of the same population through dispersing breeders (Chesser 1991a,b). In the present study, we combine fine-scale and population-based genetic analyses to separate family-related from population-related genetic variance to address the following questions: (i) what is the relative degree of sex-biased dispersal and at what spatial scale, (ii) is sex-biased dispersal dependent of habitat connectivity, e.g. if separation by habitat is more important for sex-biased dispersal than separation by territoriality and (iii) is dispersal related to body mass, indicating that there might be alternative dispersal tactics?

Materials and methods

Study area

The study took place from August to November 2008 in the Goegap Nature Reserve, Northern Cape Province, South Africa, during the breeding season of striped mice. The vegetation is succulent Karoo dominated by *Zygophyllum retrofractum* and *Lycium cinerum* shrubs (Rösch 2001). Both plants are important food sources and nesting sites for striped mice (Schradin *et al.* 2006). In winter,

from May to August, the temperature varies between 1.5 and 24 °C, and between 5 and 40 °C in summer (C. Schradin, unpublished). The average rainfall is 160 mm/year and occurs mainly during winter (Rösch 2001).

Study species

The diurnal striped mouse (*Rhabdomys pumilio*; Sparrman 1784) is a medium sized rodent with an adult body weight of 30–80 g (David & Jarvis 1985; Schradin & Pillay 2005a). Males can follow one of three alternative reproductive tactics: (i) natally philopatric males that attempt matings with females from neighbouring groups, (ii) solitary roamers that leave their natal groups and attempt matings with any female they encounter, or (iii) dominant territorial polygynous breeders that disperse from their natal group and immigrate into groups of up to four breeding females (Schradin *et al.* 2009). Male territoriality is influenced by body condition; heavy males being dominant (Schradin 2004). Females are either philopatric and breed in a communal group of closely related females that is defended by a territorial male or they breed singly without territorial males (Schradin *et al.* 2010a). The level of polygyny is influenced by population density, with more females living in communal groups and more males being territorial breeders under high population density (Schradin *et al.* 2010a). Behavioural observations have shown that both males and females may stay in the natal group after reaching adulthood in the year of birth (breeding season is August to November) and groups can contain up to 30 individuals of both sexes (Schradin & Pillay 2004). Males and females living in territorial groups share a common nest but forage as solitary individuals within the group territory (Schradin 2006). The territory is defended by all group members against mice from neighbouring groups and solitary roaming males (Schradin 2004).

Study populations

1. To analyse fine-scale genetic structure, mice were caught in traps set up every 20 m in the seven km transect (Fig. 1). The 7 km transect constitutes a continuous and homogenous dry riverbed environment (Appendix S1, Supporting information) that only carries water for one or few days a year after heavy rainfall; in some years the river never flows. The population density at the start of the 2008 breeding season was 10.4 mice/ha, which was below an eight year average of 14.4 ±12.9 mice/ha, range: 1.5–32.4 (Schradin *et al.* 2010a). Food and nesting sites were continuously distributed throughout the riverbed.

2. For analyses of among-population differentiation, a total of seven spatially separated breeding habitats covering an area of approximately 30 km^2 were analysed, each breeding habitat located along a dry riverbed (Fig. 1). The two 580 m transect endpoints of the dry riverbed (subpopulations 1 & 2, Appendix S1, Supporting information) were included as separate subpopula-

