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Original Article

Consequences of natal philopatry for reproductive success and mate choice in an Alpine rodent

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Quantifying the interaction between dispersal, kinship, and genetic structure can provide insights into the factors that shape kin-structured mammal societies. Here, we first employ a combination of 8 years of capture–mark–recapture and molecular data to characterize the spatial and genetic relationships among female snow voles (*Chionomys nivalis*) in a population located in the Swiss Alps. Subsequently, we examine the individual-level consequences of kin structure in terms of fitness and mating patterns. Behavioral data, relatedness estimates, and spatial autocorrelation analyses indicate that females show strong philopatry, with spatially clustered females being characterized by high levels of genetic relatedness, leading to significant small-scale (<30 m) spatial genetic structure (SGS). In line with selection favoring female philopatry, dispersing females had a lower fitness compared with philopatric individuals. However, we found a negative association between female reproductive success and the number of neighboring females. This suggests that female kin clustering does not constitute an adaptive strategy in this species, but rather that site tenacity is a by-product of the costs of dispersal. Although dispersal is frequently invoked as a means to avoid inbreeding, our results provide no evidence for premating inbreeding avoidance, which is in line with previous studies on mammals. Instead, in the majority of years, we observed that pairs were more-closely related than expected by chance. However, we found that both males and females with related partners had reduced reproductive success, suggesting the existence of inbreeding depression and/or postmating inbreeding avoidance mechanisms. On the whole, our results show how quantification of SGS within populations can provide insights into individual dispersal behavior and its fitness consequences, and into the ways in which social and genetic structure interacts to shape the evolution of free-living populations.

Key words: ***Chionomys nivalis*, genetic relatedness, kinship, natal dispersal, snow vole, spatial genetic structure.**

INTRODUCTION

Natal philopatry, that is, the delayed or reduced dispersal of individuals away from their natal site, is a common phenomenon in many vertebrate species (Dobson 2013). In small mammals, the general trend is that females (whose reproductive success is assumed to be largely limited by environmental resources) tend to remain in their natal territory, whereas males (whose reproductive success is instead assumed to be largely limited by access to females) are more likely to disperse (Lawson Handley and Perrin 2007; Clutton-Brock and Lukas 2012). It is this pattern of female-biased natal philopatry (i.e., male-biased dispersal) that prompts the appearance of social groups comprising closely related females. This generates fine-scale spatial genetic structure (SGS; Peakall et al. 2003; Hazlitt et al. 2004), which may vary temporally and spatially depending on ecological conditions such as population density (Cutrera et al. 2005; Mabry 2014).

The existence of matrilineal clusters, and SGS in general, may have important fitness consequences. For example, female kin clusters can provide direct fitness benefits in the form of defense against unfamiliar conspecifics (e.g., infanticidal males) or intruders (Moses and Millar 1994; Le Galliard et al. 2006). Kin cooperation has therefore been proposed as a driving force behind the formation and maintenance of social groups in rodents ("kin cooperation" hypothesis: Lacey and Sherman 2007; Silk 2007). In addition, by remaining in the natal area, individuals may inherit a breeding site of proven quality, which constitutes an evolutionarily stable strategy when the probability of successful dispersal is low ("habitat saturation" hypothesis: Emlen 1982; reviewed in Solomon

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2003). Yet, site tenacity may also have negative consequences due to intragroup competition for resources (Hayes et al. 2009). For example, philopatric individuals of a subterranean rodent, the colonial tuco-tuco (*Ctenomys sociabilis*), rear significantly fewer young compared with dispersers, and per capita reproductive success of females is negatively related to the number of adults in a burrow (Lacey 2004). From this it follows that whether or not to disperse is expected to depend on its costs and benefits, which depend on the environment (e.g., level of competition) and how it shapes the probability of successful natal dispersal (Koenig et al. 1992; Lacey 2004; Waser et al. 2013).

Natal philopatry and the social and genetic structuring this generates may shape the mating strategies adopted by both sexes (Emlen and Oring 1977). For example, it is well known that dispersal can reduce the risk of inbreeding (i.e., mating with a relative), and hence the exposure to inbreeding depression in highly philopatric species (kin-structured populations; Pusey and Wolf 1996; Szulkin and Sheldon 2008). Although this negative association between dispersal and inbreeding probability may arise as a side effect of ecological constraints (e.g., local resource shortage, environmental harshness) favoring dispersal (as discussed above), direct selection for inbreeding avoidance may also play a role (reviewed in Szulkin et al. 2013). In this sense, previous studies on microtine rodents have shown that males disperse further if their mothers and sisters remain in their natal home range and males are able to discriminate against close relatives (Lambin 1994; Solomon and Rumbaugh 1997; Ishibashi and Saitoh 2008; Lemaître et al. 2012).

