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Loss of assortative pairing following colonization of a new environment by Darwin's small ground finch (*Geospiza fuliginosa*)

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ABSTRACT

Organism: Darwin's small ground finch, *Geospiza fuliginosa*.

Field sites: The arid lowlands (0–100 m above sea level) and the humid highlands (500–600 m above sea level) of Santa Cruz Island, Galápagos Archipelago.

Background: Positive assortative mating tends to maintain adaptations and individual niche specialization. However, adaptations and niche specializations are not always favoured across generations. In such cases, a loss of assortative mating could increase offspring adaptive potential and thereby offspring fitness. Range expansion into a novel habitat, with novel selection pressures, presents a scenario where assortative mating may be lost via relaxed selection on mate choice.

Hypothesis: A loss of assortative mating should be favoured in the highland colonist population of *G. fuliginosa*.

Methods: We measured the beaks of 23 nesting pairs from the highland and lowland populations in January and March 2001 and 2002. We used correlation analysis to examine assortative pairing for beak length. We determined the distribution of beak lengths for females and males within each ecological zone to rule out limited mates as a mechanism for the loss of assortative pairing.

Results: As predicted, we found positive assortative pairing for beak length in the lowland source population but not the highland colonist population. In addition, we found no evidence for limited mates.

Keywords: colonization, homogamy, parapatry, reproductive isolation, selection intensity.

INTRODUCTION

Positive assortative mating (or simply assortative mating), where individuals with similar phenotypes reproduce more often than individuals with dissimilar phenotypes, is common in natural populations (Bateson, 1983; Christensen and Kleindorfer, 2007). The likely explanation for the frequent occurrence of assortative mating is that it tends to maintain heritable adaptations

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from parents to offspring (Bateson, 1983). Such adaptations may optimize resource exploitation and/or reduce interspecific competition [following individual niche specialization theory (Bolnick *et al.*, 2002)]. In this way, assortative mating can increase an individual's fitness through an increase in its progeny's fitness. Adaptations and niche specializations that have enabled individuals to reach reproductive maturity are likely to be favoured in their progeny also, while reproduction between individuals of dissimilar phenotypes may dilute these traits.

However, the same adaptations and niche specializations are not always favoured in an individual and its progeny. First-generation individuals may over-exploit resources or overcrowd niches, reducing the fitness of the second-generation individuals. In such cases, heterotypic offspring of parents with dissimilar phenotypes could exploit different or broader niches, and thereby accrue higher fitness than homotypic offspring of parents with similar phenotypes [hybrid advantage *sensu* Grant and Grant (1994, 1996)]. This scenario would favour a breakdown or loss of assortative mating with the consequence of adaptive shifts within lineages towards under-exploited resources and available niches.

A loss of assortative mating can evolve in a number of ways. First, the cues used for mate choice can break down without a change in mate preference. Second, disassortative mating can be directly selected for – as is the case in the 'over-exploited resources' scenario we have described above. Third, a loss of assortative mating can be selected for (indirect selection for disassortative mating) – as would be the case if mates were limited and phenotype matching was therefore constrained. Fourth, a loss of assortative mating could simply *not be selected against* – that is, selection on mate choice is relaxed and mate preference is allowed to drift. Under relaxed selection on mate choice, neither homotypic nor heterotypic offspring would have an advantage and would therefore have similar fitness.

Range expansion into a novel habitat is a scenario that favours the loss of assortative mating. Here, the source and colonist populations would be subject to different environments and therefore different selection regimes. Consequently, the suite of adaptations the source population possesses would not all be favoured in the colonist population. As described above, a loss of assortative mating among the colonists could increase adaptive potential within lineages. However, not all adaptations would be disfavoured because an organism is not expected to colonize a habitat for which it is not pre-adapted (Mayr, 1965; Tonnis *et al.*, 2005). Therefore, in a novel habitat both the generation of new adaptations via disassortaitve mating and the maintenance of pre-adaptations via assortative mating would be favoured leading to relaxed selection on mate choice. In fact, novel habitats may generally exert relaxed selection because they offer ecological opportunities and reduced intraspecific competition.

