

Original Article

Song sharing correlates with social but not extrapair mating success in the white-crowned sparrow

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Bird song is a prominent example of a trait under inter- and intrasexual selection. Performance-related aspects of bird song have been shown to vary among males and to influence territorial interactions as well as female mate choice. In oscine songbirds, song is different from many other sexually selected traits in that it is learned. As a result of learning, territorial neighbors share songs in some species. Thus, social interactions may be influenced not only by how well a male performs song but also by whom he shares song with. Here, we test the hypothesis that song sharing indicates local song learning and experience from which females may benefit. We examine the prediction that song sharing correlates with reproductive success. During our 4-year field study on white-crowned sparrows *Zonotrichia leucophrys pugetensis*, we found that yearling males that shared song with at least one territorial neighbor had higher social mating success than nonsharers. At the same time, song performance did not significantly correlate with social mating success but did correlate with paternity loss. Males with high performance were more likely to lose paternity than males with low performance. No song feature correlated with gaining paternity. We conclude that song sharing may be an indicator of male quality and stable social neighborhoods which may be a direct benefit to females. Furthermore, our results may provide a functional explanation for a developmental process where songbirds adjust their song to the local social neighborhood.

Key words: bird song, reproductive success, sexual selection, vocal learning, *Zonotrichia leucophrys*. [*Behav Ecol* 23:627–634 (2012)]

INTRODUCTION

Bird song is a prominent example of a trait under sexual selection (Searcy and Andersson 1986). It is subject to both inter- and intrasexual selection because most birds use their songs for territorial defense as well as for mate attraction (Catchpole and Slater 2008). Song characteristics such as repertoire size and performance-related traits vary among males and correlate with male quality and fitness in numerous species (Gil and Gahr 2002; but see Byers and Kroodsma 2009). Due to the dual function of song, females may directly prefer certain male song traits, or males may compete with each other via song over resources that attract females including territories (Berglund et al. 1996; Buchanan and Catchpole 1997).

Song in oscine passerines is one of few sexually selected traits that is learned (Nottebohm 1970, 1972). Thus, differences in male learning ability can affect the expression of song traits (Nowicki and Searcy 2005). However, not only how well a male learns songs but also from whom he learns may affect the signal value of song. Males imitate songs of conspecifics, and consequently, territorial neighbors often share songs in large-scale geographic song dialects or small song neighborhoods (Krebs and Kroodsma 1980; Handley and Nelson 2005). Song sharing may influence male reproductive success through ter-

ritorial interactions and/or through female preference for males singing locally learned songs (O’Loughlen and Rothstein 1995; MacDougall-Shackleton et al. 2002).

Males with shared songs may have high reproductive success for several reasons. First, when song memorization is restricted to an early sensitive phase (as in closed-ended learners, Beecher and Brenowitz 2005), song sharing may be a reliable indicator that males have prior experience in the local area because they spent time learning their song(s) there and are familiar with social neighbors which may lead to fewer aggressive interactions (Vehrencamp 2000). A second hypothesis assumes that high performance singers benefit by singing a shared song because listeners can directly compare performance levels or consistency of performance among males singing similar songs (Logue and Forstmeier 2008). A third hypothesis predicts that song sharing deceives females who then confuse young pupils for their older established tutors (Craig and Jenkins 1982; Payne 1983).

Here, we test whether song sharing, song performance, and song consistency correlate with social and extrapair mating success in male Puget Sound white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). This is an excellent species to study this because males are restricted to memorizing new songs for production in the first few months of life (Marler 1970; Nelson et al. 1996). Males in their first breeding season frequently (36–57% of recruits, Nelson and Poesel 2009) sing 2 or more song types in their first few weeks on territory before retaining the single song type that matches the note complex (NC) in the song of one or more territory neighbors and deleting the remaining song types from their repertoire. This single song type is then kept for the remainder of the male’s life (Nelson and Poesel 2009). Males generally share the terminal trill part of

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their song with territorial neighbors in large-scale song dialects (Nelson and Marler 1994; Nelson 2000), and the NC in the song's introduction is shared on a local scale among 2–8 territory neighbors (Nelson and Poesel 2009).

The first hypothesis outlined above predicts that male reproductive success will correlate with song sharing if song sharing indicates a male's social competence in the neighborhood. Second, if song sharing facilitates comparison among males, we predict a statistical interaction between the effects of song performance and the song sharing on reproductive success. Third, if females are deceived by shared songs, we predict that songs of extrapair males resemble the songs of the males they cuckold. Because song may also benefit males in competition over territories that may be preferred by females, we include a measure of territory quality and male arrival date in our analyses.

