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Original Article

Territorial song sparrows tolerate juveniles during the early song-learning phase

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Avian song learning is an important model system for understanding vocal learning in humans and other animals. Laboratory studies indicate that social interactions are critical for song learning, but field observations show that territorial males are aggressive to intruders, raising the question of whether young birds are tolerated, much less tutored in the wild. We examined how adult song sparrows (*Melospiza melodia*) treat juvenile and adult intruders during different seasons important for song learning—summer, autumn, and spring—using taxidermic mounts and song playback. Territorial adults responded aggressively to adult intruders throughout the year. Adults were tolerant of juvenile intruders in the summer, displayed somewhat reduced aggression in the autumn, but treated juveniles like adult intruders by the spring. In the summer and autumn trials, wild juveniles approached our simulated "interactions" between subjects and adult mounts; these wild juveniles were also tolerated, even at close distances. That juveniles can and do closely approach adults during the early sensitive phase of song learning suggests that direct interactions with adults are possible and might be important for learning. In contrast, since young birds are treated aggressively in early spring, most late song learning likely happens through eavesdropping or long-distance singing interactions.
Key words: juvenile plumage, song learning, song sparrow, subsong, territory defense. *[Behav Ecol]*

INTRODUCTION

Many animals communicate with vocal signals, but only a fraction of these species must learn their signals. Vocal learning is not simply limited to learning to produce acoustic signals but also learning to use and comprehend communication systems (Snowdon and Hausberger 1997). Thus, vocal learning may have evolved to help allow animals to precisely match vocal features of specific individuals, groups, or population dialects, allowing for more directed or precise communication to take place. Because vocal learning is an inherently social process, whereby animals typically copy the vocalizations of other individuals, social factors are a critical aspect of the learning process. Because the effects of social influences are complex, it is important to better understand the nature of social factors in vocal learning (Snowdon and Hausberger 1997).

Vocal learning occurs in diverse taxa, including 4 orders of mammals—humans (but no other primates), cetaceans, bats, and elephants—and 3 orders of birds—songbirds, hummingbirds, and parrots (Janik and Slater 1997; Jarvis 2004; Catchpole and Slater 2008). Of these groups, the best-studied nonhuman vocal learners are the songbirds (oscine passerines). Song learning in songbirds has been intensively studied over the past 50 years (Catchpole and Slater 2008), in part because of its many parallels with human language learning and has proved to be a prime model for understanding human language learning (Brainard and Doupe 2002).

The key role of social interactions in vocal learning is one of the many parallels recognized between bird song learning and human language learning (Beecher and Brenowitz 2005; Catchpole and Slater 2008). The importance of social factors in bird song learning was revealed by the discovery that some birds learn more readily from live singing birds than from speakers playing recorded song (Baptista and Petrinovich 1984; Kroodsma and Pickert 1984; Clayton 1988; Eales 1989; Chaiken et al. 1993; but see Nelson 1998). Moreover, some of the rules of song learning derived from studies using playback of recorded song ("tape tutors") were bent or broken when the song tutors were instead actual live birds. For example, the seminal tape tutor studies of white-crowned sparrows (*Zonotrichia leuchophrys*) showed that the sensitive period for song learning closes at approximately 50 days and that heterospecific songs are uniformly rejected (Marler 1970). However, Baptista and Petrinovich (1984, 1986) showed that if a young white-crowned sparrow was exposed to a tape tutor through 50 days and thereafter exposed to a live tutor, the young bird would learn the song of the live tutor and, in some cases, would do so even if this tutor was of a different species. Furthermore, birds must learn not only how to produce their songs but also the appropriate context for using these songs to effectively communicate (West et al. 1997). Thus, live tutors add a potent factor to the song-learning mix, and social interactions between tutor and tutee may be a key ingredient.

Most laboratory experiments with live tutors have maintained the young bird and the adult tutor in intimate visual and auditory contact (though typically both are in cages) so that social interaction of some sort is unavoidable. Only a few laboratory experiments have actually tried to test the "social interaction" hypothesis by manipulating the nature and degree of social interaction. These studies have generated conflicting results, however, with close interactions having positive effects in some cases (Clayton 1987; Jones and Slater 1996),

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negative effects in others (Casey and Baker 1993; Beecher et al. 2007), and mixed in others (Nordby et al. 2000, 2001). Given that these laboratory simulations have limited ecological validity in any case, it is difficult to weigh the conflicting evidence from these experiments.

Moreover, there is good reason to expect social interaction between tutor and tutee to be fundamentally different in songbirds than it is in the analogous human system. Whereas humans typically learn language from friends and kin, songbirds typically learn their songs from birds who will be their potential territorial rivals (in this sense the term "tutor," if taken literally, is likely a misnomer). In songbirds, adults have no obvious motivation to tolerate young birds, much less to tutor them. With rare exceptions, songbird fathers do not teach their songs to sons (for 2 possible exceptions, see Grant and Grant 1996; Slater and Mann 1990); instead, in most species, song learning commences after the young bird has dispersed from the natal area (Beecher and Brenowitz 2005; Catchpole and Slater 2008). Thus we might expect territorial adult males (potential song tutors) to respond to young birds just as they respond to adult conspecifics: to signal aggressively, attack, and chase them away. Although the point has often been made that laboratory tape tutor experiments are "unnatural" because young birds never see or interact with their tutors, it is equally true that laboratory experiments with live tutors can be considered unnatural, in that young birds and tutors cannot avoid interacting.

