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Microsatellite data show evidence for male-biased dispersal in the Caribbean lizard *Anolis roquet*

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Abstract

Dispersal is a key component of an organism's life history and differences in dispersal between sexes appear to be widespread in vertebrates. However, most predictions of sex-biased dispersal have been based on observations of social structure in birds and mammals and more data are needed on other taxa to test whether these predictions apply in other organisms. Caribbean anole lizards are important model organisms in various biological disciplines, including evolutionary biology. However, very little is known about their dispersal strategies despite the importance of dispersal for population structure and dynamics. Here we use nine microsatellite markers to assess signatures of sex-biased dispersal on two spatial sampling scales in *Anolis roquet*, an anole endemic to the island of Martinique. Significantly higher gene diversity (H_S) and lower mean assignment value (mAIC) was found in males on the larger spatial sampling scale. Significant heterozygote deficit (F_{IS}), lower population differentiation (F_{ST}), mAIC and variance of assignment index (vAIC) was found in males on the smaller spatial scale. The observation of male biased dispersal conform with expectations based on the polygynous mating system of *Anolis roquet*, and contributes to an explanation of the contrasting patterns of genetic structure between maternal and biparental markers that have been reported previously in this, and other anoline, species.

Keywords: *Anolis roquet*, microsatellite, sex-biased dispersal

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Introduction

Dispersal is a key component of an organism's life history, affecting both the evolution and persistence of a species (Clobert *et al*. 2001). Dispersal influences the rate of differentiation between subpopulations and the degree to which populations function as independent demographic units (Palo *et al*. 2004). Hence, understanding the dispersal pattern of an organism is a fundamental requirement for accurate inferences about population structure and dynamics. In sexual species, dispersal often occurs predominantly in one of the sexes (sex-biased dispersal). There are three hypotheses that are commonly invoked to explain the disparity in dispersal between the sexes: (i) competition among related females for resources [local resource competition (Greenwood 1980)]; (ii) competition between related males for mates [local mate competition (Dobson 1982; Perrin & Mazalov 2000)]; and (iii) avoidance of inbreeding (Pusey 1987). These hypotheses are not mutually exclusive and share one common facet in that they predict male-biased dispersal in taxa with polygynous mating systems. Conversely, for monogamous species, only local resource competition predicts a bias in dispersal, and this bias is in favour of dispersal among females (Greenwood 1980). These predictions are broadly supported by empirical evidence from mammals and birds; in mammals (often polygynous), males normally disperse further from their natal area, whereas in birds (often monogamous), female-biased dispersal predominates (Greenwood 1980; Handley & Perrin 2007). Nevertheless, there are examples of species of mammals and birds that do not conform to the general patterns (Clarke *et al*. 1997; Gibbs *et al*. 2000; Dallimer *et al*. 2002; Moller & Beheregaray 2004; Williams & Rabenold 2005; Broquet *et al*. 2006; Handley & Perrin 2007), suggesting that mating system hypotheses cannot be applied universally. Moreover, recent studies have suggested that kin selection and sociality may play an important part in the evolution of sex-biased dispersal (Devillard *et al*. 2004).

Studies on species in other taxa, for example salmonids (Hutchings & Gerber 2002; Bekkevold *et al*. 2004; Fraser *et al*. 2004; Palstra *et al*. 2007), cichlids (Knight *et al*. 1999; Taylor