In species in which dispersal is male biased, males are able to monopolize the territories of several females (Ostfeld 1990; Solomon 2003). This results in a high probability to encounter a receptive female, and/or low search costs. Hence, males will be less likely to be limited in terms of mating opportunities, allowing them to be more selective in terms of mate choice (Härdling et al. 2008). Under these conditions, and if there is considerable variation in female quality, males could therefore be expected to bias their reproductive effort (e.g., through differential ejaculate investment) toward particular females (unmated, more compatible, or unrelated females; see Bonduriansky 2001; Reinhold et al. 2002; Parker 2006). Such male mate discrimination may be particularly common in promiscuous species, where males achieve high copulation rates and sperm depletion can limit their mating capacity (Parker and Pizzari 2010). The latter is not unlikely for arvicoline rodents, as some species have relatively small testes size (Kenagy and Trombulak 1986; Stockley and Preston 2004). For example, meadow voles *Microtus pennsylvanicus* adjust sperm allocation according to variation in the risk and intensity of sperm competition (Del Barco-Trillo and Ferkin 2004, 2006). However, although there is some evidence that male rodents may adjust their mating effort (e.g., ejaculate expenditure) in response to female reproductive value (Wedell et al. 2002), the literature on cryptic male choice is dominated by mate choice experiments on captive animals, and few studies have addressed this issue in the wild (Gowaty et al. 2003; Pizzari et al. 2004; Gillingham et al. 2009; Bergeron et al. 2011; reviewed in Kelly and Jennions 2011).

In the present study, we examine patterns of genetic structuring and their implications in terms of fitness and mate choice in an Alpine population of snow voles (*Chionomys nivalis*, Martins 1842). We do this by combining 8 years of field data on the spatial distributions of individually marked individuals with molecular data (18 microsatellite markers). First, we quantify male and female dispersal behavior, as well as the amount of SGS, and we test for a negative association between female dispersal distance and 1) population density, as predicted by the "habitat saturation" hypothesis, and 2) the degree of kinship with her female neighbors, as posited by the "kin selection" hypothesis. We then go on to test for an association between natal dispersal distance and female reproductive success, to quantify the fitness consequences of dispersal. Finally, as spatial structuring results in high relatedness among nearest neighbors, we test whether snow vole males display any evidence for premating or postmating inbreeding avoidance. Specifically, we test for the occurrence of premating inbreeding avoidance through kin-discriminative mate choice using a randomization method in which observed relatedness values are compared with to those expected under random mating. Complementarily, we test whether males adjust their reproductive investment (measured in terms of number of offspring) according to mate relatedness (postmating inbreeding avoidance) and/or whether there is inbreeding depression of mating behavior, by relating male reproductive output to parental relatedness.

MATERIALS AND METHODS

Study species and study site

The snow vole is a relatively large-sized (up to ~13 cm) rock-dwelling rodent whose distribution is mainly restricted to the mountain ranges of Southern and Eastern Europe (Pyrenees, Alps, Apennines, Carpathians) and Southwestern Asia (Nadachowski 1991; Yannic et al. 2012). Snow voles show a marked preference for rocky environments (screes, karst cliffs, limestone bedrocks), and their burrows are always located under stones. Males have large and overlapping home ranges whereas females exhibit a more territorial behavior and only share space with relatives (Luque-Larena et al. 2004; present study). Consequently, a male could monopolize the territories of several highly related females (e.g., sisters), which conform a matrilineal cluster. This pattern of spacing behavior is typical of species with a promiscuous mating system (Wolff and Sherman 2007). Indeed, most males and females mate multiply over the reproductive period, which extends from May to August. During this period, females normally produce 1 or 2 litters of 1–5 pups (Janeau and Aulagnier 1997). Because of its low fertility, this species is typically considered a *k*-strategist (Nieder and Bocchini 1993; Luque-Larena et al. 2004), which appears to be a common trait among petrophilic mammals (Mares and Lacher 1987). The average snow vole lifespan is 12–13 months, which means that most individuals do not survive the first winter (Janeau and Aulagnier 1997).

The study population of *C. nivalis* is located on the Churer Joch (Churwalden, canton of Graubünden, Switzerland; 46°48′N, 9°34′E; 2.030 m.a.s.l.). The study area consists of a west-exposed scree slope with vegetation patches composed of montane heathlands and scrub communities occurring at high altitude. The scree (~5 ha in size) is surrounded by grassland to the south and to the north, and a coniferous forest on the edge of the west side, and hence, this population is ecologically fairly isolated. More details about the study area are described in García-Navas et al. (2015).

Live trapping

For 8 consecutive years (2006–2013), snow voles have been live trapped between mid-June and early October in a standardized manner. For this purpose, the study plot is overlaid with a 10 × 10 m grid consisting of a total of 559 cells. These are divided across 4 sectors, and trapping takes place in 1 sector per night. In each cell, we set a catch-and-release Longworth trap (Penlon Ltd, Oxford, UK) filed with hay and baited with apple and peanut butter. On first capture, animals are ear-clipped (2-mm diameter, thumb type punch, Harvard Apparatus, MA) and tagged with a passive integrated transponder (mini ISO transponder 8.5 × 1.35 mm, Tierchip Dasmann, Tecklenburg, Germany) injected under the skin of the neck to allow for individual identification. Ear tissue samples are preserved in 95% ethanol + 5% Tri + EDTA (TE) buffer and stored at −20 °C until DNA extraction (see below). Trapping location, identity, weight (to the nearest gram), sex, and age (juveniles: <34 g and dark silky fur, or identified as juvenile earlier on the same year; adults: >34 g and light rough fur, or previously identified as adult) is recorded for every caught individual. Traps (100–150 per day depending on the time of the year and the part of the study plot) were set for 4 nights at approximately 20-day intervals. Traps are opened at sunset and checked around sunrise.