MATERIALS AND METHODS

Study species and site

We studied a migratory population of about 85 male Puget Sound white-crowned sparrows at Bullard's Beach State Park, Oregon (43.2033°, -124.4026°) between March and June 2005–2008. Details of field procedures are described in Nelson and Poesel (2009). We differentiated between males new to the study area (recruits) and returns, which were banded males that had defended a territory in the area in a previous year (Nelson and Poesel 2009). Based on the presence of brown rather than black-and-white crown coloration and relatively short wings most recruits were yearlings (Nelson and Poesel 2009). We restrict our analyses to recruits for 2 reasons. First, as noted above, only yearlings have the flexibility to keep a shared song in their final repertoire based on what their neighbors sing. Only 33% of surviving males that did not share song with a neighbor as a recruit shared song with a neighbor in a subsequent year (Nelson DA, personal observation). They did so because a new recruit shared song with them in their second year, not because the survivor changed his song to share. Second, returns occupy the same territory in successive years. If the female survives, she returns to the same territory

and male as in a previous year. We only observed one case of divorce during the 4-year study. Thus to ensure that observed mating patterns were not confounded by reproductive history at this site, we focus our analyses on recruits that defended a territory for the first time.

This species defends all-purpose territories, within which feeding and mating occurs (Morton 2002). To assess territory quality, we noted the number of years from 2004 to 2010 a territory had been occupied by a male. We included all years for which we monitored territory occupancy to get the best possible estimate of territory quality. This is an indirect method of assessing territory quality but has been shown to correlate with productivity and other more direct measures of territory quality in other species (Sergio and Newton 2003).

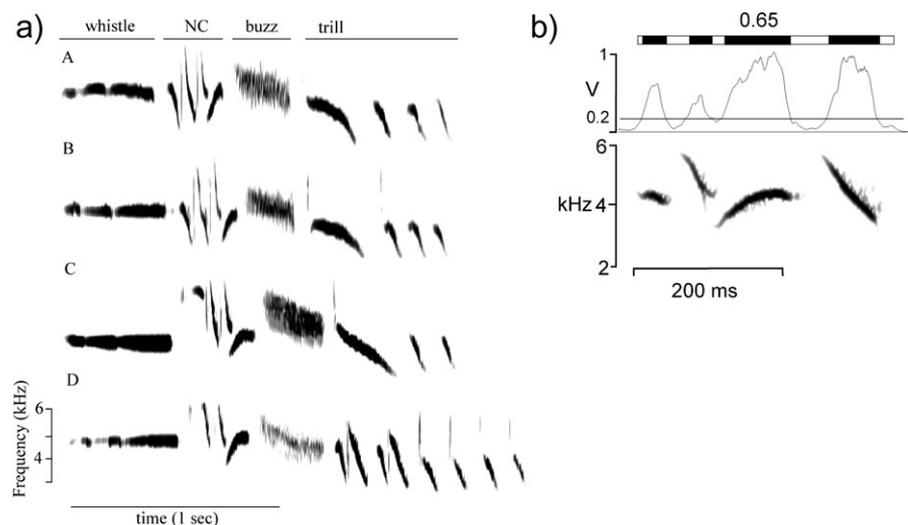
Behavioral observations and song analysis

In 2005–2007, we performed a total of 487 20-min focal watches on 197 territorial males once a week prior to pairing; 97 males were recruits. Males sing frequently prior to pairing but cease spontaneous singing once paired (Nelson and Poesel 2011). When we noted that a male was quiet in our daily observations, we searched the territory to verify that he was with a mate. For each recruit, we chose the focal watch closest to the pairing date and measured all songs within that sample. For males that did not pair, we chose a focal watch in mid-April after females had begun to arrive. We recorded 39.8 ± 3.1 (mean \pm standard error [SE]) songs per focal watch. In 2008, we chose an ad-lib sample of male singing prior to pairing or in mid-April for unpaired males with a similar number of songs. To estimate song performance for all males in the population each year, we selected focal watches of returns using the criteria described above for recruits.

