Distinguishing individual quality from habitat preference and quality in a territorial passerine

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Abstract. Theory predicts that animals breeding in heterogeneous landscapes preferentially occupy habitats likely to maximize individual fitness, but identifying those habitats has proved problematic. Many studies develop metrics of habitat quality linked to site-specific reproductive output measured in successive years, but few separate the independent effects of individual “intrinsic quality” from those due solely to the attributes of the habitats themselves. In many populations, processes such as competitive territory defense, longevity, site-fidelity, and variation in breeding density and territory size over time have the potential to limit the degree to which individual and habitat quality will be positively related in nature. However, the effects of these processes on estimates of habitat or site-specific reproductive output have not been thoroughly investigated. We show that, in an insular population of Song Sparrows (Melospiza melodia), females nested preferentially in breeding sites with high mean reproductive output assessed over 35 years, and that variation in site-specific reproductive output was positively related to female intrinsic quality, measured here as the lifetime reproductive success of individual females relative to others hatched the same year (rLRS). In contrast, vegetation traits (shrub cover, edge, and soil depth) predicted female preference for breeding sites but did not predict site-specific variation in annual reproductive output. Female quality also did not predict which females occupied more- or less-preferred breeding sites over the study period. However, mean annual reproductive output of breeding sites estimated over 35 years was strongly positively related to the quality of the females that nested in them. Overall, these results indicate that site-specific estimates of habitat quality that do not consider the quality of the individuals occupying those sites may include substantial bias due to variation in occupant quality, and thus may not reliably predict the intrinsic effects of habitat quality on individual or population fitness.

Key words: habitat preference; habitat quality; individual quality; Mandarte Island, British Columbia, Canada; Melospiza melodia; relative lifetime reproductive success; site-specific reproductive output; Song Sparrow.

INTRODUCTION

Theory suggests that habitat quality plays a key role in regulating animal populations (Andrewartha and Birch 1954, Fretwell and Lucas 1970) and that individuals preferentially occupy habitats likely to confer high relative fitness (e.g., Dhondt et al. 1992, Clark and Shuttle 1999, Gunnarsson et al. 2005, Mills 2005). However, despite decades of study, we still lack consensus on how to measure habitat quality or its influence on individual animals (Johnson 2007). Problems arise because habitat quality is often estimated by indices of vegetation structure or productivity that have uncertain links to individual fitness (Johnson 2007), and because comparisons of observed fitness across habitat gradients often fail to identify and separate the independent effects of the quality of individuals from the quality of the habitats they occupy (Sergio et al. 2009). We used a 35-year study of an insular Song Sparrow (Melospiza melodia) population to estimate correlations between habitat preference and habitat quality, and to ascribe the relative contributions of habitat quality, age, and individual female intrinsic quality (defined here as relative lifetime reproductive success; rLRS) to habitat-specific reproductive output.

It is widely assumed that habitat quality is reflected in occupancy rate and/or reproductive performance in focal species. Occupancy can be a compelling proxy for habitat quality when compiled over long periods (Sergio and Newton 2003), but is also criticized because its underlying assumption, that individuals preferentially occupy habitats that confer high relative fitness, is often false (Van Horn 1983, Bock and Jones 2004, Arlt and Pärt 2007, Rodewald et al. 2011). Another approach is to use habitat-specific estimates of reproductive output to estimate habitat quality directly (Johnson 2007). For example, in Pied Flycatchers (Ficedula hypoleuca) breeding-site selection was manipulated by relocating nest boxes of newly formed pairs and measuring fitness.
proxies to assess habitat quality at control and relocation sites (e.g., Siikamäki 1995, Huhta et al. 1999, Thomson et al. 2012). However, because we can expect positive correlations between individual and habitat quality when developmentally or intrinsically superior individuals settle preferentially in the most productive sites (Fretwell 1972, Lomnicki 1988), it has proved challenging to separate the independent effects of individual quality vs. habitat quality in natural settings (Sergio et al. 2009).