Molecular methods: genotyping, parentage analyses, and relatedness estimates

Genomic DNA was extracted from tissue samples using magnetic-particle technology (BioSprint 96 DNA Blood Kit, Qiagen, Limburg, The Netherlands). All individuals ($n = 1255$) were genotyped for 18 microsatellite loci using polymerase chain reaction conditions described previously (Wandeler et al. 2008; García-Navas et al. 2015). These loci are highly variable and informative and conform to the expectations of Hardy–Weinberg equilibrium (García-Navas et al. 2015). Amplification products were run on an ABI 3730 DNA Analyser (Applied Biosystems, Foster City, CA), and allele sizes were scored using GENEMAPPER 4.1 (Applied Biosystems).

We were able to assign maternity and paternity to the great majority of juveniles and adults captured for the first time using a maximum likelihood model implemented in COLONY 2.0 (Jones and Wang 2010) and a Bayesian approach to reconstruct pedigrees from microsatellite genotypes using the R package MasterBayes (Hadfield et al. 2006). Parentage analyses were performed for each year separately using a pool of candidate parents that included all adults sampled in that year and in the preceding one (with the exception of 2006, the first year of the study).

We used pairwise genetic relatedness as an estimate of the coefficient of kinship between 2 individuals (i.e., the proportion of alleles shared between them). Pairwise relatedness values (R_{xy}) were calculated using the moment estimator developed by Goodnight and Queller (1999) as implemented in the software COANCESTRY (Wang 2011). *Rxy* values range from −1 to 1; positive values indicate that individuals are more related than expected by chance; negative values indicate a lesser degree of relatedness than expected by chance. We constructed a matrix of relatedness estimates for all female–female and male–female dyads in each year (see more below). Furthermore, we analyzed the relationship between microsatellite-based pairwise estimates of parental relatedness (R_{xy}) and pedigree-based kin coefficients (k) using a linear mixed model with pairwise female–female relatedness as a response, k as the only predictor variable response. Mother identity and father identity were included as random effects to account for any interdependence between offspring of the same parents. We found that R_{xy} was positively associated with k (estimate: 0.60 ± 0.04, $n = 189$, $F = 177.36$, $P < 0.0001$; Supplementary Figure S1), indicating that this molecular estimator produced reliable estimates of kinship between individuals (shared ancestry). That is, our set of markers reliably captured genome-wide identity by state (e.g., Mainguy et al. 2009; Townsend and Jamieson 2013). In order to estimate relatedness between all pairs of individuals, even in those cases not connected through a pedigree at the beginning of the study period, we only employed molecular estimates (i.e., R_{xy} microsatellite-based estimates of parental relatedness) in subsequent analyses.

Spatial genetic structuring

We analyzed genetic autocorrelation patterns in order to characterize the SGS of the population and ascertain the possible existence of differences in spacing pattern of individuals among years. In a first step, we tested whether females exhibit a higher degree of philopatry than males and whether they are more likely to remain in the vicinity of their territory in certain years. To that end, we calculated 1) mean natal dispersal distances of males and females and 2) mean relatedness among neighboring females for each year. Natal dispersal distance was computed as the Euclidean distance between an adult home range center (calculated based on weighted-average locations) and the center of their maternal home range in the previous year (therefore, it was computed only for individuals captured for the first time as juveniles or individuals with a known mother). Mean relatedness among neighboring females was computed by averaging relatedness estimates for each focal female in relation to all adult females present within a 30-m radius. We chose 30 m as a cut-off because this distance has been reported to be the mean radius of the home range area in adult females (Luque-Larena et al. 2004; Pérez-Aranda et al. 2009). It is thought that males do not maintain territories but rather roam between several female territories (Luque-Larena et al. 2004; Bonnet T, personal observation; see also Gauffre et al. 2009). In addition, for each female we computed the average dispersal distances of their male and female siblings in order to examine the relationship between mother–daughter and brother–sister dispersal patterns. It allowed us to test if individuals of different sex exposed to the same environment (i.e., siblings sharing a territory) opt for a similar dispersal strategy.

We then performed spatial autocorrelation analyses using GenAlEx 6.5 (Peakall and Smouse 2012) to test for SGS in females. The spatial autocorrelation analysis estimates the maximum extent of the detectable nonrandom genetic structure from pairwise genetic and geographical distance matrices (see Peakall et al. 2003 for more details). A permutation procedure was applied (999 replicates) to test for significant deviations from zero, as well as bootstrap estimates for the autocorrelation coefficient (*rc*) at each of the 12 equal range (30 m) intervals. The autocorrelation coefficient, equivalent to Moran's *I* (see, e.g., Hardy et al. 2000), ranges from −1 to 1. Spatial genetic structuring was deemed significant when *rc* exceeded the permutation 95% confidence intervals (CI) around the null hypothesis ($rc = 0$) and when the boostrap 95% CI around *rc* did not exceed this value. This method is rather conservative for significance testing with small sample sizes (Peakall et al. 2003). Here, we focused on females because they are the most philopatric sex and they are thought to be the most important sex in microtine rodent demography (Sutherland et al. 2005). Spatial genetic autocorrelation analysis did not detect fine-scale genetic structure for males (analyses not shown). As we only consistently found significant results (i.e., the presence of SGS) within 30 m, we only report *rc* values for the first distance class. However, results (*rc* and *P* values) for all distance classes are provided as Supplementary Material (see Supplementary Table S1).

