

Sex-specific adult dispersal and its selective consequences in the brown anole, *Anolis sagrei*

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Summary

1. Dispersal behaviour is a potentially risky life-history strategy that can impact habitat use as well as competition over territories and mates.
2. I studied natural selection on dispersal behaviour over the course of four breeding seasons in a Bahamian population of brown anoles (*Anolis sagrei*).
3. Both males and females showed extremely high site fidelity over the course of each reproductive season. Movement distance in males was negatively correlated with body size at first capture in spring (small males dispersed further). Moreover, differences in body size between dispersing males and the body size of the male territory residents that they replaced were correlated with the distance that males dispersed. Relatively larger males dispersed shorter distances compared with relatively smaller males. There was no relationship between dispersal distance and body size in females. However, females were more likely to disperse away from areas of low female density and into areas of higher female density, and female dispersal distances were negatively correlated with the number of female neighbours at the site of capture in spring (before dispersal).
4. These data suggest that, whereas male dispersal is driven by inter-male competition, female dispersal is more likely related to variation in territory quality.
5. Natural selection acted on dispersal distance in conjunction with male, but not female body size. Although smaller males were the more likely to disperse, these males paid a high cost in terms of viability indicating that dispersal is a potentially risky strategy.

Key-words: dispersal, habitat use, natural selection, site fidelity, territoriality

Introduction

Movement away from natal sites or between breeding sites is an important, but potentially costly life-history trait. Dispersing individuals may avoid costs of kin competition (Olsson, Gullberg & Tegelstrom 1996; Gandon & Michalakis 2001; Perrin & Goudet 2001; Bilde 2005), find superior habitats (Ferriere *et al.* 2000), and enjoy increased access to potential mates. However, they may likewise face high rates of predation, inadvertently disperse into lower-quality habitat, and often experience physiological costs associated with movement (Clobert *et al.* 2001). The decision to either disperse or not (i.e., movement versus site fidelity/philopatry) should therefore have important consequences for selection (Olsson *et al.* 1996; Murren *et al.* 2001; Sinervo & Clobert 2003).

It is increasingly recognized that dispersal behaviour may often be context dependent. As noted above, the decision to disperse or not may depend on local population densities, which may in turn impact the likelihood of reducing competition

(Olsson, Gullberg & Tegelstrom 1996; Gandon & Michalakis 2001; Perrin & Goudet 2001; Bilde 2005), especially kin competition (Cote, Clobert & Fitze 2007). These scenarios suggest that density-dependent dispersal decisions should always favour dispersal away from high-density areas. However, high population densities may reduce the likelihood that dispersing individuals are capable of either finding or successfully entering a new settlement area (reviewed in Clobert *et al.*, in press). Thus, density dependence may also hamper dispersal at high density.

Dispersal behaviour in animals is often primarily expressed by one sex and is thought to be driven by the relative importance of competition over mates vs. competition for resources (Hamilton 1967; Stiver 2007). In most polygynous species, males compete over high-quality territories to gain access to females (the polygyny threshold model; Emlen & Oring 1977). Females may or may not be territorial, but irrespective of this distinction, females usually opt to settle on high-quality territories that provide some important resource (Brenner 1966; Brown 1969; Schoener & Schoener 1980; Calsbeek & Sinervo 2002). Thus, in polygynous species, males often disperse away from their natal sites whereas females

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tend towards philopatry (Perrin & Mazalov 2000; Leturque & Rousset 2004). Consequently, as has been shown in previous studies (Schoener & Schoener 1980), sex ratios often become increasingly female biased at high population densities, as females settle in similarly high-quality areas (Andrews & Stamps 1994). Territoriality and the opportunity for mate choice are thus intimately linked, but the mechanisms that drive dispersal behaviour into these high-quality sites differ between the sexes (Schoener & Schoener 1980).

