

Spatial and age-related variation in use of locally common song elements in dawn singing of song sparrows *Melospiza melodia*: old males sing the hits

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Abstract In many songbirds, individuals have repertoires of multiple song types, some of which may be shared with others in the local area. Hypotheses about the evolution of song repertoires differ as to whether selection acts primarily on repertoire size itself or the ability to match songs of neighbours. We used a 16-channel acoustic location system to record neighbourhoods of song sparrows (*Melospiza melodia melodia*) during the dawn chorus. We asked whether males sing all songs with similar frequency as predicted by the *Repertoire Size Hypothesis*, whether males preferentially sing highly shared songs as predicted by the *General Sharing Hypothesis*, or whether use of highly shared songs is associated with phenotype as predicted by the *Conditional Sharing Hypothesis*. Contrary to the Repertoire Size Hypothesis, most males did not sing all songs equally often. Contrary to the General Sharing Hypothesis, we found no general tendency to overproduce highly shared songs. The degree to which males overproduced highly shared songs was repeatable across days, indicating consistent individual differences, and varied across neighbourhoods. Moreover, and consistent with the Conditional Sharing Hypothesis, older males were more likely to overproduce highly shared songs. If highly shared

song is a conventional signal of aggression, with the threat of receiver retaliation maintaining honesty, older males may be more willing or able to risk conflict. Alternatively, males may learn which songs are effective signals for an area. Finally, age-related variation in vocal performance may shape the adaptive value of highly shared song.

Keywords Song repertoires · Song sharing · Repertoire size hypothesis · General sharing hypothesis · Conditional sharing hypothesis · Conventional signals

Many animals use acoustic signals in both courtship and territoriality. Songs of oscine birds (suborder Passeri) are generally learned early in life and like many animal signals, can be rich in information content. Depending upon the species and the context, there are several aspects of birdsong to which receivers may attend, but two features—song complexity and song sharing—have attracted particular attention. First, song complexity often varies among individuals; for example, some singers have more song types in their repertoire than do others. Females frequently prefer males with large repertoires as in sedge warblers *Acrocephalus schoenobaenus* (Catchpole 1980; Catchpole et al. 1984; Buchanan and Catchpole 1997; although, see Marshall et al. 2007 for an exception in this species), great reed warblers *Acrocephalus arundinaceus* (Hasselquist et al. 1996), great tits *Parus major* (Baker et al. 1986), European starlings *Sturnus vulgaris* (Gentner and Hulse 2000), and song sparrows *Melospiza melodia* (Searcy and Marler 1981; Reid et al. 2004; although, see Searcy 1984 for evidence that this preference may not affect social mate choice). The developmental stress hypothesis (Nowicki et al. 1998, 2002) explains such preferences by positing that repertoire size and other aspects of song complexity reflect the singer's ability to avoid or withstand stress during early

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life, and thus advertise quality. Second, individuals may vary in the degree to which they share whole or partial song types with neighbours or others in the local population ('song sharing'). Song sharing with neighbours predicts territory tenure in some populations of song sparrow (Beecher et al. 2000; Wilson et al. 2000) although not in others (Hughes et al. 2007) and may facilitate territorial defence through the use of shared songs to signal aggression or attention during countersinging bouts (Burt et al. 2001; Vehrencamp 2001; but see Searcy et al. 2006 for an alternative interpretation). Whether song sharing with neighbours confers additional advantages in mate attraction is less clear (O'Loughlen and Beecher 1999; Hill et al. 2011), although over larger geographic scales, females generally prefer locally typical song over nonlocal song (e.g. brown-headed cowbirds *Molothrus ater*, O'Loughlen and Rothstein 1995; white-crowned sparrows *Zonotrichia leucophrys*, Baker et al. 1981, song sparrows, Searcy et al. 2002; and swamp sparrows *Melospiza georgiana*, Anderson 2009).

Beecher and Brenowitz (2005) identify two major classes of hypothesis advanced to explain the function of song repertoires: the *Repertoire Size Hypothesis* and the *Sharing Hypothesis*. The first, referred to simply as the *Repertoire Hypothesis* by Beecher and Brenowitz (2005), suggests that repertoire size is the primary target of sexual selection (particularly mate choice, although see Krebs (1977) for discussion of how large repertoires might function in territorial defence). However, despite considerable evidence for directional selection on repertoire size, large repertoires are not ubiquitous within the songbirds. Among more than 200 species for which repertoire size data are available, the modal value is only a single song type (MacDougall-Shackleton 1997), and in some lineages repertoire size appears to have decreased over time (Irwin 1988, 1990). Moreover, many species (such as song sparrows) sing with eventual variety, repeating the same song type several times before switching to a new type, rather than showcasing their full repertoire quickly and efficiently as might be expected under the Repertoire Size Hypothesis (Slater 1981). By contrast, the Sharing Hypothesis posits that song sharing, rather than repertoire size, is the major target of sexual selection. That is, birds that share a large proportion of songs with their neighbours or others in the local population will enjoy social advantages in terms of territorial and/or mating interactions. According to this hypothesis, selection may favour increased repertoire size incidentally but only insofar as it is correlated with song sharing (Beecher 2008).