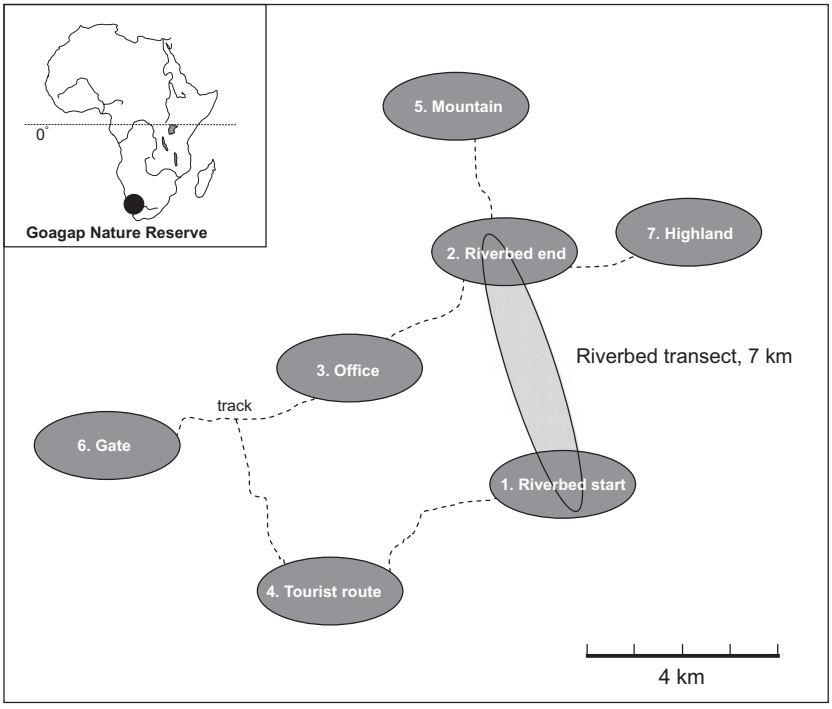

Fig. 1 Schematic presentation of sampling locations of striped mice in the Goagap Nature Reserve, South Africa. The elongated *light grey* area represents the 7 km riverbed transect for fine-scale genetic analysis. *Dark grey circles* represent 580 m transect samples for among-population analyses. The riverbed start and end, respectively, were included in the population analysis as independent sampling locations. *Broken lines* show putative dispersal tracks between sample locations via dry riverbeds. A topographic map can be viewed at Google maps, 29°40′08″S, 18°00′21″E. Details of each subpopulation are described in Appendix S1, Supporting information.

tions as these endpoints were separated by 5 km. Mice from each of the five remaining subpopulations (3–7, Appendix S1, Supporting information) were caught as described below by trapping every 20 m along 580 m transects. All subpopulation pairs, except 1–2, were separated by small hills or dry plains, which were without continuous shelter (shrubs and bushes) that are important as sources of food and for nesting sites. Distances between sample locations were 1.8–10.5 km (track distance) and 1.8–8.5 km (linear distance).

Trapping, marking and collecting of tissue samples

Stripped mice were caught with metal live traps ($26 \times 9 \times 9$cm) of the Sherman type. Two traps were placed every ca. 20 m under shrubs where walking paths and/or faeces of mice were present. Each trapping station was labelled and its geographic coordinates were recorded (eTrex Venture, GARMIN International, USA). The trapping procedure started by placing and pre-baiting closed traps for 48 h with a mixture of bran flakes, sea salt and vegetable oil. Trapping commenced immediately thereafter and continued for 3 days (72 h) using the same bait mixture. During these 3 days, traps were opened twice daily, between 7:00 am and 9:00 am and between 4:30 pm and 6:30 pm when mice were most active. Each trap was checked twice during each interval after an average time of 60 min (max. 90 min) and then closed until the next trapping event. Due to time constraints, the number of traps set per session was limited to 60, i.e., each 5-day trapping session included 580 m sub-transect. Pre-baiting of the next 580 m sub-transect commenced at day 4 or 5 of the previous sub-transect. The entire 7 km transect was sampled in 12 intervals and, allowing for 1–2 days between intervals, in 60 days (21 August 2008–21 October 2008). Mice for the population data set were sampled between 24 October 2008 and 14 November 2008. Individuals with a bodyweight below 30 g were categorised as juveniles, and not included in genetic analyses. All mice caught were weighed and sexed, and individually marked with ear tags (National Band and Tag Co., USA) or hair dye. For genetic analysis, 2 mm of the tail tip were carefully cut off and preserved in 90% ethanol. Thereafter, the mice were immediately released. Because adult mice were sampled after natal dispersal and during the breeding season when they were territorial, the prolonged sampling period should not have influenced the estimation of relatedness.

