Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*

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Male song sparrows sing repertoires of 4–13 distinct song types and have proved a valuable model for testing hypotheses concerning the function and evolution of song complexity. Captive female song sparrows solicit more copulations in response to playback of larger repertoires, yet it remains unclear whether male repertoire size influences female mate choice in natural situations. We used long-term data from free-living song sparrows inhabiting Mandarte Island, British Columbia, Canada, to investigate whether male song repertoire size predicted three components of reproductive performance during the first year: territory acquisition, mating success and laying date. Across males whose song was recorded, males with larger repertoires were not more likely to acquire a territory, to acquire a larger territory or to settle sooner. However, after we controlled for territory size and between-year variation in the population sex ratio, first-year males with larger repertoires were more likely to mate. This was because they were more likely to pair with newly settled females, not because they were more likely to acquire territories where older females were already resident. After we controlled for territory size and between-year variation in breeding date, newly settled females laid earlier when mated with males with larger repertoires. Together with the results of previous mate choice experiments, these patterns are consistent with the hypothesis that male song repertoire size is a sexually selected trait that influences female mate choice in song sparrows.

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One explanation for the evolution of exaggerated, ornamental male traits is that ornamentation enhances an individual's mating success and thus fitness (Andersson 1994; Kokko et al. 2003). Ornamentation could increase a male's mating success by improving his performance during intrasexual competition for females or breeding territories (Krebs et al. 1978; Andersson 1994). Alternatively, females may use male ornaments as a cue for optimal mate choice in terms of maximizing direct or indirect fitness benefits (Andersson 1994; Kokko et al. 2003). However, the extents to which females choose mates based on ornamentation, and to which female preferences may drive ornament evolution, remain controversial (Andersson 1994; Kokko et al. 2003). Evidence for intersexual selection requires evidence that male mating success increases with ornamentation in natural populations, and that this to some extent reflects female choice for more ornamented males.

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Simply observing a correlation between ornamentation and a male's success in attracting females does not prove that the focal trait, rather than some unmeasured correlated trait, functions in female choice. Instead, choice is most rigorously demonstrated by observing female preference for an experimentally enhanced trait, while other conditions are held constant (e.g. Andersson 1982; Møller 1988; Hill 1991). However, ornaments and mating preferences are often difficult to manipulate and measure in free-living individuals. The necessary mate choice experiments are therefore often carried out using captive individuals under controlled conditions (Searcy & Marler 1981; Andersson 1994; Godin & Dugatkin 1996). In such cases, detailed correlative studies of mating patterns in natural populations can provide valuable corroborating evidence that cues identified under controlled experimental conditions also significantly influence mate choice in free-living individuals (Searcy 1992; Benton & Evans 1998). The clearest evidence of female choice for exaggerated ornaments is therefore gathered by combining experimental and observational approaches (Searcy & Yasukawa 1996).

In songbirds, song repertoire size is a classical example of an ornamental male trait that has been suggested to function in both male–male competition and female choice and therefore to be sexually selected (Searcy 1992; Catchpole & Slater 1995; Searcy & Yasukawa 1996). Playback experiments suggest that large repertoires may facilitate territorial defence, thus enhancing a male's reproductive opportunity (Krebs et al. 1978; Yasukawa 1981 although Beecher et al. 2000 suggested that defence also depends on song sharing). Laboratory experiments show that females of several species perform more copulation solicitation displays, a measure of mating preference, in response to playback of larger repertoires (Searcy & Marler 1981; Searcy 1992; Searcy & Yasukawa 1996; see also Lampe & Sætre 1995). However, it is less clear whether male repertoire size influences female mate choice in natural populations. Song repertoires are difficult to manipulate in free-living males, so evidence has been gathered by correlating a male's repertoire size with aspects of his life history, such as mating success and pairing date, which are interpreted to reflect female choice (Catchpole 1987; Searcy & Yasukawa 1996; Buchanan & Catchpole 1997). Although male sedge warblers, *Acrocephalus schoenobaenus*, and starlings, *Sturnus vulgaris*, with larger repertoires paired earlier (Catchpole 1980; Mountjoy & Lemon 1996; Buchanan & Catchpole 1997), studies on other species showed no such relationship, or that patterns varied between years (e.g. McGregor et al. 1981; Searcy 1984, 1992; Gil & Slater 2000). In other cases, initial correlations between repertoire size and indexes of female choice disappeared when confounding variables, such as male age, territory quality or spring arrival date, were statistically controlled (e.g. Yasukawa et al. 1980; Catchpole 1986; Searcy 1992; Hasselquist 1998). Repertoire size has consequently been suggested to function primarily as a cue in extrapair rather than social mate choice in natural populations (Searcy 1992; Hasselquist et al. 1996).