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et al. 2003) and frogs (Austin *et al*. 2003; Lampert *et al*. 2003; Palo *et al*. 2004) are relatively few and the patterns of sex-biased dispersal are equivocal. Likewise, there are relatively few published studies that examine patterns of sex-biased dispersal in lizards. Monogamy in lizards is relatively rare; however, in the few known examples microsatellite data has revealed that slight female bias in dispersal appears to be the norm (Bull 2000; Gardner *et al*. 2001; Stow *et al*. 2001; Chapple & Keogh 2005) in line with predictions from mating system and local resource competition. In lizards with polygynous mating systems, patterns of sex-biased dispersal vary. In the common lizard (*Lacerta vivipara*) a mark–recapture study shows slight male-biased dispersal, where dispersal rates are dependent on female density and kinship (Lena *et al*. 1998), while microsatellite data showed an indication of male-biased dispersal in *Anolis oculatus* (Stenson *et al*. 2002) and, from mark–recapture data, in *Sceloporus occidentalis* (Massot *et al*. 2003). Mark–recapture studies in *Uta stansburiana* showed that males disperse further than females in some years, but not in others (Doughty & Sinervo 1994; Doughty *et al*. 1994). However, mark–recapture data from *Lacerta agilis* suggest that juvenile females disperse further than males (Olsson *et al*. 1996). Both natal and breeding dispersal are also higher in females of the alpine lizard, *Niveoscincus microlepitodus*, according to mark–recapture data (Olsson & Shine 2003). Hence, with only a limited number of studies in lizards, no strong general pattern of sex-biased dispersal seems to emerge. Further investigation of sex-biased dispersal in different taxonomic groups is necessary in order to make cross-taxa comparisons with the patterns observed in birds and mammals, and to develop a more general framework for the evolution of sex-biased dispersal.

Anoles have long been recognised as important model organisms in various biological disciplines (Roughgarden 1985; Losos 2004; Lovern *et al*. 2004; Schluter 2000; Thorpe *et al*. 2004), but there have been only limited field (Andrews & Rand 1983) and genetic (Stenson *et al*. 2002) studies of dispersal in this genus. Here we investigate genetic evidence for sex-biased dispersal in *Anolis roquet*, one of the nine species in the *roquet* series of anole lizards that inhabit the Southern Lesser Antilles. *A. roquet* is an arboreal insectivorous lizard that is endemic to Martinique, and which is found in high densities across most of the island. A recent phylogenetic study on *A. roquet* revealed four very distinct mitochondrial DNA (mtDNA) lineages that were found to be closely associated with geographical regions (Thorpe & Stenson 2003). These regions correspond to peripheral precursor islands that were joined by the uplifting of a central region (Andreieff *et al*. 1976; Bouysse *et al*. 1983; Maury *et al*. 1990; Sigurdsson & Carey 1991). The phylogeographic pattern suggests that young precursor islands were colonized by anoles, and individual *A. roquet* lineages evolved in geographical isolation (allopatry) until the joining of the precursor islands (Thorpe & Stenson 2003). Following secondary contact, a distinct geographical pattern of mtDNA lineage distribution persists and lineage transitions occur over very short geographical distances (Ogden & Thorpe 2002; Thorpe *et al*. 2008). In contrast, nuclear microsatellite data has revealed a pattern of high nuclear gene flow across these secondary contact zones (Ogden & Thorpe 2002; Thorpe *et al*. 2008). This type of pattern is commonly seen in organisms with male-biased dispersal (Taberlet & Bouvet 1994; Gibbs *et al*. 2000; Waits *et al*. 2000; Castella *et al*. 2001; Petit *et al*. 2001), a hypothesis that has not been tested in *A. roquet*. Given that anoles generally have polygynous mating systems (Jenssen *et al*. 2001) predicting male-biased dispersal, it is important to test hypotheses of sex-biased dispersal as a contributing factor to the contrasting patterns between mtDNA and nuclear DNA in this and other anoline species (Stenson *et al*. 2002).

Direct estimations of dispersal through mark–recapture studies are time-consuming and expensive due to the extensive fieldwork required (Berry *et al*. 2004). Furthermore, *A. roquet* is a small, arboreal, often cryptic animal that inhabits a complex tropical habitat. Hence, it would be particularly difficult to survey dispersing juveniles efficiently. Moreover, in anoles there is a high turnover, particularly among juveniles (Andrews & Rand 1983), which would require a very high number of individuals to be marked in order to reliably estimate dispersal. An indirect approach based on microsatellite frequencies offers an attractive alternative to mark–recapture studies (Goudet *et al*. 2002; Prugnolle & de Meeus 2002; Berry *et al*. 2004; Handley & Perrin 2007). Sex-biased dispersal affects genetic structure between and within populations, which can be detected by calculating indices from polymorphic genetic data. Results from these methods based on genetic data have been favourably compared with mark–recapture studies (Favre *et al*. 1997).