DNA procedure

Genomic DNA was isolated from tissue samples using Roche Diagnostics High Pure PCR Template Preparation Kit. The DNA concentrations varied from 20 to 300 ng/μl. Genetic variation was analysed at 12 microsatellite loci. Amplifications were carried out via two multiplex reactions. The first master mix had primers for seven loci (chr7_64, chr1_12, chr1_21, chr13_1, chr2_35, chr2_3, chr16_11). The second master mix included primers for five loci (D3Mit211, chr11_81, chr19_18, D7Mit124, chr5_38) (Appendix S2, Supporting information) (Thomas 2006). To each multiplex reaction we added 20 μl Hi-Di-Formamide, 0.13 μl Gene Scan-500 LIZ (orange) standard and 1μl DNA. PCR's of both master mix solutions were performed using the standard Qiagen® multiplex PCR Kit procedure: an activation step at 95 °C for 15 min, denaturation for 30 s at 94 °C, annealing for 90 s at 60 °C, and final extension for 2 min at 72 °C (35 cycles). PCR products were sequenced with an ABI 3730. Allele lengths were automatically scored by GENEMAPPER 4.0 (Applied Biosystem). All alleles were assigned to bins and new alleles checked by hand.

Gene diversity

Gene diversity was estimated as expected heterozygosity (GENEPOP v. 4.0, Raymond & Rousset 1995) and allelic richness (HP-RARE, Kalinowski 2005) per population. The allelic richness estimate of each subpopulation was weighted by the smallest sample size (15 individuals = 30 genes). Deviation from random mating (Hardy–Weinberg disequilibrium) and linkage disequilibrium was analysed within each location with GENEPOP v.4.0. All loci were checked for null alleles with MICRO-CHECKER (Van Oosterhout *et al.* 2004). We tested for null-alleles in the seven subpopulations (see above), which were assumed to constitute random samples unaffected by social structure. Only one locus, D7Mit124, showed indication of a null-allele in four out of seven sub-populations (frequencies = 0.08–0.15) and was omitted in the estimates of inbreeding coefficients (F_{IS}) and Hardy–Weinberg (HW) disequilibrium, which both are based on observed genotypes. D7Mit124 was included in relatedness analyses (relatedness coefficient in autocorrelation analysis) because the relatedness coefficient with constant gene flow parameters it is not influenced by the ploidy level or the selfing rate (Hardy & Vekemans 1999). D7Mit124 was included also in analyses of F_{ST}, which is based on the expected heterozygosity.

Fine-scale spatial genetic structure

Fine-scale spatial genetic analysis was based on autocorrelation analysis (SPAGeDI, Hardy & Vekemans 2002) by comparing average between-individual relatedness (Queller & Goodnight 1989) among geographic distance

classes from 25 m to 7500 m. The analysis is unbiased by equilibrium assumptions. All spatial genetic structure analyses were performed on adults only and separately for males and females. The autocorrelation analysis was based on striped mice caught in the essentially one-dimensional 7 km continuous dry riverbed habitat. Significant positive spatial genetic structure (relatedness $R > 0$) within each distance category was tested with permutation tests (SPAGeDI, Hardy & Vekemans 2002). Differences in mean relatedness between the sexes within each distance category were tested with two sided *t*-tests (JMP, SAS Institute 1995). Isolation-by-distance (IBD) in the continuous riverbed habitat was estimated for each sex with the slope of regression of relatedness and geographic distance (Hardy & Vekemans 2002). If IBD exists in the presence of fine-scale genetic structure, autocorrelations are expected to be positive at short distances, decreasing to zero at intermediate distances and finally becoming negative (Sokal & Wartenberg 1983; Smouse & Peakall 1999).

As suggested by Vekemans & Hardy (2004), we estimated an independent degree of spatial genetic structure with the *SP*-statistic for cross-species comparisons, $SP = -bR/(1 - R_{(1)})$, where $-bR$ is the regression slope (transformed prefix from negative to positive) on distance classes and $R_{(1)}$ is the mean relatedness between individuals in the first distance category.

Population level analyses

Differentiation between *a priori* defined subpopulations, F_{ST}, was estimated among the five sampling transects separated by unsuitable habitat (subpopulations 3–7) and the two 580 m endpoints of the riverbed. The two endpoints were included as they were beyond positive relatedness ranges (see Results, fine-scale genetic structure). Overall and sex-specific differentiation between subpopulations was based the method of Weir & Cockerham (1984) with FSTAT v. 2.9.3.2 (Goudet 1995). Mean relatedness, *R*, among mice of the same sex was estitamed as $R = 2xF_{ST}/(1 + F_{IT})$ where F_{IT} is the inbreeding coefficient of individuals relative to random mating in the total population. Pair-wise differentiation between populations was analysed with the programme Arlequin 3.5 (Excoffier *et al.* 2005). Estimates of sex-specific gene flow and relatedness by this method assume that individuals are sampled after the dispersal phase, which was the case for adults >30 g (David & Jarvis 1985; Schradin & Pillay 2005b).