Male song sparrows sing complex songs consisting of 4–13 distinct song types, performed with eventual variety as a series of song bouts (e.g. AAA…BBB…CCC…AAA…DDD…., Searcy & Marler 1981; Cassidy 1993; Beecher et al. 2000). Although individuals can sing minor variations within each song type, song sparrows regard types as natural categories that transcend these variations, and respond more strongly to different types than to variations (Stoddard et al. 1988; Horning et al. 1993; Searcy et al. 1995, 1999). The number of discrete song types is therefore a biologically relevant measure of song complexity in this species. Song sparrows have consequently proved a valuable model species in which to investigate the function and evolution of repertoire size and other song components (e.g. Beecher et al. 1994, 2000; O'Loghlen & Beecher 1997; Hughes et al. 1998; Nowicki et al. 2002). Song sparrows provided the original experimental evidence that females display more in response to playback of larger song repertoires (Searcy & Marler 1981; Searcy 1984; Catchpole 1987). However, there is scant evidence that female song sparrows preferentially mate with males with large repertoires in the wild. In the well-studied song sparrow population on Mandarte Island, British Columbia, Canada, Hiebert et al. (1989) found that males with larger repertoires acquired territories earlier, held them longer and reared more offspring to independence. The relation between repertoire size and mating success was not explicitly measured. Studies on other song sparrow populations showed no correlation between repertoire size and male phenotype or territory tenure (Searcy et al. 1985; Beecher et al. 2000), and males with larger repertoires did not pair earlier or obtain replacement females sooner after their original mate was experimentally removed (Searcy 1984). Relations between song repertoire size and mating success therefore merit further investigation in this model species (Catchpole 1987).

Using a long-term data set from the island of Mandarte (greatly expanded since Hiebert et al. 1989), we investigated whether male song sparrows with larger song repertoires were more likely to acquire territories, to mate or to breed earlier during their first year. A crucial stage in correlative analyses is to control for potentially confounding covariates (Buchanan & Catchpole 1997). Song sparrow pairs frequently remain together over successive years, so we focused on performance by age 1 (first year) to ensure that observed mating patterns were not confounded by male age or reproductive history. We also statistically controlled for territory size, female age and reproductive history, and for between-year variation in reproductive performance and population structure.

METHODS

Study Population

Mandarte lies 25 km north of Victoria, British Columbia, Canada. The rocky island covers 6 ha and holds a continuous band of low deciduous scrub surrounded by meadow. The resident song sparrow population has been intensively studied since 1975 (Smith, in press). During this time, almost all nests have been located and

all sparrows hatched on the island have been marked with unique combinations of metal and coloured plastic rings. Colour-ringed sparrows are easily observed across the whole island, allowing each individual's reproductive activities to be documented accurately with minimal disturbance (Smith, in press).

Territoriality and Mating

Song sparrows can breed from age 1 (Arcese et al. 2002; Smith & Marr, in press). On Mandarte, where song sparrows are resident and primarily monogamous, males defend scrub territories where females feed and nest. Territories and pairs are typically established during winter and early spring, and breeding occurs from April to August (Arcese 1989; Smith & Marr, in press). Surviving pairs typically remain together over consecutive years. A female that outlives her mate either remains on the same territory or moves to a new one. Newly settling males can establish new territories or take over existing ones, which may or may not hold a previously resident female (Arcese 1989). Newly settling females have been observed to visit multiple males or territories before settling (P. Arcese & J. M. Reid, personal observation). New pairings may therefore reflect female choice between territorial males or arise as a de facto consequence of male acquisition of a territory where a female is already resident (Arcese 1989). The population sex ratio on Mandarte is usually male biased, so some territorial males remain unmated (Arcese 1989; Smith & Marr, in press). Furthermore, some males fail to establish territories and remain in the population as nonterritorial floaters (Arcese 1987, 1989). The presence of unmated males has been interpreted to imply strong sexual selection (Jennions et al. 2001). Although the basic social structure of the population is set when breeding begins in April, some partial or complete territory takeovers occur through the breeding season (Arcese 1987, 1989).

Each April during the study, the identities of the sparrows remaining on Mandarte were recorded and the population sex ratio (males/females) was calculated. The territorial and mating status of each surviving male was noted (Arcese 1987, 1989). We used these data to test whether males with larger song repertoires were more likely to acquire a territory or mate during their first year. In migratory populations where all males eventually mate or unmated males cannot be easily observed, indirect indexes of male quality and female choice, such as spring arrival, settlement and pairing dates, are commonly used (e.g. Møller 1988; Buchanan & Catchpole 1997; Gil & Slater 2000). These indexes are not relevant or cannot be easily measured in resident populations such as Mandarte's song sparrows. However, we used the date on which breeding began in a male's first year as an additional indicator of his mating success; breeding date may reflect pairing date and individual quality (Wiktander et al. 2001; Daunt et al. 2003). For each pair, laying date (the date on which the first egg was laid) was recorded directly if nests were found before clutch completion, or back-calculated from hatch date or chick age for nests

found subsequently. Additional winter fieldwork during 1982–1987 (Arcese 1989; Hiebert et al. 1989) and 2002–2003 permitted recording of the month in which territories were acquired (settlement age) for some males. The territory size (area of scrub, m^2) defended by each male in April each year was estimated from detailed observations of song perches and interactions between neighbouring males (Arcese 1989).

Song Repertoire Size

Territorial male song sparrows sing throughout the breeding season, although song rates peak during pair formation and incubation, and unmated territorial males sing more than mated males (Arcese et al. 2002). Non-territorial floaters typically remain silent (Arcese 1989). Song sparrows are 'age-limited' learners; a male's song repertoire is crystallized during his first winter and does not change subsequently (Searcy et al. 1985; Cassidy 1993; Nordby et al. 2002).