Distinguishing between the Repertoire Size and Sharing Hypotheses has proven difficult, in part because many studies focus on the fitness consequences of either repertoire size or song sharing to the exclusion of the other

(Beecher 2008). However, these two aspects of song are not necessarily independent of one another, and in some cases are positively associated (Beecher et al. 2000; MacDougall-Shackleton et al. 2009). Thus, simply measuring how fitness correlates to some feature of song repertoires, whether size or sharing, may not reliably determine its relative importance. A promising alternative to relying on observations of repertoire *content*, which remains static throughout adulthood in closed-ended learners like song sparrows, is to investigate patterns of repertoire *use*. Singing behaviour has traditionally been examined by stationing human observers on the territories of free-living birds, but even when observers attempt to be unobtrusive, human presence can alter singing behaviour (Gutzwiller et al. 1994). Moreover, standard techniques involve recording song from one or two birds at a time, such that different individuals are recorded at different times of day or over different days, increasing the likelihood that temporal or weather variation may obscure underlying patterns in song use. Recent advances in technology offer a solution to these problems. Acoustic location systems (ALS) now allow researchers to continuously and unobtrusively monitor vocalizations over many territories simultaneously, using multiple omni-directional microphones placed throughout a field site (e.g. Blumstein et al. 2011; Mennill 2011). With very little intrusion by humans, a neighbourhood of individuals can thus be recorded simultaneously, providing a powerful new approach to understanding how birds use the songs within their repertoires.

We used a 16-channel ALS to investigate repertoire use in a migratory Ontario population of song sparrows (*M. melodia melodia*). Song repertoire size varies from five to 12 song types per male, and is positively related to various measures of condition (cell-mediated immune response, Reid et al. 2005; body condition, Pfaff et al. 2007) in this and other populations of song sparrows. Whereas neighbouring males often share entire song types in sedentary western (*Melospiza melodia morphna*) populations, such complete song sharing is rare in migratory eastern populations (Hughes et al. 1998; Stewart and MacDougall-Shackleton 2008; although see Foote and Barber 2007 for an exception). Despite the lack of complete song sharing, males often share portions of song ('song elements'); such sharing appears salient in territorial interactions (Anderson et al. 2005). In our study population, males vary in the degree to which their song elements are shared with others (Fig. 1). Some males' repertoires consist mainly of song types with very common elements that are shared with many males in the local area, whereas other males' repertoires contain elements shared with no other birds at the site. Genetic work suggests that the latter males have immigrated from outside our study population (Stewart and MacDougall-Shackleton 2008).

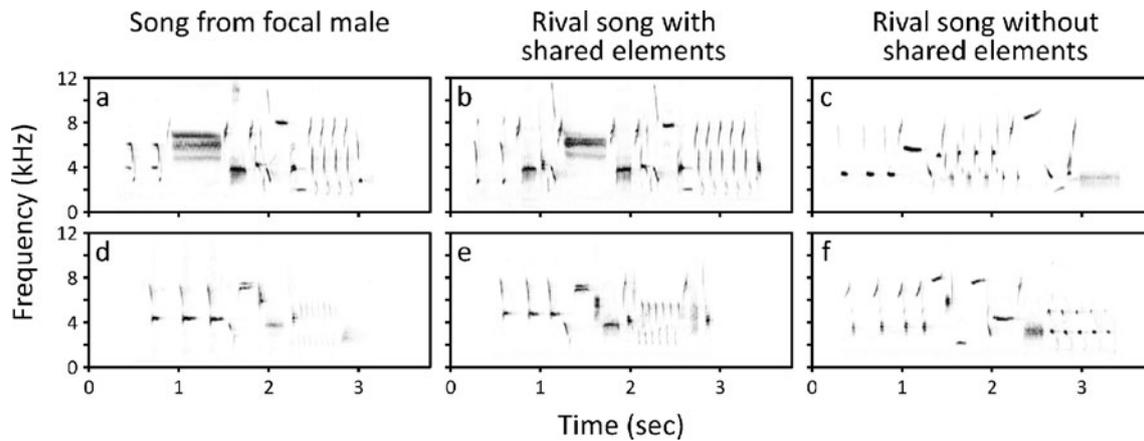


Fig. 1 Spectrograms of songs recorded from male song sparrows, showing pairs of songs with and without shared elements. Song type A (produced by a focal male) shares six elements with song type B

(produced by a neighbouring male) but none with song type C (produced by a third male). Similarly, song type D shares five elements with song type E but none with song type F

Our main objective in this study was to use patterns of repertoire use to distinguish between the Repertoire Size and Sharing Hypotheses in our study population. If repertoire size is the major target of selection on song, then all else being equal, males should produce all song types within their repertoire with approximately equal frequency because this arrangement should maximize apparent repertoire size. The probability that a receiver (a rival male or a prospective mate) will fail to detect one or more song types, and thus underestimate the singer's repertoire size, is minimized when all song types are produced equally often. Conversely, if song sharing is the primary target of selection males may overproduce song types with highly shared elements and underproduce song types with less common elements in order to maximize the apparent degree of shared song content and potentially reduce aggression through the dear-enemy effect (e.g. Briefer et al. 2008). We refer to this idea as the *General Sharing Hypothesis*. However, an alternative interpretation of the Sharing Hypothesis is that individuals may vary in the degree to which they advertise highly shared song. Although previous studies suggest that the *ability* to produce highly shared song (that is, having such songs available within one's repertoire) may enhance fitness, heavy *use* of this signal could incur costs as well as benefits. In several species, including song sparrows, matching the song of an opponent may signal aggressive intent (Krebs et al. 1981; Nielsen and Vehrencamp 1995; Burt et al. 2001; Vehrencamp 2001; Searcy and Beecher 2009; but see Searcy et al. 2006) and can thus increase the risk of eliciting an aggressive response (Vehrencamp 2001; although see Anderson et al. 2008 for an example to the contrary). If so, preferential use of highly shared songs may be restricted to individuals with high resource holding potential; we refer to this idea as

the *Conditional Sharing Hypothesis*. Thus, producing shared song may act as a conventional signal (Vehrencamp 2001), with the threat of receiver retaliation maintaining signal honesty.

