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Original Article

Sex-biased juvenile dispersal is adaptive but does not create genetic structure in island lizards

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Dispersal is a potentially risky behavior that has several important implications for demography. Dispersal may be measured directly through behavioral observations or indirectly using genetic analyses. The direct approach is accurate but labor-intensive, whereas the indirect approach depends on population subdivision to infer dispersal events. Here, we combine field studies of behavior and natural selection in an island lizard (*Anolis sagrei*) to provide direct estimates of sex-specific dispersal and then compare these estimates to measures of population subdivision at both nuclear (biparental inheritance) and mitochondrial (uniparental inheritance) genetic markers. Juvenile males dispersed 4 times further than juvenile females. Natural selection acted against long-distance dispersal in females, but we measured no such selection on dispersal distance in males. Despite strong evidence for sex-biased dispersal accompanied by selection, we detected no population genetic signature of dispersal at either nuclear or mitochondrial loci. In closed populations, such as those occurring on small islands, repeated dispersal events may have important demographic consequences and yet produce no population genetic signature owing to continuous admixture of genotypes.

Key words: **dispersal, island, lizard, selection, sex bias.**

INTRODUCTION

Dispersal, the movement away from one's natal site, is an important life-history trait. Dispersal influences a variety of ecological and evolutionary processes that can have cascading effects on populations (Janzen 1967; Holbrook et al. 2002; Glor et al. 2005; Cote et al. 2010). Examples of the factors influenced by dispersal include predator–prey dynamics (Clobert et al. 2000), competition for resources (Le Galliard et al. 2005), the search for mates (Doligez et al. 1999), and the possible costs associated with kin-based competition and mating (Cote and Clobert 2010). Moreover, dispersal may establish local variation in population density, which in turn influences many types of social interactions among individuals (Sinervo and Clobert 2003; Le Galliard et al. 2005; Sinervo et al. 2006; Sinervo et al. 2010).

Dispersal is a potentially adaptive behavior because, by moving away from natal sites, individuals are more likely to reduce their chances of inbreeding (Pfenninger et al. 1996; Boinski et al. 2005). Dispersal may also result in acquisition of a higher quality territory (Bensch and Hasselquist 1991), increased access to potential mates (Doligez et al. 1999), and reduced competition or predation risk (Boinski et al. 2005). Although dispersal provides many benefits, it is also known to be a potentially costly behavior (Cote and Clobert 2010; Schoepf and Schradin 2012). The risks associated with dispersal include the possibility of moving from a high to low quality environment (Gill and Stutchbury 2010), the energetic costs of movement, and increased exposure to predation during movement (Cote et al. 2013). Both the risks and rewards of dispersal imply that the behavior should have consequences that are measurable in terms of natural selection (Leturque and Rousset 2002; Bonte and Lens 2007; Calsbeek 2009). Indeed, interactions between dispersal and natural selection have well-established ties to the dynamics of populations, including important roles in the persistence of populations and in the action of frequency-dependent social interactions (McPeek and Holt 1992; Sinervo et al. 2006). Moreover, if the costs and benefits of dispersal equilibrate differently between males and females, then sex biases in patterns of dispersal are predicted to evolve (Urquhart et al. 2009).

Documenting the influence of dispersal on evolutionary processes, such as local adaptation (Corn 1971) and speciation (Turelli et al. 2001), depends on the ability to measure changes in allele frequencies that arise due to dispersal. Whether or not these changes occur, and can be documented, may depend on the spatial and

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temporal scales over which dispersal is measured (Janzen 1967; Hertz et al. 1993; Leturque and Rousset 2002; Singhal and Moritz 2012). Historically, studies of dispersal have relied on direct estimates of dispersal, that is, capture-mark-recapture measures of how far individual organisms move across a landscape. The direct approach is extremely powerful, since observing marked individuals provides precise estimates of movement from one location to another and can reveal differences among groups (e.g., sex or morphotype) in patterns of movement. However, the feasibility of observing dispersal is limited, especially in open populations (e.g., marine organisms with planktonic larval stages; Palumbi and Kessing 1991; Palumbi 1996; Mitchell et al. 2013) or in taxa for which marking large numbers of individuals is prohibitively expensive. Moreover, direct studies of dispersal cannot provide quantitative insights into the population genetic impacts of individual movements.