Repertoire sizes of 16 male song sparrows were recorded on Mandarte Island in 1984 (Hiebert et al. 1989). Two additional males were recorded in 1985, using identical protocols and equipment. We recorded repertoire sizes of a further 36 males during 1988–1993 (Cassidy 1993) and 22 males during 2003. Seventy-six males were therefore recorded in total, representing 20 cohorts (hatched 1980–1992 and 1996–2002). Songs were recorded using a WM-6DC Sony Professional Walkman and Sennheiser ME80 microphone (1988–1993) or an Optimus CTR-117 recorder and Sennheiser ME67 microphone (2003). Songs were digitized and visualized using a Multigon Uniscan II real-time analyser (songs recorded during 1988–1992; Cassidy 1993) or the Syrinx sound analysis program (songs recorded in 1993 and 2003; J. Burt, www.syrinxpc.com). Sonagrams were visually grouped into song types to enable counting of the total number of types (repertoire size). Different song types were typically clearly distinguishable. In the few cases where the distinction between type and variation was not clear, we defined types based on the similarity of the first few syllables. Early syllables are more consistent than later syllables within song sparrow song types (Beecher et al. 2000). Categorizations were consistent across different observers (Hiebert et al. 1989; Cassidy 1993). Recommended criteria for documenting a song sparrow's complete repertoire have been refined over time. Hiebert et al. (1989) assumed that 3 h of continuous recording was sufficient, and in practice observed no new song types after 1.5 h. During 1988–1993 and 2003, we estimated repertoire sizes by typing a minimum of 210 continuously recorded songs for each male; plots of recording effort against cumulative song types show that 210 songs is sufficient to estimate repertoire size with 95% confidence on Mandarte (Cassidy 1993). In most cases, the number of songs analysed hugely exceeded this threshold (median 347, maximum 2558; 225 songs is sufficient to estimate repertoire size with 99% confidence; Cassidy 1993). More recent studies have estimated repertoire size by analysing a minimum of approximately 17 song bouts (Beecher et al. 2000; bouts

typically comprise 5–20 songs). In 1993 and 2003, we therefore imposed an additional minimum criterion of 20 bouts, exceeding the suggested quantity. Each individual's repertoire size was measured with no knowledge of its life history parameters.

Analysis

We used logistic and linear regression to investigate whether a male's song repertoire size predicted his territory acquisition, mating success or laying date. We distinguished between males that acquired territories where older females were already resident and males that mated with newly settling females, which is more likely to reflect female choice. We included potentially confounding covariates, such as territory size and female age, where relevant. Territory location and fine-scale habitat attributes do not repeatedly predict territory occupancy patterns or breeding success on Mandarte, suggesting that habitat quality does not vary markedly across the island (Hochachka, in press; P. Arcese, unpublished data). We therefore did not consider these variables further. Variables were eliminated from regression models if $P > 0.10$. We present the test statistic and probability associated with each retained variable. For eliminated variables, we present statistics associated with their reintroduction to the final model.

The males whose song repertoires were recorded were hatched during 1980–1992 and 1996–2002. Parameters such as mean territory size, population sex ratio and laying date have varied markedly on Mandarte over this time (Arcese et al. 1992; Smith et al., in press). When relating a male's performance to his song repertoire size, we corrected for this temporal variation by including the year-specific, population-wide, mean performance as a covariate. For example, we examined whether a first-year male's repertoire size predicted his mate's laying date while controlling for mean laying date in the relevant year. In our case, this approach was more robust than simply modelling 'year' as a random factor, because it incorporated data from the whole population rather than solely the few males from each cohort whose song was recorded. An alternative approach is to subtract the population mean life history performance from each observation and divide by the population-wide standard deviation, then use the resulting 'z scores' in regression analyses. However, the variance in life history parameters did not differ markedly between the years that we studied. The covariate and z score approaches therefore gave qualitatively identical results. For simplicity, we present the results of only the covariate approach. Although the extent to which life history parameters vary with song repertoire size cannot be measured accurately without correcting for year effects, the absolute magnitude of variation is difficult to discern from year-standardized scores. We therefore also present unstandardized mating success data. To allow direct comparison of the observed effect size with previous studies, we calculated the overall Pearson correlation coefficient for the relation between song repertoire size and mating success (Gontard-Danek &

Møller 1999). All tests were two tailed, and means are presented $\pm$ SD. Analyses were carried out in SPSS v.10.0 (SPSS 1999).

RESULTS

Song Repertoire Size

Across the 76 recorded males, repertoire size averaged 8.0 ± 1.6 song types (range 4–12, coefficient of variation 20.7) and did not differ between cohorts (ANOVA: $F_{19,56} = 1.0$, $P = 0.44$). Across the 58 males recorded during 1988–2003, estimated repertoire size did not increase with the number of songs analysed (Spearman rank correlation: $r_S = -0.11$, $N = 58$, $P = 0.41$). This result suggests that sampling effort was sufficient to record each male's full repertoire. Males were recorded at 1–7 years of age. Repertoire size did not vary with male age at recording ($r_S = 0.13$, $N = 76$, $P = 0.28$).