Darwin's small ground finch (*Geospiza fuliginosa*) on Santa Cruz Island, Galápagos Archipelago, provides an opportunity to examine differences in mating strategies between source and colonist populations. This is because (1) assortative mating is known in Darwin's finches (Grant, 1999; Huber *et al.*, 2007), and (2) *G. fuliginosa* on Santa Cruz Island underwent a recent range expansion (post-1960) from the arid coastal lowlands to the high rainfall central highlands (Bowman, 1961; Kleindorfer *et al.*, 2006; Kleindorfer, 2007; Kleindorfer and Mitchell, 2009). We think the range expansion in *G. fuliginosa* was facilitated by anthropogenic alteration to the highlands, which increased the abundance of preferred prey for *G. fuliginosa* – namely, plants that produce small seed – and the local extinction of the ecologically similar sharp-beaked ground finch (*G. difficilis*). At present, highland *G. fuliginosa* are undergoing niche expansion and showing character shifts in ecologically significant traits (beak length, foot span) (Kleindorfer *et al.*, 2006); thus, we predict that assortative mating has been relaxed in highland *G. fuliginosa*.

We focus our examination on assortment for beak length because of the adaptive significance of beak length in Darwin's finches (e.g. Bowman, 1961; Grant, 1999; Kleindorfer *et al.*, 2006), its high heritability (e.g. Boag and Grant, 1978; Boag, 1983), and its role in mate selection (e.g. Christensen *et al.*, 2006; Huber and Podos, 2006; Christensen and Kleindorfer, 2007; Huber *et al.*, 2007; but see Grant and Grant, 2008). We do not possess data on maternity and paternity, and therefore examine assortative pairing rather than assortative mating.

Following our hypothesis that assortative mating would be lost in a novel habitat, we predict that lowland *G. fuliginosa* will show assortative pairing for beak length, but highland *G. fuliginosa* will not. We test our hypothesis using correlation analysis. In addition, we compare the distribution of female and male beak length within each ecological zone to reject the hypothesis that a loss of assortative pairing in the colonist population is the result of a limited number of potential mates with similar phenotypes. We address two alternative hypotheses for a loss of assortative pairing (breakdown of mate choice cues and selection for disassortative pairing) in the Discussion.

MATERIALS AND METHODS

Study site and species

This study was conducted between January and March in 2001 and 2002 on Santa Cruz Island, Galápagos Archipelago. The arid lowlands (0–100 m above sea level) are dry-deciduous open forest dominated by Palo Santo (*Bursera graveolens*); the humid highlands (500–600 m above sea level) are evergreen closed forest dominated by scalesia trees (*Scalesia pedunculata*). *Geospiza fuliginosa* has been observed to breed in the lowland and highland zones since 2000 (Kleindorfer, 2007; Kleindorfer and Dudaniec, 2009; Kleindorfer *et al.*, 2009), but was not present in the highlands before the 1960s (Bowman, 1961).

Darwin's finches are socially monogamous (Grant and Grant, 1989). Males establish territories, construct display nests, and sing to attract females (Grant and Grant, 1989). Females visit several male territories prior to pairing (Grant and Grant, 1989; Kleindorfer, 2007). Levels of extra-pair paternity are unknown for *G. fuliginosa* on Santa Cruz Island. For medium ground finch (*G. fortis*) on Daphne Major Island, 20% of offspring were the result of extra-pair paternity (Keller *et al.*, 2001); extra-pair paternity was reported to be less than 8% in the cactus finch (*G. scandens*) (Petren *et al.*, 1999). Therefore, females may pay assortatively with the pair male, but disassortatively with the extra-pair male and vice versa, although this remains to be tested.

Analysis of assortative pairing

We used mist-netting to catch breeding pairs at active nests within four randomly allocated plots (100 × 200 m) in the lowlands and highlands. Individuals were marked with a unique combination of colour bands, which were used to confirm pairings after release. Each colour-banded individual belonged exclusively to one nesting pair. We measured beak length from the anterior edge of the right naris to the beak-tip using dial calipers to an accuracy of 0.01 mm (see Kleindorfer *et al.*, 2006).

Beak length was normally distributed, also between the sexes (Kolmogorov-Smirnov test). We measured the level of assortment in each ecological zone by calculating Pearson correlation coefficient (r_p) for female and male beak length. We tested for a significant difference between r_p by converting these values to z-scores and calculating z_{obs} using the formula outlined in Pallant (2007). A significant difference is indicated by a z_{obs} that is either less than or equal to −1.96 or greater than or equal to 1.96. In addition, we calculated Spearman rank correlation (r_s) for female beak length and the absolute value of male residuals of beak length (generated from regression analysis) to determine whether assortment was *true*, as opposed to *apparent* (Crespi, 1989; Arnquist *et al.*, 1996). True assortment, indicated by a non-significant r_s value and a symmetrical distribution around the regression line, means that females and males with short beaks are paired at the same frequency as females and males with long beaks (Arnquist *et al.*, 1996). Apparent assortment, indicated by a significant r_s value and a triangular distribution around the regression line (an increase or decrease in variance in male beak length with an increase in female beak length), means that there is a female preference for either short or long beaks in males (Arnquist *et al.*, 1996). Thus, true and apparent assortments have different evolutionary consequences. We used PASW version 18.0 (SPSS Inc., 2009) for all statistical analyses.