Although work on dispersal behaviour has been extensive (see Clobert *et al.* 2001), one shortcoming in the literature is that few studies have measured natural selection acting on animal dispersal in the wild (Soulsbury 2008, but see Murren *et al.* 2001). This is in part because there are few study systems in which one can confidently differentiate between individual deaths and dispersal away from an area. Here I report on dispersal behaviour and its selective consequences in subadult and adult *Anolis* lizards living on islands in The Bahamas. Although considered highly successful dispersers among islands in the Caribbean (Calsbeek & Smith 2003), almost all of the previous studies of dispersal in anoles have been aimed at understanding long-distance (especially overwater) dispersal events (Schoener & Schoener 1984; Glor, Losos & Larson 2005). Considerably less is known about within-population dispersal behaviour of anoles (Andrews & Rand 1983). However, anoles provide an excellent opportunity to study the selective consequences of dispersal because their short life span (*c.* 1 year) and the small (*c.* 1500 m²) islands that they inhabit permit studies of entire populations of individuals throughout their life span. I use 4 years of longitudinal data to test the hypothesis that male dispersal is driven by intrasexual competitive interactions, whereas female dispersal reflects movement towards high-quality habitat. I compared the different motivating factors that appear to drive dispersal in males vs. females and subsequently measured the selective consequences of dispersal.

I predicted that if competition determined dispersal behaviour of males, then traits such as body size, which are important in determining contest outcomes (Calsbeek & Smith 2007), should be important for dispersal by males but not females. For example, I predicted that relatively large males would disperse shorter distances compared with relatively small males, because large body size would make it easier for these males to supplant other territory residents. By contrast, if female dispersal decisions are based on territory quality rather than competitive interactions, then dispersal by females should depend on the spatial distribution of resources, and female densities should increase in those high-quality areas. Although I do not present genetic data in the present study, I briefly discuss implications of the observed levels of philopatry in the context of previous studies that have noted a striking degree of population genetic structure over very small spatial scales in these and related lizards (Kolbe *et al.* 2004; Marnocha *et al.* submitted). Patterns presented here may inform those studies and suggest a mechanism by which highly structured populations of *Anolis* lizards have evolved.

Methods

The brown anole, *Anolis sagrei*, is a small (< 70 mm snout-vent-length; SVL) semi-arboreal lizard that has a broad tropical and subtropical distribution. At the study site described in this paper, 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 late March and have a highly polygamous breeding system (e.g., females are known to store sperm from up to four different males; Calsbeek *et al.* 2007). Females lay one or two eggs at approximately 10-day intervals throughout the breeding season, which typically ends by September (Calsbeek *et al.* 2007). 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 & Smith 2007). However, a small subset of individuals that had been marked the previous year is typically recaptured in subsequent years. These individuals provide an opportunity to measure viability selection as a function of dispersal behaviour.

DISPERSAL BEHAVIOUR

I studied site fidelity and dispersal behaviour from spring to fall in a population of Bahamian anoles during 2003 (*N* = 29) and 2005–07 (*N* = 67, 127, and 99). Larger numbers of lizards were initially marked in each year (population sizes range from ~250–350 individuals in any given year) and these sample sizes reflect only individuals that survived to the fall census and thus were used to estimate dispersal distance upon recapture. I studied the lizard population on Kidd cay, a small (1600 m²) island situated 80 m offshore and adjacent to the town of Georgetown, Great Exuma (23°31'N, 75°49'5"W). Each spring (May–June), I weighed [to the nearest 0.1 g using a Pesola spring scale (Rebmattli, Baar, Switzerland)], measured (SVL; to the nearest 0.5 mm using a ruler), and uniquely marked all individuals on the cay. Lizards were permanently marked with unique combinations of coloured elastomer dyes injected subdermally into the ventral side of their hind and forelimbs. Tags are invisible to predators and other lizards and so do not affect survival or social interactions (Nauwelaerts, Coeck & Aerts 2000). During 2003 and 2005, temporary unique paint markings were made on the dorsum to facilitate home-range estimations. I captured lizards systematically, such that local neighbourhoods of lizards were all removed at the same time. I did this to limit changes in social interactions among individuals that may have otherwise occurred if only subsets of neighbourhood residents had been removed. All lizards were returned to their original point of capture within 4 to 6 h.

Each year in fall (late September–early October) I conducted a recapture census of the entire island. I attempted to recapture all surviving lizards (mean survival = 38%), weighed and measured them, and marked them with a small spot of white paint on the hind limb to prevent immediate recapture (recapture rates of 97–99% of survivors; I failed to catch at least two male lizards during 2005 and at least one male evaded recapture during the other years). I measured changes in body size (Δ SVL) between the first capture in spring and recapture in fall. Individuals that survived to be recaptured again the following spring were used to estimate viability selection on dispersal behaviour (see below).