Methods

Study site and population

Field work was conducted during spring 2008 and 2009, on the Bracken property owned by the Queen's University Biological Station, near Newboro, Ontario, Canada (44° 38.6' N, 76° 19.0' W). This site supports approximately 35–40 breeding pairs of song sparrows (*M. melodia melodia*) that have been studied by our research group since 2002. Song sparrows in this area are migratory, but philopatric as adults (40–60% return rates, <75 m territory movement between years).

Shortly after birds returned from spring migration in April, we captured adult males in seed-baited Potter traps or mist nets and provided each with a unique combination of coloured leg bands. We measured mass to the nearest 0.2 g using a spring-loaded scale, and measured right tarsus length to the nearest 0.1 mm using dial callipers. Body condition was estimated as the ratio of mass to tarsus length. We determined age (range=1–5 years) based on banding records dating back to 2002. Two males had been banded as nestlings in previous years, so their ages were known with certainty. Others were first captured and banded as adults; we considered these *adult recruits* to be yearlings. In support of this assumption, adult recruits have shorter wings than birds known to be 2 years or older (unpublished data). Moreover, each spring we exhaustively

search the study area to capture and band all breeding adults. Given the short distance of territory movement by banded birds between years, we assume that adult recruits are breeding for the first time. We determined pairing status through field observations, and monitored nests to confirm the breeding status of all males in the study.

ALS recording and analysis

The ALS consisted of an array of 16 omni-directional microphones, similar to the eight-channel ALS described by Mennill et al. (2006), distributed over five to 11 song sparrow territories. Microphones were protected by rain guards made from polyvinyl chloride tubing and plastic mesh, and mounted with shelf brackets onto 3-m wooden poles that had been painted in a camouflage pattern and attached to trees or stakes using elastic cords. Microphones were connected by 2,200 m of cable to a central laptop computer, where data from all 16 simultaneously recording channels were digitized using a multichannel data acquisition card (National Instruments DAQ-6260) and stored as a 16-channel AIFF sound file using Chickadee recording software (version 1.8; J. Burt, Seattle, WA). ALS recording began at sunrise; we annotated the first 30 min of song recorded each day. We have previously shown that 30 min is sufficient to achieve repeatable measures of song output in this population (MacDougall-Shackleton et al. 2009). This interval encompassed most of the dawn chorus, as song rates declined substantially by 30 min after sunrise, and was long enough for most singers to use most or all of the songs within their repertoire (Table 1). To minimize disturbance, we did not intrude onto territories while the ALS was operating.

Social context, and thus song matching, is expected to vary with breeding stage (Krebs et al. 1981); to address this possibility, we investigated patterns of song use during two different times of the breeding season. In 2008, we conducted ALS recordings from 5 to 16 May, corresponding to the egg-laying and incubation periods for most birds in our study population. For this year, we restricted our analysis of repertoire use to males that had already attracted a social

mate that had begun nest construction ('nesting' males, $N=16$). In 2009, we conducted ALS recordings between 20 and 29 April, corresponding to shortly before nest construction for most birds in the population. For this year, we restricted our analysis of repertoire use to males who were either unpaired at the time of recording, or whose mates had not yet initiated nest construction ('pre-nesting' males, $N=26$). Nine males were recorded by the ALS in both years.

We divided the study site into three areas (hereafter, 'neighbourhoods'), corresponding to three different ALS configurations. Only males whose territories were completely contained within one of the three neighbourhoods were included as focal males in this study. The ALS remained in place for 2–4 days before being moved to a new location. For each neighbourhood, wind and weather conditions were taken into account and the best two (2009, pre-nesting) or three (2008, nesting) days of recording were retained for analysis. These days were consecutive where weather permitted. The smaller number of recording days in 2009 reflects efforts to ensure that all neighbourhoods could be recorded before nesting activity began.

We visualized ALS recordings using Syrinx-PC (version 2.6h; J. Burt, Seattle, WA) and noted how often each male produced each of the song types within his repertoire. Because complete song types are almost never shared by more than one male in this population, identifying ALS recordings to song type also allowed us to identify the singer by referring to individual repertoire recordings (see below). For many males, we further confirmed identities by triangulating the position of several songs following the same protocol outlined in Mennill et al. (2006) and matched these positions with our territory maps from behavioural observations.

Repertoire recording and analysis

In addition to ALS recordings, we also individually recorded song repertoires of focal males and their neighbours, i.e. immediate neighbours plus those one territory away (Beecher et al. 2000; Hughes et al. 2007). In all, we recorded repertoires from 40 territorial males, 33 of which were involved directly in this study ('focal males'). The remaining seven males were not included as subjects in our analysis of song use ('non-focal males'), either because their territories were at the periphery of the recording neighbourhoods or because they were not at the appropriate breeding stage at the time of recording. However, because they were neighbours of one or more focal males, we included their repertoires in our calculations of neighbourhood song element sharing (see below).