The song of male white-crowned sparrows in our study population begins with a whistle, followed by a NC, a buzz, and a terminal trill (Figure 1a). Across the population, the NC and trill can be categorized into types based on the structure of notes (Baptista 1977; Nelson et al. 2004). In total, we recorded 14 common NC and 5 trill types in this population. We generated spectrograms in SIGNAL 4.04 (Engineering Design) with a 256

Figure 1

Song sharing and measuring singing performance. (a) Sonograms of songs of 4 male *Zonotrichia leucophrys pugetensis*. Songs consist of 4 phrases: whistle, NC, buzz, and trill, each composed of one or more notes. Songs A, B, and C contain the shared trill notes of the local dialect at Bullard's Beach State park, Oregon; song D represents a foreign dialect, 70 km north of Bullard's Beach State park. Within the local dialect songs, A and B share NC types whereas B and C do not. (b) Sonogram of a NC with the amplitude envelope above. The bars on top of the figure indicate the time intervals (in milliseconds) when song above (filled) or below (open) the threshold value of 20% (horizontal line at 0.2 V) of the maximum amplitude is produced. This male reached peak performance 65% of the duration of the NC.



point Fast Fourier Transform length from a file digitized at 25 kHz, step size 3 ms (frequency resolution = 98 Hz, temporal = 10 ms). We determined visually whether a male sang the same NC as one or more of his territory neighbors (Figure 1a). Visual classification of NC types is repeatable across independent observers (Nelson et al. 2004). We grouped the number of neighbors that a male shared the NC with into not sharing, sharing with 1 neighbor, and sharing with 2 or more neighbors (only 4 males shared with 3 neighbors and 1 male with 4 neighbors). We determined whether a male sang a local or foreign trill. The majority of males in this population sang dialect 1 which we termed local (Nelson et al. 2004).

We also derived 2 measures of how NCs were performed: residual NC performance and consistency of NC performance. Two considerations led us to focus on NC performance rather than trill performance. NCs consist of a series of broadband frequency sweeps delivered in rapid succession. Other evidence suggests that NCs are difficult to imitate (Nelson et al. 2004; Nelson and Poesel 2009). In contrast, the terminal trill consists of narrow band frequency sweeps (1–2 kHz) delivered at a slow rate (7–8 notes per second), with the number of syllable repetitions varying with context (Nelson and Poesel 2011). It is unlikely that trills are subject to motor constraints on production (sensu Podos 1997). In contrast to the NC, the fine details of trill structure are not shared among neighboring males (Nelson and Poesel 2009). We measured the performance of NCs in male song using a semiautomated program in SIGNAL 4.04. Each recording was first high-pass filtered above 2 kHz to remove low-frequency background noise. We used a gate function to measure the total duration of the NC and the duration of individual notes and silent intervals within NCs. The total duration of the NC was defined as the time during which the signal remained 9 dB above the background noise level including the quiet intervals in-between notes. We chose the 9 dB threshold and gate function parameters to minimize triggering the gate function on transient background noise. The level of background noise was measured from the quiet interval imme-

diately preceding the NC. NC performance was defined as the percentage of the total duration that the signal exceeded 20% (–14 dB) of peak amplitude within the NC (Figure 1b, Forstmeier et al. 2002). We restricted analysis to NCs not masked by other sounds and with a signal to noise ratio of at least 23 dB.

For each recording session of a male, we then calculated the mean and standard deviation (SD) of NC performance. Mean performance varied significantly among the 6 most common types but not across years within types (Nelson DA, unpublished data). Thus, we calculated residual performance as the male’s mean performance relative to the population mean performance (returns and recruits) for a particular type (Forstmeier et al. 2002).

To express consistency of NC performance, we used the coefficient of variation in performance ($100 \times \text{SD}/\text{mean}$). For 3 birds that did not have performance data, we assigned them the mean residual performance for their NC type (zero by definition) and the population mean coefficient of variation. We measured repeatability of NC performance following Lessells and Boag (1987) by measuring the performance of NCs in the songs of 31 banded males recorded on 2 different days each prior to pairing in 2005. In each recording, we measured an average of 53.7 songs (range 10–97). Repeatability was very high ($R = 0.88$, $F_{30,31} = 12.17$, $P < 0.001$). This agrees with previous measurements of variation in frequency and temporal parameters of NCs made on songs recorded on 2 different dates for each male and confirms that NC structure is highly stereotyped within males (Nelson and Poesel 2007).