We know very little about the relationships between young birds and their song tutors in nature, but most songbirds learn songs from birds who will be their territorial neighbors in their first breeding seasons (Beecher and Brenowitz 2005). Thus for song learning to occur via direct interaction between a young bird and adult tutor in the wild, the young bird must dare to encroach on the adult's territory and the adult must permit him to do so. Both of these conditions need be met if any kind of interaction-based song tutoring is to occur. Note that early juvenile song (especially subsong and early plastic song sung in the natal summer) is very quiet in most species, so young birds are not capable of any sort of long-distance singing interaction with adults until some later time and any early song learning through direct interaction must take place in close proximity to the adult tutors. In the present study, we examine the social relationships necessary for song learning by asking whether young male song sparrows (*Melospiza melodia*) can and do interact with older birds, their potential song tutors, in nature.

Song sparrows have been intensively studied in the laboratory and field and are an important model system for the study of vocal learning (see Beecher 2008 and studies reviewed within). In this species, males learn to sing a repertoire of 6–12 song types during their first year of life, after which time their repertoire does not change (Beecher 2008). There is a sensitive developmental phase during the first few months of life when most song memorization probably occurs (Marler and Peters 1987), but the composition of the young bird's song repertoire is strongly affected by events happening well into the next (the young bird's first) breeding season (Nordby et al. 1999, 2001, 2007). In particular, although song sparrows may memorize most of their songs during their natal summer, they retain few songs of adult birds that fail to survive into the next breeding season (Nordby et al. 1999). Young birds go through a period of low amplitude and unstereotyped "subsong" and then a somewhat better developed plastic song period during the first autumn or winter and much of this singing necessarily takes place on the territories of adult conspecifics. By the first breeding attempt, all song sparrows have developed a stereotyped set of songs with the end product being a set of neighborhood-specific song types where each bird typically shares several songs in his repertoire with each of his neighbors (Beecher 2008). These matching song types are the basis of the intrasexual territorial communication system and possessing shared songs is positively related to territory tenure (Beecher 2008), perhaps because they provide the means for effective communication among neighbors. Because song sparrows possess a sophisticated communication system where the same signals have different meanings depending on the specific way in which they are used (Beecher 2008), there is good reason to believe that song sparrows must learn now only how to produce their vocalizations but also how to use these songs for effective communication. They may do so by directly interacting with other birds or by eavesdropping on other birds' interactions, but social factors of some sort are likely critical for the ontogeny of vocal communication in song sparrows.

In a previous field study, we found that during the early part of this learning period, young birds are especially attracted to adult counter-singing interactions (Templeton et al. 2010). Young sparrows with radio transmitters actively approached playback of adults' counter singing, but essentially ignored playback of a single adult singing broadcast song. This result corroborated laboratory findings (Beecher et al. 2007; Burt et al. 2007), and suggested that young birds may be attracted to interacting adults in order to learn songs and perhaps the social rules for using songs to communicate. Although we suggested in Templeton et al. (2010) that young song sparrows might learn songs (and how to use them) by eavesdropping on adult counter-singing interactions, this hypothesis does not exclude the possibility that they could also learn via directly interacting with an adult tutor.

Here, we examine whether song learning (in part or in whole) by direct interaction between a young bird and adult is even possible during the song-learning period: how do adults react when they encounter young birds singing on their territories? We used simulated territorial intrusions to examine aggression levels toward juvenile intruders at various time periods known to be important for song learning. We challenged each subject on his territory with a life-like taxidermic mount of a juvenile male song sparrow accompanied by concurrent age-appropriate song in each of 4 seasons (late summer, autumn, early spring, and late spring) and compared this with responses to adult male mounts. Specifically, we asked whether the juvenile phenotype would permit the young bird to get close enough to interact directly with an adult. Would the adult male treat a young male more tolerantly than he normally treats adult intruders on his territory, and what sorts of interactions might young birds have with potential tutors at different life stages? In addition, because in our earlier study (Templeton et al. 2010) we had noted that young birds were attracted to interactive singing, we looked for young birds appearing on territory during the simulated interactions between the subject and the mounts, and noted how these intruding juveniles were received by the territorial adult.

MATERIALS AND METHODS

Study site and subjects

Field work was conducted in Discovery Park, a 3 km^2 primarily undeveloped park bordering Puget Sound in Seattle, WA, USA (47°39′N, 122°24′W). Song sparrows are common throughout the forests, forest edges, and shrub lands in the park, and we have banded most individuals with unique combinations of colored leg bands for individual identification.

Subjects were 16 territorial males who were each at least 2 years old ("After Second Year," or ASY) in summer 2008. Tests were carried out in each of 4 seasons relevant to different stages of a young bird's song development (see below and Table 1). Several birds from our original sample disappeared (likely died) in the summer, autumn, or winter and so were not tested in all seasons (see below). Consequently, we added new subjects to replace them (some of these disappeared as well). Eight birds were tested in all 4 seasons, 1 bird in 3 seasons, 4 birds in 2 of the seasons, and 13 individuals in just 1 season, for a total of 16 (summer and autumn) or 12 (early spring and late spring) subjects receiving all treatments.