Fitness consequences of natal philopatry

We used the number of offspring produced per season and the number of offspring per season and per mate as individual measures of fitness. We examined whether female fitness was influenced by the following variables: natal dispersal distance (in meters), average degree of kinship (*k*) with neighboring females, number of neighboring females (number of adult females captured within a 30-m radius), number of neighboring males (number of adult males captured within a 30-m radius), relative proportion of sexually active males to fertilizable females (local operational sex ratio [OSR]) and male/s genetic similarity. We constructed a generalized mixed model with number of offspring as a response variable and the above-mentioned variables as predictors assuming a quasi-Poisson distribution. Female identity and study year were included as the random effect and fixed factor, respectively. Our initial sample size was 209 females (27 of them bred in 2 consecutive years and 5 did so in 3 consecutive years) but information on natal dispersal or relatedness was missing for several of them (as some females had unknown mothers or bred alone, i.e., without other females in the surroundings, respectively). Therefore, we constructed 2 models; one model including all explanatory variables (n = 153) and a second one excluding dispersal distance and degree of kinship in order to test the association between female fitness and the remaining variables with the complete dataset (n = 246). Lastly, in order to discard that dispersal patterns are influenced also by its impact on male reproductive success we examined the relationship between male dispersal distance and offspring production (n = 86 males). All analyses were performed using the R package *lme4* (Bates et al. 2015). Estimates are presented ± standard error.

Mate choice

In a first step, we used a Cochran–Armitage permutation test with 10 000 Monte Carlo randomizations as implemented in the R package *MCPerm* (Jiang et al. 2014) to test whether observed mating pairs had more often than expected negative (i.e., less-closely related) rather than positive estimates (i.e., more-closely related) of pairwise genetic relatedness compared with all potential non-mating pairs ("all mates" scenario sensu Szulkin et al. 2009). We considered all females present in the population in a given year as potential partners because male snow voles have large home ranges and patrol widely for prospective partners (Luque-Larena et al. 2004; Pérez-Aranda et al. 2009).

We then tested if male snow voles have more offspring when mating with more genetically dissimilar partners and/or skew their reproductive investment (number of offspring) at the expense of more genetically similar females (n = 170 breeding males). Mark–recapture analyses (not shown) revealed high among-session recapture probabilities for juveniles (81%) and goodness-of-fit tests provide no evidence for the existence of heterogeneity in trapability, indicating that most individuals present in a given year are caught at least once. Indeed, only 2 capturing sessions are required to capture 97% of juvenile individuals. Thus, we managed to identify the majority of matings and their resulting offspring.

First, we compared mean relatedness to the partner between polygamous (n = 106) versus monogamous (mated more than once with the same female; n = 64) males. We constructed a model including (mean) parental relatedness as a dependent variable, mating type (monogamous; polygamous) and study year as explanatory factors, and male identity as a random effect. In a second step, we tested in a similar way for a relationship between male fitness (per mate productivity as a response variable) and mean pairwise relatedness (averaging all relatedness values in the case of mating multiply) correcting for year and assuming a Poisson distribution. In this way, we tested if males mating with more genetically dissimilar females (in absolute terms) have higher fitness than those mating with more genetically similar partners. Third, we tested whether within the group of males that had mated with multiple females, a male had the smallest proportion of his offspring with the female he was most closely related to. Relative genetic relatedness was calculated as the female's relatedness estimate in relation to the rest of the partners of the focal male. With this procedure, for a given male, the relative sire success of a dam is negatively linked with the sire success of the other male's partners. Thus, to assess significance of relationship and avoid problems of pseudoreplication, we consistently chose the female with the highest relatedness value (i.e., the more similar partner). We included the number of offspring sired by a dam as the response variable (event) and the total number of offspring sired by their partner as a binomial denominator (trial). Explanatory variables were relative maternal relatedness and study year. Male identity and the number of mates observed for each male were fitted as a random effect and offset term, respectively. Only polygamous males that sired 3 or more juveniles were included in this analysis (n = 84).

RESULTS

Dispersal patterns and spatial genetic structuring

On average, natal dispersal distances were longer for males than for females ($F_{1,227}$ = 92.99, $P < 0.001$; Table 1, Supplementary Figure S2), but this sex difference varied across years (*study year* × *sex*: $F_{6,215}$ = 2.48, P = 0.024). Post hoc comparisons revealed that sex differences were significant in the first 5 years, but not in the last 2 years, in which female dispersal distances were larger than the average female home range size. Most females (78%) remained in their natal territory (mean distance: 24.05 ± 4.11, range: 0–171.8 m) and more than half (54%) shared space with one or more (range: 1–4) relatives ($k \geq 0.125$), whereas males dispersed 2–5 times further than females (mean: 79.89 ± 5.26, range: 5.0–401.1 m; see Table 1). Accordingly, daughters dispersed further from the maternal territory than did sons (19.72 vs. 73.35 m). Curiously, there was no congruence in dispersal patterns of male and female siblings (n = 32, r = −0.02, P = 0.91), which suggests that each sex assesses the costs and benefits of dispersing differently. No clear trend emerged when examining the relationship between mother–daughter dispersal patterns (n = 68, r = −0.03, P = 0.78); daughters did not resemble her mother' dispersal behavior.