Microsatellite genotyping and parentage analyses

In 2005–2007, we took blood samples from adults (10–40 µl) and nestlings (5–25 µl; 1–9 days posthatch). We determined paternity of 168 offspring in 52 broods based on 5 microsatellite loci (Zole_A02; Zole_B01; Zole_C11; Zole_C12; Zole_H02) from a set of 21 previously developed microsatellite primers for

Table 1
Results of logistic regression models with maximum-likelihood estimation on the probability of (a) pairing and (b) paternity gain in male *Zonotrichia leucophrys pugetensis*

Characteristic	Odds (95% CI)	Likelihood-ratio test	
		Chi square, df = 1	P value
(a) Pairing success, N = 97; full model: $\chi^2_8 = 20.84$; P = 0.008			
Shared NC	–2.03 (–3.92 to –0.15)	4.89	0.03
Local trill	–0.12 (–1.41 to 1.18)	0.03	0.86
Variation in performance	–0.02 (–0.16 to 0.12)	0.12	0.73
Residual performance	3.93 (–6.39 to 14.25)	0.56	0.45
Shared NC × variation in performance	0.09 (–0.06 to 0.24)	1.47	0.23
Shared NC × residual performance	1.66 (–7.58 to 10.89)	0.13	0.72
Relative arrival date	1.27 (–0.36 to 2.90)	2.38	0.12
Territory quality	–0.25 (–0.49 to 0.003)	3.93	0.05
(b) Paternity gain, N = 71; full model $\chi^2_8 = 5.33$; P = 0.72			
Shared NC	–1.64 (–5.24 to 1.95)	0.78	0.38
Local trill	0.77 (–2.03 to 3.57)	0.31	0.58
Variation in performance	–0.06 (–0.44 to 0.32)	0.09	0.76
Residual performance	–8.13 (–41.79 to 25.53)	0.24	0.63
Shared NC × variation in performance	0.08 (–0.23 to 0.40)	0.28	0.60
Shared NC × residual performance	–2.32 (–24.50 to 19.86)	0.04	0.84
Relative arrival date	–0.52 (–4.24 to 3.20)	0.08	0.78
Territory quality	–0.37 (–0.98 to 0.24)	1.66	0.20

Shown are song and territory characteristics, the effect sizes as univariate odds ratios with 95% confidence interval (CI, Bland and Altman 2000), and chi-square statistics for the difference in –2 log-likelihoods between the full model and a reduced model with the particular independent variable removed; see also Figure 2. Sharing NC or trill was coded as “1,” nonsharing as “0.” A positive odds ratio indicates that song sharing higher than average song performance, little variation in performance, early arrival date or high quality territory increased the probability of mating. × indicates a statistical interaction; social mating success was measured in 2005–2008, paternity gain in 2005–2007. df, degree of freedom.

the Puget Sound white-crowned sparrow (Poesel et al. 2009). Sixteen broods and 51 offspring were attended by recruits. We followed methods in Poesel et al. (2009) to genotype samples. Briefly, all 5 primer pairs were combined in one multiplex PCR (QIAGEN Multiplex kit), and genotyping was performed on an ABI 3730 DNA Analyzer using GENEMAPPER v.3.0 software. All 5 loci had a combined exclusion probability of 0.983 for the first and 0.998 for the second parent. We used CERVUS v.3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007) to determine maternity and paternity. Details of the parentage analysis are described in Poesel et al. (2011). First, we assigned the female attending the nest and nestlings as the genetic mother for 63.1% offspring in our analyses. For the remaining 36.9% offspring, the mother was unknown because we did not obtain blood from the female attending the nest. Second, we accepted the social male as the genetic father if his genotype matched the offspring's genotype at all loci ($N = 111$) or had only a single mismatch ($N = 5$) but was more likely (at $\geq 80\%$ confidence level) than any other male in the population to have fathered the chick (see also Hill et al. 2011). When we found 2 or more mismatches between the male attending the nest and the offspring, we rejected the putative male as the genetic father ($N = 46$). Third, we assigned 98.1% of young with rejected social fathers to an extrapair male in the population.

To investigate paternity gain, we selected each recruit in 2005–2007 and determined whether the male had gained

extrapair paternity in any of the sampled broods in that year. Our measure is conservative because we may not have sampled all broods in which males could have possibly gained paternity.