Study periods

We measured the response of our adult subjects toward simulated territorial intrusions in each of the 4 seasons when juveniles might interact with potential tutors during their first year of life (Table 1): late in the breeding season (summer; 11–21 July 2008), postbreeding (autumn; 30 September–2 October 2008), prebreeding (early spring; 14–20 January 2009), and early breeding (late spring; 7–8 April 2009). July is the last month of the breeding season and most juveniles have fledged and are independent from their parents in this month. July would be part of the classical "sensitive period" for birds fledged in May or June (most birds in our population). The end of September and beginning of October is well after the breeding season and adult molt (which takes place in August), but adults are still territorial and many juveniles are "prospecting" for a territory, with a fair number of them singing early plastic song (Nice 1943; Arcese et al. 2002). January is the first month of the prebreeding season in our population (Seattle, Washington has a maritime climate and is quite temperate for its latitude). Song sparrows in our population increase their rates of singing and other territorial behaviors with the lengthening days after the winter solstice (Templeton CN, Campbell SE, Beecher MD, in preparation). April marks the beginning of the breeding period and is therefore theoretically the last time that some juveniles might be intruding on adult territories while searching for a breeding territory of their own.

In the first 3 seasons (summer, autumn, and early spring), we tested each subject's response to both adult and juvenile intruders. In April, we only tested responses to adult intruders because young birds hatched the previous year are now indistinguishable from older birds in song as well as plumage. Trial order (adult or juvenile) was randomized in each season, and the 2 trials for each subject were spaced 2 days apart to avoid habituation.

Mount and playback stimuli

We simulated intrusions using song playback coupled with presentation of a taxidermic mount. The mounts had their bill open and wings slightly out and backward, as if singing. For the adult treatment, we used an adult male song sparrow mount with playback of one of the subject's own songs, with a single song broadcast every 10 s. Self song was chosen to standardize playback stimuli across subjects: songs were population appropriate, not associated with specific known individuals with whom subjects may have previously interacted, and provided the same opportunity to vocally interact (e.g., through song matching, an important signal used to modulate aggressive interactions Beecher 2008).

For the juvenile treatment, we used an age-appropriate mount; in the summer trials, the mount was a young male in drab juvenile plumage, but for the autumn and spring trials, the mount was a bird in adult plumage (juveniles typically molt into adult plumage in early August). Although young birds (and our mount presentation) become progressively more like adults over the seasons, we use here the term "juvenile" for all seasons to refer to the young intruder mount presentation in each of the first 3 seasons to clearly distinguish between the 2 treatments.

Song playback stimuli for the juvenile treatment were similarly age and season appropriate. We played juvenile subsong in the summer, early plastic song in the autumn, and late plastic song in the spring (examples are shown in Figure 1). Because subsong is often quiet (low amplitude), making it difficult to obtain high-quality field recordings, we used recordings from juvenile song sparrows living in the laboratory. These birds had been collected recently from the same field population and therefore their songs were of both the appropriate "dialect" and developmental stage. We used 10 exemplars from 4 individual birds. Plastic songs used in the autumn and early spring were recorded from wild juveniles in our population a few days before each set of trials began to ensure that our stimuli matched the appropriate song development level of wild juveniles in our population. We used 8 exemplars from 4 different individuals for each set of plastic song playbacks. Juvenile song playback stimuli were structured to use a duty cycle similar to that of the adult stimuli. All playback stimuli were compiled in Syrinx (Burt JM; www.syrinxpc.com) and stored as high-quality uncompressed wave files.

Trial procedure, behavioral measures, and data analyses

The mount was placed on a 1.5-m pole, which was then positioned in the center of each subject's territory in a location that provided both good visibility of the mount and also numerous perches at varying (standardized) distances from the mount. We placed a playback speaker (Pignose 7-100) on the ground below the mount and controlled it with an Apple ipod touch located approximately 15 m away. We played song sparrow songs (details above) at approximately 75dB (sound pressure level at 1 m) until the bird approached close enough (~4 m from the mount) that we could be sure that he had visually located the intruder. We then continued playback for one additional minute. During each trial, we recorded all of the subjects' behaviors and songs for 20 min after the initial approach or

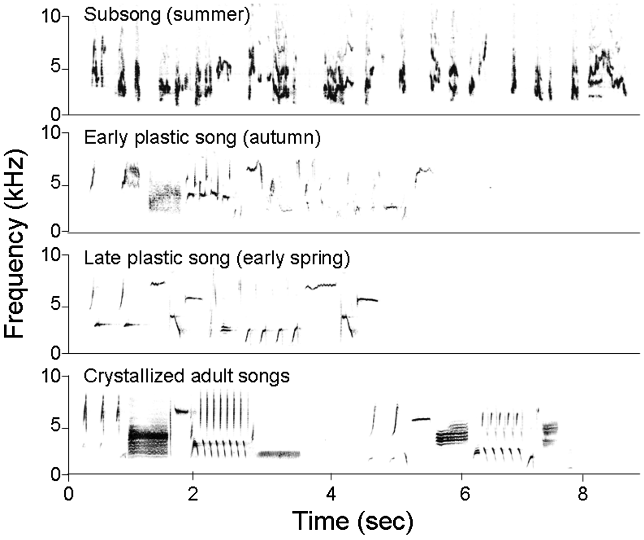

Figure 1
The songs of young song sparrows slowly develop throughout the seasons, with birds passing through subsong and plastic song phases before crystallizing their adult song repertoires (typically 8–10 different song types, 2 examples are shown). In this experiment, we matched our juvenile song playback to the appropriate development stage of wild birds in each season. Adult playback songs remained stable throughout the year.