Isolation by distance between sample sites was estimated for both sexes combined and for each sex separately. In contrast to the fine-scale analysis above, IBD in this analysis is population-based and two-dimensional. IBD among sample sites was analysed with the Mantel test using GENEPOP (Raymond & Rousset 1995). The geographic distances were defined as (1) the distance between populations via dry riverbeds, as these could act as dispersal routes, and (2) linear distances. Genetic distances were estimated as F_{ST} and $F_{ST}/(1 - F_{ST})$. The geographic distances were not transformed in the analysis of IBD because sampling sites were regularly dispersed at short distances without outlier samples.

Sex-biased dispersal was further considered by estimating first generation migrants and comparing the estimated number of first generation male and female migrants with the actual number of trapped mice. Male-biased dispersal is indicated when males are over-represented in the migrant estimate. In this analysis, we evaluated if first generation migrants came predominately from neighbour sites. If dispersal follows an IBD pattern, we expect that those sites with the highest number of migrants should be neighbours. First generation migrants were calculated with the program Geneclass2 (Piry *et al.* 2004) using the algorithm of Rannala & Mountain (1997) with the significance level set to 0.01.

To assess genetic cohesion of the study population without *a priori* assumptions of deme structure, the number of genetic clusters, *K*, was estimated using Bayesian inference with the program Structure (Pritchard *et al.* 2000). Structure estimates *K* by optimising Hardy–Weinberg equilibrium and minimising linkage disequilibrium within clusters. These features can be problematic in family-based populations where disequilibrium may be expected for both estimators. We therefore used Structure to evaluate for each sex the extent of genetic cohesion, i.e. individuals collectively influenced by certain alleles/genotype combinations, rather than the level of differentiation. We studied *K* between 1 and 10, assuming an admixture model with correlated allele frequencies (Falush *et al.* 2003). We ran 10 independent runs for each *K* and calculated the mean of the posterior probabilities for each *K*. Each run was started with a burn-in of 10 000 iterations and was run for 100 000 iterations. The number of genetic clusters, *K*, was inferred as the *K* with the highest mean likelihood, and if *K* reached a likelihood-plateau, the smallest *K* in the plateau. Significant difference in mean likelihood between the inferred *K* and *K* - 1 was tested with *t*-tests. *K* was estimated for all individuals combined ($N = 192$) and for each sex separately ($N_{females} = 100$, $N_{males} = 92$).

Dispersal and body weight

The mean weight difference between mice determined to be migrants and residents by Geneclass2 was analysed with *t*-tests (JMP, SAS Institute 1995). Males and

Table 1 Genetic diversity estimates and tests for Hardy–Weinberg (HW) proportions for striped mice sampled along a 7 km transect and between subpopulations

Sample scale	Location	N_{tot}	N_{female}	N_{male}	A_R	H_o	H_e	P_{HW}
Transect	Riverbed	343	204	137	11.3	0.84	0.89	0.04
Subpopulation	1. Riverbed Start	32	23	9	10.4	0.84	0.89	0.06
	2. Riverbed End	28	15	13	10.0	0.83	0.88	0.00*
	3. Office	22	9	13	11.2	0.82	0.88	0.00*
	4. Tourist Route	31	19	12	11.1	0.86	0.90	0.45
	5. Mountain	30	14	16	11.1	0.82	0.88	0.05
	6. Gate	34	15	19	10.2	0.80	0.86	0.04
	7. Highland	15	5	10	10.3	0.87	0.89	0.00*
	Total	192	100	92				

N = number of sampled individuals, A_R = allelic richness over all loci, H_o = observed heterozygosity, H_e = expected heterozygosity, P_{HW} = probability of deviation from HW proportions, * significant at the 0.05 level after Bonferroni correction.

females were studied separately. Weight assessments were based on morning resting weights, which are the least biased by daily foraging increments (Schradin & Pillay 2005c; this study, unpublished).