Statistical analyses

We used SPSS 17.0 for statistical analyses. All tests are 2-tailed, and we report mean \pm SE. To estimate the effect of song and territory traits on the probability of pairing and paternity gain, we used logistic regression models with maximum-likelihood estimation. We included first-order interaction effects between NC sharing and performance (residual and consistency). We included male arrival date relative to the average arrival date of all males in a year and territory quality as covariates in the models. We report full models following Mundry and Nunn (2009). To estimate the importance of single independent variables, we report results from likelihood ratio tests that compare the difference in -2 log-likelihoods between the full model and a nested model that omits one independent variable. Arrival date and territory size were log-transformed to meet assumptions of normality. Data on paternity loss were available for 16 of 97 recruits in 2005–2007; in 2008, we studied social mate choice only. We used t -tests to compare males that lost and did not lose paternity. For 2 extrapair males that had sired offspring in the same nest, we

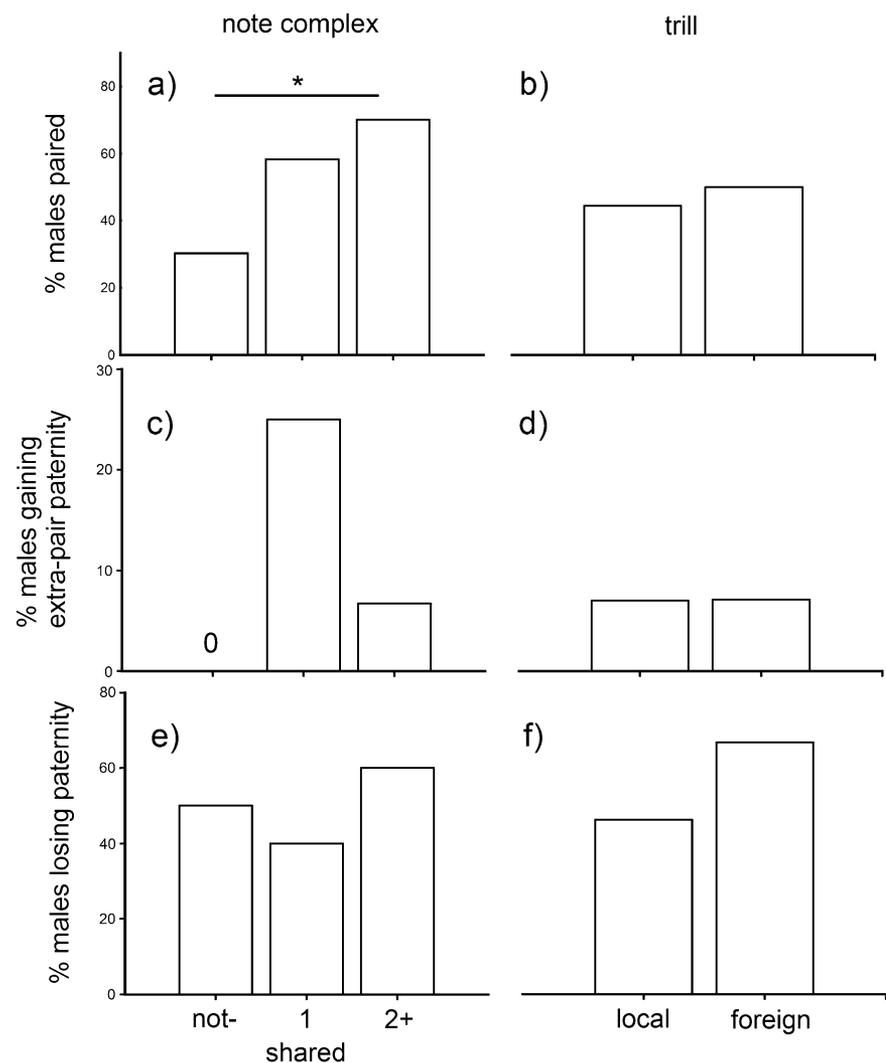


Figure 2 Percentage of recruits *Zonotrichia leucophrys pugetensis* that attracted a social mate (paired; $N = 44$), gained extrapair paternity ($N = 5$), or lost paternity ($N = 8$) while (a, c, e) not sharing the NC with a neighbor, sharing with one or sharing with 2 or more neighbors, and (b, d, f) singing local (shared) or foreign trill. The horizontal line connects groups that are significantly different in the logistic regression model in Table 1.