In this study, we combine mark-recapture estimates of dispersal with measures of resultant natural selection and population genetic structure to determine the evolutionary implications of dispersal in an island population of lizards. Although dispersal is well represented in the scientific literature, relatively few studies have examined how natural selection acts on dispersal behaviors (Leturque and Rousset 2002; Bonte and Lens 2007; Calsbeek 2009) or how such selection may differ between the sexes (Calsbeek 2009). In this study, we first assess the demographic effects of dispersal by testing for sex biases in juvenile dispersal prior to establishment of adult home ranges. Next, we test the adaptive significance of sex-biased juvenile dispersal by examining the survival of breeding adults as a function of juvenile dispersal. Finally, we test whether sex-biased dispersal has resulted in population-level genetic structure at mitochondrial and nuclear loci. Specifically, we test the hypothesis that the observed pattern of male dispersal and female philopatry, which is common in mammals (Schoepf and Schradin 2012) and routinely observed in reptiles (Gill and Stutchbury 2010) including anoles (Johansson et al. 2008; Calsbeek 2009), should leave a signal of greater population substructuring at mitochondrial loci, which are maternally inherited, compared to nuclear loci, which are biparentally inherited.

METHODS

Study system

The brown anole, *Anolis sagrei*, is a small, semiarboreal lizard that has a broad tropical and subtropical distribution. In our primary study population on Kidd Cay, a small (120m by 60m; ~1600 m^2 total vegetated area) island situated 80 m offshore and adjacent to the town of Georgetown, Great Exuma, The Bahamas (23°31′ N 75°49.5′ W), both males and females defend small home ranges that often overlap with the home ranges of several other individuals. Lizards in this population usually begin breeding in March. Females lay 1 or 2 eggs at approximately 10-day intervals throughout the breeding season, which typically ends by September (Calsbeek et al. 2007). Hatchlings emerge approximately 50 days after eggs are laid and receive no parental care. Most individuals (>85%) in this population mature and die in a single year and the bulk of mortality occurs during the summer months (May–October; Calsbeek and Smith 2007).

We captured gravid females from Kidd Cay in May of 2009 (N = 59) and 2010 (N = 81) and housed them under standard conditions in the laboratory (see Cox and Calsbeek 2010b for details). Briefly, gravid females were housed individually in 10-gal glass terraria placed under a 40-W incandescent bulb in a reflective hood for heat (diurnal temperature range = 26–35 °C) and 2 Repti Glo 5.0 full-spectrum fluorescent bulbs for ultraviolet radiation (5% UVB; Hagen, Montreal, Canada). We allowed females to lay their eggs in potted plants within their cages and left the eggs undisturbed until hatching. We fed all animals an ad libitum diet of fruit flies (*Drosophila* for hatchlings) and crickets (*Acheta* for juveniles and adults). Food was dusted weekly with vitamin and mineral supplements (Repta-Vitamin, Fluker Farms, Port Allen, LA).

We identified the sex of each hatchling on the basis of enlarged postanal scales (present only in males) and dorsal color pattern (females express a dorsal pattern polymorphism that is absent in males; Calsbeek et al. 2010). These sexing methods have proven completely accurate over 6 years of captive breeding involving thousands of individual hatchlings (Calsbeek and Bonneaud 2008; Cox and Calsbeek 2010a). Hatchlings were weighed (g) and measured (Snout-Vent-Length [SVL], mm) immediately upon hatching and then shipped back to The Bahamas and released within 3 weeks of their hatch date. Immediately prior to release, we measured each individual a second time and permanently marked each hatchling with a unique toe-clip. Hatchlings were randomized with respect to maternal ID and were released in groups of 10–13 individuals per each of 10 specific locations on the island from which gravid females had been captured the previous spring. To minimize the time spent in the laboratory, we released hatchlings in 3 sequential groups (August, September, and October) per year. We released 237 and 290 juvenile lizards during 2009 and 2010, respectively.