Table 1

Territorial behavior and song learning of young song sparrows relative to the testing dates

Season	Test dates	Young of the year	Song learning
Late breeding	11–21 July 2008 (Summer)	Most young fledged and independent of parents, some singing subsong	Sensitive period for song learning of most young birds
Postbreeding	30 September–2 October 2008 (Autumn)	Some birds in the cohort begin prospecting for territories, some singing early plastic song	Song learning still possible[a]
Prebreeding	14–20 January 2009 (Early spring)	Most birds prospecting for territories, some singing late plastic song	Late song learning possible, both de novo and selective retention[a]
Early breeding	7–8 April 2009 (Late spring)	Many young birds have established territories, some still prospecting, all singing crystallized song	Song learning probably over

[a] However, young birds may be less inclined to learn songs in the autumn than in the subsequent spring (Nulty et al. 2010).

song response. If the subject attacked the mount before this time, the trial was terminated to prevent damage to the mount. During each trial, we measured behavioral variables that are consistently associated with aggression in song sparrows (Nice 1943; Searcy et al. 2006; Akçay et al. 2009): the number of flights, the distance of the focal bird to the mount, the number of soft songs, and the number of wing waves. Distances were measured continuously during the 20-min trial with the aid of markers and branches of known distance and later converted to percentages in various distance categories. Because we were interested primarily in aggressive behavior and the potential for direct interactions, we focus our analysis on the percentage of time each subject spent within the closest distance category (<1 m from the mount). Soft songs are a specific vocal display that are not simply softer, but are also often qualitatively different in acoustic structure from normal broadcast repertoire songs (Anderson et al. 2008). They occur primarily in aggressive contexts, when a bird is close to his opponent, and are the best predictor of attack in song sparrows (Searcy et al. 2006). Wing waves are visual displays (Nice 1943) that are also linked with aggression (Ballentine et al. 2008), though generally not as strongly as soft songs or flights (Searcy et al. 2006). In addition, we measured 2 other conspicuous behaviors, high chips and loud song production. High chips are high-frequency vocalization that are emitted under a variety of situations usually related to distress or agitation (Nice 1943), and loud songs are long-distance signals which also do not reflect aggression (Searcy et al. 2006).

We coded data from the recordings and calculated rates and averages for each trial using JWatcher v1.0 (Blumstein DT, Daniel JC, and Evans CS; http://www.jwatcher.ucla.edu). Because several of the behavioral variables we measured were correlated, we used principal components analysis (PCA) to reduce the number of variables. We retained all principal components with eigenvalues >1 (Table 2), reducing the data to 3 uncorrelated variables which explained 80% of the data. The first PC loaded primarily on variables associated with aggressive signalling (soft songs, flights, time near mount, wing waves) (Searcy et al. 2006; Akçay et al. 2009, 2011), so we refer to PC1 as the "aggression score." The other 2 components loaded primarily with the other 2 types of vocalizations (Table 2) and we refer to PC2 as "loud songs" and PC3 as "high chips." This PCA confirms previous studies on song sparrows (Stoddard et al. 1991; Beecher 2008) showing that loud song is not a component of aggressive response, that is, not correlated with other variables related to aggression. The function of high chips is less clear but they seem to be a general type of alarm/distress vocalization and are typically used in place of other aggressive behaviors (Nice 1943; Searcy et al. 2006). Although attacks on the mount are clearly related to aggression, we did not include them in the PCA because of their rarity and instead consider them separately.

We ran a general linear model (GLM) analysis with each of the principal components as dependent variables and treatment (adult and juvenile) and season (summer, autumn, and early spring), and their interaction as explanatory variables. Subject identity was also included as a random factor in the models. All statistics were two-tailed and were calculated using JMP v8.0 (SAS Institute, Cary, NC). We also repeated the analyses for PC2 and PC3 with the raw data (loud songs and high chips, respectively). Because we did not have a juvenile treatment in the spring, we could not include this season in the model described above, so instead, we examined variation in adult response across all 4 seasons with a separate GLM that used subject identity as a random factor and season as a fixed factor. Count data were analyzed using Fisher's exact tests.

RESULTS

The aggressive response of subjects (PC1) was affected significantly by both the treatment (adult vs. juvenile presentation, $P = 0.006$) and season ($P = 0.036$), and the 2 effects interacted ($P = 0.006$, for detailed statistics, see Table 3). Response to the adult presentation was strong in all 3 seasons, although slightly weaker in the autumn than in summer or early spring. Response to the juvenile mount was weaker throughout all 3 seasons, but only the summer difference was large and significant (Tukey tests, overall alpha = 0.05): responses to the

Table 2

Loading coefficients for the PCA. PC1 (aggression score) includes several behaviors that are generally associated with aggression

	Loading coefficient eigenvector		
Variable	PC1	PC2	PC3
Time close to mount	0.55	−0.18	0.23
Number of flights	0.46	0.50	0.08
Soft song rate	0.56	−0.07	−0.23
Wing wave rate	0.37	−0.28	−0.50
Loud song rate	0.08	0.74	0.10
High chip rate	0.17	−0.30	0.79
Eigenvalue	2.31	1.43	1.10
Cumulative % explained	38.5	62.4	80.6

Loud songs and high chipping had the highest loading on PC2 and PC3, respectively. We used the first 3 principal components, which each had eigenvalues >1.0. Together these 3 components explained 80% of the variation in the data.