Territory Acquisition

Of the 76 recorded males, 61 acquired a territory by their first April and 72 did so at some stage during their first summer. The probability that a male would acquire a territory at either stage did not vary significantly between cohorts (logistic regression: first April: $\chi^2_{19} = 24.6$, $P = 0.17$; first summer: $\chi^2_{19} = 22.8$, $P = 0.24$) and was not predicted by male song repertoire size (first April: $\chi^2_1 = 0.83$, $P = 0.36$; first summer: $\chi^2_1 = 0.38$, $P = 0.54$). Across the 61 males that held a territory in their first April, territory size was not correlated with a male's repertoire size after accounting for between-year variation in mean territory size (Fig. 1). Across 28 first-year males whose settlement date was known, males with larger repertoires did not acquire territories earlier (Fig. 1).
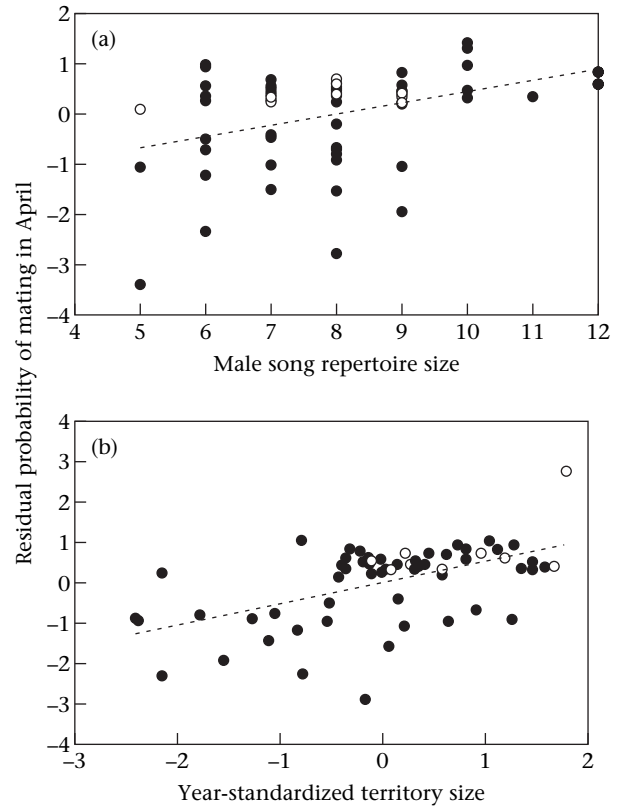
Mating Success

Of the 61 males that acquired territories by their first April, 42 mated and bred at this time. The probability that a territorial male would mate in his first April was lower in years when the population sex ratio was more skewed (when more males remained unmated), and increased with the male's repertoire size and year-standardized territory size: males with larger repertoires and larger territories were more likely to mate (Fig. 2). Furthermore, the probabilities that a male would mate after acquiring a territory at any point during his first summer, and that he would simply mate during his first summer, increased with repertoire size after controlling for between-year variation in sex ratio (logistic regressions: probability of mating given territory acquisition: $N = 72$, logistic regression: sex ratio: $\chi^2_1 = 7.2$, $P = 0.007$; repertoire size: $\chi^2_1 = 4.2$, $P = 0.041$; overall probability of mating: $N = 76$, sex ratio: $\chi^2_1 = 5.6$, $P = 0.018$, repertoire size: $\chi^2_1 = 4.6$, $P = 0.032$). Territory size was not included in the latter analyses because territories established after April were not always measured. Settlement age was
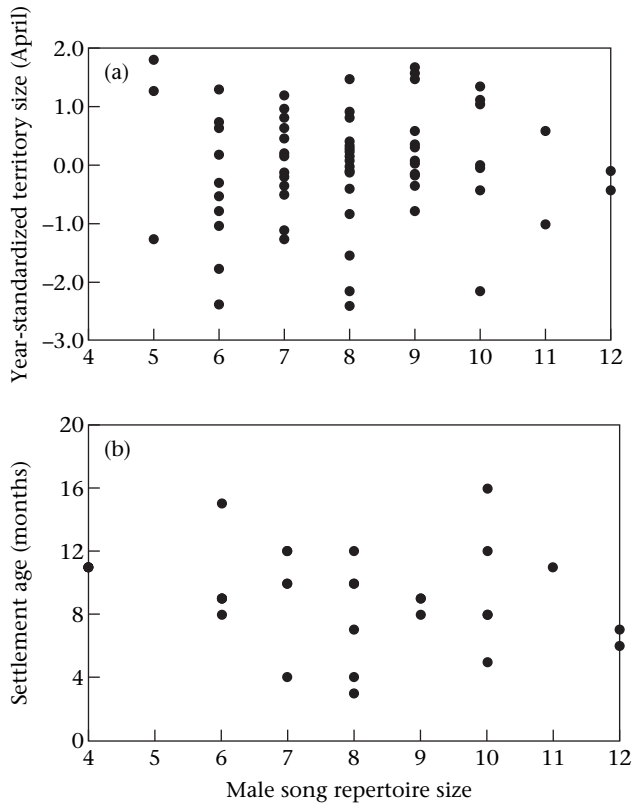
Figure 1. Relations between a male song sparrow's song repertoire size and (a) the year-standardized size of the territory defended during the male's first April (Pearson correlation: $r_{59} = 0.09$, $P = 0.51$) and (b) the male's age at territory acquisition $r_{26} = -0.22$, $P = 0.26$.