Materials and methods

Anolis roquet is a sexually dimorphic lizard; mature males are larger than females and show distinctive markings. Both males and females have dewlaps, however, the dewlap on males is larger and more brightly coloured (Lazell 1972), hence discrimination between adults from each sex is straightforward. Only adult lizards were used for this study.

We sampled a total of 17 localities on two spatial scales. Ten island-wide localities (distance between localities ranged between 4–43.6 km, the mean being 17.12 km) were sampled between March and May 2005–07. Localities were chosen to incorporate at least one locality from each mtDNA lineage and cover as many habitat types as possible. Seven further localities situated along a 4-km transect, all in the same habitat type (Fig. 1), were sampled between April and May 2007. Distances between these latter localities are likely to be a more realistic scale for juvenile dispersal. Each

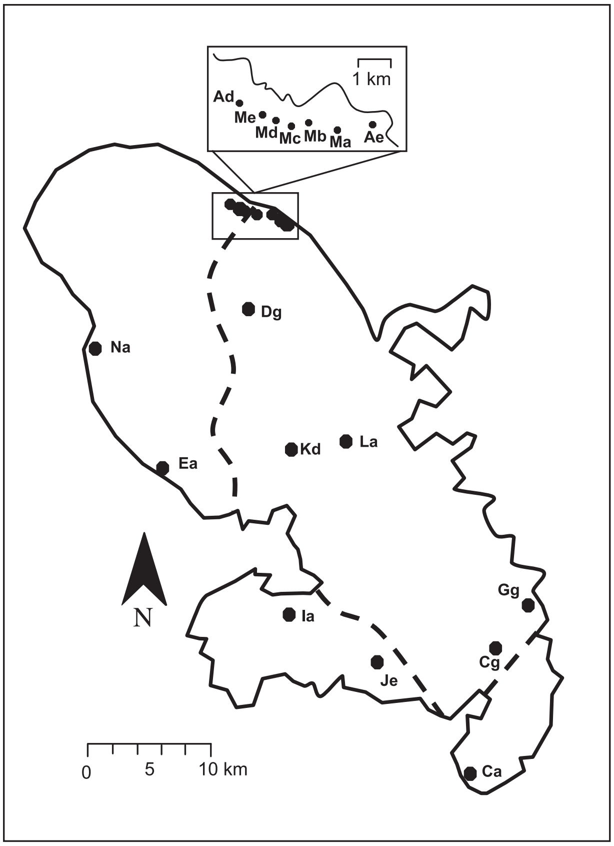

Fig. 1 Map of Martinique, showing the island-wide sampling localities and the transect at the smaller sampling scale (inset). Broken line shows the phylogenetic lineage boundaries for the four main mtDNA lineages of *Anolis roquet* on Martinique.

locality (at both sampling scales) was sampled over no more than two days in the same year. Only data from locations yielding at least 28 adult individuals and approximately equal numbers of females and males were included in this study.

Autotomised tail tips were collected for DNA analysis and stored in 100% ethanol. Genomic DNA was extracted by the Chelex method described by Estoup *et al*. (1996). Individuals were typed at nine microsatellite markers (Ogden *et al*. 2002; Gow *et al*. 2006; Johansson *et al*. 2008). Loci were amplified in a multiplex polymerase chain reaction (PCR) (primer concentrations: 0.05 μm for ARO-035, ARO-062, ARO-065 and ARO-HJ2, 0.1 μm, for ARO-120 and 0.2 μm for ABO-P4A9, AAE-P2F9 and ALU-MS06) using QIAGEN Multiplex PCR kit following the manufacturers instructions, with the exception of an annealing temperature of 55 °C. The amplified products were then analysed on an ABI 3130xl genetic analyser with the internal size standard 600-LIZ, and genotypes scored using GENEMAPPER version 4.0 (Applied Biosystems).

From the ten localities sampled island-wide, a total of 372 individuals were genotyped, ranging from 28–48 individuals per population (mean 39.5), of which 184 were female and 188 were male. The proportions of sexes genotyped from each locality can be found in Table 1. From the transect, a total of 281 individuals were genotyped, with 36–44 individuals per locality (mean 40.1), totalling 140 females and 141 males (Table 1).