During spring of 2003 and 2005, I mapped home-range boundaries by walking multiple daily transects across the entire study site for 2 weeks and recording the location of each individual relative to known landmarks (> 1000 sightings per year, average unique sightings = 7.2 per male and 5.2 per female). Lizard positions were

recorded as distance measurements and compass bearings from previously surveyed locations on the study site (Calsbeek, Bonneaud & Smith 2008). I constructed maps of neighbourhoods (minimum convex polygon method) using the software package MACTURF (Sinervo & DeNardo 1996), and defined neighbours as individuals with coincident or overlapping home-range borders. Neighbourhoods were readily defined by the patchiness of habitat on the cay and lizards aggregated in and around these clumps of cover vegetation. I compared numbers of neighbours estimated directly from these neighbourhood maps with estimates made by counting the total number of neighbours within 3 m of the centre of each home range (the average home range diameter). The two measures produced qualitatively similar results, and the latter, simpler method was used during 2006 and 2007 in lieu of mapping actual territories. In this case, I assumed that locations at first capture were the centre points of home ranges. Numbers of neighbours are reported as estimates of local population density.

I considered animals to have dispersed if the distance between capture locations in spring and fall was greater than 3 m [approximately one home range diameter (Calsbeek *et al.* 2008)]. If dispersers were captured at a site that had been previously occupied by a lizard that was not recaptured in fall, then I compared the relative body sizes of the dispersing lizard to the former territory residents. I then used this difference to test the hypothesis that relatively large males would disperse shorter distances compared with relatively small males.

The distributions of both dispersal distance and the numbers of females at spring capture sites were non-normally distributed. Log transformation brought the distribution of female numbers closer to normality, but did not help the distribution of dispersal distances. Therefore, analyses of dispersal distance were performed using nonparametric tests (figures show least squares regressions for illustrative purposes only). One long-distance dispersing male was a statistical outlier and after briefly considering the effects of this individual on the data set, I exclude his data from all subsequent analyses (noted below and indicated in Fig. 2). I tested for year effects in each model, but the factor for year never explained a significant portion of the variance in these tests and I subsequently dropped this effect from each model. These nonsignificant year effects are not discussed further.

SELECTION ANALYSES

I estimated viability selection on males and females, by measuring survivorship of all animals from the fall census to the following spring. Because body size had a significant effect on dispersal behaviour, I measured the strength of selection on dispersal behaviour including body size as a covariate and year as a random factor. All tests were two-tailed and were performed using JMP version 6.0.2 for the Macintosh. Selection gradients were calculated from the regression coefficients of standardized fitness (individual fitness standardized by the population mean) and standardized traits (mean zero, unit variance) (Lande & Arnold 1983). Because survival has a binomial distribution (live/die), I calculated significance values for selection differentials and gradients using logistic regression (Janzen & Stern 1998). The degree of multi-collinearity among traits was assessed by estimating variance inflation factors (VIF; Petraitis, Dunham & Niewiarowski 1996), all of which were less than five.

Fitness surfaces were estimated separately for each sex using projection pursuit and the multivariate techniques implemented by Schluter and Nychka (1994). Data were standardized (mean zero, unit variance) before performing a grid search to find a value for the smoothing parameter (λ) that minimized the generalized-cross-validation (GCV)

score. The best-fit surface was then estimated using this value of λ and estimates of the survival probabilities.

Results

Average distance moved from spring to fall (Fig. 1) was significantly greater for males (all males: mean \pm SE = 3.18 m \pm 0.37) compared with females (all females 1.25 m \pm 0.40) (two-sample Kruskal–Wallace test: $Z = -4.70$, $P < 0.0001$) (Table 1), but not when considering only those individuals that dispersed greater than one home-range diameter (male dispersers: 8.23 m \pm 7.74 vs. female dispersers: 6.85 m \pm 5.62; $P = 0.4$). Hereafter, unless otherwise noted, all results are reported for all individuals whether philopatric or dispersive. Comparing all individuals, males that were smaller in spring moved greater distances compared with larger males (Spearman's $\rho = -0.21$, $N = 171$, $P = 0.004$). This relationship was partially obscured by one outlier, a male whose dispersal distance (44 m) was 6.8 standard deviations larger than the mean (data point indicated in Fig. 2a). After excluding this male from the data set, the relationship became stronger (Spearman's $\rho = -0.24$, $N = 170$, $P = 0.002$). There was no effect of body size on dispersal behaviour in females (Spearman's $\rho = 0.04$, $N = 147$, $P = 0.64$ Fig. 2b).