Figure 2. Relations between (a) a territorial male song sparrow's song repertoire size and his residual probability of mating during his first April after controlling for year-standardized territory size and population sex ratio and (b) a male's year-standardized territory size and his residual probability of mating during his first April after controlling for repertoire size and population sex ratio. Open symbols show males that mated with long-term resident females. (logistic regression: $N = 61$; sex ratio: $\chi_1^2 = 4.4$, $P = 0.035$; repertoire size: $\chi_1^2 = 5.2$; $P = 0.023$; year-standardized territory size: $\chi_1^2 = 9.8$, $P = 0.002$.) Odds ratios for repertoire size and territory size were 1.7 and 2.8, respectively.

known for 22 males that acquired territories by their first April. Across this relatively small subsample, the tendency for males with larger repertoires to be more likely to mate was not significant (logistic regression: $N = 22$, $\chi_1^2 = 2.1$, $P = 0.15$). However, across these individuals, there was no indication that mating success was instead predicted by a male's settlement age ($\chi_1^2 = 0.6$, $P = 0.44$).

In Mandarte's resident song sparrow population, it is not always clear which sex occupied a territory first and so how pairs formed. First-year males with large repertoires may be more likely to mate because females preferentially settle with them, or because they are more likely to acquire territories where older females are already resident possibly reflecting male–male competition more than female choice. Nine (15%) of the 61 males that were territorial by their first April acquired territories with long-term resident females (that had bred on that territory the previous year). The probability that a male would acquire a territory with a resident female rather than an un-occupied territory did not increase with his song repertoire size (logistic regression: $N = 61$, $\chi_1^2 = 0.1$, $P = 0.80$). Of the 52 males that acquired unoccupied territories, 33 mated with a newly settled female (females that were themselves aged 1, or had moved from a different territory) and 19 remained unmated. Across these 52 males, the probability that a male would mate with a newly settled female increased with his repertoire size and territory

size after controlling for between-year variation in the population sex ratio (logistic regression: $N = 52$, sex ratio: $\chi_1^2 = 6.7$, $P = 0.010$; repertoire size: $\chi_1^2 = 6.0$, $P = 0.015$; year-standardized territory size: $\chi_1^2 = 5.0$, $P = 0.025$). The unstandardized proportions of males with repertoire sizes that were small (six songs or less), median (eight songs) or large (10 or more songs) that mated during their first year differed considerably: approximately 90% of males with large repertoires mated, but only half of males with small repertoires did so (Table 1).

Laying Date

Laying date was known for 41 of the 42 males that bred during their first April. Across these males, laying date was negatively correlated with male song repertoire size after controlling for between-year variation in the timing of breeding; females mated to males with larger repertoires laid earlier (Fig. 3). Laying date did not vary significantly with standardized territory size or female age across these

Table 1. The proportion of male song sparrows with small ($\leq$6 song types), median (8 song types) and large ($\geq$ 10 song types) repertoire sizes that mated

	Repertoire size			
	Small ($\leq$6)	Median (8)	Large ($\geq$ 10)	*r*
Mated by first April	0.50 (N=12)	0.59 (N=17)	0.91 (N=11)	0.34 (0.38)
Mated during first year	0.53 (N=15)	0.68 (N=19)	0.86 (N=14)	0.37 (0.38)

Proportion of males that mated by their first April, given that they had acquired a territory, and at any time during their first year. The categories indicate mating success at median and extreme repertoire sizes. The effect size (*r*) is the Pearson correlation coefficient for the relation between song repertoire size and standardized mating success for all males and, in parentheses, excluding males that mated with long-term resident females.

individuals (Fig. 3). The time of territory acquisition was recorded only for 16 males that bred during their first April. Across these males, laying date tended to decline with repertoire size ($N = 16$, ANOVA: year mean lay date: $F_{1,13} = 6.6$, $P = 0.024$; repertoire size: $F_{1,13} = 4.1$, $P = 0.065$) but did not vary with a male's settlement date ($F_{1,12} = 0.01$, $P = 0.91$).

The negative correlation between repertoire size and laying date remained significant across 32 males (whose laying date was known) that bred after acquiring a territory with no long-term resident female; newly settled females laid earlier when mated with males with large repertoires ($N = 32$, ANOVA: year mean lay date: $F_{1,29} = 20.0$, $P < 0.001$; repertoire size: $F_{1,29} = 5.8$, $P = 0.023$). Laying date did not vary with territory size or female age (standardized territory size: $F_{1,28} = 0.2$, $P = 0.63$; female age: $F_{1,28} = 0.1$, $P = 0.77$). However, across the nine first-year males that mated with long-term resident females, laying date varied with female age but not with the male's repertoire size, although statistical power to detect an effect was low; older resident females laid earlier ($N = 9$, female age: $F_{1,7} = 28.7$, $P = 0.001$; year mean lay date: $F_{1,6} = 0.01$, $P = 0.92$; repertoire size: $F_{1,6} = 3.9$, $P = 0.10$; standardized territory size: $F_{1,6} = 0.9$, $P = 0.39$). Males that mated and bred later during their first summer, for example, with females that switched males after their first breeding attempt, were not considered in these analyses, because laying dates in these cases depended primarily on the outcome of the female's first attempt.

DISCUSSION

To understand the evolution of ornamental male traits, we require knowledge of the extent to which male mating success varies with ornamentation in natural populations, and whether this variation reflects intrasexual competition or female mate choice (Andersson 1994; Kokko et al. 2003). Although song complexity in songbirds is commonly cited as a classical example of a sexually selected trait, studies on free-living populations have inconsistently supported the basic prediction that a male's mating success should increase with his song repertoire size (Searcy 1984, 1992; Gil & Slater 2000; although see Catchpole 1986; Hasselquist et al. 1996; Mountjoy & Lemon 1996; Buchanan & Catchpole 1997).