The level of relatedness among neighboring females (mean value: 0.186 ± 0.01) decreased significantly during the period 2008–2012 (r = −0.83, P = 0.02) and increased sharply in the last year of study (Table 2; Supplementary Figure S3). Spatial autocorrelation analyses confirmed this pattern; we found that, within a 30-m radius, females were genetically more similar than expected by chance in 5 out of the 8 study years (Table 2, Supplementary Table S1). The regression slope (*rc*) was positive and significant, with the exception of 2009, 2011, and 2012, in which density was lowest (Table 2). In line with this, we observed a positive relationship between average pairwise female–female relatedness and annual abundance, leveling off when density reaches around ~8 females/ha (Figure 1).

Fitness consequences of natal philopatry

The annual number of offspring produced decreased significantly with the number of adult females in a 30-m radius (slope: −0.261 ± 0.061, t = −4.22, $P < 0.001$), whereas it increased significantly with the number of male neighbors (0.119 ± 0.024, t = 5.03, $P < 0.001$). A qualitatively similar result was obtained when considering female productivity per mate (*number of females*

Table 1

Descriptive statistics for the study population

	Year							
	2006	2007	2008	2009	2010	2011	2012	2013
Total number of individuals	215	232	158	190	159	82	99	122
Number of adults	79	80	67	57	78	40	40	47
Adult sex ratio (proportion of females)	0.38	0.43	0.43	0.53	0.46	0.53	0.55	0.38
Mean number of ♀ neighbors[a]	2.27 (0–6)	1.90 (0–4)	1.56 (0–4)	0.77 (0–2)	1.85 (0–4)	0.84 (0–2)	0.53 (0–2)	0.90 (0–2)
Mean number of ♂ neighbors[a]	5.47 (2–11)	5.34 (1–11)	4.40 (0–8)	5.57 (0–11)	3.88 (0–11)	2.73 (0–5)	2.26 (0–5)	3.86 (0–8)
♀ Natal dispersal distance (meters)	19.36	16.55	20.34	17.24	23.89	36.83	34.13	—
♂ Natal dispersal distance (meters)	100.87	70.20	60.05	96.90	113.72	66.13	51.37	—
Proportion of ♀ mating multiply (%)	62.1	54.5	68.0	81.8	39.4	54.5	72.7	64.7
Proportion of ♂ mating multiply (%)	58.0	71.4	58.3	75.0	61.5	50.0	46.1	64.7
Number of mates per ♀	1.53	1.62	1.20	2.07	1.24	1.31	1.55	1.54
Number of mates per ♂	1.70	1.73	1.51	1.89	1.34	1.32	1.45	1.54
Number of offspring per ♀	2.65	2.70	1.95	4.21	1.57	1.79	2.17	2.83
Number of offspring per ♂	4.06	3.72	2.74	4.24	2.10	1.15	1.85	3.17

Values in parentheses are the minimum and maximum value observed.
[a]Mean number of females/males captured within a 30-m radius per female.

Table 2

Statistics summarizing the observed variation in the spatial extent of female relatedness across years

Year	*N* females	♀♀ Relatedness (± SE)	*rc* (± SE)	*P*
2006	49	0.245 ± 0.029	0.240 ± 0.146	0.001
2007	46	0.160 ± 0.031	0.074 ± 0.049	0.001
2008	38	0.127 ± 0.033	0.084 ± 0.051	0.001
2009	27	0.141 ± 0.048	−0.178 ± 0.352	0.164
2010	42	0.188 ± 0.031	0.119 ± 0.055	0.001
2011	19	0.047 ± 0.053	−0.041 ± 0.043	0.843
2012	18	−0.058 ± 0.082	−0.075 ± 0.063	0.921
2013	29	0.398 ± 0.046	0.570 ± 0.213	0.001

The following information is given: total number of adult females, average pairwise relatedness among neighboring females (i.e., females present within a 30-m radius), and genetic autocorrelation coefficients (*rc*) (± error as determined by bootstrap resampling) and associated *P* values obtained from spatial autocorrelograms (0- to 30-m distance class). SE, standard error.

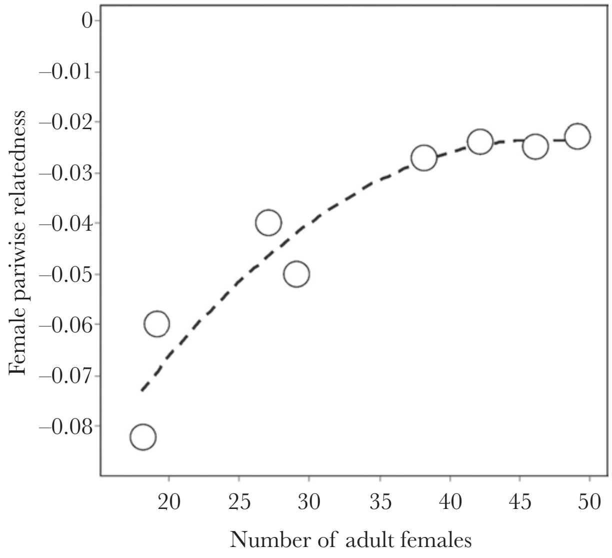

Figure 1
Annual mean degree of genetic relatedness among adult females in relation to the number of adult females present in the population.

slope: −0.17 ± 0.05, $F_{1,243} = 10.85$, $P = 0.001$; *number of males* slope: 0.32 ± 0.06, $F_{1,232} = 35.15$, $P < 0.001$). In line with the opposite effects of the number of females (negative) and the number of males (positive), we found a negative and significant relationship between female productivity and local sex ratio (relative abundance of females in a 30-m radius) (slope: 0.782 ± 0.168, $t = -4.64$, $P < 0.001$; Figure 2).