The number of females at the initial capture site predicted whether individuals dispersed or remained philopatric in both females (logistic regression, $N = 131$, Wald $\chi^2 = 4.46$, $P = 0.03$) and males ($N = 150$, Wald $\chi^2 = 5.6$, $P = 0.02$) (Fig. 3). The number of females at each initial capture site (spring) predicted the magnitude of distance moved for females (Spearman's $\rho = -0.35$, $N = 148$, $P < 0.001$), but this result was not significant for males (Spearman's $\rho = -0.09$, $N = 129$, $P = 0.35$ Fig. 4). For the small subset of individuals that survived from one spring capture to the next, growth (Δ SVL) showed a weak and positive correlation with dispersal distance (log transformed) in males (ANOVA $F_{1,32} = 3.83$, $P = 0.05$) but not females (ANOVA $F_{1,31} = 0.01$, $P = 0.92$). Thirty-one males and seven females had to be excluded from this analysis owing to missing body size measurements at either the first or second capture event.

VIABILITY SELECTION

Over the 4 years of this study, 73 individuals (33 females and 40 males) survived from one spring to the next. Because survival to a second breeding season is rare, analyses could not be performed separately by year. I detected no selection on male body size ($\beta = 0.07 \pm 0.15$, $F_{1,173} = 1.28$, $P = 0.24$; effect of year $P = 0.18$) or female body size ($\beta = -0.07 \pm 0.15$, $F_{1,150} = 0.26$, $P = 0.61$; effect of year $P = 0.002$). Across all years pooled and considering all individuals irrespective of dispersal distance, there was a weak tendency towards directional selection favouring greater dispersal distances in males that was nonsignificant ($\beta = 0.28 \pm 0.15$, $F_{1,170} = 3.71$, $P = 0.07$; effect of year $P = 0.20$). However, there was a significant interaction between dispersal distance and male body size (ANCOVA SVL \times dispersal distance; $F_{1,167} = 6.64$, $P = 0.01$;