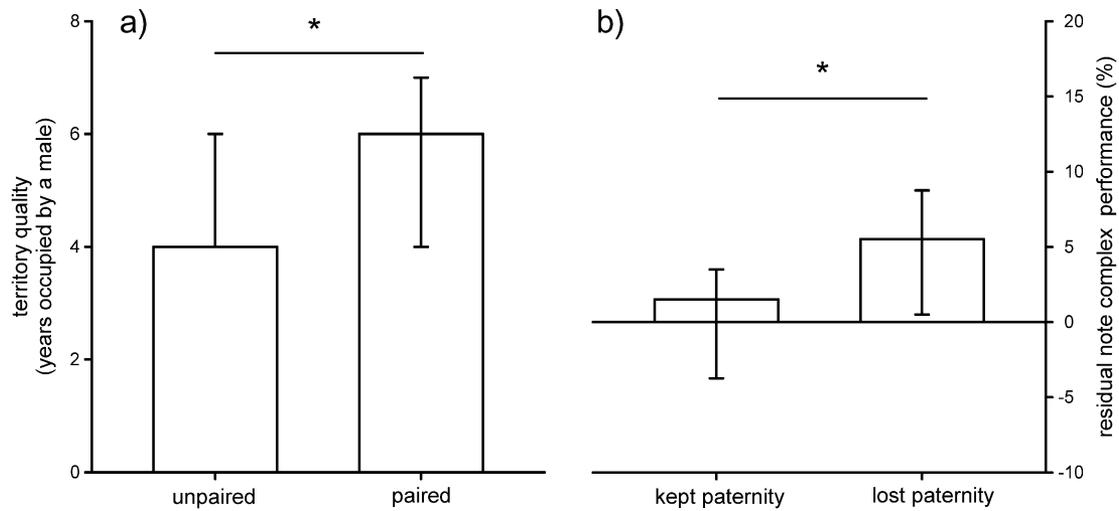


Figure 3 Relation between (a) territory quality and pairing success and (b) residual performance and paternity loss in *Zonotrichia leucophrys pugetensis*. Horizontal lines connect groups that are significantly different in the logistic regression model in Table 1. Error bars indicate the first and third quartiles. A residual performance of zero indicates that a male performed at the population mean for a given NC type.

calculated average values of song performance and arrival date to compare with the cuckolded male. We report effect sizes and their associated 95% confidence intervals (Nakagawa and Cuthill 2007).

RESULTS

Eighty-nine of 97 (91.8%) recruits sang the local trill dialect, whereas 44 of 97 (45.4%) recruits shared the NC. Mean NC performance varied from 58% to 95%, and the coefficient of variation of performance averaged 10.1% (range 3.0–22.3%).

Pairing success

Each year 39–67% of recruits remained unpaired. NC sharing and territory quality were the only 2 variables significantly related to pairing success, the latter marginally (Table 1a). Recruits that shared their NC with at least one neighbor were more successful in attracting a social mate than were recruits that did not share their NC (Figure 2a). Recruits that occupied a high quality territory were more likely to attract a mate than recruits that occupied a low quality territory (Figure 3a). NC sharing and territory quality were each important in predicting pairing success and could not be removed from the model without decreasing the model fit (Table 1a). Comparison of odd ratios indicates that NC sharing was somewhat

more important than territory quality in explaining variation in social mating success.

Paternity gain and loss

None of the song variables or arrival date or territory quality correlated with paternity gain (Table 1b; Figure 2c,d). The 5 recruits that gained extrapair paternity all shared their NC with at least one neighbor. In the subsample of 16 recruits for which paternity was known, 50% (8/16) lost paternity. The best predictor of paternity loss was residual performance (Table 2). Recruits that lost paternity were more likely to have a higher than average NC performance than recruits that did not lose paternity (Figure 3b). NC sharing, territory quality, and arrival date did not differ between recruits that lost or did not lose paternity (Table 2). Three males with foreign trills were not more likely to lose paternity than 13 males with the local trill (Figure 2f).

A comparison of extrapair males and the recruits they cuckolded showed that 3 of 8 (38%) extrapair males shared the NC with the cuckolded recruit, whereas the cuckolded recruits shared the NC with on average $35.4 \pm 12.8\%$ (0–100%) of their neighbors. Thus, the proportion of extrapair males sharing their NC with the cuckolded recruit was not significantly different from expected among neighbors (binomial exact $P = 0.57$). Within- and extrapair males did not differ in residual performance, variation in performance, or relative arrival date

Table 2 Comparison of characteristics (mean \pm SE) of male *Zonotrichia leucophrys pugetensis* that lost ($N = 8$) and males that did not lose ($N = 8$) paternity