Further complicating this issue, the term “individual quality” can be ambiguous or inconsistently applied (Wilson and Nussey 2010). For example, studies that contrast individual and habitat quality often use cross-sectional data and equate age with quality (e.g., Balbontín and Ferrer 2008). However, because reproductive success tends to increase and decrease with age across a wide range of taxa (reviewed in Nussey et al. 2008), this definition implies that individual quality varies temporally. In contrast, quantitative genetic theory implies that individual quality is better estimated as the permanent environmental and genetic effects of phenotype on survival and reproductive success, which is consistent with its characterization as a repeatable, intrinsic trait of individual animals that is positively related to relative fitness (Arcese 2003, Steele and Hogg 2003, Kruuk 2004, Wilson and Nussey 2010, Bergeron et al. 2011). However defined, estimating the independent contributions of individual and habitat quality to site-specific annual reproductive output requires that reliable metrics of habitat and individual quality are available, and that the processes acting to distribute animals across focal habitats and the relationships between individual and habitat quality are known.

We used 2543 breeding records by 528 female Song Sparrows (Melospiza melodia) over 35 years to quantify long-term preference for individual breeding sites on Mandarte Island, British Columbia, Canada, and to test if the long-term mean and annual reproductive output assessed in preferred sites was predicted better by the vegetation traits measured in those sites or the mean rLRS or age of the females that nested in them annually or on average. Specifically, we asked the following questions. (1) Were breeding sites occupied nonrandomly by females across the study period? (2) Did preferred breeding sites produce more offspring on average? (3) Were preferred breeding sites occupied primarily by prime-age females or those displaying high rLRS, on average? (4) Could female preference for particular breeding sites be predicted by the vegetation traits measured in those sites? (5) What were the relative contributions of female age, rLRS, and site-specific vegetation traits to annual variation in site-specific reproductive output measured over 35 years?

The population of Song Sparrows resident on Mandarte Island is ideally suited to these questions because more than 98% of the birds breeding there after 1975 were hatched locally, individually marked as nestlings, and resighted thereafter to quantify lifetime fitness (e.g., Smith et al. 2006c, Sardell et al. 2012). Moreover, because female population size has varied widely (4–71 females) over time, the area of habitat used by nesting females is limited in extent and described in detail, territory ownership is dynamic in both sexes, and individual differences among birds affect territory tenure, there exists the potential for many different females to have nested in many different breeding sites, and for most breeding sites to have been occupied by many different females over 35 years of study (Arcese 1987, 1989a, b, Smith et al. 2006a).

**Methods**

**Study system**

Song Sparrows are an archetypal, open-cup nesting passerine species in which females alone incubate eggs and both parents provide care for young (Arcese et al. 2002). The resident, individually marked population of Song Sparrows on Mandarte Island (6 ha) has been monitored in detail since 1975 (Smith 2006) by recording the life histories of all locally hatched birds (99% of all breeders, on average) that recruit to the population for survival and reproductive output over their lifetimes. Song Sparrows are socially monogamous but genetically polygamous (Sardell et al. 2010). Both sexes engage in sometimes protracted contests for breeding sites, and individual phenotype can predict the outcome of these contests (Arcese 1987, 1989a, b). Once settled, Song Sparrows typically breed within a neighborhood of adjacent sites on Mandarte Island (Smith et al. 2006a). However, because territory size varies inversely with the number of adults on the island (Smith et al. 2006a), the range of sites available to any individual female depends mainly on population size.

Each year all nests were located using a coordinate system based on an aerial photo, composed of 157 grid cells (20 × 20 m each) representing potential nesting habitat (i.e., including grass and/or shrub cover), which we define as “breeding sites.” Habitat preference and quality were estimated at the scale of grid cells instead of “territories” because grid cell location was static over the study, whereas territory size varied dramatically and inversely to population size (Smith et al. 2006a). We focused on 146 breeding sites with at least one known nesting attempt between 1975 and 2010, but excluded estimates of reproductive output for nests potentially influenced by feeding experiments in 1979 (n = 65), 1985 (n = 85), and 1988 (n = 113) due to the demonstrated effects of supplemental food on reproduction (Arcese and Smith 1988).