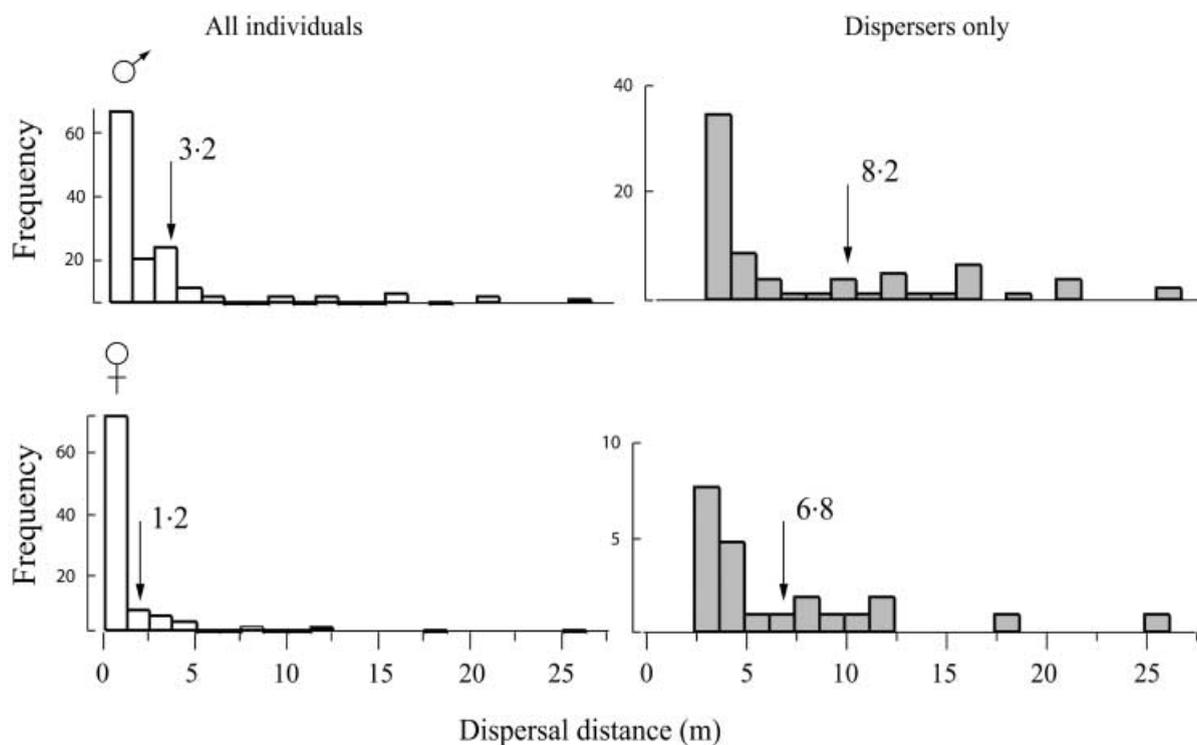


Fig. 1. Frequency distributions of dispersal distances for all males and females (white bars) and the subset of those males and females with nonzero dispersal distances (gray bars). Arrows indicate mean values. Distributions show pooled data from all 4 years of study because there were no significant among-year differences in dispersal.

Table 1. Summary table of the average dispersal distances (\pm SE) for each sex during each year of the study. Data on dispersal distance do not include philopatric individuals

Sex	Year	No. of philopatric individuals	No. of dispersing individuals	Average dispersal distance (SE)
M	2003	20	7	10.93 (8.99)
F	2003	2	0	NA
M	2005	20	19	9.08 (7.23)
F	2005	24	4	4 (0.82)
M	2006	45	18	6.14 (4.92)
F	2006	53	11	8.64 (6.51)
M	2007	27	17	8.39 (10.04)
F	2007	47	8	5.81 (5.26)

effect of year $P = 0.14$; Fig. 5) indicating that selection acted differently on large and small males. I detected no linear selection on female dispersal distance ($\beta = -0.16 \pm 0.16$, $F_{1,145} = 1.71$, $P = 0.19$; effect of year $P = 0.003$), nor did female body size interact with dispersal distance as it did in males (SVL \times dispersal distance; $F_{1,141} = 0.02$, $P = 0.91$; effect of year $P = 0.003$; Fig. 5). This difference in the selective consequences of body size for dispersal distance was significant between the sexes (SVL \times dispersal distance \times sex; $F_{1,321} = 6.25$, $P = 0.01$).

Discussion

Dispersing through the habitat, whether during the period before sexual maturity or between breeding episodes, is an important component of the life history. The act of dispersal is potentially costly (Boinski *et al.* 2005) as it puts individuals at risk of predation (Stamps 1983), of ending up in an area that is of lower quality than the one they left, and may heighten the probability of agonistic encounters with conspecifics (Clobert *et al.* 2001). It may also be costly in terms of energy expenditure. The potential costs of dispersal can, however, be balanced by the benefits of increased access to mates and higher-quality territories (i.e., a trade-off). These costs and benefits may depend on how dispersal behaviour responds to density conditions (either positively or negatively; Clobert *et al.* in press, Cote *et al.* 2007). Especially in polygynous species, male dispersal may be constrained by competitive interactions with other males. In such cases, females may show a higher degree of flexibility to move around the habitat (Calsbeek & Sinervo 2002) and are more likely than males to disperse based on territory quality per se (Schoener & Schoener 1980).

Lizards in this study population showed a high degree of site fidelity over the course of the breeding season. More than 65% of males and 85% of females were recaptured in fall within 3 m of their spring capture site and the mean movement distance of all individuals was less than 2.5 m. Such high site fidelity is frequently observed in passerines (Sedgwick 2004; Bruinzeel 2007) and colonial breeding mammals (Wolf & Trillmich 2007). Studies of adult dispersal in lizards are less

