



Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size

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Song repertoires may be a product of sexual selection and several studies have reported correlations of repertoire size and reproductive success in male songbirds. This hypothesis and the reported correlations, however, are not sufficient to explain the observation that most species have small song repertoire sizes (usually fewer than 10, often fewer than five song types). We examined a second important aspect of a male's song repertoire, the extent to which he shares songs with his neighbours. Song sharing has not been measured in previous studies and it may be partially confounded with repertoire size. We hypothesized that in song sparrows, *Melospiza melodia*, song sharing rather than repertoire size per se is crucial for male territorial success. Our longitudinal study of 45 song sparrows followed from their first year on territory showed that the number of songs a bird shares with his neighbourhood group is a better predictor of lifetime territory tenure than is his repertoire size. We also found that song sharing increases with repertoire size up to but not beyond eight to nine song types, which are the most common repertoire sizes in the population (range in our sample 5–13). This partial confound of song sharing and repertoire size may account for some earlier findings of territory tenure–repertoire size correlations in this species and other species having small- or medium-sized repertoires.

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In the majority of songbird species, a bird has not one song but a 'repertoire' of distinct song types. The prevailing theoretical view is that song repertoires are a product of sexual selection (Catchpole 1980; Krebs & Kroodsma 1980; Searcy & Andersson 1986; Kroodsma 1988). This view is plausible because a single song seems sufficient for song's basic functions in male–male competition and mate attraction, as in fact it is for approximately a quarter of the songbird species and most of the nonsongbird species. The view that song repertoires are sexually selected implies strong directional selection pressure on repertoire size (the number of song types in the repertoire). Songbirds with repertoires of more than 100 songs, such as northern mockingbirds, *Mimus polyglottus*, and common nightingales, *Luscinia megarhynchos* (Kroodsma 1996) are consistent with this view. A problem for this view, on the other hand, is the prevalence of songbirds with small to moderate-sized repertoires: most repertoire species have fewer than 10 types, and many have fewer than five types. For example, consider the modest song repertoire sizes of some well-studied species: great tit, *Parus major*, 2–5; chaffinch, *Fringilla coelebs*, 2–4; swamp sparrow, *Melospiza georgiana*, 2–4; red-winged blackbird,

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Agelaius phoeniceus, 2–6; western meadowlark, *Sturna neglecta*, 5–9; and the song sparrow, *Melospiza melodia*, 5–11.

There are two ways the sexual selection hypothesis can be squared with the prevalence of small to moderate repertoire sizes. First, sexual selection theory predicts that sexually selected traits are prevented from further exaggeration by opposing selection pressures, such as the energetic costs or increased predation correlated with these potentially expensive, conspicuous traits (Andersson 1994). In this view, sexual selection may be more intense, or the opposing selection pressures less intense, in large-repertoire species than in small-repertoire species. In this paper we focus on a second hypothesis, that selection has acted on a song trait distinct from, but partially correlated with, repertoire size. In this view, song repertoire size, rather than being the target of selection, is only incidentally related to the true target of selection.

We examine the hypothesis that sharing of song types with several neighbours, rather than the number of types per se, is the target of selection in the song sparrow, a species with a moderate repertoire size of 5–11 song types (Beecher et al. 1997). If neighbours have different song types, and if it is advantageous to share these songs with these different neighbours, then song repertoires may be

indirectly selected as a consequence of selection for learning songs that are shared with these different neighbours.

To date, a correlation between song sharing and reproductive success has been found only in one species, the single-song indigo bunting, *Passerina cyanea*: first-year buntings that share their single song type with an adult neighbour tend to be more successful in mating and in fledging young than those that do not (Payne et al. 1988). The relation of song sharing to measures of reproductive success has not yet been examined in a repertoire-singing songbird.