Analysis of beak length distribution

We used non-targeted mist-netting to assess the distribution of beak length for females and males in each ecological zone. We sampled from the same plots described above and used colour banding to avoid resampling individuals. We tested the significance of the difference in beak length between the sexes in each ecological zone.

RESULTS

Analysis of assortative pairing

We collected data from a total of 23 nesting pairs (2001, $n = 11$; and 2002, $n = 12$). Split by ecological zone, we examined data from 12 lowland pairs and 11 highland pairs. We found no significant differences in beak length within either ecological zone across years, and therefore pooled data for further analysis. As we predicted, we found positive assortative pairing for beak length in the lowlands ($r_p = 0.80$, $P = 0.006$; Fig. 1a), but not in the highlands ($r_p = 0.07$, $P = 0.847$; Fig. 1b). These r-values were significantly different ($z_{obs} = 1.99$). Assortment in the lowlands was confirmed to be true ($r_s = -0.07$, $P = 0.855$).

Analysis of beak length distribution

We collected beak length from 30 females (2001, $n = 17$; and 2002, $n = 13$) and 64 males (2001, $n = 37$; and 2002, $n = 27$) in the lowlands, and 32 females (2001, $n = 22$; and 2002, $n = 10$) and 55 males (2001, $n = 38$; and 2002, $n = 17$) in the highlands. We found no significant difference in beak length between years for data split by sex and ecological zone. A two-way analysis of variance (ANOVA) found a significant effect of ecological zone ($F = 17.54$, d.f. = 1, $P < 0.001$), but not sex ($F = 0.17$, d.f. = 1, $P = 0.682$) or the interaction term ($F = 0.01$, d.f. = 1, $P = 0.910$) on beak length. In addition, the variance around the mean beak length was not significantly different between females and males in either

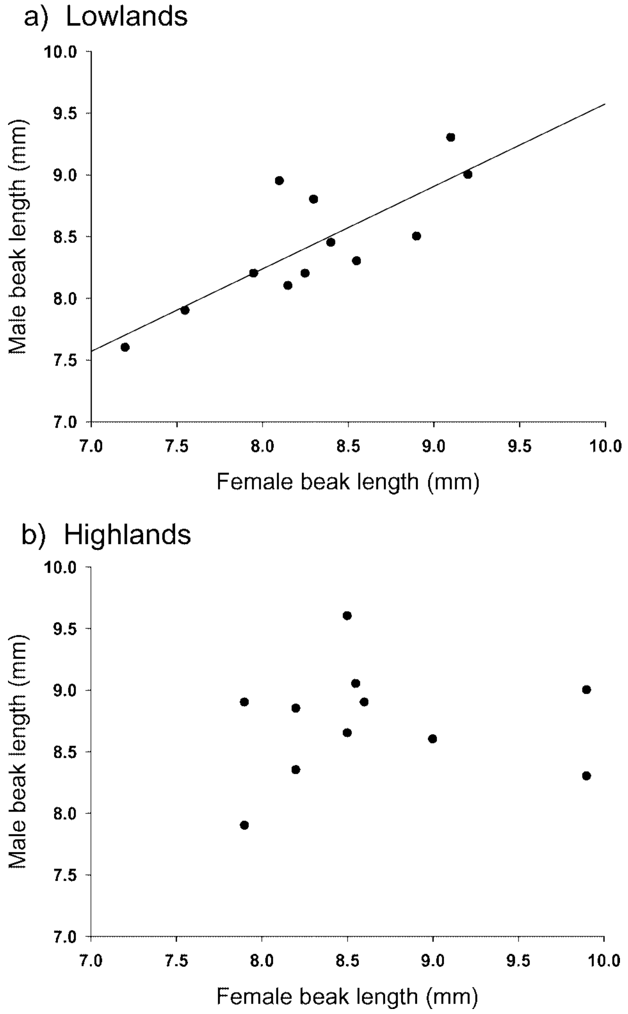
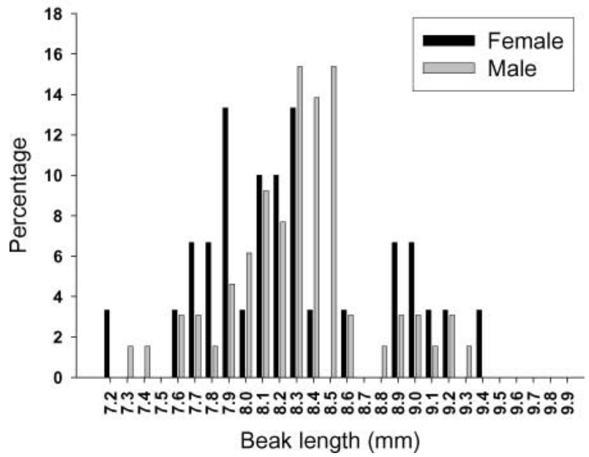