Table 3
Results from the GLMs

Variable	Source	DF	F	P
Aggression (PC1)	Treatment (Adult, Juvenile)	1	13.35	0.0006
	Season (July, Oct, Jan)	2	3.49	0.036
	Treatment × Season	2	5.58	0.006
Loud songs (PC2)	Treatment (Adult, Juvenile)	1	0.11	0.74
	Season (July, Oct, Jan)	2	2.13	0.13
	Treatment × Season	2	0.38	0.68
High chips (PC3)	Treatment (Adult, Juvenile)	1	9.24	0.003
	Season (July, Oct, Jan)	2	0.45	0.64
	Treatment × Season	2	0.42	0.66
Latency to Respond	Treatment (Adult, Juvenile)	1	11.49	0.001
	Season (July, Oct, Jan)	2	7.50	0.001
	Treatment × Season	2	6.50	0.003

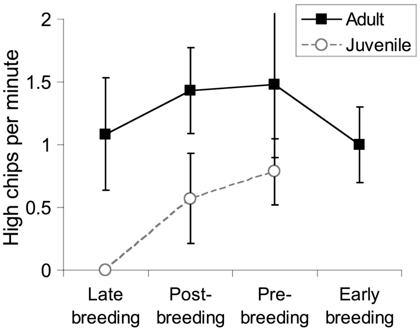

Figure 3
Song sparrows produced more high chipping calls (shown as means ± standard error of mean) when they encountered an adult in their territory than a juvenile intruder, regardless of the season.

juvenile became progressively more similar to those to the adult across seasons (Figure 2). The summer difference between response to adult and juvenile is actually somewhat larger than suggested by Figure 2, which omits 6 of 16 subjects who failed to show up at all for juvenile subsong playback (only one failed to show up for adult song). There was only one other no-show in all of the October and January trials. If we include these individuals in the analysis by examining the overall latency to respond to the intruder (by singing or approaching the mount), subjects' responses were much slower for the juvenile intruder's subsong playback in the summer trials than the adult or plastic song playback at other times of the year (Figure 4). In the summer trials, even the subjects who did show up took longer to do so to juvenile subsong than to adult song (means 3.4 ± 0.8 vs. 0.7 ± 0.2 min, respectively). Attacks on the mount followed a similar pattern. In July, subjects often attacked the adult mount (8 of 16 cases) but only one subject attacked the juvenile mount (1/16; Fisher's exact test: $P = 0.015$) and that attack occurred only at the very end of the 20-min trial. Attacks generally diminished in subsequent seasons but increased again in the spring (October: to adults 3/16, to juveniles 2/16; January: to adults 2/12, to juveniles 1/12; April: to adults 5/12) so that attack rates were higher overall in the breeding season than nonbreeding season, but this pattern was not statistically significant (Fisher's exact test: $P = 0.08$; Figure 5).

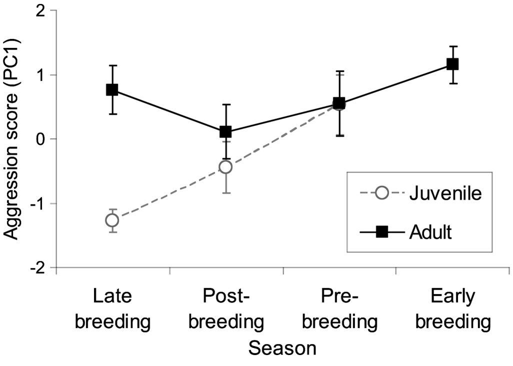

Figure 2
Aggression levels of subjects in response to adult and juvenile territorial intruders varied by season and intruder type. The *y* axis shows mean (±standard error of mean) aggression score, a composite measure of aggression derived from the rates of soft songs, flights, wing waves, and the proportion of the trial each subject spent less than 1 m from the intruder.

Nonaggressive behaviors (PC2 and PC3) showed different patterns (Table 3). Loud songs (PC2) did not vary by either treatment or season. More high chips (PC3) were produced in response to the juvenile mount than the adult mount, though this behavior was not affected by either season or the season–treatment interaction (Figure 3). Examining the raw data provided very similar results. Loud songs did not vary at all by treatment or season ($P > 0.28$). More high chips were produced in response to the juvenile mount than the adult mount ($F_1 = 10.56$, $P = 0.002$), though neither season ($F_2 = 2.04$, $P = 0.14$) nor a season–treatment interaction ($F_2 = 0.19$, $P = 0.83$) affected chipping rates. When we limited the data to adult intruders and examined nonaggressive responses in all 4 seasons (including late spring data from April), we found no effect of season for any of the behaviors we measured ($P > 0.3$ for all), indicating that subject's response to adult intruders did not vary much across season.

