Mind the gap: genetic distance increases with habitat gap size in Florida scrub jays

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Habitat gap size has been negatively linked to movement probability in several species occupying fragmented landscapes. How these effects on movement behaviour in turn affect the genetic structure of fragmented populations at local scales is less well known. We tested, and confirmed, the hypothesis that genetic differentiation among adjacent populations of Florida scrub jays—an endangered bird species with poor dispersal abilities and a high degree of habitat specialization—increases with the width of habitat gaps separating them. This relationship was not an artefact of simple isolation-by-distance, as genetic distance was not correlated with the Euclidean distance between geographical centroids of the adjacent populations. Our results suggest that gap size affects movement behaviour even at remarkably local spatial scales, producing direct consequences on the genetic structure of fragmented populations. This finding shows that conserving genetic continuity for specialist species within fragmented habitat requires maintenance or restoration of preserve networks in which habitat gaps do not exceed a species-specific threshold distance.

Keywords: fragmentation; dispersal; gene flow; Aphelocoma coerulescens; habitat gaps

1. INTRODUCTION

Habitat fragmentation has been recognized as a major threat to biodiversity [1,2]. One of its consequences on landscape structure is the generation of gaps that separate habitat patches. Depending on the spatial scale at which these gaps occur, foraging and/or dispersing organisms may have to cross them in order to find energetic resources and/or a place to breed. Habitat gaps can be more or less hostile to moving organisms, depending on the biotic and abiotic characteristics of the gaps, and on the movement abilities and the degree of specialization of the organisms. Modelling studies have suggested that gap structure might be more important than patch structure in determining dispersal success in a landscape [3]. A number of studies, mainly involving birds, have used behavioural experiments to investigate how gap characteristics affect gap-crossing decisions and movements. They have shown that gap-crossing probability often decreases gradually with gap width, until a maximum distance above which individuals will not cross [4]. How these effects on movement behaviour in turn affect the genetic structure of the populations is less clear. Because gene flow depends on dispersal movements, gaps ought to affect the genetic structure of populations, and these effects ought to be inversely correlated with gap width, but field documentation of this relationship remains lacking [5]. We tested this hypothesis for the Florida scrub jay (FSJ, Aphelocoma coerulescens), a species potentially highly sensitive to fragmentation because of its low dispersal abilities and high degree of habitat specialization [6,7].

2. MATERIAL AND METHODS

For range-wide analyses, we drew blood samples from FSJ s throughout peninsular Florida between 1999 and 2006. Among the full set of samples, we selected paired groups of individuals that had been sampled from adjacent habitat patches separated by natural habitat gaps of various sizes. We limited our selections to cases in which gaps were naturally present and unmodified at least since the early 1900s according to aerial photos, and most probably much longer, as evidenced by soil maps. Limiting the analysis to natural gaps avoids potential effects of delays between human-imposed landscape changes and their subsequent outcome on genetic structure. Soil type is an excellent predictor of vegetation type, and this is especially true for the xeric-sand soils that support FSJ habitat [8,9]. We delineated naturally occurring oak scrub distributions based on county soil lists and maps using a geographic information system (GIS). Having identified all natural gaps separating groups of sampled individuals, we used post-2000 aerial photographs to select all those cases in which the original gaps were still naturally present in the current landscape.

DNA was extracted from the blood samples and the individuals were genotyped at 20 microsatellite loci previously developed for the FSJ (see Stenzer & Fitzpatrick [10], Coulon et al. [11]).

To test for the effect of gap sizes on gene flow among groups of individuals, we performed multiple linear regression of genetic distances between the groups on the natural logarithm of Euclidean distance between the centroids of each of the two sampled groups (function lm from the 'stats' package in R [12]). We included Euclidean distance in the regression in order to control for its potential confounding effect with gap size on genetic differentiation. We ln-transformed the geographical distances in order to linearize their relationship with genetic distances and make them more suitable to linear regression. Because they are recognized as probably the most reliable estimators of population genetic distances [13], we estimated FST between groups with Genalex [14] (Weir and Cockerham's estimator, 1000 permutations). Gap size was measured using ArcGIS v. 9.1 (ESRI), as the shortest distance between the edges of the habitat patches in which the two groups of individuals were sampled. Euclidean distance was represented by the linear distance between the geographical centroids of the groups. We selected the best statistical model explaining the genetic distances between groups, through a stepwise backward selection procedure starting with the most complex model that included Euclidean distance, gap size and their interaction. As a comparison, we also performed a linear regression of genetic distances on the natural logarithm of geographical distances between groups of individuals living in areas in which the habitat is continuously distributed. We chose pairs of groups separated by the same range of distances as those used in the previous analyses.

3. RESULTS

We sampled 18 pairs of groups of individuals whose populations were separated by natural habitat gaps of various sizes (min = 600 m; max = 31.8 km; mean = 7.2 km; electronic supplementary material, S1, S2 and S4). Sample sizes averaged 22.3 individuals per site (min = 5; max = 80; s.d. = 16.1), for a total of...
579 individuals, most of them (560/579) sampled between 2003 and 2006 (electronic supplementary material, S3). Sixteen of the 18 $F_{ST}$ values were significant at the 5 per cent threshold (electronic supplementary material, S4). Genetic distances between the groups were significantly correlated with the size of the gaps separating them ($p < 0.001$; $r^2 = 0.48$; $F_{1,16} = 16.62$; figure 1). This correlation did not result from a confounding effect of the geographical distances between the groups: genetic distance was not significantly correlated with Euclidean distance ($p = 0.12$; $r^2 = 0.09$; $F_{1,16} = 2.77$; figure 1). The stepwise backward selection procedure selected the model including gap sizes only (tables 1 and 2).