We recorded songs using Marantz Professional PMD 671 solid state recorders and Telinga Twin Science Pro parabolic microphones. Following Pfaff et al. (2007), we considered a repertoire complete when either 300 consecutive songs or

Table 1 Total song output per individual, and percentage of songs in the repertoire that were used, across multiple day ALS recordings of male song sparrows singing at dawn

Breeding Stage	<i>N</i>	Song output	Percentage of repertoire
Pre-nesting	26	126.0±93.1	88±16
Nesting	16	237.8±136.9	91±14

Pre-nesting males were annotated for two 30-min intervals, and nesting males for three 30-min intervals. Values are means±SD

450 non-consecutive songs had been recorded. We recorded complete song repertoires from all 33 focal males, and six of seven non-focal males. The remaining non-focal male had fewer than 300 consecutive songs recorded, but was included in the neighbourhood song element sharing analysis based on the ten song types identified within his (presumably) partial repertoire. Several additional males (five in 2008 and four in 2009) had territories near those of study subjects, but had no repertoires recorded. As a result, nine males in each year of the study had at least one neighbour unrepresented in the calculation of song element sharing (mean±SD=2.11±0.93 and 1.22±0.44 for 2008 and 2009, respectively). Adult song sparrows do not alter their repertoire composition from year to year (Nordby et al. 2002), so we did not re-record males whose repertoires were collected in previous years.

We used Syrinx-PC to generate spectrograms of repertoire recordings, then visually sorted each male's songs and classified them into distinct song types following Pfaff et al. (2007). We then identified each song type's component song elements, defined as traces on the spectrogram that always occurred together (Stewart and MacDougall-Shackleton 2008). In 2008, we identified 227 different song types and 214 different song elements within the repertoires of focal males and their neighbours. In 2009, we identified 229 distinct song types and 222 different song elements; 193 song elements were common to both years of the study. The total number of song types at the study site often exceeds the total number of song elements because although each song type is composed of multiple elements (Fig. 1), these elements can be combined in many different ways, and most elements occur in multiple song types.

Song element sharing

To determine how closely each song type matched the songs of neighbours, we used visual and acoustic inspection of spectrograms and recordings to generate a catalogue of song elements based on all available repertoires. We then scanned each song type within each male's repertoire for the presence of each song element. Because song sparrows sing their song types with variation, occasionally deleting or substituting certain elements, we considered an element to be present in a song type if it occurred in any of the variants recorded for that song type. Next, for all pairwise combinations of song types, we determined the degree to which they shared song elements. This was calculated as Jaccard's coefficient of similarity, using the equation

$$J_{AB} = c/(a + b + c - d).$$

Here, c represents the number of elements common to song types A and B; a is the number of elements present in

song type A but not song type B; b is the number of elements present in song type B but not song type A; and d is the absolute value of the difference in number of elements in song types A and B (Tracy and Baker 1999). Finally, for each song type, we calculated the average of the Jaccard's coefficients of similarity between it and all the song types produced by all neighbouring males. This calculation included all neighbours (adjacent and one away) for whom repertoires were available, regardless of their status as focal or non-focal males. We, thus, obtained a single coefficient of neighbourhood-scale element sharing for each song type, hereafter referred to as that song type's *neighbourhood sharing coefficient*. In principle, this coefficient can range from zero (a song composed entirely of elements unique to the singer and present in no neighbours' songs) to one (a song composed entirely of elements that are present in every song type of every neighbour). We also calculated for each song type of each focal male a larger-scale coefficient of sharing (*population sharing coefficient*) based on its element sharing with songs from all males recorded at the study site that year, following Stewart and MacDougall-Shackleton (2008).

Data analysis

We used chi-square analyses to test whether males used all song types in their repertoire similarly often, as predicted by the Repertoire Hypothesis. Heterogeneity testing (Zar 1999) indicated that pooling data across individuals would be inappropriate (data not shown), so we compared observed versus expected rates of use for each male individually. For each focal male, the two song types within his repertoire having the highest neighbourhood sharing coefficients were categorized as 'most shared'; the two song types having the lowest neighbourhood sharing coefficients were categorized as 'least shared'; and the remaining song types (one to six per male, depending on repertoire size) were considered 'moderately shared'. We then calculated the male's song output, combined across all days of recording, for each of the three categories of song and compared the observed patterns of use to random (even) expectations. Expected outputs were calculated by dividing total song output by the male's repertoire size, then multiplying by the number of song types within a given category (most, least or moderately shared). Finally, we compared males that did versus did not deviate from random expectations with respect to age, repertoire size and dawn song output.

To characterize the degree to which a given male preferentially sang the more shared songs within its repertoire, we calculated Spearman's correlation coefficient (ρ) between a given male's output of each song type (combined across all days of recording unless otherwise

noted) and that song type's neighbourhood sharing coefficient, across all the songs within the male's repertoire. We considered this correlation coefficient to reflect that male's *sharing strategy*. Positive values of ρ denote birds that sang their most-shared songs more often than their least-shared songs, whereas negative values denote birds that sang their least-shared songs more often. To determine whether our sampling regime characterized consistent sharing strategies, we investigated repeatability of strategy across different days of recording (2 days for pre-nesting males and 3 days for nesting males). Specifically, we calculated each male's sharing strategy for each 30-min annotation window, separately for each day of recording. We used ANOVA to compare within- and among-male components of variance, following Lessels and Boag (1987).

To test the hypothesis that males preferentially sing highly shared song types, as predicted by the General Sharing Hypothesis, we compared the observed distribution of ρ (combined across all days of recording) to a null value of zero using a one-sample *t* test. In a related analysis, we used a paired *t* test to compare neighbourhood sharing coefficients of each individual's most versus least produced song types.