During many of these adult mount trials, we observed wild juveniles approach the subject and mount and watch the "interaction" between them. Juveniles approached during at least 5 of the adult trials, and in one trial, we observed at least 3 different juveniles approach within 3–4 m. In the summer, juveniles approached close to the adult–mount interaction, sometimes perching as close as 1–2 inches from the adult subject. However, even when the juveniles perched this close (nearly touching), adults directed all aggression toward the adult mount and essentially ignored the juveniles. We never witnessed any aggressive behaviors (wing waves, soft songs, flights toward, attacks, etc.) directed toward these young birds in the summer trials. No juvenile was observed singing during these "interactions." In the autumn, most of the young birds we observed tended to stay farther away (3–10 m) from the subject and mount. Only in one trial did we observe a juvenile approach the juvenile mount; during this trial, a juvenile female approached the juvenile mount and then performed the copulation solicitation display to the mount. In the spring trials, the young birds that approached the mount did so as territory holders (i.e., the previous adult territory holder had died or disappeared).

DISCUSSION

For most hatch year song sparrows in our population, July is part of the classical sensitive period for song learning, the period when most song memorization occurs (Marler and Peters 1987). In our experiment, we found that adult male song sparrows were tolerant of juveniles during this period. In the autumn test, they were still less aggressive toward juveniles, but the difference was smaller, and by early spring

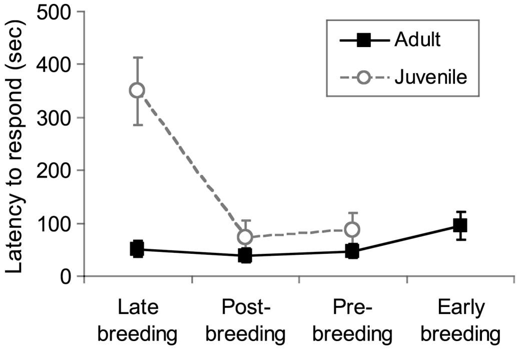

Figure 4
Subjects responded, by singing or approaching, to subsong playback (late breeding) more slowly than to playback of plastic (postbreeding, prebreeding) or adult song. Mean latency (±standard error of mean) to approach within 10 m of the mount or sing after the first intruder playback is shown for both juvenile and adult intruders in each season.

(January tests), they treated adults and juveniles essentially the same. At the proximate level, the decreasing differences in response to adult and juvenile presentations track the phenotypic differences, which in July were large (different plumage and quite different, subsong, song), in October much less (the same adult plumage and more similar plastic song), and in January, the least (the same plumage and more similar late plastic song). Although previous studies have shown that plumage is important for reducing aggression levels toward young birds (Rohwer et al. 1980; Greene et al. 2000; Ligon and Hill 2009), our results indicate that undeveloped song (subsong or plastic song) also reduces aggression levels, as evidenced by the long latency to approach subsong playback. Although it is not possible to tell simply from the latency whether adults were less interested in undeveloped song or it was more difficult to detect compared with adult song, the other behavioral measures (scored after approach) indicate that undeveloped song reduces aggression. Most striking was the persistent difference in high chipping rates even in the autumn and early spring after the juvenile intruder had full adult plumage (i.e., the only difference was acoustic). Clearly both plumage and song are important for mediating aggressive interactions and both likely work in concert with a bird's behavior. At the ultimate level, the progressive change through the seasons also makes sense given that a young bird represents an increasing threat over the course of the year and by January is a full or near-full territorial competitor (Arcese et al. 2002).

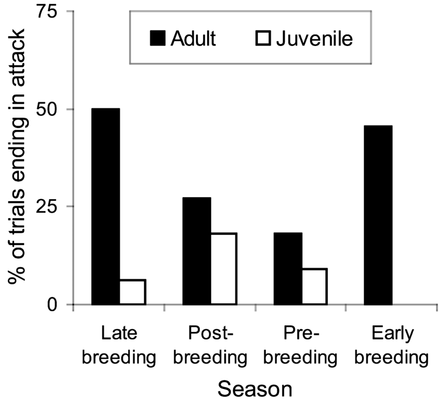

Figure 5
Subjects were less likely to attack young juvenile intruders (late breeding) than adult intruders. Attack rates were generally lower outside of the breeding season, despite similar levels of aggressive signaling (see Figure 2).

These findings indicate that in the summer and perhaps into the autumn, a juvenile bird may be able to get quite close to an adult. Moreover, during the July and October trials, we often observed one or more young birds fly in to witness the "interaction" between subject and challenger (adult mount). As noted earlier, in another field study on this population (conducted just prior to the present study), we found that young song sparrows preferentially approached simulated singing interactions between 2 adults but essentially ignored simulated solo-singing adults (Templeton et al. 2010). Note that in the present study, juveniles were similarly attracted to an ongoing "interaction" between the subject and the mount, and frequently approached the territorial adult during these interactions. The results of these 2 studies confirm that juveniles are attracted to adult singing interactions and indicate that they can closely approach one or both of the singers to thoroughly observe these interactions. Because juveniles are not themselves chased or attacked, they are free to observe singing interactions of potential tutors, and these observations may be critical for song learning or the gathering of other information relevant to future territory establishment. Thus, the opportunity exists for young birds to memorize songs or learn the rules for communication through social eavesdropping.