Fig. 1. The relationship between female and male beak length (mm) for breeding pairs of Darwin's small ground finch (*G. fuliginosa*) in (a) the arid lowlands and (b) the humid highlands on Santa Cruz Island, Galápagos Archipelago (2001–2002).

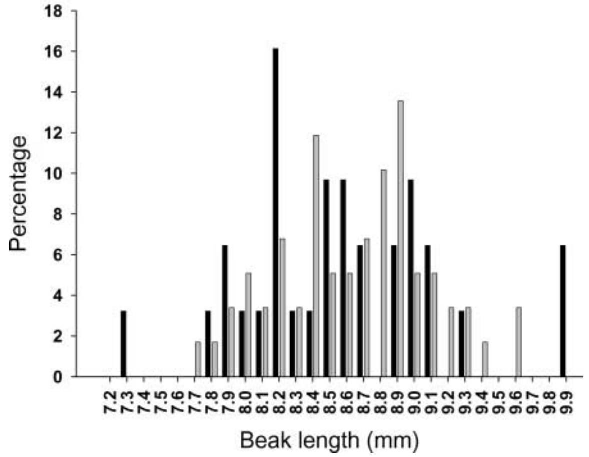
ecological zone (Levene's test: lowlands $F = 3.14$, $P = 0.080$; highlands $F = 1.83$, $P = 0.179$). Percentage distributions of female and male beak length (to an accuracy of 0.1 mm) for each ecological zone are shown in Fig. 2.

DISCUSSION

We predicted that a colonist population in a novel habitat would experience loss of assortative mating under conditions of relaxed selection for assortment. Our findings support this prediction. On Santa Cruz Island, the lowland source population of *G. fuliginosa* showed assortative pairing for beak length (an ecologically significant trait for foraging and song), whereas the highland colonist population did not. We found no



a) Lowlands



b) Highlands

Fig. 2. The distribution of beak length (mm) for female and male small ground finch (*G. fuliginosa*) sampled in (a) the arid lowlands and (b) the humid highlands on Santa Cruz Island, Galápagos Archipelago (2001–2002). Data are given as the percentage of individuals of each sex within 0.1 mm bins.

evidence that the number of potential mates of similar phenotype was a limiting factor and therefore reject this explanation for the observed loss of assortment in the highlands.

The loss of assortative mating/pairing may alternatively evolve via a breakdown of mate choice cues or direct selection for disassortative mating/pairing. We argue that neither alternative explanation is likely in the present study.

Assortative pairing may be lost through a breakdown of cues used for detecting and assessing assortment. This breakdown of cues may occur when the transmission or detection of cues is modified in the new environment (Seehausen *et al.*, 1997). In Darwin's finches, females use male morphology and song in mate choice (Grant, 1999). Experiments have shown that ground finches (*Geospiza* spp.) can discriminate conspecifics based on visual assessment of overall beak and/or body dimensions, and auditory assessment of overall song characteristics (Grant, 1999). Song characteristics (trill rate, frequency bandwidth) can reliably be used to indicate beak morphology in Darwin's finches (Podos, 2001; Christensen *et al.*, 2006). As a result, mate choice is expected to occur in two stages: first, males use song to attract females over longer distances; and second, males use morphology to attract females over shorter distances (Grant, 1999). While the more complex vegetation structure of the highland forest may impede the detection of song (Slabbekoorn and Smith, 2002), it is not expected to impede visual cues at short distances. From a mate choice perspective, it is likely that homotypic and heterotypic phenotypes are discriminated by females in the same way, and that there has been no notable change in mate choice cues in the novel habitat.