To test the hypothesis that sharing strategy reflects some aspect of individual phenotype, as predicted by the Conditional Sharing Hypothesis, we first constructed an exploratory general linear model for each of the two time periods (pre-nesting and nesting) using PROC GLMSELECT in SAS version 9.2 (SAS Institute, Cary, NC). We used the Schwarz Bayesian Information criterion and backward elimination to identify candidate variables associated with sharing strategy (calculated across all days of recording). Predictors entered into these exploratory models included number of neighbours (range=6–16), repertoire size, average neighbourhood sharing coefficient (calculated across all song types within a male's repertoire), song output (mean number of songs produced per 30 min), age and body condition. Mass data were unavailable for two males, so we used mean substitution for their body condition in the exploratory models. Neighbourhoods did not differ in male age, body condition, repertoire size, or average neighbourhood sharing coefficient, nor did we observe neighbourhood differences in clutch size or nest success (data not shown). However, to account for daily variation in weather and breeding stage at the time of recording, as well as spatial variation, we included 'neighbourhood' as a factor in the exploratory models. We calculated variance inflation factors for all continuous predictors using PROC REG in SAS 9.2: these ranged between 1.05 and 1.99, all below the threshold of 10 which would indicate problematic multicollinearity (Chatterjee et al. 2000). We used general linear model regression (PROC GLM in SAS 9.2) to evaluate the selected models.

Results

Distribution of song use

Individual chi-square analyses of song use at dawn indicated that slightly more than half the males (15 of 26 during pre-nesting recordings and nine of 16 during nesting recordings) deviated significantly from patterns expected if all song types were used equally. Of these, during the pre-nesting period, six males overproduced their most-shared song types, five overproduced intermediately shared song types and four overproduced their least-shared song types. During the nesting period, three males overproduced their most-shared song types, one its intermediately shared song types and five their least-shared song types. Post hoc comparisons between males that deviated significantly from equal use expectations during pre-nesting and those that did not revealed no differences in song output (*t* test; $t_{24}=-0.23$, $p=0.82$), repertoire size ($t_{24}=-1.50$, $p=0.15$), average neighbourhood sharing coefficient ($t_{24}=-0.53$, $p=0.60$) or age ($t_{24}=1.49$, $p=0.15$). During nesting, males that deviated from equal use expectations had lower song output than those that did not (mean \pm SD=53.6 \pm 37.3 and 112.2 \pm 38.0, respectively; $t_{14}=-3.09$, $p=0.01$) but did not differ significantly in repertoire size ($t_{14}=-0.72$, $p=0.49$), average neighbourhood sharing coefficient ($t_{14}=1.01$, $p=0.33$) or age ($t_{14}=-1.62$, $p=0.13$).

General patterns in sharing strategy

We found no general tendency for males to sing songs containing highly shared elements more often. Sharing strategy, or the degree to which a male preferentially produced highly shared song types, was not significantly different from zero during either pre-nesting (one-sample *t* test; mean \pm SD=-0.002 \pm 0.457, $t_{25}=0.03$, $p=0.98$) or nesting (mean \pm SD=0.030 \pm 0.449, $t_{15}=0.26$, $p=0.80$; Fig. 2). Similarly, the most and least frequently used song types did not differ in neighbourhood sharing coefficients during either pre-nesting (paired *t* test, pre-nesting: $t_{25}=-0.18$, $p=0.86$) or nesting ($t_{15}=-0.061$, $p=0.95$). Sharing strategy did not differ on average between pre-nesting versus nesting breeding stages ($t_{40}=0.07$, $p=0.79$).

Individual variation in sharing strategy

Sharing strategy was repeatable across days (pre-nesting $F_{25,28}=2.23$, $p=0.02$, repeatability=0.38; nesting $F_{15,35}=2.45$, $p=0.02$, repeatability=0.33), indicating consistent individual variation in this trait. Among pre-nesting males, age was the only predictor of sharing strategy in the optimal model identified by the exploratory GLM. Among nesting males, the exploratory model identified neighbourhood as the only predictor of sharing strategy.

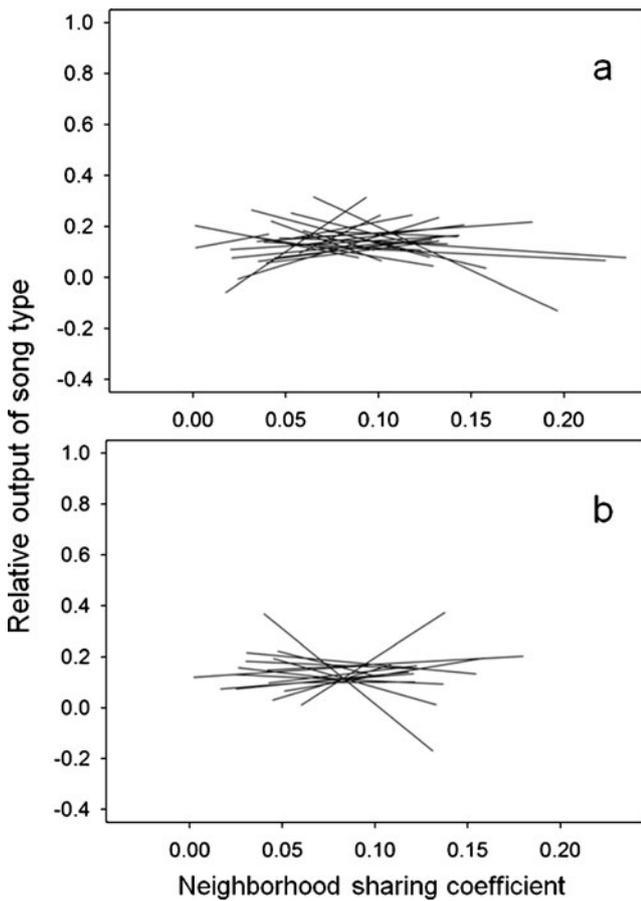


Fig. 2 Male song sparrows showed no consistent pattern in how often they produced highly shared song types during dawn singing bouts. Relative output for each song type was calculated as the proportion of the singer’s total output. Each line represents one bird and shows the linear regression of each song’s relative output on that song’s neighbourhood sharing coefficient, across the song types within his repertoire. Birds are separated based on the time of year: **a** $N=26$ males recorded in the pre-nesting season, **b** $N=16$ males recorded during the nesting season