In contrast, correlations between repertoire size and measures of male reproductive success, such as pairing date and mating success, have been found in several cross-sectional studies. Most of these findings have two limitations, however. First, in many cases, the correlation is confounded with age and sometimes with territory size as well. Such correlations have been found for northern mockingbirds, red-winged blackbirds, great reed warblers, *Acrocephalus arundinaceus*, yellow warblers, *Dendroica petechia*, and western meadowlarks (Howard 1974; Yasukawa et al. 1980; Catchpole 1986; Cosens & Sealy 1986; Horn et al. 1993). The confound with age occurs because males in these species add songs with age (although the strength of the evidence for an age-repertoire size correlation varies between cases). In many songbirds, on the other hand, repertoires do not increase in size past the first breeding season. Second, in none of these studies was song sharing with neighbours measured. The above argument suggests that repertoire size may be indirectly selected as a consequence of selection for song sharing with neighbours, so to evaluate the relative roles of these two song parameters, both must be measured. In contrast to repertoire size, song sharing with neighbours has rarely been measured, perhaps because to do so requires measuring the song repertoires of all of the subject's neighbours in addition to the repertoire of the subject.

We believe that song sharing with multiple neighbours is the central feature of song learning and song communication in the song sparrow. In our study population, song sparrows typically share song types with near neighbours (average 20–30% sharing between adjacent neighbours) but not with birds four or five territories away. Similar patterns of neighbour song sharing have been found in many other songbird populations, including corn buntings, *Miliaria calandra*, tufted titmice, *Baeolophus bicolor*, great tits, field sparrows, *Spizella pusilla*, and rufous-sided towhees, *Pipilo erythrophthalmus* (McGregor 1980; Schroeder & Wiley 1983; McGregor & Krebs 1989; Nelson 1992; Ewert & Kroodsma 1994), although not in all, for example, chaffinches and western meadowlarks (Slater & Ince 1982; Horn & Falls 1988). In some cases the degree of sharing varies geographically, for example, in song sparrows sharing is common in western populations (Cassidy 1993; Nielsen & Vehrencamp 1995; C. E. Hill, unpublished data) but not, apparently, in eastern populations (Kramer & Lemon 1983; Hughes et al. 1998). In our study population we have traced this pattern of neighbour song sharing to a particular strategy of song learning, the essential features of which are the following. A young

song sparrow: (1) learns his eight or so song types from several older birds that are territorial neighbours in the young bird's hatch-year summer; (2) learns or retains the song types shared among these tutor-neighbours in preference to song types unique to particular tutors; (3) establishes his territory, if possible, close to his tutors, sometimes replacing one that does not survive to the next spring; (4) preferentially retains the song types of those tutor-neighbours that do survive to the next spring, the young bird's first breeding season; and (5) in at least some cases, learns new songs *de novo* from new neighbours after the natal summer. The bird does not modify his song repertoire after his first breeding season. These findings are based on extensive field observations (Beecher et al. 1994; Nordby et al. 1999) and have been confirmed in laboratory experiments using multiple live-song tutors and simulating natural conditions (Nordby et al., *in press*, unpublished data). Taken together, these findings suggest a strategy of song learning designed to provide the bird with songs he shares with his neighbours in his first breeding season. Supporting this hypothesis is the observation that song sparrows preferentially use shared types in countersinging interactions: for example, a bird will typically reply to a neighbour with one of the songs he shares with that particular neighbour (Beecher et al. 1996, 2000).

The hypothesis that shared songs are advantageous in male–male competition suggests that song sparrows sharing more songs with their neighbours will hold their territories longer than birds sharing fewer songs. We tested this prediction in the present study, comparing the ability of repertoire size and song sharing to predict the territory tenures of the birds in our sample. Territory tenure is the major component of lifetime reproductive success in male song sparrows (Smith 1988) and it is the component most directly related to male–male competition (Arcese 1987, 1989). We examined the role of song sharing for song sparrows in intersexual contexts elsewhere (O'Loughlen & Beecher 1999; C. E. Hill, unpublished data).

METHODS

Our study site is a 200-ha undeveloped city park along Puget Sound in Seattle, Washington, with ca. 100–150 colour-banded males on territories per year. The population is sedentary and the birds can be found on territory all year long, although they are fully territorial only during the breeding season.

Our sample consisted of 45 males born in 1990–1993. Of these, 17 survived a single breeding season, eight survived two seasons, four survived three seasons, five survived four seasons, seven survived five seasons, two survived six seasons, one survived seven seasons and one survived eight seasons. At the end of the 1999 breeding season, only one subject was still alive (born in 1991, 8 years old).