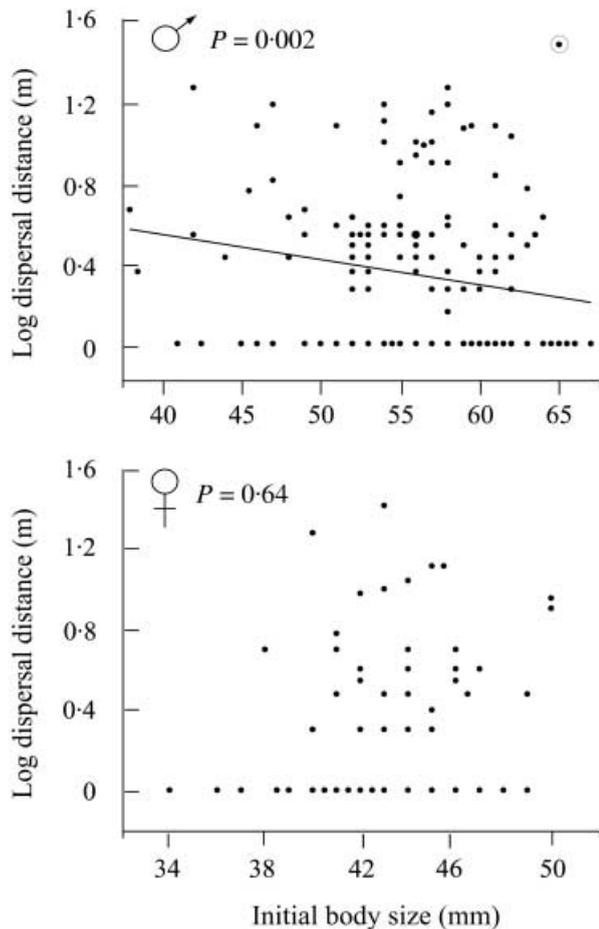


Fig. 2. Dispersal distance in males (top panel) was negatively correlated with body size at first capture in spring, such that small males dispersed further compared with larger males. There was no significant relationship in females (bottom panel). The least squares regression line is for illustrative purposes only, *P* values come from nonparametric tests (see methods).

common, but one such study (Olsson *et al.* 1996) found that the average dispersal distance of male and female sand lizards was in excess of 60 m between breeding seasons. In a 7-year study of anoles in Panama, Andrews & Rand (1983) documented extremely limited dispersal (e.g., 3–5 m) of *Anolis limifrons* on Barro Colorado island. They suggested that a uniform resource distribution and high population turnover (*A. sagrei* and *A. limifrons* are both essentially annuals) reduced selection for dispersal in this species. High site fidelity is therefore common in at least these two species of anole.

These results suggest that dispersal in male *A. sagrei* may be driven by competition with other males. Male dispersal distance was negatively correlated with body size measured in spring (Fig. 2). That is, large males were more likely to be philopatric compared with smaller males. This suggests that small males could have initially been in less favourable areas compared with larger males, and thus were more likely to disperse into better sites after they grew (Andrews & Stamps 1994). Indeed, when I compared the body sizes of males that dispersed into new territories with the body size of the previous residents at those sites, relatively larger dispersing

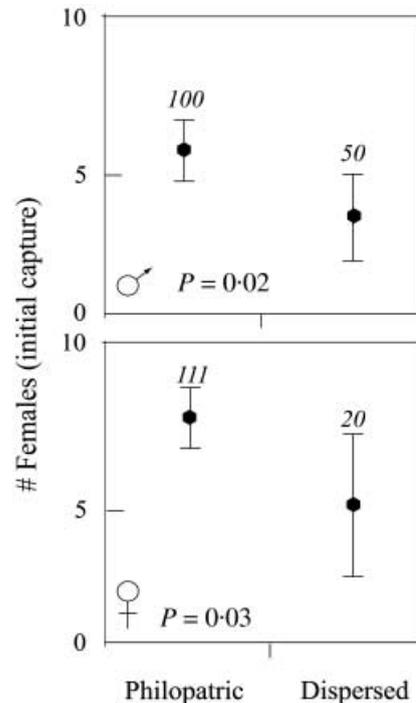


Fig. 3. Twice as many males (top panel) and nearly five times as many females (bottom panel) remained philopatric as dispersed (i.e., moved more than the diameter of an average home range between spring and fall). Patterns of dispersal were related to the numbers of females at the initial capture site in spring; males and females with fewer female neighbours were more likely to disperse. Test statistics are based on logistic regression, but for ease of interpretation, panels show mean values with standard errors.

males moved shorter distances compared with dispersing males that were much smaller than the resident that they replaced. It is impossible to discern whether dispersing males filled vacancies left by residents that had already died, or whether dispersing males evicted territory residents and thus hastened their demise. However, both scenarios could be consistent with the hypothesis that male–male competition limits dispersal if small males filled vacancies left by dead residents, whereas large males usurped territories from smaller neighbours. Experimental studies with *A. sagrei* have shown that the stability of territory boundaries may be mediated through the dear enemy effect (Paterson 2002; Calsbeek & Marnocha 2006) whereby neighbour recognition reduces the costs of territory defence. Moreover, removing territory residents increases rates of territory takeover by males on nearby territories (Paterson 2002). These results further support the hypothesis that dispersal by males is limited by interactions with other males.