Genetic data from the two sets of localities were analysed separately. The software ARLEQUIN version 3.01 (Schneider *et al*. 2000: http://lgb.unige.ch/arlequin/) was used for exact testing of Hardy–Weinberg equilibrium (Guo & Thompson 1992) and calculation of linkage disequilibrium (Slatkin & Excoffier 1996) for each population and locus. Departure from Hardy–Weinberg equilibrium was considered with, and without, Bonferroni correction. For all calculations of F-statistics we used Weir & Cockerham's (1984) unbiased estimators. To test for overall genetic differentiation in the two samples and for pairwise differentiation between individual populations, we used FSTAT version 2.9.3 (Goudet 1995: http://www2.unil.ch/popgen/softwares/fstat.htm) to calculate global and pairwise F_{ST}, respectively.

To test for sex-biased instantaneous dispersal we calculated the gene diversity (H_S), F_{IS}, F_{ST}, mean assignment index (mAIC) and variance of the assignment index (vAIC) separately for each sex. Statistical significance for these indices was determined by 10 000 randomizations as implemented in FSTAT version 2.9.3. A bias in dispersal between the sexes should be reflected in statistically significant dissimilarity in the estimated parameters. The higher-dispersing sex should have a higher F_{IS}: in the dispersing sex individuals sampled from one single patch will be a combination of residents and immigrants, hence a heterozygote deficit is expected due to the Wahlund effect (Goudet *et al*. 2002). More similar allele frequencies are expected between sampling sites in the dispersing sex and less differentiation between populations. Thus F_{ST} is expected to be higher in the philopatric sex and within-site gene diversity (H_S) is expected to be lower (Goudet *et al*. 2002). The measure of F_{ST} (i.e. among-population differentiation) on the island-wide sampling scale is unlikely to be informative with respect to actual dispersal rates as it is unlikely that populations exchange migrants over these distances. The probability of a genotype originating in the population from which the genotyped individual was sampled can be calculated as an assignment index, from which the sample mean (mAIC) can be found (Paetkau *et al*. 1995). A relatively higher frequency of rarer genotypes is expected in populations of the dispersing sex and this is indicated by a negative assignment index (Paetkau *et al*. 1995; Prugnolle & De Meeus 2002). Finally, the vAIC can be estimated from mAIC, where variance is expected to be larger for the sex that disperses (Favre *et al*. 1997). In the case of microsatellite data (or other biparental markers), these methods detect only short-term dispersal,

Table 1 Locality names, GPS position (UTM Easting and UTM Northing), total number of genotyped samples ($N_{(T)}$), number of females ($N_{(F)}$) and number of males ($N_{(M)}$) for each locality

Locality	UTM Easting	UTM Northing	$N_{(T)}$	$N_{(F)}$	$N_{(M)}$
Island-wide localities					
Ca	728245	1593645	28	15	13
Cg	730021	1604099	38	19	19
Dg	709480	1632216	35	17	18
Ea	702159	1618280	48	25	23
Gg	732909	1607713	32	14	18
Ia	712794	1606954	41	22	19
Je	720504	1603147	34	17	17
Kd	713197	1621052	43	19	24
La	717409	1621378	38	19	19
Na	696124	1629433	35	17	18
Transect localities					
Ad	708108	1640748	40	20	20
Ae	711603	1640234	36	18	18
Ma	710657	1640090	40	20	20
Mb	709933	1640253	44	22	22
Mc	709442	1640153	38	19	19
Md	709089	1640332	40	20	20
Me	708722	1640418	43	22	21

Table 2 Deviations from Hardy–Weinberg expectations (F_{IS}), F_{ST}, gene diversity (H_S) mean assignment index (mAIC) and variance of mean assignment index (vAIC) for the ten island-wide localities for females (F) and males (M). *P*-values are from two-tailed tests where; ** = significant at $P < 0.01$

	F_{IS}	F_{ST}	H_S	mAIC	vAIC
F	0.012	0.062	0.756	0.502	9.719
M	0.022	0.057	0.778	–0.491	11.533
P-value	0.597	0.404	0.005**	0.003**	0.406

Table 3 Deviations from Hardy–Weinberg expectations (F_{IS}), F_{ST}, gene diversity (H_S) mean assignment index (mAIC) and variance of mean assignment index (vAIC) for the seven transect localities for females (F) and males (M). *P*-values are from two-tailed tests where; ** = significant at $P < 0.01$, * = significant at $P < 0.05$

	F_{IS}	F_{ST}	H_S	mAIC	vAIC
F	–0.009	0.014	0.791	0.345	9.211
M	0.044	0.006	0.795	–0.347	13.574
P-value	0.003**	0.025*	0.301	0.047*	0.014*

since this signal disappears after the dispersing individuals mate, due to the Mendelian segregation of biparental markers (Goudet *et al*. 2002).