We recorded the song repertoires of the 45 subject birds and 140 additional birds that were their neighbours. Songs were recorded with a Sennheiser ME88 directional

microphone and Sony TC-D5M tape recorder, and analysed on a Kay DSP-5500 sonagraph. We estimated a repertoire to have been completely measured (all song types) when we had recorded 16 or more consecutive switches (method and rationale described in Kroodsma 1982).

To measure song sharing, we compared the bird's song repertoire in his first breeding season with that of all neighbours with territories adjacent to or one territory removed from the bird. These neighbour groups ranged in size from seven to 18 birds (mean 12.0, median 12). Our measure of song sharing was the number of songs in the neighbours' repertoires that were also in the subject's repertoire, summed over the entire neighbour group. Song sharing, unlike repertoire size, is not a fixed quantity, but changes whenever birds in the neighbourhood die or move and are replaced by other birds (most of this happens between breeding seasons). We took song sharing in the first breeding season as our measure for all birds, for several reasons. First, 17 of the 45 birds lived only the first breeding season. Second, any changes in song sharing in subsequent years were due to turnover in neighbours, rather than changes in the subject's repertoire. Thus song sharing in the first year is strongly determined by the bird's song learning strategy, but any changes in sharing in subsequent years are not. Third, song sharing does not show a consistent pattern of change in later seasons for the birds that survive longer than one season. Even though a song sparrow will lose some of his old neighbours each year after the first year and does not learn the songs of his new neighbours, the young birds that become his new neighbours will usually learn some of his songs, hence his song sharing is as likely to increase as it is to decrease. In fact, for birds in the present sample for which we had information on later breeding seasons, sharing actually increased slightly on average after the first year, so the choice of the first season was conservative with respect to the hypothesis being tested.

To be considered shared, two songs had to match at least half of their component phrases. In borderline cases, we put more weight on the more invariant early portions of the song and less on later parts of the song, which are more variable and less important in individual recognition (Nice 1943; Podos et al. 1992; Horning et al. 1993). We considered all recorded variations when looking for shared types (e.g. see Fig. 1, and examples in previous papers). Although a more stringent criterion could be used, the 50% criterion is appropriate for several reasons. First, a song sparrow varies his different renditions of a particular song type (Stoddard et al. 1988; Podos et al. 1992; Nowicki et al. 1994). Although in general between-type variation is larger than within-type variation, it is not unusual for one of a bird's variants on a type to be 50–75% different from another of his variants on that type. Nevertheless, even relatively large within-type variation has been shown to be perceptually less salient than between-type variation in both laboratory and field contexts (Stoddard et al. 1992b; Searcy et al. 1999). Second, we have shown, in both laboratory and field contexts, that song sparrows perceive, and respond to, hybrid song

types (the first half of one song type and the second half of a different song type) as if they are similar to the 'parental' song types, even though hybrid and parental types are 50% different, with the first half of the song being more salient than the second half (Horning et al. 1993). In summary, it seems reasonable to use a sharing criterion that is as permissive about types as the birds are themselves. Finally, our experience with sharing criteria is that when you shift from a looser to tighter criterion, you shift the obtained number up or down correspondingly, but you do not affect the general pattern of results (for a clear example see Nordby et al. 1999).

Territorial success was measured as years on territory (hereafter called territory tenure). A year was counted if the bird survived on territory through to at least 1 June of the year. A bird not found on his territory or elsewhere in the study site was presumed not to have found a territory anywhere (and probably to have died). In more than 10 years of studying this population, we have never found a bird that moved his territory more than four to five territories away (and a move of even that extent is highly unusual).

It is possible that territorial success depends on how early the young bird establishes his territory, which in turn could be correlated with first-season song sharing or repertoire size. To assess this possibility, we extracted from our field notes the date the bird was first observed singing on territory; we were able to do this for all but the 1990 birds (i.e. for 39 of the 45 subjects). Date of first singing is a key step in the process of territory establishment. Although territory establishment is a process, not a discrete event, the date of first singing provides a reasonable measure of whether a bird began this process early or late. In our sample, this date ranged from late in the natal summer to early the next spring.