**Breeding site use**

To estimate breeding site use and preference by female sparrows, we used ArcMap (ESRI 2006) to map the locations of 2543 nests with one or more eggs to a resolution of ~2.5 m. We then created 100-m² circular buffers around each nest to define the “nest area,” under
the assumption that buffers reflect habitat used intensively by the parents and offspring associated with each nesting attempt. We then used Hawth’s Tools (Beyer 2004) to allocate a proportion of each 100-m² nest area to each breeding site that it intersected (i.e., overlap in square meters). Allocated in this way, each nest area overlapped 1–4 breeding sites, depending on its location near the center of a site or intersection of adjacent sites.

Estimates of habitat preference

We quantified habitat preference as the number of years a breeding site included at least some fraction of one nest area, and also by calculating the fraction of all nest areas in a year that overlapped a given breeding site. We then calculated the mean fractional use by females of all breeding sites in all years to create a long-term metric of female preference for particular sites, defined here as “habitat preference.”

Estimates of annual reproductive output per breeding site

We used the number of offspring that survived to independence from parental care (~24 d after hatch) as the metric of reproductive output for each mapped nest. To estimate annual reproductive output at individual breeding sites, we distributed independent young from each nest to one or more sites in proportion to overlapping nest area. Because annual reproductive success on Mandarte varies with breeding density (Arcese et al. 1992), climate (Wilson and Arcese 2003), weather (Marr et al. 2006), and Cowbird parasitism (Arcese et al. 1996), we also standardized reproductive output at each occupied breeding site in each year using Z scores:

\[
\frac{R_{\text{site}}} - \mu_t}{\sigma_t}
\]

where \(R_{\text{site}}\) represents the total yearly reproductive output of a site (yearly sum of reproductive output of each nest in a breeding site, proportional to nest area overlap) in year \(t\), and \(\mu_t\) and \(\sigma_t\) represent the mean and standard deviation of reproductive output for all occupied sites in year \(t\). Thus, our final data set included one estimate of the reproductive output of each occupied breeding site in each year.

Estimates of female quality per breeding site: age and rLRS

We assessed individual female quality in two ways: as a developmental trait, female age (years since hatch) and as an intrinsic trait of females, their lifetime number of independent young, relative to other females hatched in the same year (relative lifetime reproductive success; rLRS). The mean age of females observed in each breeding site annually was calculated as female age, weighted by fraction of each female’s nest area overlapping the site. We then standardized annual mean values to reduce the influence of age structure of the population on annual estimates of reproductive output (Smith et al. 2006c). Females of unknown age in 1975 were considered to belong to a single hatch-year cohort \((n = 34)\). As with mean age and annual reproductive output of breeding sites, we then calculated the annual weighted mean rLRS of females with a nest area overlapping the breeding site, and standardized those values by the annual mean and SD of all occupied sites.

Vegetation characteristics of breeding sites

To examine the vegetation characteristics of breeding sites, we selected a number of predictors believed to be related to Song Sparrow habitat preference in our study system. More than 99% of nests occur in or adjacent to shrubs on Mandarte Island (Smith 2006). Thus, in 1986 and 2006, we surveyed each breeding site to record the total area (m²) of shrub cover, as well as the cover (m²) of the nine most common shrubs occurring on the island (snowberry [Symphoricarpos albus], Nootka rose [Rosa nutkana], serviceberry [Amelanchier alnifolia], Pacific willow [Salix lucida], trailing blackberry [Rubus ursinus], Himalayan blackberry [Rubus armeniacus], currant [Ribes divaricatum], oceanspray [Holodiscus discolor], and red elderberry [Sambucus racemosa]), each of which may be subject to preference/avoidance by Song Sparrows as a potential nesting substrate. In addition, we surveyed the linear distance (m) of shrub/grass interface (“edge”) in each breeding site as Song Sparrows typically prefer to nest in edge habitat (Arcese et al. 2002). We also measured the mean soil depth (cm above rock) and shrub height (m) at five evenly spaced points in each breeding site, as these predictors may reflect microhabitat variation related to the size or age of shrubs not accounted for by the total shrub area or shrub species composition of a breeding site. We then averaged estimates from each survey (1986 and 2006) to describe “vegetation traits” at each site.