Final GLMs for each time period are summarized in Table 2. Sharing strategy was positively associated with age during pre-nesting recordings, with older males singing more shared song elements than younger males (Fig. 3). This pattern reflects age-related variation in repertoire use, not in repertoire composition, as we found no relationship between male age and either repertoire size (Pearson’s correlation; $r_{24}=0.04$, $p=0.85$) or average neighbourhood sharing coefficient ($r_{24}=0.31$, $p=0.12$). Post hoc analysis of

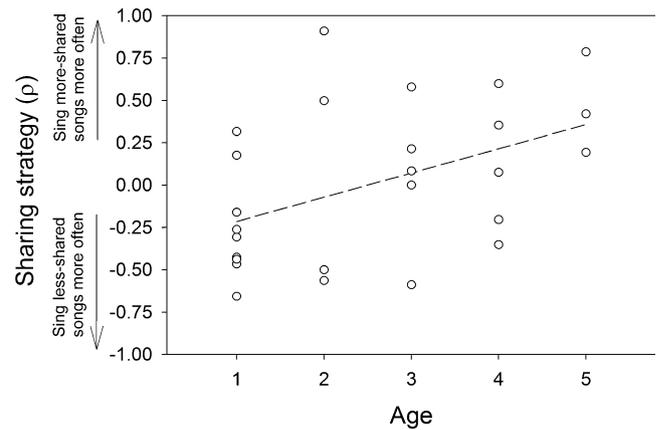


Fig. 3 The tendency to overproduce highly shared song types during dawn song increased with age in male song sparrows recorded during the pre-nesting season. $N=26$ males

overwinter returns revealed no effect of pre-nesting sharing strategy on the likelihood of returning to the study site in the following year (logistic regression; likelihood ratio, $\chi^2=0.02$, $p=0.88$).

Among nesting males, a significant proportion of variation in sharing strategy was explained by neighbourhood (Fig. 4; Table 2). Other variables, including age, did not explain a significant proportion of the variation in sharing strategy during this time period.

Neighbourhood- versus larger-scale sharing

In both years studied, the degree to which a song type shared elements with songs of neighbouring males (neighbourhood sharing coefficient) was highly correlated to the degree to which it shared elements with songs of all males recorded at the study site (population sharing coefficient; 2008, $r_{123}=0.87$, $p<0.001$; 2009, $r_{190}=0.96$, $p<0.001$). Neighbourhood sharing coefficients did not differ on average from population sharing coefficients for a given song type (paired t test, 2008; $t_{124}=1.69$, $p=0.09$; 2009, $t_{191}=0.0004$, $p=0.66$).

Discussion

Over half the males in our study did not produce all song types equally often. We found no general tendency for

Table 2 Results of final general linear model regressions predicting sharing strategy of male song sparrows during dawn song

Context	<i>N</i>	Predictor	β (SE)	<i>F</i>	R^2	<i>P</i>
Pre-nesting	26	Age	0.15 (0.06)	6.69	0.22	0.016
Nesting	16	Neighbourhood	–	10.99	0.63	0.002

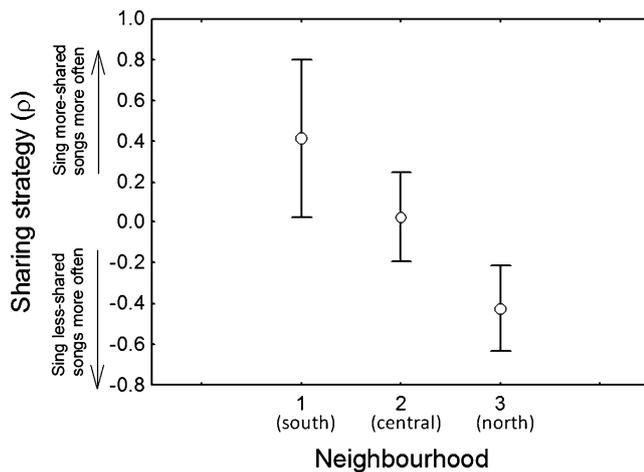


Fig. 4 The tendency to overproduce highly shared song types during dawn song varied among neighbourhoods in male song sparrows recorded during the nesting season. Values are means \pm SD. $N=16$ males

highly shared songs to be overproduced relative to random expectations; instead, the degree to which males used highly shared song types was consistent within individuals. Prior to nesting, variation in sharing strategy corresponded to variation in male age, such that old males were more likely than young males to overproduce songs composed of highly shared elements; this finding provides support for the Conditional Sharing Hypothesis. During nesting, sharing strategy varied among neighbourhoods, suggesting that extrinsic factors may also affect the degree to which individuals overproduce highly shared song.