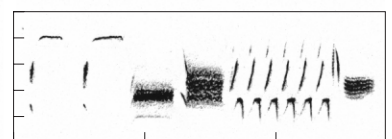
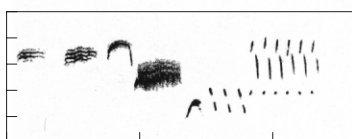
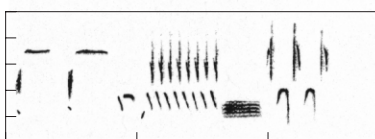
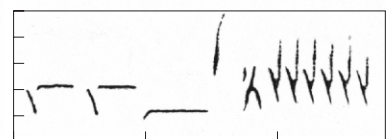
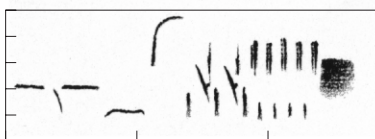
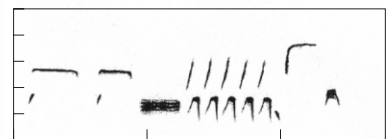
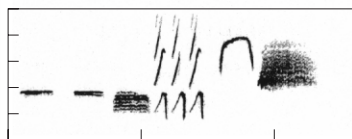
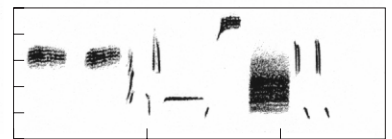
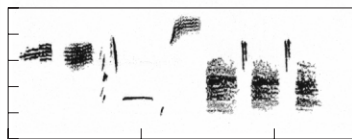
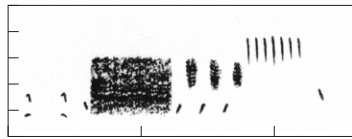
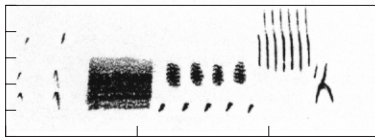
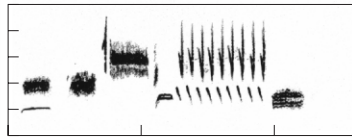
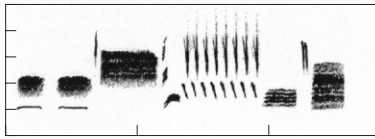
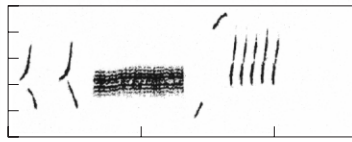
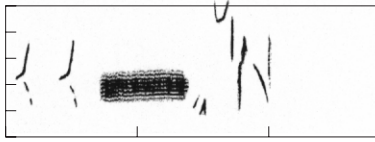
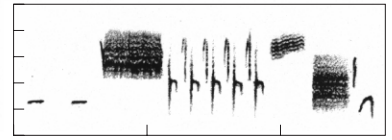
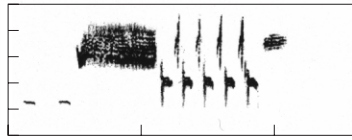
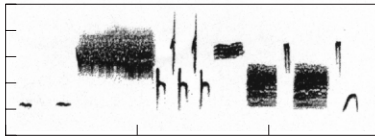
In an earlier study involving this same population, we traced the song tutors of all young birds in the 1992 cohort of our population (Nordby et al. 1999). We found that a young bird typically learned his songs from several neighbouring adult males and usually settled next to them. When birds did not settle next to their tutors, it was because the tutors had died, or, alternatively, because few or none of their tutors died, so that few or no vacancies opened up in the tutor area. Seventeen of the 41 birds of that study are common to the 45 birds of the present study. To assess whether or not the tutor status of the birds in the neighbour group is important, for this subsample we examined the relation of number of tutors in the neighbour group to territory tenure, song sharing and repertoire size.

Repertoire sizes in our sample ranged from 5 to 13 song types (mean 8.64, median 8); except for one repertoire size of 13, all repertoire sizes were in the range of 5 to 11. Number of shared songs ranged from 3 to 31 songs (mean 14.8, median 14). Both parameters were approximately normally distributed, with a slight skew at the higher end. In grouped analyses, the highest category was made larger than the rest to remove outlier effects. Specifically, in the grouped analyses, we categorized song sharing into groups of four values each (1–4, 5–8, etc., except for the

yygm

bymp

ppom



Frequency

Time

largest category, 21–31). Repertoire size fell into natural integer groups, but was grouped at the two extremes (5–6, and 11–13). Statistical analyses were done in SYSTAT (Wilkinson 1986).