In contrast to males, female dispersal behaviour does not appear to be constrained by intrasexual interactions. Female body size did not influence dispersal behaviour, and there was no relationship between the body size of dispersers and the former residents that they replaced. Moreover, females tended to actively disperse into areas with higher densities of females, rather than avoiding such areas. Patterns of dispersal based on local female density were similar, although not significant

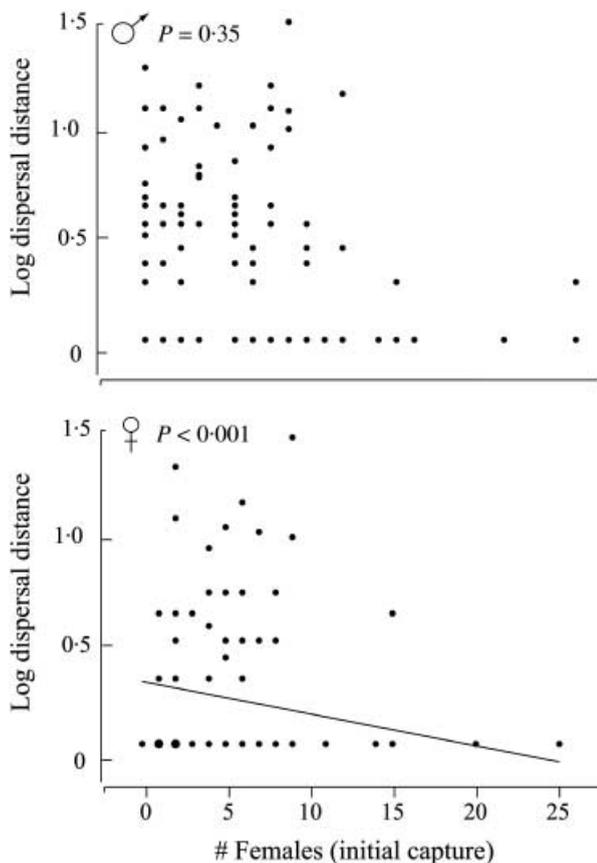


Fig. 4. Dispersal distance in females (bottom panel) was negatively correlated with the number of neighbouring females at first capture in spring, females with fewer female neighbours dispersed further compared with females that had more female neighbours. There was no significant relationship in males (top panel). The least squares regression line is for illustrative purposes only, P values come from nonparametric tests (see methods).

for males, further providing at least partial support for the idea that male movement may be influenced by competition over access to females. This suggests that certain regions of the habitat are more attractive to females, and that females in suboptimal habitats are more likely to disperse (Fig. 3). This interpretation is consistent with the hypothesis that whereas female dispersal is driven by territory quality, male dispersal is driven by differential access to females (and potentially also territory quality per se) (Brenner 1966; Brown 1969; Schoener & Schoener 1980; Calsbeek & Sinervo 2002). Although I did not attempt to quantify territory quality in this study, anecdotal evidence indicates that high quality *A. sagrei* habitat is characterized by a high degree of structural complexity (e.g., brush piles and/or dense vegetation; personal observation) that may provide an individual with ample retreat sites and greater thermal heterogeneity.

Although the literature on dispersal spans decades (Clobert *et al.* 2001) and includes a wide variety of taxa, studies that simultaneously measure dispersal distance and the selective consequences of this movement remain rare. This is because it is often difficult to differentiate between death and dispersal when an individual is not recaptured during the