If repertoire size is the primary target of selection on song, we would expect male song sparrows to sing all song types more or less equally often in order to maximize apparent repertoire size. Our finding that a majority of males deviated from this pattern is contrary to general predictions of the Repertoire Size Hypothesis, as is the widely recognized fact that song sparrows sing with eventual rather than immediate variety. Previous studies on song sparrows have shown that although females prefer large over small repertoires, they also prefer song bouts arranged with eventual variety over song that has been artificially organized with immediate variety (Searcy and Marler 1981). Moreover, repertoire size appears to have little effect on territory tenure when song sharing is controlled for (Beecher et al. 2000). Taken together, these patterns suggest that song sparrows do not use their song types interchangeably and that advertising repertoire size rapidly and efficiently may not be of primary importance in this species, at least during the time periods we surveyed. Of course, the non-uniform distribution of song use we observed does not rule out other aspects of song complexity (besides repertoire size) being important targets of selection.

Likewise, it should be noted that some males did use their song types more or less evenly, and moreover that during nesting males singing at high rates were particularly likely to use songs evenly. This individual variation suggests that the Repertoire Size Hypothesis cannot be conclusively dismissed at this time. Although a majority of males produced some songs more often than others, we observed no overall tendency to overproduce songs with highly shared elements. Sharing strategy did not differ, on average, from zero either before or during nesting, and individual chi-square analyses showed comparable numbers of males overproducing their least shared or moderately shared as most-shared songs. These findings suggest that heavy use of highly shared song types may not be advantageous across all contexts. Instead, we observed substantial and repeatable variation among individuals in the degree to which they over- or underproduced highly shared song.

During the pre-nesting period, older males were more likely than younger males to preferentially use highly shared song types (Fig. 3). Traits can become correlated with age either because individuals change their expression of the trait as they age, or because of differential mortality related to trait expression (e.g. Kipper and Kiefer 2010). In western song sparrows, for example, the number of shared songs within an individual's repertoire predicts territory tenure such that on average, older males share more songs with neighbours than do younger males (Beecher et al. 2000) despite the fact that repertoire size remains static over time (Nordby et al. 2002). In our study, the low number of males sampled in both years, and confounds with breeding stage, limit our power to document longitudinal changes in behaviour. However, dawn sharing strategy did not predict return the following spring. This parallels findings by Hughes et al. (2007) that song sharing does not predict territory tenure in this subspecies and suggests that age-related variation in sharing strategy results from changes in song use as individuals age not from a survival or territorial advantage associated with singing shared songs.

Our finding that sharing strategy varies with male age is consistent with the Conditional Sharing hypothesis but conclusively evaluating this idea requires determining whether our measure of highly shared song is indeed a signal of willingness to escalate: future playback studies will examine this possibility. In western populations of song sparrows, use of shared song does appear to signal aggressive intent (Burt et al. 2001; Vehrencamp 2001). However, these studies investigated song in a highly directional context, dyadic interactions during countersinging. In contrast, both our measure of similarity (sharing of elements with all neighbours rather than with a specific rival) and the context in which song occurred (dawn chorus, which in many species is associated with broadcast singing behaviour, as opposed to pairwise song contests; e.g.

Mennill and Otter 2007) were less specific. The song bouts we recorded represent a combination of spontaneous song, countersinging contests between two males and more complex multi-male interactions. Unfortunately, further disentangling these contexts using remote sensing data is problematic, because the high rate of song throughout a neighbourhood that characterizes the dawn chorus also reduces the reliability of temporal and spatial cues in identifying countersinging bouts (Burt and Vehrencamp 2005). In this situation, the use of shared song types can be informative as to whether or not two singing males are interacting with one another (Burt and Vehrencamp 2005) but using song matching to identify countersinging events then testing whether such bouts involve more matching than non-countersinging bouts would necessarily be circular.

Another methodological difference involves our measure of song similarity, based on proportion of shared elements rather than on whole-song sharing as in studies of western song sparrows. Our measure weights all elements equally, despite evidence that in some populations song sparrows attend mainly to introductory elements (Horning et al. 1993). Importantly, however, a similarly weighted measure (proportion of locally copied elements) has been implicated in female song preference in a Pennsylvania population of this subspecies (Nowicki et al. 2002). Moreover, sharing of introductory trills does not predict territory tenure better than whole-song sharing in that study population (Hughes et al. 2007). Thus, we think it likely that our measure of song sharing captures a reasonable proportion of behaviourally salient variation. We also observed a strong positive correlation between a song type's neighbourhood sharing coefficient and its population sharing coefficient; moreover, neighbourhood sharing coefficients were not higher on average than population sharing coefficients. These results demonstrate that (partial) song sharing is not greater within neighbourhoods than at a larger geographic scale, consistent with findings from the Pennsylvania population studied by Hughes et al. (1998). Thus, whereas the *use* of shared song content may be relevant to territorial interactions, in contrast to sedentary populations (e.g. Beecher 2008) the *amount* of shared content in a male's repertoire appears unrelated to the neighbourhood in which he establishes a territory.

The Conditional Sharing interpretation also requires that old males are better able and/or more motivated than young males to carry the risk of eliciting an aggressive response from rival males. Consistent with this idea and with our findings, Hyman et al. (2004) observed higher levels of territorial defence by returning males than first-year males in a Pennsylvania population of song sparrows. Such a pattern could arise for several reasons. First, insofar as high-quality individuals are more likely to survive to old age, age may covary with resource holding potential (although see Arcese 1987 for an example of nonlinear

age effects in this species). Second, if older males tend to occupy more desirable territories they may be more motivated to defend these territories and/or encounter more territorial challenges. Undermining this possibility, however, we observed no relationship between male age and either clutch size or fledging success (data not shown), although we cannot dismiss the possibility that some other unmeasured aspect of territory quality or mate quality might vary with age. Third, age can influence the optimal balance between current and future reproduction, as predicted by terminal investment models (Clutton-Brock 1984). Similarly, previous experience at the breeding site can increase the value of a territory to its owner (e.g. 'bourgeois strategy'; Maynard Smith 1982), such that old males may benefit more than young males from high levels of defence regardless of territory quality.