RESULTS

To evaluate the relationship of territory tenure to repertoire size and song sharing, we carried out a planned comparison analysis of variance (ANOVA) for each song measure, testing the hypothesis that territory tenure should be greater for larger song values of the song measure (repertoire size or song sharing). We found that song sharing predicted territory tenure ($F_{1,39}=6.46$, $P=0.015$) but repertoire size did not ($F_{1,39}=0.21$, NS).

The results are illustrated with the grouped data in Fig. 2. The relationship between territory tenure and song sharing was linear but that between territory tenure and repertoire size appeared to be curvilinear, peaking at nine songs.

We also computed product-moment correlations ($N=45$) between territory tenure and each song measure (Table 1). The correlation between territory tenure and song sharing was significant ($r=0.43$, $P=0.003$), while that between territory tenure and repertoire size was not ($r=0.03$). Because song sharing and repertoire size were themselves correlated ($r=0.47$), we computed partial correlations. The correlation between territory tenure and song sharing with repertoire size held constant was 0.47 ($P=0.002$), while that between territory tenure and repertoire size with song sharing held constant was negative and nonsignificant ($r=-0.21$).

The song sharing correlations were not due to confounds with neighbourhood size: the correlation between song sharing and neighbourhood size was $r=0.01$, while the correlation between territory tenure and neighbourhood size was $r=0.07$.

Figure 3 shows that the correlation between repertoire size and number of shared songs was primarily due to low and medium repertoire sizes. There was no apparent relationship between the two variables for repertoire sizes of nine or larger.

The date on which the subject was first observed singing on territory correlated weakly with song sharing ($r=-0.34$, $N=39$, $P<0.05$) and repertoire size ($r=-0.23$, NS). It did not, however, correlate with territory tenure ($r=0.04$, NS).

For the 17 birds born in 1992 whose song tutors were traced in Nordby et al. (1999), only 16% of their neighbours in their first breeding season were tutors. The number of identified tutors in the neighbour group ranged from zero to four (out of the average 12 neighbours per bird) and was correlated with the number of songs shared with birds in that group ($r=0.64$, $N=17$, $P<0.01$), but not with territory tenure ($r=0.23$, NS) or repertoire size ($r=0.24$, NS).

DISCUSSION

In summary, in our study population of song sparrows, song sharing predicts territory tenure while repertoire size does not. These results support the hypothesis that a song sparrow benefits by having songs in his repertoire that he shares with his male neighbours. The results are purely correlational of course, and it is possible that the key variable is some third variable that is incidentally correlated with song sharing. The most obvious candidate would be a variable relating to how early a bird moves into the area and/or first begins to establish his territorial status. The territory establishment process in song sparrows has been well described in the papers of Arcese (1987, 1989). Birds that begin the process of territory establishment earlier might also learn more songs of their neighbours, but it might be the early start, and/or greater familiarity with the area, that provides them an advantage, not the fact that they share more songs with their neighbours. In the present study, however, the date of first singing on territory, a key step in the process of territory establishment, did not correlate with lifetime territory tenure (although it did correlate weakly with song sharing). It remains possible, however, that some better measure of arrival in the area, which is difficult to obtain given the inconspicuous habits of 'floater' song sparrows (Arcese 1987, 1989), might reveal a correlation with lifetime territory tenure.

As mentioned above, in an earlier study we showed that young birds attempt to settle next to their song tutors (Nordby et al. 1999). They sometimes fail, because the tutors die or move (although moves are usually only a territory or two away), or because none of the tutors dies, so no vacancies open up. The young bird can, however, ultimately settle next to birds with whom he shares songs but which are not his tutors. For example, a particular tutor of the young bird might die before the breeding