Statistical analysis

Long-term patterns in habitat preference and quality.—Analyses were performed in R 2.15.1 (R Development Core Team 2012). We used Pearson’s chi-square to test if sparrows nested randomly with respect to breeding site location across years by comparing the distribution of the number of years a site was occupied vs. expected values generated from the Poisson distribution, and pooling the number of years a site was occupied into 14 categories \((\leq 12, 13, 14, \ldots, 23, 24, \geq 25)\) with expected frequencies greater than 5 to meet the assumptions of the \(\chi^2\) statistic. We used the “ncf” package (Bjornstad 2009) to test for spatial autocorrelation in habitat preference using Moran’s \(I\), which calculates the summed covariance from each sampling location at a given distance, divided by the number of location pairs, to estimate spatial autocorrelation (Fortin and Dale 2005). However, none was detected beyond 20 m (i.e., the width of one breeding site; Moran’s \(I < 0.2\) for increments over 20 m). Estimates of habitat preference
were then normalized by square-root transformation and used as the dependent variable in linear analyses to test if breeding sites occupied in a greater number of years were also occupied preferentially.

To test if preferred breeding sites also produced more offspring, on average, we used a random-effects model with breeding site identity as a random factor to calculate a best linear unbiased predictor (BLUP) of the standardized reproductive output of each site over all years, and then used linear regression to test if site-specific reproductive output increased with habitat preference. We then repeated this procedure for female age and female rLRS to test if breeding site preference was predicted by the age or intrinsic quality of its female occupants. BLUPs are to be used with caution in populations where many individuals have few observations (or a single observation) for traits under investigation (e.g., Hadfield et al. 2010). In our application of BLUPs to estimate breeding site quality, we observed all breeding sites in all years to precisely estimate the proportion of all nests in each breeding site in each year.

To identify the vegetation traits that characterized preferred breeding sites, we adopted an information-theoretic (IT) approach and used linear multiple regression with habitat preference as the response variable and 11 site-specific vegetation traits as predictors (all related at r ≤ 0.7: shrub area, edge, soil depth, rose, serviceberry, oceanspray, willow, trailing blackberry, Himalayan blackberry, elderberry, and currant). Each species of shrub in this predictor set formed the substrate of at least one Song Sparrow nest over the 35 year study. In total, we ran 2048 models (all possible combinations of 7 predictor variables excluding interactions), and selected those with partial support as predictors (Anderson 2002). We chose a cutoff of ΔAIC ≤ 7 rather than ΔAIC ≤ 2 to incorporate all models that fall within the range of plausibility described by Burnham and Anderson (2002) and Burnham et al. (2011). We ran models from this subset again to recalculate relative AIC weights and to assess the relative support for each predictor by summing its AIC weight for each model in which it was included. Relative support for predictors ranged from 0 (absent from all models) to 1 (present in all models); we included all those with ≥0.5 relative support as potential predictors of habitat preference.

Contributions of habitat vs. individual quality to reproductive output.—Our data consisted of 2741 observations of the annual reproductive output of breeding sites overlapped by one more nest areas in that year. To estimate the relative contributions of female and habitat quality to observed variation in annual reproductive output at a breeding site, we again applied an IT approach, linear mixed-effects models, and model averaging. Specifically, we used standardized annual reproductive output at a breeding site as the response variable and breeding site identity as a random effect. As predictors, we included total nest overlap (TNO; the annual fraction of all nest areas that overlapped a site) to estimate what fraction of annual variation in site-specific reproductive output was accounted for solely by the sum of nest area overlap in a site and year. We did so because we expect that if female settlement were random across sites with respect to rLRS or age, the total overlap in a site would account for most of the variation observed in relative reproductive output between years, and thus would reflect only the shared preference of females for a site rather than the mean phenotype of females nesting there. We also included mean age and rLRS, the interaction of these variables with total nest overlap, and four vegetation traits with relative support ≥0.5 (see Results) because these were our main predictors of interest. Vegetation traits and total nest overlap were standardized to mean = 0, SD = 1 to reduce any influence of measurement scale (White and Burnham 1999). Because equal numbers of observations are required to compare AIC in competing models (Burnham and Anderson 2002), we pruned our data set to a sample of 2555 observations across 144 breeding sites by excluding females of unknown age. We ran a tailored model set of 208 models (all possible combinations of 7 predictor variables plus age × TNO and rLRS × TNO interaction terms) and estimated parameters by averaging models with ΔAIC ≤ 7 from the best model, following Burnham and Anderson (2002).