Results

Gene diversity

A total of 475 adult individuals were trapped and analysed at 12 microsatellite loci. Gene diversity was similar in all population samples. Expected heterozygosity (H_e) per population was high in all localities H_e = 0.86–0.91 (Table 1). After Bonferroni correction, three subpopulations deviated significantly from HW proportions, while the three marginally significant populations (P = 0.04–0.06) did not. Mean allelic richness (A_R) per locus ranged between 10 and 11.1 (Table 1). No consistent linkage disequilibrium between pairs of loci was detected across populations ($P > 0.05$, Fisher's exact test).

Fine-scale spatial genetic structure

In total, 204 adult females and 137 adult males from the riverbed population were included in fine-scale analysis. The highest number of within-distance-category relatedness comparisons was 7602 at 1669 m for females, and 3 334 at 1639m for males. The lowest sample was 12 females at 5180 m and 11 males at 5 172 m (Appendix S3, Supporting information).

Female and male relatedness were significantly positive at short distances (Fig. 2). Mean female relatedness was highest at intervals of 25 m, R = 0.21 (locus range R = 0.15–0.28), decreasing continuously to zero at ca. 500 m (R = 0.001; P = 0.03) and becoming significantly negative between 1000 m and ca. 5000 m. Mean male relatedness was also highest at intervals of 25 m but only reached an estimate of R = 0.06 (locus range R = 0.03–0.16). Positive male relatedness was not significantly different from zero at 100 m (R = 0.015; P = 0.10) (Appendix S3, Supporting information). Female relatedness was significantly higher than male relatedness in all distance categories, except the two furthest distance points (5000–7000 m). The mean relatedness difference between females and males was significantly (P = 0.026) higher at shorter distances (25—100 m, mean difference R = 0.083) than at longer distances categories (250–5 000 m, mean difference R = 0.009). Isolation by distance estimates based on the regression slopes of autocorrelation over all spatial distances with overall genetic relatedness (over all loci) were negative and significant in both sexes: females b-log (slope log distance) = −0.02, $P < 0.001$; males b-log (slope log distance) = −0.009, $P < 0.001$), intercept 0.054. The *SP*-statistic was higher in females (*SP* = 0.025) than in males (*SP* = 0.008).

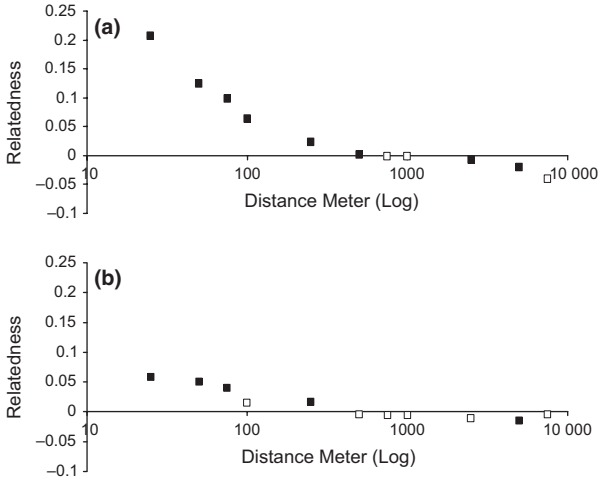

Fig. 2 Fine-scale genetic analysis showing the mean individual relatedness (Queller & Goodnight 1989) within distances categories of females (a) and males (b) of the riverbed population. Filled squares indicate relatedness significantly different from zero (permutation tests, SPAGeDI, Hardy & Vekemans 2002).

Population-level analysis

Genetic differentiation among subpopulation samples was based on 192 individuals (92 males and 100 females) sampled at seven sites. Overall differentiation was F_{ST} = 0.021 (P < 0.01). Differentiation between pairs of population-samples ranged between F_{ST} = 0.010 and F_{ST} = 0.046. All pair-wise estimates differed significantly from zero (P < 0.05) after Bonferroni correction (Appendix S4, Supporting information). Females were significantly more structured among sample sites, F_{ST} = 0.039, and more related within sample sites, R = 0.074, than males, F_{ST} = 0.015, R = 0.028 (P < 0.01). The within-sample site inbreeding coefficient was significantly higher in males, F_{IS} = 0.085, than in females, F_{IS} = 0.018 (P < 0.01).