In the Introduction, we described the 'over-exploited resources' and 'novel habitat' scenarios that would favour selection for disassortative mating and relaxed selection on mate choice respectively. Direct selection for disassortative mating is not the likely cause of the loss of assortative pairing in this system. Direct selection for disassortative mating in a novel habitat would require the existence of markedly different resources and niches to those in the original habitat. In this case, source populations would have a homotypic advantage and colonist populations would have a heterotypic advantage. While we acknowledge that such a pattern is possible (given the right selection pressures), we think that a shift from assortative mating to disassortative mating during the colonization process that does not involve an intermediate stage of relaxed mate choice is highly improbable. As previously stated, colonization of a novel habitat requires colonists with pre-adaptations (Mayr, 1965; Tonnis *et al.*, 2005). These pre-adaptations may arise intrinsically, through mutation or recombination, or extrinsically, through changes in the environment, which facilitate colonization. In the present system, anthropogenic alteration to the highland zone has facilitated the invasion of mostly exotic small-seeding plants, which may have facilitated the expansion of *G. fuliginosa*, a species pre-adapted to foraging on small seeds. A diet shift in highland *G. fuliginosa* towards increased insectivory is linked with an abundance of invertebrate prey (Tebbich *et al.*, 2002) and the local extinction of the insectivorous sharp-beaked finch, *G. difficilis*, in the highlands (discussed in Kleindorfer *et al.*, 2006, Kleindorfer and Mitchell, 2009). However, seeds remain an important component in the diet of highland *G. fuliginosa* (Kleindorfer *et al.*, 2006). Therefore, the maintenance of seed-foraging pre-adaptations in some highland *G. fuliginosa*, alongside the generation of invertebrate-foraging adaptations in other highland *G. fuliginosa*, is favoured. This logic is parsimonious with the loss of assortative mating, and not selection for disassortative mating, in this system in particular and for range expansions into novel habitats in general.

The data support the idea that loss of assortative pairing was caused by relaxed selection for assortative mating in a novel habitat, given that novel habitats offer ecological opportunities and reduced interspecific competition. We suggest that the ecological contrast between the lowland and highland zones on Santa Cruz Island (and other elevated islands of the Galápagos Archipelago) has intensified the contrasting pattern of assortative and disassortative pairing observed. The arid lowlands represent a 'severe' habitat that would favour strict assortative pairing; the humid highlands represent a 'benign' habitat that would favour relaxed assortative pairing.

This difference in selection intensity between ecological zones is the product of differences in rainfall and, subsequently, food supply. During the prevailing La Niña climatic conditions on the Galápagos Archipelago – La Niña periods typically span 2–11 years (Snell and Rea, 1999) – annual rainfall in the lowland zone was less than 250 mm on average, defining it as a desert; highland rainfall was never less than 650 mm (based on records over the past decade). La Niña periods are interspersed by El Niño periods, spaning 1–2 years, which bring high rainfall to both lowlands and highlands (Snell and Rea, 1999). While we did not measure differences in food supply between ecological zones, Tebbich *et al.* (2002) showed a higher diversity and abundance of invertebrate prey in the highlands than the lowlands. Invertebrate prey constitute a large portion of the diet in *G. fuliginosa* (Kleindorfer *et al.*, 2006).

As a consequence of the ecological contrast between source and colonist population in our study, selection pressure driven by food supply is expected to be more intense in the lowlands than in the highlands. Therefore, the maintenance of tested foraging adaptations (a specific beak length) via assortative mating would be favoured in lowland *G. fuliginosa*, not only because most niches in the original habitat are expected to be filled, but because food supply is limited. In contrast, the greater number and diversity of prey and available niches in the highlands could favour deviations from tested foraging adaptations, and thereby tolerate mating between dissimilar phenotypes.

Studies that have examined beak size bimodality in populations of medium ground finches (*Geospiza fortis*) in the lowlands of Santa Cruz Island indirectly add support to our findings. At the location *El Garrapatero*, strong disruptive selection (Hendry *et al.*, 2009) and assortative pairing (Huber *et al.*, 2007) maintain divergence between small and large beak morphs. Interestingly, there was a trend for stronger assortment in years with low rainfall than years with high rainfall (Huber *et al.*, 2007), which is analogous to the arid lowlands and humid highlands in our study, respectively. Such a trend suggests that assortative pairing in Darwin's finches can be plastic and has a propensity to relax with selection pressure (as suggested here). Furthermore, at a second location on Santa Cruz Island – Academy Bay – where the environment has changed substantially as a result of anthropogenic modification, historic beak size bimodality, and presumed assortative mating in *G. fortis*, has been lost (Hendry *et al.*, 2006). Hendry *et al.* (2006) suggest that beak size bimodality (and assortative mating) may have been lost via relaxed selection in a 'more benign' environment created by humans (exhibiting a diversity of seeding plants, permanent water, direct and indirect hand-feeding, etc.). Therefore, the loss of assortative pairing in highland *G. fuliginosa* that we observed appears to be a repeatable phenomenon in finch populations that experience relaxed selection.

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