We recaptured surviving progeny during May of 2010 and 2011 and recorded the compass bearing and distance moved from their release site. Distance was measured to within 0.01 m using a geosystems laser distance gauge (Leica model 776149). Animals were weighed (g) and measured (SVL, mm), marked with a small spot of white paint to prevent recapture, and were immediately released to their capture location. We repeated this process in September of each year and in May of the following year to assess viability selection following dispersal. We quantified viability selection by regressing relative survival (0 or 1 divided by mean survival) on dispersal distances standardized to the population mean in unit variance (Arnold and Wade 1984). We calculated relative survival and standardized trait values separately for each sex. We calculated directional selection gradients from the partial regression coefficients of ordinary least squared regressions on dispersal distance, including both sex and year as factors. We also included condition at release (estimated as the residuals from a regression of log-mass vs. log-SVL) in these analyses to account for subtle differences in growth during the few weeks that animals spent in the laboratory prior to release. We measured selection over the period from our initial recapture census in May through to the following fall. For this analysis, we pooled data from both years of our study because sample sizes of individuals that survived long enough to record both dispersal (total N = 34 males and 49 females) and selection following dispersal (total N = 22 males and 16 females) were small within each year. We assessed statistical significance ($P < 0.05$) using a generalized linear model (GLM) with a logit link function to account for the binomial distribution of survival (Janzen and Stern 1998). We inferred sex differences in selection from significant Sex × Trait interactions in these analyses.

DNA extraction

We haphazardly selected 96 of our post-dispersal adult study animals for genetic analysis and obtained a thin slice of tissue from tail samples using a sterile scalpel. Tissues were placed in 200-μL strip tubes with 150 μL of 5% Chelex (Bio-Rad, Inc.) in purified water and 1.0 μL of Proteinase-K (20 mg/mL). We extracted whole genomic DNA by incubating samples for 180 min at 55 °C followed by a denaturation step of 10 min at 99 °C using a DNA Engine Thermal Cycler (Bio-Rad). Samples were then centrifuged for 15 min at 3000 rpm and 30 L of the supernatant was collected and stored at −20 °C until amplification by PCR.

Amplification of microsatellite loci

Each individual dam and sire was genotyped at 6 microsatellite loci: AAAG-70, AAAG-68, AAAG-91, AAGG-38, AAAG-77, and AAAG-94 (Bardelbeden et al. 2004). We performed PCR in 10 μL reaction volumes comprised of 1 μL Chelex supernatant, 1× PCR Buffer (Invitrogen), 1.5 mM $MgCl_2$, 0.4 mM dNTPs, 0.25 M of each primer (forward and reverse), and 0.3 U of Taq polymerase (Invitrogen). PCR cycles consisted of an initial denaturation step at 94 °C for 5 min followed by 29 or 35 cycles of 45 s at 94 °C, 1 min at primer-specific annealing temperatures, and 1 min at 72 °C, followed by a final extension for 5 min at 72 °C (see Cox et al. 2011 for PCR conditions).

Genotyping and microsatellite analysis

Loci were pooled into 2 groups for analysis on an ABI 3730 Genetic Analyzer (Applied Biosystems) using fluorescent dye-labeled primers (see Cox et al. 2011 for pooling protocols). All genotypes were scored by visual inspection of electropherogram traces using GeneMapper 3.7 software (Applied Biosystems) against a GeneScan 500 LIZ size standard (Applied Biosystems). Prior to analysis, we verified that loci were in Hardy–Weinberg equilibrium and were not subject to linkage disequilibrium using Arlequin (Gunderson and Leal 2012).

Amplification and sequencing of mitochondrial DNA

A 673 bp section of the mitochondrial gene cytochrome *b* was sequenced for the same 96 individuals described above for microsatellite analyses, using previously designed primers (Thorpe and Stenson 2003). PCR was conducted in 25 μL volumes consisting of: 5 L Chelex template DNA, 1× PCR Buffer (Invitrogen), 2.5 mM MgCl2, 0.4 mM dNTPs, 0.5 mM of each primer (Mt-A and Mt-F; Thorpe and Stenson 2003), and 1 U of Taq polymerase (Invitrogen). PCR conditions were adapted from Thorpe and Stenson (2003) and consisted of an initial denaturation step at 94 °C for 3 min followed by 5 cycles of 30 s at 94 °C, 1 min at 45 °C and 1 min at 72 °C, which was followed by 30 cycles with the annealing temperature increasing to 51 °C, followed by a final extension for 5 min at 72 °C. Diffinity RapidTips (Sigma) were used to purify PCR products before samples were sent to the Dartmouth College sequencing core facility, where Big-Dye terminator (Applied Biosystems) cycle sequencing reactions were performed and the products analyzed on an ABI 3730 automatic sequencer (according to manufacturer's protocol; Applied Biosystems). Purified PCR products were diluted to 100 ng total DNA template and sequenced in both directions using the PCR primers, Mt-A and Mt-F at 3.2 pM (Thorpe and Stenson 2003).