Results

Occupied breeding sites had 2.5 ± 1.6 overlapping nest areas annually over 35 years (all values given as mean ± SD), with an overlap of 95.6 ± 93.4 m² per year. Individual female sparrows bred a mean of 2.2 ± 1.4 years, and occupied 12.7 ± 9.8 breeding sites over their lifetimes. Females in a given cohort produced a total of 6.46 ± 3.17 independent offspring over their lifetimes.

Long-term habitat preference and habitat quality

Female Song Sparrows nested nonrandomly with respect to breeding site location over 35 years (Fig. 1), and the number of years a site was occupied was strongly positively related to habitat preference, indicating that sites occupied in more years were also more densely overlapped by female nest areas, on average (Fig. 2). Breeding site identity accounted for 19.8% of the observed variance in reproductive output over 35 years (Table 1), indicating modest repeatability in the performance of sites across years. Preferred breeding sites also displayed high average reproductive output (Fig. 3a). In contrast, breeding site identity accounted for only 2.3% of variation in the mean age of females whose nest areas overlapped the site, and only 5.4% of variation in mean female rLRS (Table 1). Neither female age nor rLRS was related to habitat preference (Fig. 3b, c).

Vegetation traits in preferred habitat

A global model of vegetation traits in preferred breeding sites was a good fit to the observed values of
habitat preference ($R^2 = 0.78$). Of 2048 total models (see Methods), 261 were within $\Delta\text{AIC} \leq 7$ of the best model and summed to a cumulative AIC weight of 0.90. This subset included four traits with strong support as predictors of habitat preference (Fig. 4): edge, shrub area, and soil depth (positive predictors), and service-berry cover (negative predictor; see Supplement for parameter estimates and standard errors for all models in this subset). Only edge and total shrub area were included in all 262 subset models.

**Contributions of habitat and individual quality to reproductive output**

A global model of female- and habitat-specific contributions to reproductive output at a breeding site was moderately well fit to the observed values of site-specific reproductive output ($R^2 = 0.55$). Of 208 original models, two were within $\Delta\text{AIC} \leq 7$ from the best model, and the cumulative AIC weight of all three models in this subset was 0.94. Variables included in one or more of these models were total nest overlap (TNO), age, rLRS, edge, and the interaction of age $\times$ TNO and rLRS $\times$ TNO (Table 2). AIC weights for this model subset and model averaging indicated that TNO, rLRS, and the interaction rLRS $\times$ TNO emerged as strongly supported predictors of the annual variation in reproductive output of breeding sites (Table 2). Edge, age, and age $\times$ TNO were relatively weak predictors of site-specific reproductive output (Table 2). In particular, rLRS was 2.8 times more influential in predicting site reproductive output than female age, and 85 times more influential than edge, the only vegetation trait that emerged as a predictor from our IT approach.
Female Song Sparrows preferentially nested in breeding sites that produced high relative numbers of young, on average. However, because the number of breeding females varied from four to 71 over 35 years (Smith et al. 2006b), most breeding sites were occupied by a wide range of females with respect to age and rLRS. Annual variation in the reproductive output of breeding sites was strongly predicted by the mean rLRS of females that occupied the site, but was not closely related to vegetation traits or mean female age in sites. Nevertheless, vegetation was a good predictor of long-term preference for high-quality breeding sites by female Song Sparrows. Thus, while habitat preference and quality were positively related, on average, annual reproductive output at particular breeding sites was mainly a consequence of the rLRS, or quality, of the females that occupied them. We will now address our earlier questions and discuss the implications of our finding that individual quality and habitat preference were not positively related.