Characteristic	Lost paternity	Did not lose paternity	Standard effect size	95% CI	t_{14}	P
Shared NC (% males)	62.5	62.5	0	-0.98 to 0.98	0.69 ^a	0.99
Local trill (% males)	100	100			NA	NA
Variation in performance (%)	8.90 \pm 1.0	8.80 \pm 1.6	0.04	-0.94 to 1.02	-0.07	0.94
Residual performance	0.05 \pm 0.02	-0.01 \pm 0.02	3.53	1.82 to 4.85	-2.66	0.02
Relative arrival date (days)	3.38 \pm 3.91	2.0 \pm 4.26	-0.12	-1.10 to 0.87	-0.46	0.65
Territory quality (years)	5.9 \pm 0.58	5.8 \pm 0.62	-0.05	-1.02 to 0.94	-0.15	0.89

We report the standardized mean difference effect size and its 95% confidence interval (CI) and results from an independent samples t -test; NA indicates that all males that lost paternity shared the trill, and the variable was excluded from analysis.

^a For NC sharing, we report results from a Chi-square test and the exact P value.

(Table 3). Five of 8 extrapair males were older than the cuckolded recruit.

DISCUSSION

We found that song sharing and performance correlated differently with social mating success and paternity loss in the Puget Sound white-crowned sparrow. Males that shared the NC with one or more neighbors were more successful in attracting a social mate than males that did not share song. Males that sang with higher performance lost paternity. None of the song traits correlated with extrapair paternity gain, which may indicate that extrapair matings are not due to active mate choice as discussed below. Song traits may influence a male's mating success through female choice and/or male competition over territories, possibilities which we cannot distinguish in this correlational study.

Our results suggest that male characteristics correlate differently with social and extrapair matings as in other species (pied flycatcher *Ficedula hypoleuca*, Saetre et al. 1994; Lifjeld et al. 1997; sedge warbler *Acrocephalus schoenobaenus*, Marshall et al. 2007). This supports theory that extrapair and social mating success depend on different criteria because females derive different benefits from social and extrapair mates (Mays and Hill 2004). Social males, besides providing favored genes, can provide direct benefits to females through access to a high-quality territory and/or paternal care (e.g., Alatalo et al. 1986; Buchanan and Catchpole 1997). To distinguish between female preferences for social and extrapair mates, a future experiment could compare social mate choice in the field with copulation solicitation displays of the same females in laboratory settings. Searcy (1992) hypothesized that copulation solicitation displays in the lab may reflect preferences in the context of choosing extrapair mates rather than social mates.

Pairing success

Our result that males that shared song with a neighbor were more likely to attract a mate than males that did not share is consistent with several suggestions that song sharing may be an index to male quality (O'Loughlen and Rothstein 1995; Vehrencamp 2000; Hughes et al. 2007). Vehrencamp (2000) postulated that song sharing in a closed-ended learner indicates a male's ability to return to the site of learning and establish a territory with familiar neighbors. If males that share songs suffer fewer territorial intrusions than males that do not share songs (Wilson and Vehrencamp 2001), females could gain direct benefits from living in a stable social neighborhood. Arguing against this interpretation, our indirect measure of male quality, relative arrival date, did not explain variation in social or extrapair mating success in recruits, even when NC sharing was removed from the model (data not shown). Alternatively, the high social pairing success of males with shared songs could result from mate choice copying, if newly arrived females copy mate choice of older females (Pruett-Jones 1992; Freed-Brown and White 2009). We also

found that males on high-quality territories tended to be more likely to attract a mate. Still, when all variables were included in one statistical model, NC sharing had effects independent of, and somewhat stronger than, territory quality on pairing success. We emphasize that in the absence of observations of how song sharing males and their mates behave, we cannot identify the mechanism(s) underlying the correlation with male mating success.

Paternity gain

The benefits that extrapair mates provide are indirect in most species, that is, "good" or compatible genes. Song sharing did not correlate with success in extrapair matings. We would expect a correlation between song sharing and extrapair matings if song sharing indicated local males with locally adapted genes (Nottebohm 1972; Baker and Cunningham 1985). However, this seems unlikely because the song neighborhoods based on shared NCs are too small (2–8 males) and ephemeral to differ genetically (Nelson et al. 2004). Even for large-scale geographic song dialects, evidence that assortative mating based on shared songs leads to restricted gene flow is limited (Soha et al. 2004). Females may not choose particular males for extrapair copulations but follow a bet-hedging strategy where they mate with several males to produce offspring with various genotypes in an unpredictable environment (Loman et al. 1988; reviewed in Yasui 1998). Alternatively, copulating with males outside the social pair bond may insure against unfertilized eggs if mated to an infertile male. We observed one incidence of an apparently infertile male where the female continued incubating the eggs for much longer than the usual period until the clutch was finally depredated (Poesel A, unpublished data). If males are seeking extrapair copulations, the cost of accepting copulation may be lower for females than to attempt resisting copulation (e.g., Arnqvist and Kirkpatrick 2005).