Adults were surprisingly tolerant of the juveniles they encountered during the summer sensitive phase of song learning. Only 10 of 16 adults were attracted to playback of juvenile subsong despite it being played from the center of the territory; in contrast 15 of the 16 subjects rapidly approached adult song playback. Of the 10 subjects that were attracted to juvenile subsong, only one interacted strongly with the juvenile mount. Subjects were nonaggressive not only toward the juvenile mount but also toward wild juveniles who approached within the adult's territory, even when they came extremely close to the adult (within 2 inches of an adult that was signalling aggressively toward the mount) or when several approached at the same time. We previously found that young song sparrows form stable social networks and have high song sharing rates with males they associated with early in life (Templeton et al. 2012), and it is plausible that shared social eavesdropping experiences like we observed in this study may contribute to this interesting learning pattern. The results of summer trials with the juvenile mount and our observation of juveniles closely approaching adults in both the summer and autumn trials, indicate that adults are surprisingly tolerant of juvenile intruders at this time.

The finding that juveniles can closely approach adults without fear of aggression during the sensitive phase for song learning, suggests that they have the potential to learn to sing by directly interacting with adults, but it is not clear exactly what form these interactions might take. Tolerating nearby juveniles does not necessarily indicate that adults actively tutor or even do much more than ignore them. However, even if adults simply tolerate juveniles and do not actively interact with them, they create the opportunity for juveniles to interact with them. In this way, the "interaction" wherein an adult sings and a juvenile responds may be perceived differently by both players: juveniles may perceive a two-way interaction (responding to the adult) even if the adult is simply singing to advertise his territory or communicating with a distant rival. Although this situation perhaps resembles "parallel play" more than it does a strong social interaction, it could nevertheless be a key context for song learning. Over the years, we have made numerous anecdotal observations of juveniles "interacting" in this way with adults. In fact, juveniles may even be attracted to adult interactions primarily because they provide this type of continued opportunity to "interact" with an adult (even if he is actually interacting with a neighbor) in the realistic context of a counter-singing interaction.

Although it is likely that a song sparrow in our population memorizes most of his songs during the natal summer (Marler and Peters 1987), he memorizes many more than he retains for his final repertoire of 7–10 songs, and generally, he retains only songs of adults who survive into his first breeding season (Nordby et al. 1999, 2001, 2007) through a process of selective retention (Nelson and Marler 1994). That is, the song-learning process that began the previous spring and summer continues into the early part of the next spring. The results of the present study suggest that this later phase of learning might proceed differently from the early memorization phase, for the young bird would not be able to get close to the older bird without being challenged and attacked. It is possible that aggressive interactions that the young bird has with adults during this late phase help solidify song learning (Clayton 1987; Jones and Slater 1996). However, song sparrows generally stop singing or switch to soft warble song and visual displays when they get close (Nice 1943; Searcy et al. 2006) so there are likely to be few opportunities to learn loud song during these interactions. At this stage, however, the young bird is singing well-developed plastic song (Figure 1), and it is possible that he could sing interactively at a distance with a territorial adult. This interactive singing could be the social basis for late learning, regardless of whether it is de novo song learning or selective retention of the best-matching previously memorized songs (Nelson and Marler 1994). However, in the absence of direct observational data on this point, it is just as possible that the birds hone their final repertoire on the basis of eavesdropping, perhaps especially on counter-singing interactions of their future territorial neighbors.

In conclusion, our results indicate that song learning by young song sparrows could involve both direct interactions with the adults and eavesdropping on counter singing between adults. The 2 processes are not mutually exclusive, but which process dominates likely varies over the course of the young bird's first year. During the summer critical period, adult song sparrows are tolerant of juveniles, even at close range and even when these adults are engaged in aggressive territorial interactions with rivals. Direct interactions with adults are possible but less likely in the autumn as adults become less tolerant of juveniles. Song learning early the next spring (January through March) probably does not involve close contact, because adults are intolerant of young birds at that time. Song-learning at this stage probably involves distant learning, either the young bird counter singing with the adult or eavesdropping on counter-singing interactions between adults. Territorial song sparrows tolerate juveniles during the early song-learning phase.

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REFERENCES

Akçay Ç, Tom M, Holmes D, Campbell SE, Beecher MD. 2011. Sing softly and carry a big stick: soft song as an aggressive signal in song sparrows. Anim Behav. 82:377–382.

Akçay Ç, Wood WE, Searcy WA, Templeton CN, Campbell SE, Beecher MD. 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. Anim Behav. 78:97–102.

Anderson RC, Searcy WA, Peters S, Nowicki S. 2008. Soft song in song sparrows: acoustic structure and implications for signal function. Ethology. 114:662–676.

Arcese P, Sogge MK, Marr AB, Patten MA. 2002. The Birds of North America Online. In: Poole A, editor. Ithaca: Cornell Laboratory of Ornithology [Internet]. Available from: The Birds of North America Online database: http://bna.birds.cornell.edu/ [cited 2012 April 16].

Ballentine B, Searcy WA, Nowicki S. 2008. Reliable aggressive signalling in swamp sparrows. Anim Behav. 75:693–703.

Baptista LF, Petrinovich L. 1984. Social-interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. Anim Behav. 32:172–181.

Baptista LF, Petrinovich L. 1986. Song development in the white-crowned sparrow: social factors and sex differences. Anim Behav. 34:1359–1371.