Female Song Sparrows strongly preferred particular breeding sites over the 35-year period, leading to nonrandom patterns of site occupancy (Fig. 1). Sergio and Newton (2003) concluded that birds occupied breeding habitat nonrandomly in all 22 studies and 17 species included in a review of site occupancy as a

**Table 1.** Role of breeding site identity in three random-effects models partitioning variation in site-specific reproductive output, female age, and female rLRS of Song Sparrows on Mandarte Island, British Columbia, Canada.

<table>
<thead>
<tr>
<th>Model and response</th>
<th>Variance component</th>
<th>SE</th>
<th>Percentage of variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproductive output</td>
<td>Site identity</td>
<td>0.20</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>0.80</td>
<td>0.90</td>
</tr>
<tr>
<td>Age</td>
<td>Site identity</td>
<td>0.02</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>0.97</td>
<td>0.99</td>
</tr>
<tr>
<td>Female rLRS</td>
<td>Site identity</td>
<td>0.05</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>0.95</td>
<td>0.03</td>
</tr>
</tbody>
</table>

*Note:* For reproductive output and female rLRS (relative lifetime reproductive success), n = 2740 observations across 146 breeding sites; for female age, n = 2555 observations across 144 breeding sites.

**DISCUSSION**

Female Song Sparrows preferentially nested in breeding sites that produced high relative numbers of young, on average. However, because the number of breeding females varied from four to 71 over 35 years (Smith et al. 2006b), most breeding sites were occupied by a wide range of females with respect to age and rLRS. Annual variation in the reproductive output of breeding sites was strongly predicted by the mean rLRS of females that occupied the site, but was not closely related to vegetation traits or mean female age in sites. Nevertheless, vegetation was a good predictor of long-term preference for high-quality breeding sites by female Song Sparrows. Thus, while habitat preference and quality were positively related, on average, annual reproductive output at particular breeding sites was mainly a consequence of the rLRS, or quality, of the females that occupied them. We will now address our earlier questions and discuss the implications of our finding that individual quality and habitat preference were not positively related.

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**Fig. 3.** Relationships between habitat preference and site-specific reproductive output, the mean age of females occupying the site, and the relative lifetime reproductive success (rLRS) of the individual females that initiated those nests. All response variables were standardized at each occupied breeding site in each year using Z scores. Habitat preference was positively related to (a) the reproductive output of a breeding site ($R^2 = 0.63$, $F_{1,144} = 242.53$, $P < 0.0001$), but unrelated to (b) the mean age of females that nested in those sites ($R^2 = 0.0006$, $F_{1,142} = 0.09$, $P = 0.76$) or (c) their mean rLRS ($R^2 = 0.02$, $F_{1,144} = 2.20$, $P = 0.14$).
measure of quality, indicating that habitat preference may act as a reliable proxy for habitat quality. In contrast, several studies report nonideal patterns of habitat occupancy, wherein individuals preferentially occupy sites with low reproductive output (i.e., “ecological traps”; Van Horne 1983, Bock and Jones 2004, Arlt and Pärt 2007, Rodewald et al. 2011). On Mandarte Island, habitat preference by female Song Sparrows was positively related to long-term, site-specific reproductive output (Fig. 3a), indicating that habitat preference in this system is adaptive. Adaptive habitat preference is posited in many systems (e.g., Southwood 1977, Lurz et al. 1997, Clark and Shutler 1999), but relatively few studies estimate the components of variation in site-specific reproductive output that are a consequence of variation in the quality of the animals that occupy them annually or over longer periods. Our results suggest that where individual quality is not easily estimated, site-specific estimates of reproductive output based on short time frames (relative to the longevity or site fidelity of its occupants) cannot be assumed to represent a repeatable trait of sites that will be conferred to different occupants.