Across the song sparrows that we recorded, males with larger repertoires were not more likely to acquire a territory
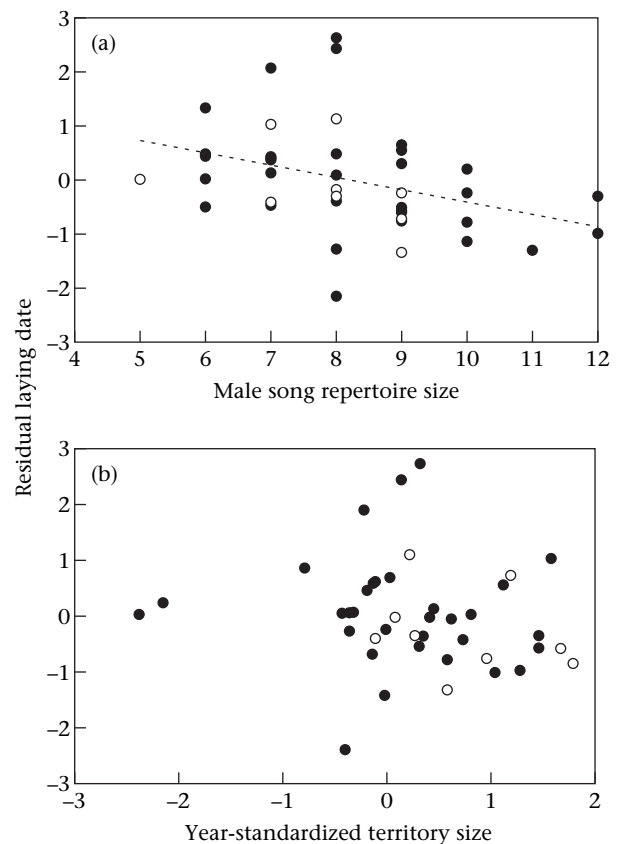
Figure 3. Relations between (a) a first-year male song sparrow's song repertoire size and female laying date after controlling for between-year variation in the timing of breeding and (b) a first-year male's year-standardized territory size and female laying date after controlling for repertoire size and between-year variation in the timing of breeding. Open symbols show males that mated with long-term resident females. ($N = 41$, year mean lay date: $F_{1,38} = 22.2$, $P < 0.001$; repertoire size: $F_{1,38} = 6.4$, $P = 0.016$; territory size: $F_{1,37} = 0.8$, $P = 0.37$; age: $F_{1,36} = 2.6$, $P = 0.12$; age^2: $F_{1,36} = 2.5$, $P = 0.13$.) The effect size for the relation with repertoire size was -2.3.

by their first April or at any point during their first year. Furthermore, territorial males with larger repertoires did not hold larger territories or acquire them earlier (see also Searcy 1984; Hiebert et al. 1989). We therefore found no evidence that repertoire size facilitates competition for territories in song sparrows. However, nonterritorial song sparrows rarely sing (Arcese 1989; Arcese et al. 2002), so we characterized repertoires only of males that acquired territories on Mandarte at some stage during their lives. Therefore, although we documented a wide range of repertoire sizes, we cannot exclude the possibility that, across all Mandarte-born males, individuals with larger repertoires were more likely to become territorial. Previous studies have suggested that large song repertoires facilitate territorial defence in birds (Krebs et al. 1978; Yasukawa 1981; Catchpole & Slater 1995), although the number of songs that a male shares with his neighbours (which may be correlated with total repertoire size) may affect defence more than repertoire size per se (Beecher et al. 1994, 2000). The relation between repertoire size and territorial defence, rather than acquisition, requires further investigation on Mandarte.

Across all song sparrows that we recorded, and across just those that acquired territories, males with larger repertoires were more likely to mate during their first year. Furthermore, females mated with males with larger repertoires bred earlier. We specifically studied first-year males, so these results cannot be confounded by male age or reproductive history, and they remained significant after controlling for territory size, female age and between-year variation in population sex ratio and laying date. Although the time of territory acquisition was known for few males, there was no indication that relations between repertoire size, mating success and laying date were confounded by settlement age. Thus, on Mandarte Island, first-year males with larger song repertoires achieved greater mating success and bred earlier.

Variation in mating success and breeding date are often interpreted to reflect female choice between males (Searcy 1992; Buchanan & Catchpole 1997; Gil & Slater 2000). Given the complex process of pair formation within the resident Mandarte population, it is difficult to conclude with certainty that mating success increased because females preferentially settled with males with large repertoires. However, first-year males with large repertoires were more likely to mate because they were more successful in pairing with newly settled females, not because they were more likely to acquire territories where older females were already resident. Furthermore, although laying dates of established females varied with the female's age (as is generally true in song sparrows, Smith & Marr, in press), newly settled females bred earlier when mated with males with larger repertoires. Laying date did not vary with territory size and territory size was not correlated with repertoire size, so there is no evidence that females that paired with males with larger repertoires laid earlier because they had access to more resources after settling. These females may therefore have settled earlier or have been in better condition when they did so; either possibility is consistent with models of preferential settlement with males with large song repertoires (Benton &

Evans 1998). Correlative studies cannot conclusively prove that a specific male trait is subject to female choice, since it is difficult to exclude the possibility that choice in fact focuses on some correlated cue. However, together with experimental evidence that captive female song sparrows solicit more copulations in response to larger repertoires (Searcy & Marler 1981; Searcy 1984), our field data support the hypothesis that free-living female song sparrows preferentially mate with males with large song repertoires.