Mitochondrial DNA analysis

We edited forward and reverse sequences by eye using Sequencher 4.7 software (Gene Codes). We used the online FASTA sequence toolbox FaBox 1.40 (Villesen 2007) to trim all sequences to the length of the shortest sequence and we used FaBox (Villesen 2007) to visualize variation among the distinct haplotypes identified by Arlequin.

Genetic analyses of spatial structure

We used Structure 2.3.2 (Pritchard et al. 2000; Schrag 2012) to determine whether there was any genetic structure present on our study island. We tested for a range of possible population subdivisions (K values ranging 1–5, where K indicates the number of genetic demes that best describes the genetic variation within a population) using a burn-in period of 10 000 iterations of the default Markov Chain Monte Carlo model. We did not include any a priori population delimiters since the distribution of individuals on the islands is approximately continuous.

Bootstrap simulations of spatial structure

Direct measures of dispersal revealed a strong male bias in dispersal distances (see Results). Given this pattern of male dispersal and female philopatry, we predicted that mitochondrial loci would exhibit spatial structure in adult females, but not males (because juvenile dispersal by males should produce an admixture of mitochondrial haplotypes across the island), and that nuclear loci would show no structure in either sex (since dispersal by males would homogenize variation in both sexes). However, initial spatial analyses of genetic data (from post-dispersal adults) revealed the opposite pattern; males appeared more likely than females to share mitochondrial haplotypes with their nearest same-sex neighbors (see Results). Given this unexpected result, we used a randomization procedure to further test the probability that such a pattern would arise by chance.

We used mapping coordinates from our field measures of dispersal to generate XY coordinates for each individual in our study. Using these XY coordinates, we calculated nearest neighbor distances and recorded haplotype values for each nearest neighbor of the same and opposite sex. To randomize the spatial arrangement of the haplotypes carried by male and female lizards from our data set, we sampled without replacement from these data and assigned each individual's haplotype to a randomly selected pair of XY coordinates. We then compared each individual to its nearest same-sex and opposite-sex neighbor and recorded the frequency of like versus un-like haplotypes between these pairs. We repeated this process 1000 times to generate a frequency distribution of nearest neighbors with like-haplotypes. We performed this bootstrap procedure for comparisons of males and their nearest male neighbors and for females with their nearest female neighbors. Bootstraps were carried out in R (R Development Core Team).

RESULTS

Of the 237 and 290 progeny released as hatchlings during 2009 and 2010, respectively, 52 (21.9%) and 31 (10.7%) survived to the subsequent spring census, which permitted us to measure dispersal on this subset of juveniles. Of these dispersing individuals, 20 (38%) and 13 (42%) individuals from the 2009 and 2010 cohorts, respectively, survived to the end of their respective breeding seasons and were recaptured during our fall censuses.

Juvenile growth, measured from initial release to recapture in May, differed by sex and also between years. In both years of our study, males grew significantly more than females in snout-vent length (analysis of covariance [ANCOVA] sex: $F_{1,67} = 65.06$, $P < 0.0001$; effect of SVL at release: $F = 10.29$, $P = 0.002$; year: $F = 18.58$, $P < 0.0001$) and body mass (ANCOVA sex: $F_{1,57} = 43.13$, $P < 0.0001$; effect of mass at release: $F = 2.03$, $P = 0.16$; year: $F = 14.65$, $P = 0.0003$). Degrees of freedom differ for analyses of mass and SVL because we did not record mass for 10 individuals following recapture. Year effects reflect the fact that growth was greater in the 2009 cohort, as was the magnitude of the difference in growth between males and females (Figure 1). This resulted in significant Year × Sex interactions for growth in SVL ($F_{1,66} = 10.57$, $P = 0.002$) and mass ($F_{1,56} = 11.37$, $P = 0.001$).