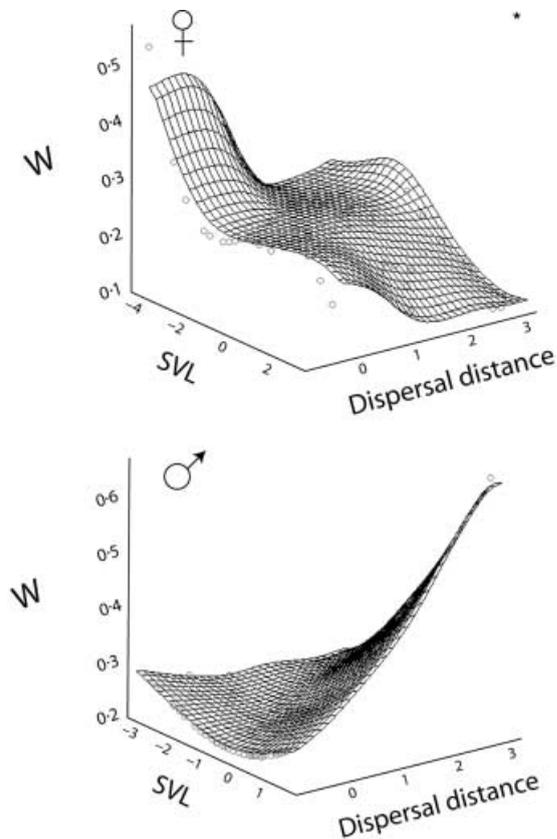


Fig. 5. Individual fitness surfaces (Schluter & Nychka, 1994) for females (top) and males (bottom) showing the interaction between body size and dispersal distance (both traits standardized) with relative survival (W). The surface for females is not significant. The * indicates data from one female that was excluded to simplify surface construction but that was included in statistical analyses. The surface for males illustrates significant multivariate selection favouring greater dispersal distances in large males. The difference in selection acting on males and females was statistically significant (see text).

course of study. This difficulty was at least partially overcome here by studying lizards on an island large enough to facilitate dispersal, but small enough to reliably track the entire population through time. A caveat however, is that for those individuals that did not survive to the fall census, it is impossible to know whether they remained philopatric or died in the act of dispersing. Thus, estimates of selection presented here should be interpreted with caution.

Viability analyses conducted over the span of a year suggest that dispersal may be a risky strategy, at least for small males. As noted above, small males were more likely than large males to disperse, but viability selection favoured small males that remained at their initial capture location (i.e., philopatry) and only favoured dispersal for larger males. Although body size had an important influence on the tendency of males to disperse, there was no overall pattern of selection on male or female body size. Thus, it is reasonable to conclude that the results presented here are not simply the spurious side effect of nonrandom survival of large versus small males. Results in females were not significant, although it is difficult to interpret this result because only about a third as many

females dispersed compared to males and the power to detect an effect in females was low.

Multivariate selection on dispersal behaviour and body size acted differently in males and females. This result is consistent with previous studies of selection acting on this system (Calsbeek & Bonneaud 2008) in which traits such as body size, stamina, and immunocompetence have all been shown to experience antagonistic selection between males and females. Genetically based traits that experience opposing selection pressures should put the genome under tension and are thought to drive the evolution of mechanisms that can resolve this sexual conflict (e.g., sex-limited trait expression, sexual dimorphism). This has been shown in a handful of other studies (Ferguson & Fairbairn 2000; Bjorklund & Senar 2001; McGlothlin *et al.* 2005) and the implications of these studies are discussed in detail elsewhere (Cox & Calsbeek 2008). If dispersal behaviour also has a genetic basis, then the results presented here add to the list of traits that may contribute to sexual conflict in *Anolis* lizards. This will be the case despite the result that dispersal behaviour was not under selection in female, because females effectively shelter dispersal genes from selection and can thus pass suboptimal trait values on to their sons.

Finally, if dispersal influences the distribution of territories and hence mate choice, then it can, as a result, influence population genetic structure (Griffiths & Magurran 1998; Sinervo *et al.* 2006). That is, the greater the proportion of individuals that disperse, or the greater the average dispersal distance between sites, the lower will be the likelihood that genetic structure will evolve within populations (Dobzhansky 1941; Mayr 1963; Endler 1986; Hendry, Taylor & McPhail 2002). By contrast, philopatric parents and their progeny may, through limited dispersal, establish genetic substructure within a population, or in extreme cases may experience a greater probability of inbreeding (Bensch & Hasselquist 1991; Olsson *et al.* 1996). Recent studies have documented extremely fine-scale genetic structure in populations of *Anolis* lizards (Ogden & Thorpe 2002). Genetic differentiation on such small spatial scales (e.g., neighbourhoods of lizards separated by less than 50 m) is surprising, and uncommon among highly mobile vertebrates. However, limited dispersal may be responsible for promoting the patterns of genetic differentiation described in these studies, and may also be a root cause of the patterns of rapid evolutionary diversification that have been widely documented in this group.

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