Results

The mean number of alleles scored per population (averaged over all loci) from the ten island-wide localities sampled was 10.4. There was no evidence of consistent departures from Hardy–Weinberg equilibrium or of linkage disequilibrium in the samples (Table S1). The global F_{ST} was estimated at 0.059, with pairwise F_{ST} values ranging from 0.0157 to 0.1227, suggesting moderate levels of genetic differentiation on the sampled spatial scale. Males display significantly higher gene diversity, H_S (males = 0.778, females = 0.756, $P = 0.005$) and significantly lower mAIC values (males = – 0.491, females = 0.502, $P = 0.003$). The remaining indices (F_{IS}, F_{ST} and vAIC) were compatible with male-biased dispersal, but did not reveal statistically significant differences (Table 2).

The mean number of alleles scored per population on the transect was 10.62. No consistent departures from Hardy–Weinberg equilibrium and no linkage disequilibrium were detected. The global F_{ST} was estimated at 0.011, with pairwise F_{ST} values ranging from 0.0024–0.0213, suggesting low levels of genetic differentiation. Four tests of sex-biased dispersal were found to be significant on this sampling scale. Females had a negative F_{IS} (–0.009) compared to the positive value for males (0.044), showing a highly significant difference ($P = 0.003$). The variance of assignment index also showed a significant difference ($P = 0.014$), with males having a higher index (13.574) compared to females (9.211). Females also showed significantly higher differentiation compared to males (female $F_{ST} = 0.014$, male $F_{ST} = 0.006$, $P = 0.025$). Furthermore, males and females differed significantly in mAIC, with males returning a negative value of –0.347, while females showed a positive value of 0.345 ($P = 0.047$). The difference in gene diversity was not significant, although the level in males was on average higher (Table 3).

Discussion

We included island-wide sampling (covering lineages and habitats) so that, in spite of limitations, we could generalize some of our findings to the entire species. The distances between the island-wide populations are well beyond the distance juvenile anoles are expected to disperse, on account of their small size. Furthermore, the ten island-wide localities were sampled during different years. These two factors mean that among-population indices (pairwise F_{ST}'s) cannot be used to infer sex-biased dispersal at this scale (Goudet *et al.* 2002), but the within-population indices are informative as they are not affected by the sampling protocol. The transect localities were sampled in the same year and in the same habitat, and given the short distance between the localities, pairwise comparisons are expected to be reliable.

All of the indices estimated, on both spatial sampling scales, suggest that males have a higher dispersal rate than females in *Anolis roquet*. Highly significant differences between males and females were observed in the estimates of mean assignment index and gene diversity on the island-wise sampling scale, whereas F_{IS}, F_{ST}, mAIC and vAIC showed significant differences on the transect. The evaluation by Goudet *et al.* (2002) of the efficiency and power of these tests showed that test performance was dependent on dispersal rates, strength of bias, polymorphism of the markers and the sampling. These tests generally have a low power in detecting bias, unless the sex-bias in dispersal is at least 80:20 and all populations involved are sampled exhaustively (Goudet *et al.* 2002). Within this context, the significant indices detected in this study provide strong evidence for male-biased dispersal in this species. The results for *A. roquet* are in concordance with the prediction of male-biased dispersal in polygynous species, which was first suggested by Greenwood (1980). However, not all polygynous lizards show male-biased dispersal (Olsson *et al.* 1996; Olsson & Shine 2003), and several reasons can be postulated for the results observed in *A. roquet*.