We found that preference for individual breeding sites by female Song Sparrows was not closely related to the mean age or rLRS of the females that occupied them (Fig. 3b, c). This indicates that the ability of females to settle in preferred breeding sites was largely independent of their age or intrinsic quality, measured as rLRS. These results are in contrast to the idea of “Resource Holding Potential” (Parker 1974), which assumes a positive correlation between habitat preference and individual quality as an outcome of contest competition and individual variation in competitive ability (see also Fretwell 1972, Lomnicki 1988). Although many studies report that adults or socially dominant individuals regularly restrict access by young or subordinate animals to resource-rich habitats (e.g., Arcese and Smith 1985, Petit and Petit 1996, Marra 2000, Buston 2003, Clutton-Brock et al. 2006, Wittemyer et al. 2007), few studies use longitudinal data to quantify variation in habitat use over an individual’s lifetime, or to identify repeatable indices of habitat quality that are closely linked to individual fitness (but see Pärt 2001, Reid et al. 2006). On Mandarte Island, breeding site acquisition and loss depends in part on transient aspects of individual phenotype that are related to development (e.g., maturation, senescence, learning, experience), leading to frequent turnover in site ownership (Arcese 1987, 1989a, b). Female numbers also varied greatly over 35 years, allowing all females to breed in high-quality sites at low density, but preventing many high-quality females from access to those same sites at high density, because the year-round nature of territoriality in this population limits opportunities for the reassortment of females annually (Keller and Arcese 1998). As a consequence, strong correlations between habitat preference and female rLRS did not develop.

Four of 13 vegetation traits that we measured were strongly supported as predictors of habitat preference (Fig. 4). Vegetation traits are often used to characterize habitat and predict demographic performance across habitat gradients, particularly where habitat preference

![Fig. 4. Relative support (based on AIC weights) for 11 vegetation traits used to predict habitat preference by nesting female Song Sparrows. The dashed line indicates a cutoff at 0.5 relative support using all models within ∆AIC ≤ 7 subsets (n = 268). Common shrub species included are: serviceberry (Amelanchier alnifolia), red elderberry (Sambucus racemosa), trailing blackberry (Rubus ursinus), Nootka rose (Rosa nutkana), currant (Ribes divaricatum), Pacific willow (Salix lucida), Himalayan blackberry (Rubus armeniacus), and oceanspray (Holodiscus discolor).](image)

### Table 2. Parameter estimates (with SE in parentheses) for variables identified as predictors of site-specific reproductive output in top-ranked models (∆AIC ≤ 7).

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Intercept</th>
<th>TNO</th>
<th>Female age</th>
<th>Female rLRS</th>
<th>Edge</th>
<th>Female age × TNO</th>
<th>Female rLRS × TNO</th>
<th>ΔAIC</th>
<th>AIC wt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>−0.001 (0.02)</td>
<td>0.70 (0.01)</td>
<td>−0.06 (0.01)</td>
<td>0.17 (0.014)</td>
<td>Edge</td>
<td>0.01 (0.01)</td>
<td>0.11 (0.01)</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>−0.001 (0.02)</td>
<td>0.70 (0.01)</td>
<td>−0.06 (0.01)</td>
<td>0.17 (0.014)</td>
<td>Edge</td>
<td>−0.03 (0.01)</td>
<td>0.12 (0.01)</td>
<td>3.82</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>−0.01 (0.02)</td>
<td>0.69 (0.01)</td>
<td>−0.06 (0.01)</td>
<td>0.17 (0.014)</td>
<td>0.03 (0.02)</td>
<td>0.11 (0.01)</td>
<td>5.46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Averaged model</td>
<td>−0.002 (0.02)</td>
<td>0.70 (0.01)</td>
<td>−0.06 (0.01)</td>
<td>0.17 (0.014)</td>
<td>0.002 (0.002)</td>
<td>−0.004 (0.002)</td>
<td>0.11 (0.01)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** Parameter estimates for averaged model are calculated via AIC weights (see Burnham and Anderson 2002). TNO and rLRS refer to total nest overlap and relative lifetime reproductive success, respectively. Where a variable was not used as a predictor for a model, the cell is blank.
is related to the reproductive output of its occupants (reviewed in Johnson 2007, Homayack 2010). Vegetation traits can reflect breeding resources (e.g., nest sites, food; Burke and Nol 1998, Rodenhousen et al. 2003), as well as shelter from predators (Chalifoun and Martin 2008) or inclement weather (D’Alba et al. 2009). However, relatively few studies that use vegetation traits to assess habitat quality demonstrate clear links between preference for particular habitats and the fitness of occupants (but see Rodenhousen et al. 2003). We show that although female Song Sparrows strongly preferred breeding sites that could be identified by vegetation cover and composition, vegetation traits were up to 85 times less influential on site-specific reproductive output than were the attributes (age and rLRS) of the females that occupied them, on average (Table 2). This result indicates that the vegetation traits that predict habitat occupancy and are sometimes assumed to indicate habitat quality, may be of little value in predicting the fitness of different female occupants (see also Morrison 2001, Johnson 2007).