Figure 1. Partial repertoires of three neighbouring song sparrows: ygym, bymp and ppom. Each row shows shared songs except for the bottom row, which shows three unshared songs. To be considered shared, two songs had to match at least half of their component phrases. In borderline cases, we put more weight on the more invariant early portions of the song and less on later parts of the song. The number of elements in the phrase was generally disregarded, as this is a feature that the bird often varies from one rendition to another (e.g. fourth shared song, middle phrase, following the buzz: in these renditions, ygym has five elements, bymp has three elements, but the phrase is considered the same because the component elements are the same). A borderline case is the sixth shared song: the two songs differ in terms of the initial paired elements and the end phrase. The middle three phrases (buzz, trill and high sweep) are the same, so the song is considered more than half similar. Also borderline are ygym's and ppom's songs in the bottom row. Although both songs begin with the same paired elements and contain a similar (not identical) trill, they are less than half similar overall and are classified 'unshared'. To illustrate the computation of the number of shared songs (our measure of sharing in this paper): if bymp and ppom were the only neighbours sharing songs with ygym, and if the remaining songs (not shown here) of these three birds were unshared, then the number of songs ygym shares with his neighbours would be seven. Frequency scale 0–10 kHz, markers at 2-kHz intervals, time marker 1 s.

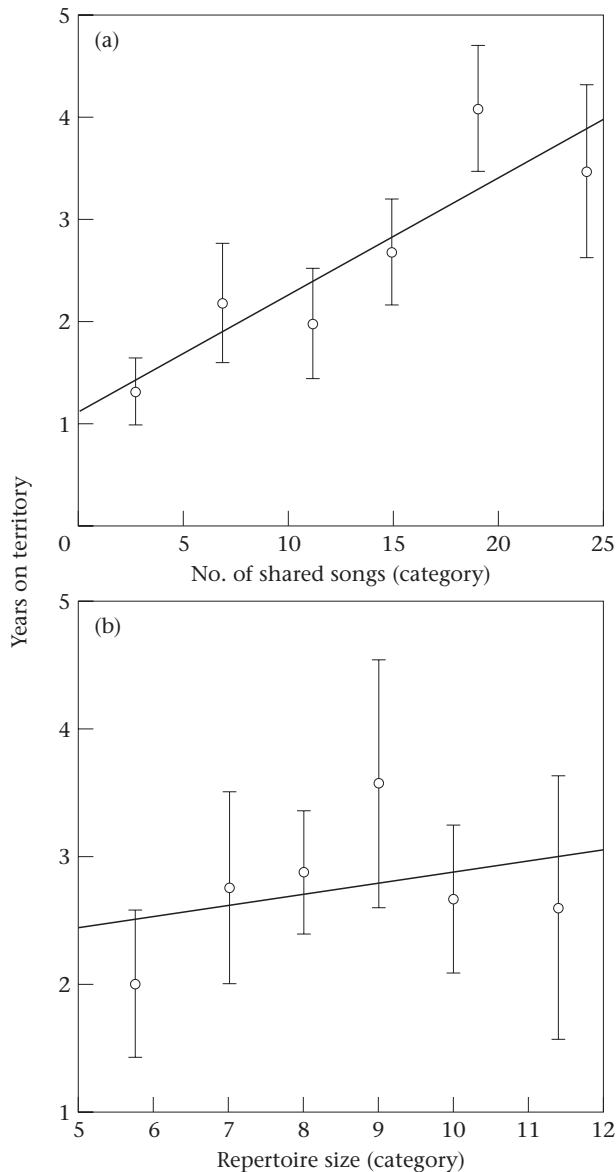


Figure 2. (a) Territory tenure as a function of number of shared-songs category. Categories are 1–4 ($N=3$), 5–8 ($N=5$), 9–12 ($N=10$), 13–16 ($N=10$), 17–20 ($N=9$) and 21–31 ($N=8$). Mean sharing in each of the six categories is 2.67, 6.8, 11.1, 14.9, 19.0 and 24.2. Product-moment correlation: $r=0.89$, $P=0.029$. (b) Territory tenure as a function of repertoire-size category. Categories are 5–6 ($N=4$), 7 ($N=4$), 8 ($N=17$), 9 ($N=7$), 10 ($N=9$) and 11–13 ($N=5$). Mean repertoire size in each of the six categories is 2.67, 6.8, 11.1, 14.9, 19.0 and 24.2. Product-moment correlation: $r=0.36$, NS.