Paternity loss

Males that sang with higher than average performance were more likely to lose paternity than males with lower than average performance. This result does not support the hypothesis that shared songs facilitate comparison of males in terms of their song performance. Logue and Forstmeier (2008) predicted that males with high performance should be successful, and indeed, female dusky warblers *Phylloscopus fuscatus* prefer males with high song performance as extrapair partners (Forstmeier et al. 2002). In white-crowned sparrows, as in sedge warblers (Marshall et al. 2007), song may be less important in extrapair than social mate choice because males stop singing right after acquiring a social mate (Nelson and Poesel 2011). Extrapair males were mainly neighbors (73%, Poesel A, unpublished data), and other cues, such as visual cues or simply proximity, may have been important besides song. Consistency of song performance which may reflect song learning accuracy (Nowicki et al. 2002) did not correlate with mating success. This is in

Table 3

Pairwise comparison of characteristics of within- and extrapair male *Zonotrichia leucophrys pugetensis* ($n = 8$) that fathered offspring in the same nest

Characteristic	Cuckolded male	EP male	Z	P
Variation in performance (%)	10.09 (5.63–10.96)	10.56 (5.78–13.71)	–0.84	0.40
Residual performance (%)	5.50 (0.5–8.75)	3.5 (0.25–9.5)	–0.63	0.53
Relative arrival date (days)	1.0 (–3.25–5.0)	–2.75 (–7.0–12.25)	–0.70	0.48

We report median (first and third quartile) values and results from a Wilcoxon Signed-rank test.

contrast to other studies that found consistency of performance important in male–male or male–female interactions (Byers 2007; Holveck and Riebel 2007; Botero et al. 2009).

Our results do not suggest that females were deceived by males that share their song with the social mate as proposed by Payne (1982). Less than half of the extrapair males shared their song with the cuckolded male. Our sample was small ($N = 8$) but similar to other studies that found an effect of song variables on extrapair matings (e.g., Hasselquist et al. 1996; Forstmeier et al. 2002). Overall, this finding is not surprising because female songbirds have been shown to discriminate their mate from other males (Lampe and Slagsvold 1998; O’Loughlen and Beecher 1999), even when song differences are very small (Blumenrath et al. 2007).

Singing the local dialect did not correlate with reproductive success. The power to detect an effect of song dialect in the current study was low because, as is typical in this species, only few males sang foreign dialects and did not share the trill with a neighbor. Still, the finding of an apparent female indifference to trill variation is in accordance with previous results indicating that females do not favor the local dialect in field playbacks, whereas males give stronger responses to the local dialect (Nelson and Soha 2004).

To date, few studies have investigated song sharing and mating success. The pioneering study of Payne et al. (1988) found an effect of song sharing on social mating success in male indigo buntings *Passerina cyanea*, but it predated the common use of molecular techniques and thus could not investigate the role of extrapair paternity as a contributor to male reproductive success. Song sharing did not influence social pairing success in either yellow warblers (*Setophaga petechia*, Cosens and Falls 1984) or great tits (*Parus major*, McGregor and Krebs 1984). Hill et al. (2011) studied genetic mating success only and found that song sharing did not predict extrapair mating success in song sparrows.

The correlation between song sharing and pairing success provides a functional explanation for the developmental process of song overproduction and repertoire attrition in this and possibly other songbird species that adjust their song to the social environment (e.g., song sparrows, Beecher et al. 1994; American redstarts *Setophaga ruticilla*, Lemon 1994; sedge warblers *Acrocephalus schoenobaenus*, Nicholson et al. 2007; nightingales *Luscinia megarhynchos*, Kiefer et al. 2010). Male white-crowned sparrows learn from several adults in the hatching year, often overproduce songs at the beginning of their first breeding season, and retain the song type that resembles the song type of a territory neighbor at the end of the song attrition process (Nelson 2000; Nelson and Poesel 2009). Learning from several males in the hatching year and overproducing songs may be a mechanism to provide multiple options of where to breed and share songs when future territory vacancies cannot be predicted.

To conclude, our results show that song sharing correlates with social mating success, adding to the role it plays in territory defense (Beecher et al. 2000). If females chose males based on song sharing, then song sharing may be one of many song traits reflecting the dual function of bird song as a trait under inter- and intrasexual selection.

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