It has been shown that in cases where males compete for females (local mate competition) and females compete for resources (local resource competition), the association between male-biased dispersal and polygyny is strengthened (Perrin & Mazalov 2000). Similarly, higher levels of competition between males than between females in a polygynous system increase the likelihood of a male-bias in dispersal. This occurs in the female defence polygyny observed for sexually dimorphic members of *Anolis* (Trivers 1976; Schoener & Schoener 1980; Jenssen *et al.* 2001). Female anoles choose their territory before they reach sexual maturity and several females can hold home ranges that overlap considerably (Trivers 1976; Jenssen *et al.* 2001). Males subsequently enter female territory and dominant males defend their access to, and mate with, several females (Schoener & Schoener 1980; Jenssen *et al.* 2001). Therefore, females may benefit from dispersing only to the extent to which they are able to obtain adequate resources for survival and reproduction (Stamps 1977), whereas males may have to disperse further to find territory that is unoccupied by superior males. In those anoles that have polygynous mating systems it appears that intrasexual aggression levels are consistently higher in males than in females (Trivers 1976; Jenssen *et al.* 2000), and this aggression has been hypothesised to cause juvenile or subadult males to leave their natal area (Trivers 1976; Schoener & Schoener 1980; Schoener & Schoener 1982).

Conversely, philopatry is typically favourable for the sex that invests highly in their offspring, given that knowledge of the territory and potential social interactions with kin may provide benefits (Greenwood 1980; Waser & Jones 1983). In anoles, as in most species of lizard, there is no post-hatchling parental investment, however, females invest more energy in reproduction (for egg production) than males (Orrell *et al.* 2004) suggesting benefits for philopatric females. As described above, there is a very strong mtDNA structure in *A. roquet*. Specific lineages are associated with the different precursor islands, even after an estimated 1.5 million years of secondary contact and in the absence of physical or ecological barriers (Ogden & Thorpe 2002; Thorpe *et al.* 2008). Such a pattern has been described in several species (Taberlet & Bouvet 1994; Gibbs *et al.* 2000; Waits *et al.* 2000; Castella *et al.* 2001; Petit *et al.* 2001) and has been explained by very high philopatry in females. A comprehensive study of this type of pattern comes from the greater mouse-eared bat *Myotis myotis* (Castella *et al.* 2001). In this species females aggregate to form nursing colonies in spring and summer, and the females have been shown to exhibit strong fidelity to their natal colonies, whereas the geographic origin of males is usually unknown. Castella *et al.* (2001) show that dispersal of effectively a single sex in *M. myotis* is sufficient to homogenize nuclear DNA structure whilst preserving mtDNA structure, when the other sex is philopatric. Similar conclusions were drawn by Bowen *et al.* (2005), in a study on loggerhead turtles. Hence the structure observed in *A. roquet* mtDNA is probably due to strong female philopatry, as observed previously in *Anolis oculatus* by Stenson *et al.* (2002).

In species with strong philopatric tendencies, sex-biased dispersal is beneficial since it decreases the risk of mating with related individuals (Pusey 1987). Furthermore, the potential cost of inbreeding associated with philopatry may also be reduced by multiple paternity in anoles. Some female anoles have been shown to be highly promiscuous, and able to store sperm for more than two months (Fox 1963; Calsbeek *et al.* 2007; Eales *et al.* 2008). Offspring of promiscuous females are genetically more diverse, thereby allowing maternal half-siblings to mate with a decreased risk of inbreeding (Calsbeek *et al.* 2007).

In conclusion, this study shows strong evidence for male-biased dispersal in a species for which direct dispersal estimation by mark–recapture methods would be very difficult to obtain. This result contributes to an explanation of the conflicting patterns of gene flow between nuclear and mitochondrial markers observed by Thorpe *et al*. (2008). Indeed, it seems likely that pronounced female philopatry produced the strong mtDNA lineage structure observed across the island (Stenson & Thorpe 2003), while nuclear gene flow across the lineage contact zones may be predominantly maintained by means of male dispersal.

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The authors belong to the Molecular Ecology and Evolution of Reptiles Unit in Bangor. This paper is part of the team's investigation into population genetics and speciation in the *Amolis roquet* complex and forms part of Helena Johansson's research for a PhD. Yann Surget-Groba is interested in the molecular ecology of lizards, including the evolution of viviparity. Roger S Thorpe is interested in natural selection, population genetics, molecular phylogeography and speciation of island lizards.