Female Song Sparrows preferred to nest in breeding sites that contributed more offspring to the population, on average (Fig. 3a). As expected, the best predictor of annual reproductive output at a site was the annual fraction of nests overlapping the site (total nest overlap), which should be the only predictor of output under the null hypothesis of random settlement (Fretwell 1972, Lomnicki 1988; see Methods). However, we also found that the mean rLRS of female occupants and interaction of the mean total nest overlap of sites and female rLRS were positive predictors of annual variation in reproductive output among sites (Table 2). This indicates that annual variation in reproductive output among sites was influenced by the mean rLRS of females nesting in them, and also that the influence of female rLRS on reproductive output at a site increased with its mean total nest overlap. Thus, although females with high rLRS did not have priority of access to the most preferred sites (Fig. 3c), our results suggest that mean reproductive output in preferred breeding sites, which is often assumed to indicate habitat quality, was biased by the intrinsic quality of their occupants.

Understanding how the environmental features of habitats shape individual phenotype and estimating how genotype and phenotype affect population growth rate are shared goals in “eco-evolutionary” research (Hairston et al. 2005, Pelletier et al. 2007, 2009, Wilson et al. 2010). Gradients in habitat quality are also extensively discussed with respect to their influence on population growth and persistence (e.g., Donovan et al. 1995, Newton 1998, Rodewald et al. 2011), and much evidence suggests that fitness often covaries with genotype across habitat gradients (e.g., Nussey et al. 2005, Charmantier et al. 2008, Quinn et al. 2009). However, when estimates of habitat quality are biased by the quality of the individuals that occupy them, care must be taken to reliably estimate the influence of habitat on population growth or individual fitness.

Although vegetation traits predicted breeding site preference by female sparrows, they had little-to-no influence on site-specific reproductive output over the 35-year period. Nevertheless, site identity did account for 19.8% of the annual variation in reproductive output that we observed (Table 1), which suggests that repeatable differences between sites exist and influence the performance of the females in them. We suggest that some candidate factors not measured here include those linked to repeatable microclimate, food availability, or breeding date, all known to influence reproductive output in female Song Sparrows. Females that breed earlier on Mandarte typically produce more offspring annually (Arcese and Smith 1988, Hochachka 1990, Wilson and Arcese 2003) and also raise offspring more likely to achieve social dominance and to recruit to the population and breed (Arcese and Smith 1985, Hochachka 1990). Breeding sites with favorable microclimates may enhance female fitness by facilitating early breeding or minimizing physiological stress early in the season, when incubation costs can be high (Bryan and Bryant 1999) and poor weather can induce nest failure (Marr et al. 2006).

Our results highlight the need to estimate habitat quality independent of individual quality when the goal is to make predictions about site-specific contributions to population growth or individual fitness. Although female Song Sparrows exhibited strong preference for certain breeding sites over our 35-year study, we found that female intrinsic quality measured as rLRS, rather than habitat quality per se, accounted for most of the variation in site-specific annual reproductive output that we observed. Our findings imply that separating these contributions will be easier in populations where habitat preference, quality, and individual phenotype are not closely correlated. In general, these correlations will be lower when short life span, low site fidelity, high variation in population density, or related factors prevent the monopolization of breeding sites by a subset of individuals in populations.

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SUPPLEMENTAL MATERIAL

Parameter estimates (and standard errors) for all models in the ΔAIC ≤ 7 subset of 262 models describing vegetation-based predictors of habitat preference (Ecological Archives 895-038-S1).