Studies of two other natural song sparrow populations did not detect correlations between a male's song repertoire size and any aspect of his mating success or subsequent reproductive performance (Searcy 1984; Searcy et al. 1985; Beecher et al. 2000). This difference may arise because the long-term Mandarte data set is particularly conducive to detecting such relationships, because potentially confounding variables, such as a breeder's age and reproductive history, and broader aspects of population structure, such as density and sex ratio, can be quantified and statistically controlled. Furthermore, for mate preferences to be clearly expressed, females must sample a representative cross section of the male population (Benton & Evans 1998). Although female sampling behaviour has not been rigorously quantified on Mandarte, the small size of the island and the high population density may allow females to sample multiple males. The power of our correlative analyses to detect female preferences may therefore be relatively high (Benton & Evans 1998). Alternatively, patterns of mate choice may differ between song sparrows on Mandarte and other song sparrow populations. Where females gain direct benefits from mate choice, choice may focus primarily on aspects of resource availability, such as territory quality, rather than on male quality per se. A male's song complexity may have less bearing on mate choice where resource availability varies greatly between males (McGregor et al. 1981; Searcy 1992; Forstmeier et al. 2002). On Mandarte, survival and reproduction vary with an individual's inbreeding level (Keller 1998) and current environmental conditions (Arcese et al. 1992; Wilson & Arcese 2003), but no clear fitness consequences of territory location or structure have been detected (Hochachka, in press; P. Arcese, unpublished data). Territory quality may therefore vary relatively little within Mandarte's relatively uniform habitat. Female preferences for male characteristics such as song repertoire size may consequently be particularly evident.

The magnitude of the relation between trait expression and mating success can indicate the strength of sexual selection and thus the possibility for evolution of exaggerated ornamental traits (Gontard-Danek & Møller 1999; Jennions et al. 2001). In song sparrows, the effect size for the relation between male repertoire size and mating success was 0.38 (Table 1). This effect size exceeds the average of 0.26–0.29 across observational studies relating mating success to (morphological) ornamentation in birds (Gontard-Danek & Møller 1999). Some individual studies, however, reported effects exceeding 0.7 (Gontard-Danek & Møller 1999). Although effect sizes are often calculated from short-term studies, apparent patterns of sexual

selection can vary between years (Buchanan & Catchpole 1997; Gil & Slater 2000). Our results from multiple years suggest that song sparrows on Mandarte, on average, experience reasonably strong sexual selection for large repertoire size. In addition to the possibility that mating preferences may be easier to detect within relatively dense populations (Benton & Evans 1998), this may be because the Mandarte population is generally male biased. Male mating success is consequently skewed (Jennions et al. 2001; Hochachka, in press). The possible benefits that females gain from mate choice based on repertoire size, and the extent to which increased early mating success ultimately enhances male fitness, will be the subject of future investigation in this population.

Acknowledgments

References

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature*, **299**, 818–820.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Arcese, P. 1987. Age, intrusion pressure and defence against floaters by territorial male song sparrows. *Animal Behaviour*, **35**, 773–784.

Arcese, P. 1989. Territory acquisition and loss in male song sparrows. *Animal Behaviour*, **37**, 45–55.

Arcese, P., Smith, J. N. M., Hochachka, W. M., Rogers, C. M. & Ludwig, D. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology*, **73**, 805–822.

Arcese, P., Sogge, M. K., Marr, A. B. & Patten, M. A. 2002. Song sparrow (*Melospiza melodia*). In: *The Birds of North America*. Number 704 (Ed. by A. Poole & F. Gill), Philadelphia: The Birds of North America.

Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 1450–1454.

Beecher, M. D., Campbell, S. E. & Nordby, J. C. 2000. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour*, **59**, 29–37.

Benton, T. G. & Evans, M. R. 1998. Measuring mate choice using correlation: the effect of female sampling behaviour. *Behavioral Ecology and Sociobiology*, **44**, 91–98.

Buchanan, K. L. & Catchpole, C. K. 1997. Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. *Proceedings of the Royal Society of London, Series B*, **264**, 521–526.

Cassidy, A. L. E. V. 1993. Song variation and learning in island populations of song sparrows. Ph.D. thesis, University of British Columbia.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour*, **74**, 149–166.

Catchpole, C. K. 1986. Song repertoires and reproductive success in the great reed warbler, *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology*, **19**, 439–445.

Catchpole, C. K. 1987. Bird song, sexual selection and female choice. *Trends in Ecology and Evolution*, **2**, 94–97.

Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.

Daunt, F., Monaghan, P., Wanless, S. & Harris, M. P. 2003. Sexual ornament size and breeding performance in female and male European shags *Phalacrocorax aristotelis*. *Ibis*, **145**, 54–60.

Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society of London, Series B*, **269**, 1479–1485.

Gil, D. & Slater, P. J. B. 2000. Multiple song repertoire characteristics in the willow warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. *Behavioral Ecology and Sociobiology*, **47**, 319–326.

Godin, J.-G. J. & Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, U.S.A.*, **93**, 10262–10267.

Gontard-Danek, M.-C. & Møller, A. P. 1999. The strength of sexual selection: a meta-analysis of bird studies. *Behavioral Ecology*, **10**, 476–486.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376–2390.

Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, **381**, 229–232.

Hiebert, S. M., Stoddard, P. K. & Arcese, P. 1989. Repertoire size, territory acquisition and reproductive success in the song sparrow. *Animal Behaviour*, **37**, 266–273.

Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature*, **350**, 337–339.

Hochachka, W. M. In press. Unequal lifetime reproductive success and its implication for small, isolated populations. In: *Biology of Small Populations: The Song Sparrows of Mandarte Island* (Ed. by J. N. M. Smith, L. F. Keller, A. B. Marr & P. Arcese). New York: Oxford University Press.

Horning, C. L., Beecher, M. D., Stoddard, P. K. & Campbell, S. E. 1993. Song perception in the song sparrow: importance of different parts of the song in song type classification. *Ethology*, **94**, 46–58.

Hughes, M., Nowicki, S., Searcy, W. A. & Peters, S. 1998. Song-type sharing in song sparrows: implications for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, **42**, 437–446.

Jennions, M. D., Møller, A. P. & Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Quarterly Review of Biology*, **76**, 3–36.

Keller, L. F. 1998. Inbreeding and its fitness consequences in an insular population of song sparrows (*Melospiza melodia*). *Evolution*, **52**, 240–250.

Kokko, H., Brooks, R., Jennions, M. & Morley, J. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London, Series B,* **270,** 653–664.

Krebs, J. R., Ashcroft, R. & Webber, M. I. 1978. Song repertoires and territory defence in the great tit. *Nature,* **271,** 539–542.

Lampe, H. M. & Sætre, G. P. 1995. Female pied flycatchers prefer males with larger song repertoires. *Proceedings of the Royal Society of London, Series B,* **262,** 163–167.

McGregor, P. K., Krebs, J. R. & Perrins, C. M. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *American Naturalist,* **118,** 149–159.

Møller, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous house sparrow. *Nature,* **332,** 640–642.

Mountjoy, D. J. & Lemon, R. E. 1996. Female choice for complex song in the European starling: a field experiment. *Behavioral Ecology and Sociobiology,* **38,** 65–71.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 2002. Adult song sparrows do not alter their song repertoires. *Ethology,* **108,** 39–50.

Nowicki, S., Searcy, W. A. & Peters, S. 2002. Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society of London, Series B,* **269,** 1949–1954.

O'Loghlen, A. L. & Beecher, M. D. 1997. Sexual preferences for mate song types in female song sparrows. *Animal Behaviour,* **53,** 835–841.

Searcy, W. A. 1984. Song repertoire size and female preferences in song sparrows. *Behavioral Ecology and Sociobiology,* **14,** 281–286.

Searcy, W. A. 1992. Song repertoire and mate choice in birds. *American Zoologist,* **32,** 71–80.

Searcy, W. A. & Marler, P. 1981. A test for responsiveness to song structure and programming in female sparrows. *Science,* **213,** 926–928.

Searcy, W. A. & Yasukawa, K. 1996. Song and female choice. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 454–473. Ithaca, New York: Cornell University Press.

Searcy, W. A., McArthur, P. D. & Yasukawa, K. 1985. Song repertoire size and male quality in song sparrows. *Condor,* **87,** 222–228.

Searcy, W. A., Podos, J., Peters, S. & Nowicki, S. 1995. Discrimination of song types and variants in song sparrows. *Animal Behaviour,* **49,** 1219–1226.

Searcy, W. A., Nowicki, S. & Peters, S. 1999. Song types as fundamental units in vocal repertoires. *Animal Behaviour,* **58,** 37–44.

Smith, J. N. M. In press. Song sparrows, Mandarte Island, and methods. In: *Biology of Small Populations: The Song Sparrows of Mandarte Island* (Ed. by J. N. M. Smith, L. F. Keller, A. B. Marr & P. Arcese). New York: Oxford University Press.

Smith, J. N. M. & Marr, A. B. In press. Life history: reproduction and survival. In: *Biology of Small Populations: The Song Sparrows of Mandarte Island* (Ed. by J. N. M. Smith, L. F. Keller, A. B. Marr & P. Arcese). New York: Oxford University Press.

Smith, J. N. M., Marr, A. B., Arcese, P. & Keller, L. F. In press. Fluctuations in numbers: population limitation, regulation and catastrophic mortality. In: *Biology of Small Populations: The Song Sparrows of Mandarte Island* (Ed. by J. N. M. Smith, L. F. Keller, A. B. Marr & P. Arcese). New York: Oxford University Press.

SPSS Inc. 1999. *SPSS v. 10.* Chicago: SPSS Inc.

Stoddard, P. K., Beecher, M. D. & Willis, M. 1988. Response of territorial male song sparrows to song types and variations. *Behavioral Ecology and Sociobiology,* **22,** 125–130.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001. Age and reproduction in lesser spotted woodpeckers (*Dendrocopus minor*). *Auk,* **118,** 624–635.

Wilson, S. & Arcese, P. 2003. El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Sciences, U.S.A.,* **100,** 11139–11142.

Yasukawa, K. 1981. Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Animal Behaviour,* **29,** 114–125.

Yasukawa, K., Blank, J. L. & Patterson, C. B. 1980. Song repertoires and sexual selection in the red-winged blackbird. *Behavioral Ecology and Sociobiology,* **7,** 233–238.