Isolation-by-distance tests failed to detect correlations between genetic and linear geographic distances and between genetic and track dispersal distances in females (P > 0.17). For males, significant isolation-by-distance (P = 0.04) was found before but not after Bonferroni correction only for untransformed F_{ST} and linear geographic distance.

Geneclass2 estimated 70 individuals – about one-third of all individuals – to be first generation migrants (43 males, 27 females). The proportion of male migrants to residents (43:49) was significantly higher than for females (27:73; p < 0.01, Fisher Exact test). The majority of migrants (38) were found between only five pairs of sites (1–4, 2–5, 3–4, 3–5, 5–7), each pair with 6–10 migrants (Appendix S5, Supporting information). Two qualitative findings were reflected in the assignment tests: the five pairs with many migrants were neighbour sites and the site-pair which was connected by environmentally suitable and occupied habitat (1–2) had no migrants.

Structure analysis inferred five genetic clusters when considering all individuals, mean K5 Ln(P) = −11 218 (Fig. 3a) (t = 4.5415; d.f. = 1, P < 0.001 between K = 5 and K = 4), 3 clusters for females, mean K3 Ln(P) = −5 783 (Fig. 3b) (t = 2.72, d.f. = 1, P = 0.014 between K = 3 and K = 2) and one cluster for males, mean K1 Ln(P) = −5 658 (Fig. 3c). Hence, subdivision in the total population was explained predominately by female genetic variance, whereas males consisted of a single genetic unit in this analysis.

Dispersal and body weight

For males caught in morning, those determined by Geneclass2 to be migrants (N = 27) weighed on average significantly less than resident males (N = 35), 43.85 ± 1.70 g standard error vs. 48.40 ± 1.49 g standard error (t = 2.014, d.f. = 60, P = 0.048). There was no significant difference in morning weight between resident females (N = 46), 46.11 ± 2.50 g standard error and migrant females (N = 19) 49.54 ± 1.57 g standard error (t = 1.152, d.f. = 63, P = 0.25).

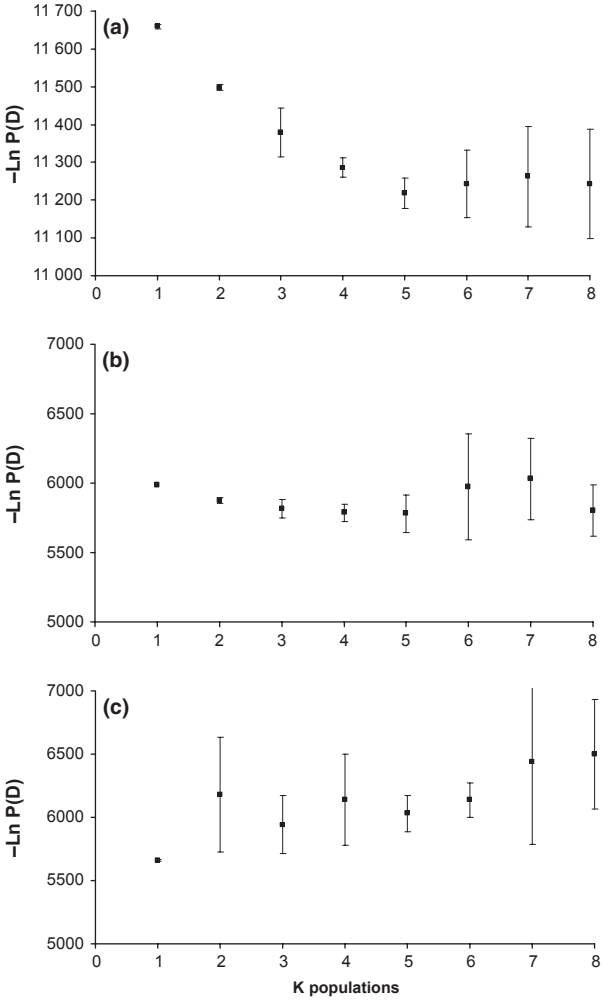

Fig. 3 Bayesian clustering analysis of striped mice sampled at seven locations in the the Goagap Nature Reserve, showing the mean and standard deviation –Log-likelihood values of 10 runs for K = 1–8 populations, (a) all individuals, (b) females only, (c) males only. Minimum values for females and males were estimated at 3–4 clusters and 1 cluster, respectively.