An alternative explanation for why older males overproduce shared songs is that prior experience rather than the cost of receiver retaliation maintains signal honesty. That is, males may learn which song types are particularly effective signals for a given neighbourhood, either through trial and error or through eavesdropping. This mechanism requires high site fidelity during adulthood (Kiefer et al. 2010), but our study population appears to meet this requirement; returning males nearly always settle on the same territory as the previous year or one territory away (unpublished data). In common nighthingales *Luscinia megarhynchos*, which are open-ended song learners, males add and drop songs between their first and second breeding seasons such that the repertoires of males aged two and older are more representative of the surrounding area than those of yearling males (Kiefer et al. 2010). Song sparrows are closed-ended learners and the content of their repertoires is static during adulthood, with selective attrition of song types (Nelson and Marler 1994) generally occurring within the first breeding season and not thereafter. In contrast, the age-related variation in repertoire use we observed seems relatively continuous (Fig. 3), rather than changing dramatically between yearlings versus older males, although our ability to address this is constrained somewhat by sample size. Another way in which learning may be implicated in age-related variation in sharing strategy is if elements contained in the 'favourite' songs of older males are more likely to be learned or retained by their younger neighbours. Our finding that, on average, song element sharing within a neighbourhood was highly correlated to (and not generally higher than) element sharing within the entire study population suggests that this explanation is unlikely. Still, testing this idea would ideally involve a combination of captive learning studies, and longitudinal analyses to examine whether 'favourite' songs remain consistent between years. Finally, the adaptive value of matching all or part of an opponent's song may depend upon relative vocal performance (Logue and Forstmeier 2008).

That is, high-performance singers (e.g. those capable of greater stereotypy or more closely approaching performance constraints) may preferentially sing songs containing highly shared elements in order to showcase superior vocal performance, while low-performance singers preferentially sing song types composed of less shared elements, which are, thus, less matchable and more difficult for eavesdroppers to compare (Logue and Forstmeier 2008). If vocal performance varies with age, as it does in swamp sparrows (Ballentine 2009) then variation in sharing strategy may reflect the divergent tactics of high-performance versus low-performance singers.

Whereas sharing strategy prior to nesting was best explained by male age, during the nesting period we found substantial variation between neighbourhoods in sharing strategy (Fig. 4). Similarly, in a Pennsylvania population of this subspecies, Hyman et al. (2004) reported spatial autocorrelation in territorial aggression: males that responded aggressively following song playback tended to be spatially clustered. Collectively, these findings support the idea that the behaviour of one territory holder may be affected by that of his neighbours, as predicted by the ‘challenge hypothesis’ (Wingfield et al. 1987). Targeted playback experiments, assessing the behavioural and physiological responses of males to highly versus less highly shared song types, should help resolve this possibility.

During the pre-nesting period, we found that variation in sharing strategy was best predicted by male age, whereas later in the season most variation was explained by neighbourhood effects. The relative importance of intrinsic (e.g. age) and extrinsic factors (e.g. song use by neighbouring males) in determining sharing strategy, and thus the reliability of sharing strategy as an indicator of male quality, may vary seasonally. Alternatively, because pre-nesting and nesting song bouts were recorded in two different years, differences between years may explain the different findings for pre-nesting versus nesting males. Differences in statistical power could in theory explain why we observed age-related variation in sharing strategy during the pre-nesting but not the nesting stage ($N=26$ and 16 males, respectively), but the fact that we found neighbourhood effects on sharing strategy during nesting suggests that the sample size in that year was large enough to detect age effects as well. Variation in breeding ecology between years could also explain why sharing strategy varied with age in 1 year and with neighbourhood in another. Although the 2 years of study did not differ in the average age of focal males ($t_{40}=1.38$, $p=0.18$) or in the proportion of yearlings ($\chi^2=0.10$, $p=0.75$) we cannot rule out subtle variation in sex ratio, neighbourhood stability, breeding density or synchrony that might affect territorial interactions, the costs and benefits of singing highly shared song, and the relative importance of different factors in shaping sharing strategy.

Most hypotheses concerning the evolution of song repertoires have focused on repertoire content, which in closed-ended learners such as song sparrows is fixed throughout adulthood and reasonably straightforward to examine. Repertoire use, in contrast, has received relatively little study. The advent of nonintrusive, neighbourhood-scale recording systems now facilitate detailed studies of repertoire use. In our study population, efficiently showcasing repertoire size does not appear to be of primary importance, as most males deviated from the even distribution of song use that would best accomplish this. Of course, this finding does not demonstrate that selection has not acted on repertoire size, but it does suggest that song types are not used interchangeably. At the same time, we observed no general tendency for males to overproduce highly shared songs. Instead, the use of highly shared song types was age dependent, suggesting that highly shared song may be constrained by the risk of receiver retaliation, by familiarity with the song of the local neighbourhood or by relative vocal performance. In contrast to repertoire content, which in closed-ended song learners is static throughout adulthood, our findings suggest that repertoire use is relatively plastic, potentially providing a snapshot of shorter-term variation in condition and circumstances. Future studies addressing the fitness consequences of different strategies within a population, and between populations that differ in their song-learning programmes, should cast light onto the evolution of song repertoires.

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Conflicts of interest The authors declare that they have no conflict of interest.

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