Dispersal distances also differed by sex and the pattern was qualitatively the same in both years (Figure 1). Males dispersed further than females in 2009 (median dispersal distance = 16.5 and 4.7 m for males and females, respectively; Anova on log-transformed values: $F_{1,41} = 23.38$, $P < 0.0001$) and 2010 (median dispersal distance = 10 and 5.3 m for males and females, respectively; Anova: $F_{1,28} = 4.68$, $P < 0.04$). When we pooled results from both years, the sex bias in dispersal was highly significant (Anova effect of sex: $F_{1,71} = 23.75$, $P < 0.0001$; sex year: $P = 0.07$).

Dispersal distances were influenced by interactions between sex and hatch date and between hatch date and body condition at release. Early-hatching females tended toward philopatry, while later-hatched females exhibited greater dispersal distances, whereas the opposite was true of males (ANCOVA Sex × Hatch date: $F_{1,56} = 8.08$, $P = 0.007$), although in all cases males still dispersed greater distances than females. In addition, individuals that hatched early and in good condition tended to disperse, whereas individuals that hatched later and in good condition tended to remain philopatric (and vice versa) and this was true for both males and females (ANCOVA Body condition × Hatch date: $F_{1,56} = 4.04$, $P = 0.05$).

Dispersal was risky for females, such that philopatric female lizards were more likely to survive over the subsequent breeding season. Though sample sizes were small owing to the time frame needed to measure dispersal and subsequent survival, we report standardized selection gradients here for completeness. However, we do so with the caveat that regression coefficients have large associated standard errors (SEs) and should be interpreted cautiously. We measured directional selection for reduced dispersal distances in females ($\beta = -0.08 \pm 0.06$; $\chi^2 = 6.66$; $P = 0.009$; effect of year: $\chi^2 = 10.16$, $P = 0.001$) but not males ($\beta = -0.02 \pm 0.09$; $\chi^2 = 0.04$; $P = 0.83$; effect of year: $\chi^2 = 5.60$, $P = 0.02$) over the period from the initial spring census to our recapture census the following fall. These GLMs included year as a factor and body condition as a covariate. Results were similar (though nonsignificant) when we pooled males and females in a single analysis (GLM: $= -1.08 \pm 0.87$, $\chi^2 = 1.92$, $P = 0.16$) and there was no difference in the slope of this relationship between the sexes (GLM sex dispersal: $\chi^2 = 0.77$, $P = 0.38$, Table 1).

Population genetics

Of our original 96 samples, we obtained high quality genotypes from 79 individuals at 6 microsatellite loci, yielding an average of 8 alleles per locus (48 total alleles) and no null alleles. All loci were in Hardy–Weinberg equilibrium and were considered suitable for further population-level analyses (Table 2). We also identified 6 distinct cytochrome *b* haplotypes within the population using Arlequin (Table 3 and Figure 2). Microsatellite analysis using STRUCTURE