season, but the young bird could still share the types he learned from that tutor with other neighbours that happened to share those song types but that had not been the young bird's tutors, or with young neighbours that were from the same cohort and that had also learned these same song types (of course, the more links in the song-learning chain, the less likely two songs derived from a 'common ancestor' are to pass the sharing criterion). For the small sample of birds common to our earlier study and the present study ($N=17$), song sharing

Table 1. Correlations of years on territory with neighbour song sharing and repertoire size

	<i>N</i>	Song sharing		Repertoire size	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Individual	45	0.43	0.003	0.03	NS
Grouped*	6	0.89	0.029	0.36	NS
Partial†	45	0.47	0.002	-0.21	NS

*Grouped: number of shared songs groups=1–4, 5–8, 9–12, 13–16, 17–20 and 21–31; repertoire size groups=5–6, 7, 8, 9, 10 and 11–13.

†Individual partial correlation coefficients (repertoire size held constant for number of shared songs, number of shared songs held constant for repertoire size).

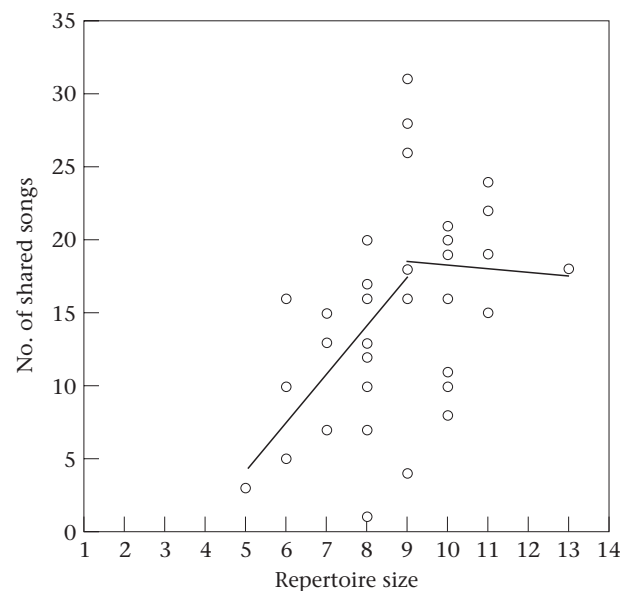


Figure 3. Correlation between number of shared songs and repertoire size. The overall correlation was $r=0.47$, $P=0.002$. However, the fit came primarily from small to medium repertoire sizes (for repertoire sizes 5–9, $r=0.46$); for larger repertoire sizes, the function flattened out (for repertoire sizes 9–13, $r=-0.04$). The best fit lines shown are for 5–9 and 9–13.

per se is a better predictor of territory tenure than is the number of surviving tutors in the young bird's first-breeding-season neighbour group. That is, the number of songs the young bird shares with its neighbours is more important to territory tenure than how he came to share them (via song tutoring or not).

The importance of song in many songbirds in territory defence has been demonstrated in many experiments, especially speaker-replacement and muting experiments (Catchpole & Slater 1995). We will examine the implications of the hypothesis that shared songs do provide male song sparrows with an advantage in male-male competition generally, and in territory defence in particular. We suspect that if such an advantage exists, it accrues from the ability to countersing with neighbours using shared songs (Stoddard et al. 1992a; Beecher et al. 1996, 2000).

An earlier study on a resident song sparrow population in British Columbia, about 200 km north of ours, reported a positive relationship between song repertoire size and territory tenure (Hiebert et al. 1989). Small-repertoire birds were purposely overrepresented in their sample of 16 birds, however, and most of their effect was due to very short territory tenures of five of their six birds with four to six song types (the average repertoire size in this population is the same as in ours, eight or nine song types). For the nine birds in their sample with repertoires of 8–12 songs, the function relating territory tenure (measured in months) to repertoire size was actually flat, or possibly negative. Because Hiebert et al. did not measure song sharing, it is possible that the effect was due to a correlation between repertoire size and song sharing. In our sample repertoire size was strongly correlated with number of shared songs up to a repertoire size of nine songs (Fig. 3); the relationship is essentially flat for larger repertoire sizes.