Discussion

We found evidence for highly male-biased dispersal as a habitat-independent trait in striped mice at a scale of up to 30 km^2 in this Succulent Karoo population using two independent analyses: individual-based analysis of fine-scale spatial structure in a continuous habitat, and population-based genetic analyses and assignment tests in a fragmented landscape. Our results further imply that body mass might be involved in male dispersal

decisions, indicating condition dependent alternative dispersal tactics.

Fine-scale genetic structure was observed in both sexes, but differed in amount and form. Female relatedness was highest at 25 m ($R \sim 0.20$), decreased continuously, reaching zero at 500 m. Maximum male relatedness was much lower ($R \sim 0.05$) and, in contrast to females, constant between 25 and 75 m, declining to zero at 100 m. Higher *SP* values for females than for males confirmed higher female spatial genetic structure. For females, $R > 0.20$ at distances up to 25 m imply that many closely related females stay in their natal groups the following breeding season and that breeding dispersal is generally restricted to neighbouring territories. For males, constant $R \sim 0.05$ between 25 and 75 m evidence that males rarely remain in the natal territory or its vicinity, while those few males that do, have a greater settling radius than females. The estimates of male relatedness lend no support for the notion that closely related males (e.g. sons or brothers) inherit territories. However, male isolation-by-distance within the riverbed population and among sample sites showed that dispersal in this sex is not completely random at this geographic scale.

Studies analysing sex-biased dispersal in small mammals have shown that population density may influence estimates of gene flow distances in social species, with the dimension of fine-scale structure in high density populations being less than in low density populations (Busch *et al.* 2009). This implies that the estimate of dispersal distance based on fine-scale structure in some instances will mirror a species' demographic situation rather than its social context (e.g. Scribner & Chesser 1993). In our study in the continuous riverbed habitat, we analysed striped mice at medium population density, which, everything being equal, indicates that the magnitude of the dispersal estimate is an average estimate. Schradin *et al.* (2010a) showed that high population density promotes group-living during the breeding season due to the lack of vacant territories which may hinder adults from dispersing. If population density affects dispersal decisions in striped mice, possibly due to territoriality, dispersal might be higher between sites that are connected by empty habitat than between sites (of equal distance) that are connected through occupied territories. Indeed, this was observed: the neighbour site-pair that was connected by suitable habitat with occupied territories had among the highest F_{ST} and the fewest first generation migrants, whereas many migrants were found between neighbour subpopulations without territories in between. This is in contrast to other studies that demonstrated that habitat characteristics can be important for fine-scale genetic structure analyses in small mammals (Peakall *et al.* 2003; Vignieri 2005). Australian bush rats (*Rattus fuscipes*), for example, do not live in complex social groups and gene flow was restricted mainly by watercourses and drainages (Peakall *et al.* 2003).

Viscous populations of social species may bias relatedness estimates and over-estimate gene coancestries within groups (Chesser 1991a; b). For striped mice, deviations from random mating was found at five out of seven sample sites and significant differentiation (F_{ST}) between subpopulations located only 3–4 km apart. Bayesian clustering analysis, on the other hand, estimated a single male genetic cluster and limited the number of female clusters to 3 (rather than 7), and assignment tests estimated that one-third of all individuals in the population analysis were first generation migrants. The assignment tests confirmed observational studies that males can easily cover distances of 1 km/day (Schradin 2006).

Although these methods of analysis produced different estimates of genetic structure, the results are not contradictory. Whereas the former analyses observed frequency distributions in pre-defined units, the latter two estimate the likelihood of genetic units. Our results show that the genetic structure in the studied area can be seen as equilibrium between female philopatry and male gene flow in what is essentially one population. Significant structure was caused by strong female philopatry in social groups and demes and, to a lesser extent, by distance between suitable habitats. The subpopulations were connected by high male gene flow. Strong philopatry in one sex may produce significantly higher inbreeding coefficients (F_{IS}) in the other, dispersing sex (males) because when individuals from different 'inbred' demes settle and mix outside the natal area, the resulting pre-mating F_{IS} will exceed zero due to the Wahlund-effect (Goudet *et al.* 2002). In contrast, females that stay in or near the natal deme will be offspring of the previous random-mating generation and thus will be more equally heterozygous, as described for the rodent *Ctenodactylus gundi* (Nutt 2008). The two-fold effects of elevated male inbreeding coefficients due to post-dispersal admixture of males from different neighbourhoods and female-related philopatry both raise the probability for inbreeding estimates deviating from random within the subpopulations. Hence, male gene diversity is influenced by deme structure based on breeding groups but differentiation among male gene lineages is alleviated due to avoidance of consanguineous mating (see Winterrowd *et al.* 2009). High female-based genetic variance suggests the potential for strong selection for female related traits such as the reproductive tactic of communal breeding or female infanticide.