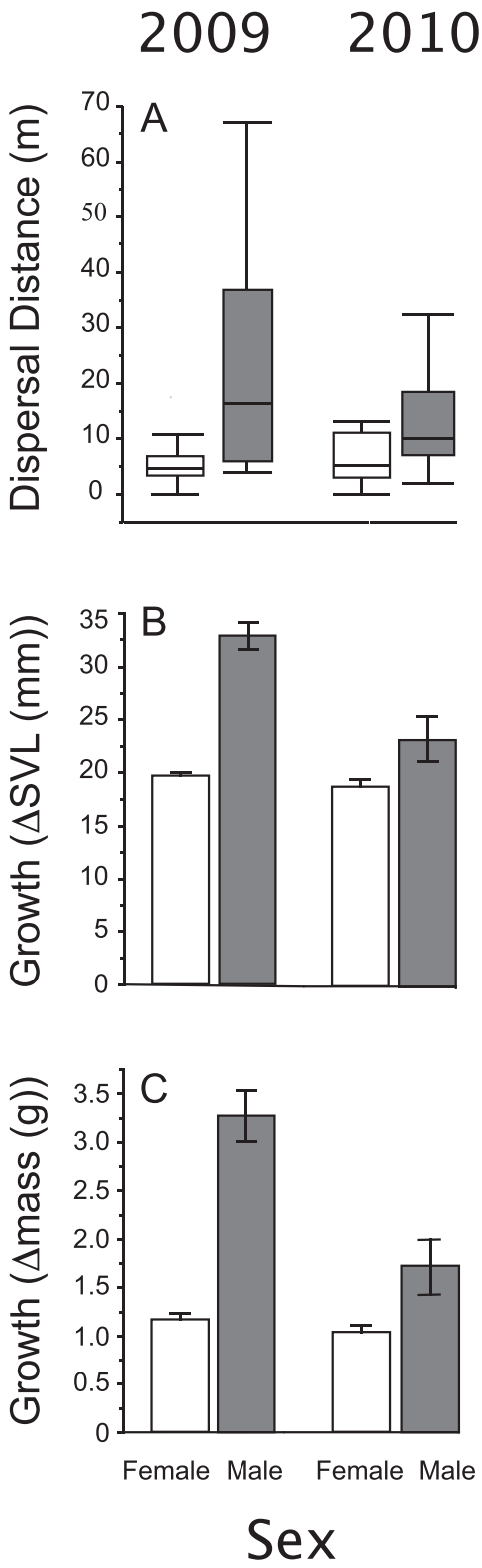

Figure 1
Sex differences in (A) dispersal distance, (B) growth in snout-vent length, and (C) growth in mass during 2010 and 2011. Box and whisker plots in panel A show median dispersal values within each box. Box heights span the 25th and 75th quantiles and whiskers show data ranges. Data in panels B and C are means ± standard error of the mean. Males dispersed further and grew more (both in terms of changes in length and body mass) than females in both years of our study.

Table 1

Viability selection using survival as the dependent variable (live/die) revealed directional selection favoring lower dispersal distance in both males and females

	df		SE	χ^2	*P* value
Males					
Dispersal distance	1	−0.02	0.09	0.04	0.83
Year	1	**−0.23**	**0.09**	**5.60**	**0.02**
Condition at release	1	−0.02	0.09	0.04	0.83
Females					
Dispersal distance	1	**−0.08**	**0.06**	**6.66**	**0.009**
Year	1	**0.12**	**0.06**	**10.16**	**0.001**
Condition at release	1	−0.08	0.08	0.99	0.32
Both sexes pooled					
Dispersal distance	1	−1.08	0.87	1.92	0.16
Sex	**1**	**−3.24**	**0.86**	**13.00**	**0.0003**
Year	1	−0.57	0.91	0.26	0.61
Condition at release	1	−0.77	1.08	0.52	0.47
Sex dispersal	1	−0.46	0.86	0.77	0.38

We included sex (in the pooled model) and year as factors in the models and condition at release as a trait in the model. Model significance was determined using a GLM with a logit link function to account for the bivariate dependent variable. Bold denotes significance. df, degree of freedom.

Table 2

Summary of microsatellite data for individuals used in this study (*N* = 79)

Locus	# Gene copies	# Alleles	H_O	H_E	Allelic range	G-W statistic
AAAG-68	158	10	0.69	0.81	36	0.27
AAAG-70	158	8	0.79	0.79	25	0.31
AAAG-91	158	8	0.83	0.83	28	0.26
AAGG-38	158	10	0.73	0.79	40	0.24
AAAG-94	158	6	0.49	0.53	24	0.24
AAAG-77	156	6	0.81	0.78	24	0.24
Mean	157.6	8	0.73	0.76	29.5	0.26
SD	0.82	1.8	0.12	0.11	6.86	0.02

Observed and Expected heterozygosities are abbreviated H_O and H_E, respectively. We used the Garza-Williams (G-W) statistic to test whether heterozygosity at each locus was outside its expected range. Locus names are from Bardelbeden et al. (2004). SD, standard deviation.

Table 3

Relative frequencies of cytochrome *b* haplotypes as a function of sex

Haplotype	Females (*N* = 33)	Males (*N* = 46)
1	0.61	0.87
2	0.12	0.07
3	0.18	0.02
4	0.06	0.02
5	0	0.02
6	0.03	0

revealed no measurable population genetic structure in nuclear loci on the island (Figure 3).