After controlling for number of neighboring females and number of neighboring males, female reproductive success tended to decreased with increasing dispersal distance (slope: −0.008 ± 0.004, $t = -1.93$, $P = 0.055$). Neither genetic relatedness with the partner/s nor degree of kinship with neighboring females had a significant influence on female productivity ($t = -1.50$, $P = 0.13$, and $t = 0.94$, $P = 0.34$, respectively).

From the male perspective, male reproductive success (measured in terms of offspring production) was not influenced by dispersal distance after correcting for interannual variability (slope: −0.002 ± 0.001, $z = -1.34$, $P = 0.18$).

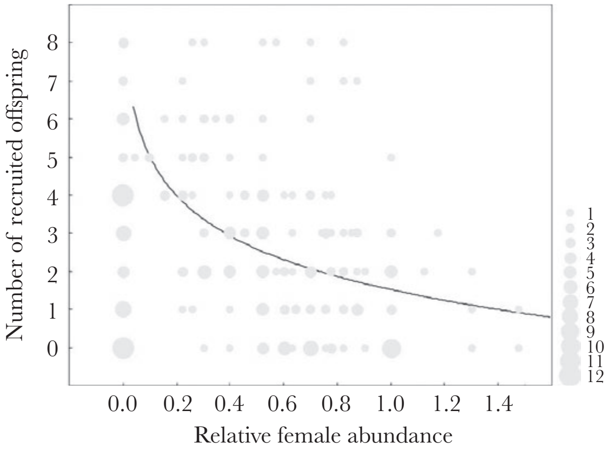

Figure 2
Female reproductive success as a function of the (log-transformed) number of neighboring females relative to the number of neighboring males (increasing values indicate a relative higher proportion of females).

Mating patterns

Averaged across years, 62.2% of the females mated with multiple males (Table 2). Females mating with only 1 male had territories with a lower density of nearby males in comparison with promiscuous females (study year $F_{7,161} = 4.08$, $P < 0.001$; mating type $F_{1,172} = 4.65$, $P = 0.03$). There was a linear relationship between the number of mates and the number of local males (i.e., within a 30-m radius) ($r = 0.28$, $n = 246$, $P < 0.001$).

Mean relatedness between partners did not differ significantly among years (mean: −0.0034, range: −0.365 to 0.453, $F_{7,372} = 0.93$, $P = 0.48$). Observed pairs were more related than expected by chance in 5 out of 8 years, whereas mean pairwise relatedness did not fall outside the simulated distribution of pairwise relatedness expected under random mating in the remaining years (2006, 2009, and 2013; Supplementary Table S1).

Among those females of which more than 1 offspring recruited into the population, those mated with a single male were less related to their mate than females that mated with multiple males (difference: -0.04 ± 0.01, $F_{1,112} = 6.48$, $P = 0.012$). Furthermore, we found a negative and significant relationship between average pairwise relatedness computed for each male and his per mate productivity ($n = 169$; estimate: -4.04 ± 0.76, $z = 5.27$, $P < 0.001$; Figure 3) after controlling for interannual variability.

The relative proportion of offspring sired by a given female (in relation to the total number of offspring sired by their partner across litters) was negatively related to the female's relative coefficient of relatedness in relation to the other partners of the focal male (estimate: -0.58 ± 0.15, $F_{1,81} = 15.09$, $P < 0.001$; Figure 4).

DISCUSSION

The selective pressures shaping dispersal strategies are generally thought to be sex specific. For example, female dispersal behavior may have mainly evolved to maximize resource availability, whereas male dispersal may have evolved to minimize inbreeding risk and maximize mating success (see Lawson Handley and Perrin 2007 and references therein). Here, we aimed at obtaining a more complete picture of the evolution of (sex-biased) dispersal and its consequences for SGS in a snow vole population, using individual-based data for an 8-year period. We first quantified male and female dispersal behavior, as well as the extent of genetic structuring, and subsequently tested for its role in shaping variation in reproductive success and mating patterns.

Dispersal and SGS

As processes other than dispersal (e.g., mating behavior) may counteract the formation of SGS (Mabry 2014), the existence of SGS does not necessarily imply strong philopatry. Hence, the combination of molecular and behavioral data is essential to comprehensively characterize the social and genetic structure of populations. For example, Matocq and Lacey (2004) reported that genetic structure was evident in a population of woodrats *Neotoma macrotis*, this despite relatively low average relatedness among neighboring females and an absence of marked female philopatry. In our study population of snow voles, we found that spatial correlation analyses characterizing fine-scale population structure were congruent with dispersal patterns inferred from mark–capture–recapture data; both approaches revealed that male snow voles disperse further than females, which is consistent with the general tendency for natal dispersal to be male biased in mammals (Pusey 1987; Dobson 2013). As a consequence of their philopatry, daughters tend to remain in their mother's territory and most females share space with relatives, resulting in the formation of matrilineal clusters. Among the factors that may have contributed to this marked SGS are those linked to the characteristically low turnover of *C. nivalis* populations (small litter size, delayed age at first reproduction, and relatively high juvenile survival; Yoccoz and Ims 1999; Allainé and Yoccoz 2003). This is in contrast to, for example, the degu, *Octodon degus*, a group-living rodent with a short lifespan and an extensive turnover of group members, and in which kin structure is absent (Quirici et al. 2011).