Migrating males responsible for gene flow between subpopulations had less average body mass. The lower

body mass might either represent the high costs of dispersing over unoccupied territory or it might be that lighter males are more likely to choose to disperse over unoccupied territory. The best solution to disentangle between cause and consequences of body mass on dispersal would be to first measure individuals at their natal site and then recapture them after dispersal. While we could not do this, we argue that most likely migrants had lower body mass already before dispersal and not just as a result of dispersal for three reasons: (i) Males can travel more than 1.6 km a day during foraging (Schradin 2006) and probably much more if dispersing, such that dispersing over a distance of a few kilometers as done by migrants in our study would cost a maximum of 1 day lost of foraging, which alone might not explain the differences in body mass. (ii) Migrants were not trapped immediately after migration, but at a random time during the breeding season and thus most likely many weeks after the migration event, giving them enough time to regain body mass. (iii) Within our main study population, philopatric males that immigrate into neighboring groups to become breeding males (and thus do not become migrants) are of high body mass (Schradin *et al*. 2009) indicating that heavy males do not become migrants but remain resident in their natal sub-population. The interpretation that males with lower body mass are more likely to become migrants needs less assumptions and is thus more parsimonious than the interpretation that we were able to measure costs of dispersal long after the dispersal event took place. However, data proving that males with lower body mass are more likely to become migrants are so far missing.

Male striped mice follow three alternative reproductive tactics, being natally philopatric before dispersal and becoming either solitary roamers or territorial breeders afterwards (Schradin *et al*. 2009). After philopatric males reached a higher body mass and thus competitive ability during the winter with high food availability, they can disperse the following breeding season in spring. Our study indicates that males might also have three alternative dispersal tactics. First, highly competitive males (that is heavy males; Schradin 2004) might show short dispersal distances, becoming the breeding males of neighbouring groups while minimizing costs of dispersal. This can explain the degree of higher genetic relatedness between males within distances of less than 100 m. Second, less competitive males might have to disperse greater distances and become roamers in their natal sub-population. Lastly, males of even lower competitive ability might not be able to disperse into areas occupied by other territorial striped mice. These males might do the best of a bad job, leaving their sub-population to avoid territoriality, dispersing over suboptimal areas unoccupied by striped mice, until they might find another sub-population. This would be a highly costly tactic, as they have to cover habitat without food and with little shelter, increasing predation risk. As body mass is correlated with age in male striped mice (Schradin *et al*. 2009) our results indicate that migrant males might also have been younger males.

Our study demonstrated how sex-biased dispersal influences the genetic structure of a population consisting of breeding groups and of subpopulations separated by unoccupied habitat. Our results suggest that less competitive males (low body mass) can be very important for genetic structure. We thus found evidence for the three dispersal tactics (short or long distance dispersal within a sub-population or dispersal over unoccupied habitat) which might correlate with reproductive tactics as well as body mass and age. These interactions should be the focus of further research.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Description of sample sites of African striped mice, *Rhabdomys pumilio*.

Appendix S2 The 12 primers with labels and allele (bp) lengths used in the study of striped mice, *Rhabdomys pumilio*, in South Africa.

Appendix S3 Summary statistics of relatedness and autocorrelation analyses (SPAGeDI, Hardy & Vekemans 2002) of fine-scale genetic structure.

Appendix S4 Genetic differentiation (F_{ST}) calculated with Arlequin 3.5 (Excoffier *et al*. 2005) and geographic distances (Dist) in kilometres between transect sampled subpopulations of striped mice.

Appendix S5 Number of migrants among seven transects estimated by Geneclass2 (Piry et al. 2004). The location of each transect is presented in Fig. 1. f = females, m = males.

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