We tested for population genetic structure in mitochondrial haplotypes using a GLM with a log link function to account for the highly skewed distribution of haplotypes. Contrary to our a priori expectations, this analysis suggested that males were more likely than females to share mitochondrial haplotypes with their nearest same-sex neighbors (GLM: $\chi^2 = 5.76$, $P = 0.01$). In other words, despite male dispersal and female philopatry, we found no evidence for spatial structure at mitochondrial loci in females but an apparent tendency for males to have mitochondrial haplotypes in common with their nearest male neighbors. However, our more conservative randomization protocol revealed that this pattern was likely an artifact of the distribution of haplotype diversity on the island. Bootstrapping the data set with randomized spatial variation revealed that nearest male neighbors were likely to share common haplotypes simply by chance ($P = 0.33$), presumably owing to the rarity of most mitochondrial haplotypes in the population. Similarly, females remained genetically unstructured in the population ($P = 0.55$). In summary, neither nuclear nor mitochondrial genetic variation showed consistent evidence of genetic structure within the population despite the relatively high degree of standing genetic variation for a small, closed population.

DISCUSSION

Despite the importance of dispersal in a variety of ecological and evolutionary processes, the spatial and temporal scales over which each of these processes is relevant remains poorly understood (Janzen 1967; Hertz et al. 1993; Bonte and Lens 2007; Singhal and Moritz 2012). We have shown that juvenile *Anolis sagrei* lizards exhibit male-biased dispersal and, by contrast, female philopatry. This pattern is very similar to the one previously demonstrated in adult lizards from the same study island (Calsbeek 2009). In that study, adult male lizards moved significantly further compared to females over the course of the breeding season, though once they had settled on territories, neither males nor females moved more than a few meters over the course of the 4-month long study. Thus, it appears that patterns of sex-biased dispersal remain fairly consistent throughout the lifespan of these lizards.

Although patterns of sex-biased dispersal appear to remain relatively consistent between juveniles and adults, patterns of natural selection acting on dispersal were different in this study compared to the earlier study on adults (Calsbeek 2009). Natural selection acting on adult dispersal favored long-distance dispersal by larger male lizards and selected against dispersal in adult females. By contrast, selection acting on juveniles acted against dispersal in females and was not significant in males. This difference may arise in part because juveniles have much lower survival than do adults. Indeed, juvenile males that survived through the dispersal phase dispersed further when they were in better condition, raising the possibility that selection culled males and females that attempted to disperse despite having poor body condition.

Taken together, the patterns of dispersal combined with natural selection acting on dispersal behavior suggest the possibility that nonrandom dispersal might establish genetic structure in the study population (Pfenninger et al. 1996; Vandewoestijne and Baguette 2004; Dornier and Cheptou 2013). This hypothesis does not rely on dispersal and/or its associated causes having an underlying genetic basis since sex-biased dispersal would set up population structure by itself. Still, growing evidence suggests that dispersal may result from a variety of nonrandom underlying processes, including frequency-dependent selection (Barrett 1990; Chaianunporn and Hovestadt 2012; Michler et al. 2013), variation in personality (Cote et al. 2010; Brodin et al. 2013), and individual variation in habitat preference (Gratton and Welter 1998). Each of these causes of variation in dispersal behavior may have a genetic basis (Edelaar and Bolnick 2012) and, as such, could also contribute to the genetic signature of variation in dispersal. Our a priori hypothesis was that

	3	2 1	2	3	3 9	5 7	1 3 8	1 4 4	1 6 2	1 6 3	1 6 8	1 9 1	1 9 8	2 0 4	2 8 8	3 4 5	3 4 8	3 4 9	3 6 6	4 2 0	4 2 7	4 3 0	4 3 1	4 1 0	5 1 3	5 1 9	5 2 5	5 3 4	5 3 7	5 6 1	6 2 8	6 4 2	6 4 8	6 6 0	6 6 2	6 3
Haplotype 1	C	G	T	G	T	A	T	A	T	C	T	C	G	A	G	G	G	A	C	C	G	A	C	T	A	T	A	A	C	C	A	C	T	T	G	C
Haplotype 2	•	**A**	**C**	**A**	**C**	•	•	•	•	**T**	**C**	**T**	**A**	•	**A**	**A**	**A**	**G**	•	**G**	**A**	**G**	**T**	•	**T**	**C**	**G**	•	**T**	**A**	•	**T**	**C**	**C**	**A**	•
Haplotype 3	•	•	•	•	•	•	•	•	**C**	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Haplotype 4	•	•	•	•	**C**	•	•	**G**	**C**	•	•	•	•	•	•	•	•	•	**T**	•	•	•	•	**C**	•	•	•	**G**	•	•	•	•	•	•	**A**	•
Haplotype 5	**T**	•	•	•	•	**G**	**C**	**G**	**C**	•	•	•	•	**G**	•	•	•	•	•	•	•	**G**	•	**C**	•	•	•	•	•	•	•	•	•	•	**A**	**T**
Haplotype 6	•	•	•	**A**	•	•	•	•	**C**	•	•	•	•	•	•	•	•	•	•	•	•	•	•	**C**	•	•	•	•	**T**	•	**G**	•	•	•	**A**	•