Beecher MD. 2008. Function and mechanisms of song learning in song sparrows. Adv Study Behav. 38:167–225.

Beecher MD, Brenowitz EA. 2005. Functional aspects of song learning in songbirds. Trends Ecol Evol. 20:143–149.

Beecher MD, Burt JM, O'Loghlen AL, Templeton CN, Campbell SE. 2007. Bird song learning in an eavesdropping context. Anim Behav. 73:929–935.

Brainard MS, Doupe AJ. 2002. What songbirds teach us about learning. Nature. 417:351–358.

Burt JM, O'Loghlen AL, Templeton CN, Campbell SE, Beecher MD. 2007. Assessing the importance of social factors in bird song learning: a test using computer-simulated tutors. Ethology. 113:917–925.

Casey RM, Baker MC. 1993. Aggression and song development in white-crowned sparrows. Condor. 95:723–728.

Catchpole CK, Slater PJB. 2008. Bird song: biological themes and variations. 2nd ed. Cambridge: Cambridge University Press.

Chaiken M, Bohner J, Marler P. 1993. Song acquisition in European starlings, *Sturnus-vulgaris*: a comparison of the songs of live-tutored, tape-tutored, untutored, and wild-caught males. Anim Behav. 46:1079–1090.

Clayton NS. 1987. Song tutor choice in zebra finches. Anim Behav. 35:714–721.

Clayton NS. 1988. Song tutor choice in zebra finches and Bengalese finches: the relative importance of visual and vocal cues. Behaviour. 104:281–299.

Eales LA. 1989. The influences of visual and vocal interaction on song learning in zebra finches. Anim Behav. 37:507–508.

Grant BR, Grant PR. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. Evolution. 50:2471–2487.

Greene E, Lyon BE, Muehter VR, Ratcliffe L, Oliver SJ, Boag PT. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. Nature. 407:1000–1003.

Janik VM, Slater PJB. 1997. Vocal learning in mammals. Adv Study Behav. 26:59–99.

Jarvis ED. 2004. Learned birdsong and the neurobiology of human language. In: Zeigler HP, Marler P, editors. Behavioral neurobiology of birdsong. New York: Annals of the New York Academy of Sciences. p. 749–777.

Jones AE, Slater PJB. 1996. The role of aggression in song tutor choice in the zebra finch: cause or effect? Behaviour. 133:103–115.

Kroodsma DE, Pickert R. 1984. Sensitive phases for song learning: effects of social interaction and individual variation. Anim Behav. 32:389–394.

Ligon RA, Hill GE. 2009. Do adult eastern bluebird, *Sialia sialis*, males recognize juvenile-specific traits? Anim Behav. 77:1267–1272.

Marler P. 1970. A comparative approach to vocal learning—song development in white-crowned sparrows. J Comp Physiol Psychol. 71:1–25.

Marler P, Peters S. 1987. A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*—a case of age-limited learning. Ethology. 76:89–100.

Nelson DA. 1998. External validity and experimental design: the sensitive phase for song learning. Anim Behav. 56:487–491.

Nelson DA, Marler P. 1994. Selection-based learning in bird song development. Proc Natl Acad Sci U S A. 91:10498–10501.

Nice MM. 1943. Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerine birds. Pt. II. Trans Linn Soc N Y. 6:1–329.

Nordby JC, Campbell SE, Beecher MD. 1999. Ecological correlates of song learning in song sparrows. Behav Ecol. 10:287–297.

Nordby JC, Campbell SE, Beecher MD. 2001. Late song learning in song sparrows. Anim Behav. 61:835–846.

Nordby JC, Campbell SE, Beecher MD. 2007. Selective attrition and individual song repertoire development in song sparrows. Anim Behav. 74:1413–1418.

Nordby JC, Campbell SE, Burt JM, Beecher MD. 2000. Social influences during song development in the song sparrow: a laboratory experiment simulating field conditions. Anim Behav. 59:1187–1197.

Nulty B, Burt JM, Akcay C, Templeton CN, Campbell SE, Beecher MD. 2010. Song learning in song sparrows: relative importance of autumn vs. spring tutoring. Ethology. 116:653–661.

Rohwer S, Fretwell SD, Niles DM. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Am Nat. 115:400–437.

Searcy WA, Anderson RC, Nowicki S. 2006. Bird song as a signal of aggressive intent. Behav Ecol Sociobiol. 60:234–241.

Slater PJB, Mann NI. 1990. Do male zebra finches learn their father's songs? Trends Ecol Evol. 5:415–417.

Snowdon CT, Hausberger M. 1997. Social influences on vocal development. Cambridge: Cambridge University Press.

Stoddard PK, Beecher MD, Horning CL, Campbell SE. 1991. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. Behav Ecol Sociobiol. 29:211–215.

Templeton CN, Akcay C, Campbell SE, Beecher MD. 2010. Juvenile sparrows preferentially eavesdrop on adult song interactions. Proc R Soc B Biol Sci. 277:447–453.

Templeton CN, Reed VA, Campbell SE, Beecher MD. 2012. Spatial movements and social networks in juvenile male song sparrows. Behav Ecol. 23:141–152.

West MJ, King AP, Freeberg TM. 1997. Building a social agenda for the study of bird song. In: Snowdon CT, Hausberger M, editors. Social influences on vocal development. Cambridge: Cambridge University Press. p. 41–56.