Although overall we found significantly positive autocorrelation coefficients within a 30-m radius, SGS was weak and not significant in 3 out of 8 years. Through its effect on dispersal behavior, some of this variation may be attributable to population density (e.g., Busch et al. 2009). Indeed, we found lower relatedness estimates

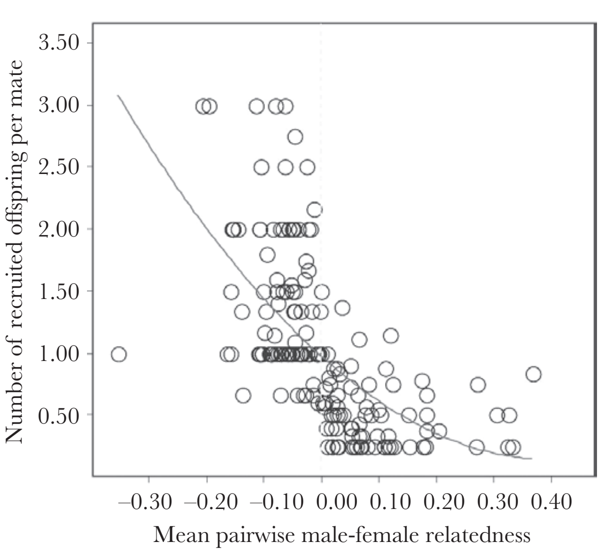

Figure 3
Relationship between mean pairwise relatedness (one value per male averaging all their partners) and male fitness.

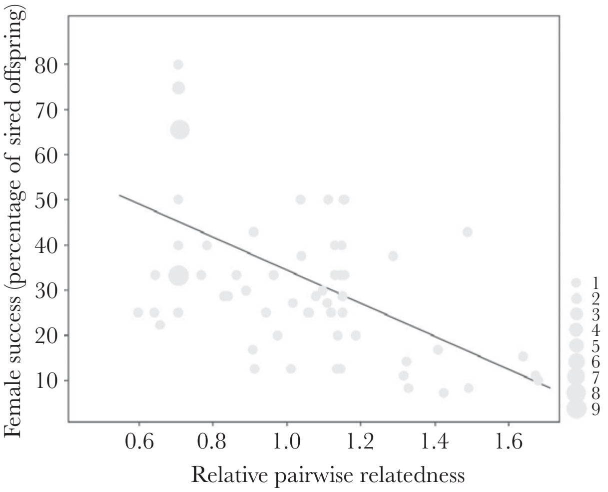

Figure 4
Percentage of offspring sired by a given female (in relation to the total number of offspring sired by their partner across litters), plotted against their relative coefficient of relatedness (in relation to the other partners of the focal male). Only one value per male (those corresponding to their more similar partner; $n = 84$, see main text) is presented.

among neighboring females and no evidence for SGS in the 3 lowest density years. This suggests that females are less prone to disperse (or less successful in settling) in high-density years (when the number of vacant territories decreases), leading to spatial clustering of related females and thereby high levels of SGS. A similar increase in proximity of female kin during high population densities has been previously observed in prairie voles *Microtus ochrogaster* (Lucia et al. 2008) and banner-tailed kangaroo rats *Dipodomys spectabilis* (Meshriy et al. 2011). Together with these studies, our study thus presents support for the habitat saturation hypothesis, which posits that a lack of suitable territories at high population densities is a primary ecological constraint on dispersal (Emlen 1982). Following this reasoning, it has been suggested that the pressure to disperse may underlie social interactions in solitary rodents (McEachern et al. 2007; Meshriy et al. 2011) and that changing environmental and demographic circumstances may sometimes favor kin clustering as an epiphenomenon of delayed dispersal (see more below). Thus, our study system, subject to erratic fluctuations in population size and unpredictable environmental conditions, meets the requirements for this process to occur.

Fitness consequences of natal philopatry

By remaining in their natal area, an individual may gain (direct) fitness benefits through social interactions with kin (e.g., defending resources or repelling intruders; Silk 2007; Armitage et al. 2011; Hoogland 2013). In this sense, there is evidence that in some vole species, relatives are more tolerant of each other's offspring, and thereby, the risk of infanticide may be lower within kin clusters (Lambin and Yoccoz 1998). Furthermore, group living can improve reproductive success by reducing the rearing costs to females. For example, a previous study on Townsend's voles *Microtus townsendii* reported that individuals with home ranges that neighbored those of kin produced more offspring than individuals with ranges neighboring non-kin (Lambin and Krebs 1993). However, we did not observe significant differences in terms of produced offspring between females that shared spaces with relatives and those that did not. Furthermore, we found a negative relationship between female reproductive success and the number of neighboring females (cluster size).