The only other longitudinal studies to date to correlate repertoire size with measures of reproductive success were done on great tits (McGregor et al. 1981; Lambrechts & Dhondt 1986). McGregor et al. (1981) found correlations between repertoire size and the three measures of reproductive success they examined: number of breeding young produced, survival to breed a second breeding season (most males survive only one), and lifetime reproductive success. In all cases, these measures were lowest for repertoire sizes of one or two songs, but the functions peaked not at the maximum repertoire size (five song types) but at three songs (lifetime reproductive success, number of breeding young) or four songs (probability of breeding in next year). Lambrechts & Dhondt (1986) found similar but weaker results. Although McGregor et al. (1981) and Lambrechts & Dhondt (1986) did not examine song sharing in their studies, McGregor & Krebs (1989) subsequently provided evidence suggesting the importance of song sharing versus repertoire size in this small-repertoire species: they showed that great tits replace songs between breeding seasons, dropping unshared songs and replacing them with songs shared with new neighbours, without increasing repertoire size. In several other species it has also been shown that birds modify their repertoires so as to increase song sharing with neighbours in later breeding seasons: brown-headed cowbirds, *Molothrus ater*, American redstarts, *Setophaga ruticilla*, and European starlings, *Sturnus vulgaris* (O’Loughlen & Rothstein 1993; Lemon et al. 1994; Mountjoy & Lemon 1995).

It seems paradoxical that song sharing was highest in our study for birds with nine types, because a bird cannot reduce the number of songs he shares with neighbours by adding a 10th or 11th song type (although he can reduce his relative sharing). An interesting possibility is that some birds may retain a larger-than-average number of songs in an effort to reach the desired level of song sharing. This might happen, for example, under circumstances of low song sharing in the neighbourhood (hence any given song will usually match only one neighbour at best). As a more general point, if maximizing sharing is the major goal of the song learning strategy, more songs

is not inherently better; in particular, the young bird should avoid winding up with unshared song types, which he does whenever a song tutor from which he learned a particular song dies, and none of the neighbours share this song. Such a tutor-unique song becomes an unshared song that ‘uses up a slot’ in the young bird’s repertoire when the tutor-neighbour dies. The young song sparrow is exposed to many more songs than he keeps and he must ‘finalize’ his song repertoire before he is a year old. Our studies indicate that he maximizes song sharing by preferentially learning or retaining songs shared by his tutor’s versus tutor-unique songs (Beecher et al. 1994; Nordby et al., in press), and by preferentially retaining songs that match his closest, most active neighbours early in his first spring (Nordby et al. 1999, in press) and perhaps by learning new songs in his first autumn or spring as well (unpublished data).

Although song sharing is a good predictor of territory tenure in our population of song sparrows, it remains to be seen how well it predicts reproductive success in other songbirds. As mentioned earlier, song sharing among neighbours appears to be minimal in some species and even in some populations of song sparrows. However, even where song sharing is not as extensive and easily measured as in our population, it may exist on a subtler scale among neighbours, as has been shown for a classical dialect species, the white-crowned sparrow, *Zonotrichia leucophrys nuttalli* (Bell et al. 1998). If such gradients of song similarity are salient to the birds themselves, neighbours could countersing with their ‘shared’ (most similar) songs or derive whatever other benefits may be correlated with having songs similar to one’s neighbours’. We are presently investigating whether birds that do not share song types by our criterion may still behave as though they have certain similar song types, for example, preferentially countersing with these particular song types.

In conclusion, our results are consistent with the hypothesis that in song sparrows selection has favoured song sharing with neighbours rather than large song repertoires per se. We suggest that in song sparrows, larger song repertoires may be favoured up to some optimum value (eight or nine types in our population) because they permit greater song sharing, but beyond this optimum they may even be disfavoured. If this is so, selection on repertoire size in this case would be both indirect and stabilizing. The general hypothesis that selection has acted on a song variable distinct from but partially correlated with repertoire size (‘indirect selection hypothesis’) should be tested in other songbird species with small or moderate repertoire sizes. The indirect selection hypothesis should be tested against the alternative hypotheses that smaller song repertoires are the result of weaker sexual selection or stronger opposition from some ‘stabilizing’ selection pressure (which would have to be identified).

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Note Added in Proof

In a recent study (Wilson et al., in press), similar results were found for another western population of song sparrows.

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