If gap size was negatively correlated with patch area, it would be possible that our results are confounded by higher drift in smaller patches (i.e. the finding that larger gaps are associated with higher genetic distances could be owing either to decreased gene flow or to increased genetic drift). However, such a confounding effect does not exist since we found no negative correlation of patch area with gap size (electronic supplementary material, S5).

We sampled 13 pairs of groups not separated by habitat gaps (electronic supplementary material, S1). The correlation between their genetic and geographical distance was somewhat higher, though still not significant ($p = 0.08$; $r^2 = 0.18$; $F_{1,11} = 3.7$; figure 2), and far lower than the correlation between genetic distance and gap size of the groups separated by gaps.

4. DISCUSSION
The body of literature describing deleterious effects of habitat fragmentation on the population biology of organisms has been growing dramatically over the past two decades. Recently, landscape genetics [15] has played a major role in this area [6,16,17].

Table 1. Results of the stepwise regression of genetic distances on the ln of gap sizes and on the ln of Euclidean distances.

<table>
<thead>
<tr>
<th></th>
<th>ln Euclidean distance</th>
<th>ln gap size</th>
<th>ln Euclidean distance × ln gap size</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st model</td>
<td>$F$</td>
<td>4.539</td>
<td>11.210</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>0.051</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>$r^2$</td>
<td>0.323</td>
<td></td>
</tr>
<tr>
<td>2nd model</td>
<td>$F$</td>
<td>4.524</td>
<td>11.173</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>0.050</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>$r^2$</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td>3rd model</td>
<td>$F$</td>
<td>2.770</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>0.116</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$r^2$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4th model</td>
<td>$F$</td>
<td></td>
<td>16.623</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>&lt;0.001</td>
<td></td>
</tr>
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</table>

Table 2. Characteristics of the model selected with the stepwise procedure.

<table>
<thead>
<tr>
<th></th>
<th>estimate</th>
<th>s.e.</th>
<th>$t$</th>
<th>$p$</th>
</tr>
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<tbody>
<tr>
<td>intercept</td>
<td>0.011</td>
<td>0.009</td>
<td>1.148</td>
<td>0.268</td>
</tr>
<tr>
<td>ln gap size</td>
<td>0.020</td>
<td>0.005</td>
<td>4.077</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

However, relatively few studies provide quantitative information about the processes underlying these responses [18]. Here, we used naturally separated habitat fragments to examine a key process by which fragmentation affects population functioning: the effects of habitat gaps on movement probabilities, through the analysis of their consequences on gene flow. We showed that in the FSJ gene flow decreases dramatically as gap size increases.
Our results are surprising on two counts. First, the range of gap sizes we tested required only relatively short distances to cross, yet their effects on gene flow were significant. This indicates a remarkably low ability to traverse suboptimal habitat successfully (i.e. reproduce in new patch after crossing), reflecting the extreme level of habitat specialization in this species and underscoring this trait as a source of extreme vulnerability from a conservation perspective. Second, we found that the effect of gaps is far stronger than the effects of genetic isolation by distance characterizing populations inhabiting continuous habitat. Moreover, a low (however not significant) signal of isolation by distance existed by gap size in contiguous areas, whereas it was absent in fragmented areas. Those two points suggest that gaps are more important than distance per se in determining population genetic structure, in this species and perhaps in any species for which suboptimal habitat strongly inhibits dispersal movements.

Our results are concordant with previous studies showing that gap-crossing probabilities in birds and small mammals tend to decrease when gap size increases [4,19]. We point out, however, that the spatial scale of those behavioural experiments was much lower (tens to hundreds of metres) than in our study (up to 32 km). Moreover, most of those studies examined non-dispersal movements (i.e. movements within the home range, or homing movements following an experimental release in a patch different from the capture patch). Our study shows that, at least for the FSJ, the effects of gaps on movement behaviour can be generalized to larger scale movements such as natal dispersal, and have consequences on the genetic structure of populations.

Some species exhibit a threshold gap size above which probability of movement abruptly decreases [4]. Our study did not directly address this question, but several tests for nonlinearity of the relationship between $F_{ST}$ and gap size, using both ln-transformed and raw values for the latter, yielded no evidence for a threshold gap size. We do note that low $F_{ST}$ values (less than 0.032; electronic supplementary material, S3) across gap sizes below about 2–3 km suggest that gaps smaller than this distance are treated by FSJs as functionally contiguous habitat.

Our study provides clear guidance for landscape management in the effort to stem the rapid decline of FSJs. Habitat gaps of even a few kilometres inhibit dispersing jays from colonizing from one population to another, thereby increasing the probabilities of local extinctions from demographic stochasticity, loss of genetic variability, or both. Therefore, minimizing gap sizes is a crucial priority for conserving this species. While gaps even as short as 600 m may reduce dispersal somewhat, we suggest that patches separated by less than 2.5 km may be treated as functionally contiguous for purposes of preserve networks.

Blood was collected under permits and the approval of Archbold Biological Station’s Institutional Animal Care and Use Committee.

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