Although sharing space with (related or unrelated) conspecifics does not appear to confer fitness benefits, philopatry may nevertheless evolve if ecological factors make successful dispersal so unlikely that the fitness benefits of remaining in the natal area outweigh those of dispersing (facultative philopatry sensu Solomon 2003, see also Waser et al. 2013). Indeed, we found a negative relationship between female reproductive success and dispersal distance. This is in agreement with the notion that female philopatry may constitute the "best of a bad job," particularly in species with a preference for harsh environments where access to food resources is demanding (e.g., rock-dwelling mammals: Nutt 2005; Nutt 2007; Galende and Raffaele 2013). For example, the habitat preferred by *C. nivalis* is characterized by rocky areas dotted with scattered vegetation patches, the latter constituting a key food resource for this species (Luque-Larena et al. 2002, 2004). By remaining in her natal area, a female is more likely to inherit a good territory and avoid the costs of seeking a suitable (and available) breeding site.

In addition to any direct fitness benefits, individual-level dispersal behavior might be also shaped by indirect fitness benefits through kin selection. Although worthy of further investigation, its quantification is beyond the scope of this manuscript.

Mate choice

The dichotomy of "discriminating females" and "indiscriminate males" has come to dominate the literature on sex roles in mate choice, particularly in mammals (Clutton-Brock 2007). As a consequence, the evolutionary significance of male mate choice has been largely neglected. However, recent studies have shown that males can be choosy too (reviewed in Edward and Chapman 2011), and it is now recognized that male mate discrimination can evolve under a wide range of circumstances (low effort required to find mates, limited ability to produce sperm, high variance in female quality) and that males may adjust their mating effort in response to female quality (e.g., Gillingham et al. 2009). In this vein, theoretical models predict that in those species in which males can encounter several mating opportunities in a narrow spatiotemporal window (i.e., almost simultaneously), selection may favor male mate choice.

Males in our study population find all of their partners in a small space (mean distance among females for a given male: 46.3 m); that is, most males mate with females belonging to the same cluster. After controlling for year effects, males paired with genetically more dissimilar partners had more descendants compared with males paired to genetically similar partners. This may be the result offspring born to closely related parents showing reduced survival due to inbreeding depression (i.e., genetic effects of elevated homozygosity; Keller and Waller 2002; see below), but it may also be the result of males increasing their mating effort (e.g., by transferring more sperm or copulating longer) when mating with unrelated mates. In line with the second option (postmating investment), we found that monogamous males (those that had several offspring with a single female) were less related to their partners than those that had offspring with multiple females. Also, we found that among those males that had offspring with multiple females, a male sired proportionately fewer offspring with the female to which he was most closely related. Therefore, although the exact mechanisms driving fertilization success remain elusive, our results are compatible with the idea that males may strategically adjust their mating effort according to mate relatedness.

Alternatively, males mating with more related females may exhibit a lower reproductive success compared with those mating with more dissimilar partners if inbred offspring have reduced survival probability. Indeed, inbreeding depression is among the main determinants of whether we expect males to differentially invest mating effort in less-closely related females (as discussed above). Furthermore, it should be noted that we may underestimate the reproductive success of genetically dissimilar partners, as they will on average have more heterozygous offspring (Supplementary Figure S4), and heterozygous individuals may be more likely to disperse beyond the boundaries of our study site (García-Navas et al. 2015).

Unfortunately, in this study system (and most natural vertebrate populations for that matter), it is quite challenging to observe copulations or to obtain an estimate of litter size before survival selection has acted. Hence, it is currently impossible to infer the relative roles of inbreeding depression and postmating parental investment in shaping the observed association between parental relatedness and offspring number. Nevertheless, it is interesting to note that we found no evidence for inbreeding avoidance through premating mate choice, and in general, inbreeding avoidance through active mate choice remains poorly supported by empirical studies on wild populations (see Szulkin et al. 2013 and references therein). As matter of fact, we found mating pairs to be more related than expected under random mating in 5 out of 8 years, and if they exist, postmating strategies could counteract any negative effects of inbreeding. Indeed, opposite patterns of premating and postcopulatory mate choice with respect to relatedness has have previously been reported in less-mobile passerines (Foerster et al. 2006; Brekke et al. 2011). A likely explanation for this strategy is that under certain circumstances (e.g., limited availability of unrelated mates or limited dispersal), postcopulatory mechanisms might be much less costly than precopulatory choosiness (Olson et al. 2012). In this sense, there is growing evidence in rodents and other taxa that postmating processes could lessen any genetic effects of mating with relatives, which in turn, could render premating inbreeding avoidance in many cases unnecessary and thus, difficult to detect (Firman and Simmons 2008; While et al. 2014; Peretti and Aisenberg 2015).

CONCLUSIONS

We have shown that this population is characterized by significant local genetic structure in females, suggesting that also in the absence of sociality, the spatial distribution and movement of individuals can significantly shape a population's genetic structure. We argue that philopatry in female snow voles is the result of their dependence on patchily distributed resources and their harsh environment (Luque-Larena et al. 2004), and dispersal is hence potentially costly. Thereby these findings support the view that fine-scale kin clustering in females has arisen as a by-product of selection acting against dispersal. The latter is in line with a lack of evidence for precopulatory inbreeding avoidance in this species. Instead, we have some evidence for cryptic mate choice strategies (e.g., Fitzpatrick et al. 2014). It suggests that at the precopulatory stage individuals may tolerate inbreeding as the costs of developing inbreeding avoidance may be high due to limited natal dispersal and/or the existence of postmating mechanisms may impede strong selection for premating inbreeding avoidance. On the whole, our study thereby shows that no single factor can account for the evolution of dispersal behavior in present-day populations, highlighting the importance of taking a comprehensive approach when studying the causes and consequences of natal philopatry.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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