Figure 2
Variation in the 6 mitochondrial haplotypes identified on our study island. Rows of nucleotides illustrate haplotypes 1–6 and columns show the location of each of the 36 variable sites along the 673 bp fragment of cytochrome *b* DNA sequence (only variable sites are shown). Variation from the template sequence (row 1) is highlighted in bold in all subsequent haplotypes. Black points indicate conservation of the base shown in haplotype 1.

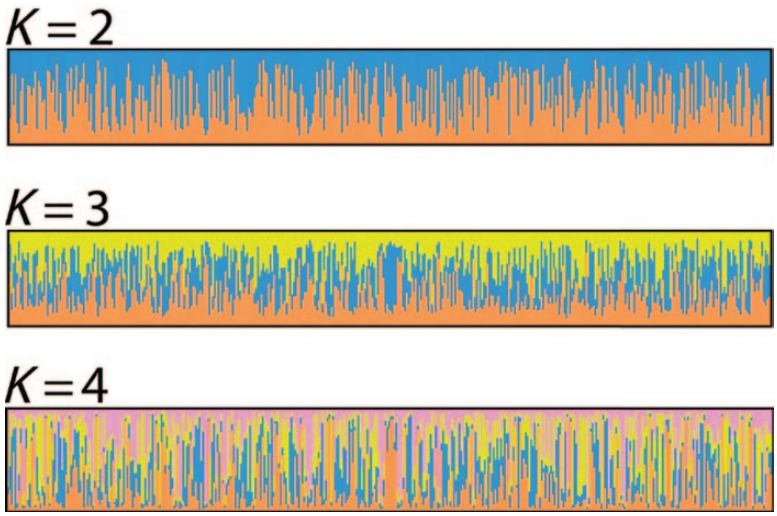

Figure 3
Variation at 6 microsatellite loci was not associated with any form of population structure, indicating that these nuclear markers are admixed across the island. *K* values refer to numbers of subpopulations and indicate test of alternative subdivision hypotheses; *y* axes show the probability of membership in hypothetical subpopulations; *x* axes delineate individuals.

mitochondrial genetic structure would be stronger than nuclear genetic structure, since dispersive males should homogenize nuclear variation across the island but philopatric females could establish structure at mitochondrial loci. Despite strong evidence for male-biased dispersal and associated natural selection acting on dispersal behavior, we found no evidence that sex-biased dispersal behavior has generated any genetic structure on our study island.

There are several potential explanations for this result. First, selection may have acted against migrants prior to reproduction, thereby preventing them from making genetic contributions to population structure. This interpretation is consistent with our selection analyses, which indicate that survival decreases with dispersal distance, particularly in females. Second, population structure may exist at molecular loci other than those we analyzed. This is possible, especially given the suggestion above that dispersal behaviors are influenced by genetic loci that influence other aspects of the organism that are related to dispersal (Edelaar and Bolnick 2012). Future studies may isolate the genes for these behaviors and provide new opportunities for a more targeted approach at finding dispersal-related genetic structure.

A third possibility is that our study island is simply too small to maintain measureable genetic structure. Given that the patterns of dispersal we measured ostensibly repeat themselves each generation, any transient genetic structure should quickly be eroded by the next generation's contribution to gene flow. Moreover, the relative isolation of our study island is likely to limit the total genetic variation, which may itself restrict any signature of structure (although we note that both the allelic variation in microsatellites and the haplotypic diversity at cytochrome *b* were higher [Tables 2 and 3] than we would have predicted a priori, a possible signature of immigration maintaining high levels of genetic diversity). This final possibility highlights the fact that when populations are small, isolated (e.g., islands), and/or harbor limited genetic diversity, the trend toward using molecular techniques to estimate dispersal may prove less useful than traditional mark-release-recapture methods like those employed here. Continued use of direct measures is important to understand the potential demographic consequences of dispersal in these circumstances.

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