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3 **Territory establishment, song learning strategies and survival in song sparrows**

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10 Running head: Territory and song learning

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12 **Acknowledgements:** We thank Veronica Reed and Chris Templeton for help with field work.

13 **Conflict of interest statement:** The authors declare that they have no conflict of interests.

14 **Abstract**

15 In most songbirds the processes of song learning and territory establishment overlap in the early life of
16 young birds who usually winds up with songs matching those of their territorial neighbors in their first
17 breeding season. In the present study, we examined the relationships among the timing of territory
18 establishment, the pattern of song learning and territorial success in a sedentary population of song
19 sparrows (*Melospiza melodia*). Males in this population show high song sharing within neighborhoods
20 deriving from their learning most of their songs from neighboring males. These shared songs are
21 preferentially used in interactions with neighbors. Males also show significant variation in the timing of
22 territory establishment, ranging from their first summer until the next spring. Using a three-year
23 dataset, we found that the timing of territory establishment did not systematically affect the
24 composition of the song repertoire of the tutee: early establishers and late establishers learned equally
25 as much from their primary tutors, and had a similar number of tutors and repertoire size. Timing of
26 territory establishment also did not have an effect on subsequent survival on territory. Therefore, the
27 song learning program of song sparrows seems versatile enough to lead to high song sharing even for
28 birds that establish territories relatively late.

29 **Keywords:** bird song learning, selective attrition, territory establishment, song sparrows, song sharing,
30 survival

31 1. INTRODUCTION

32 Bird song is unusual among vocal communication systems, because it is one of the few in which animals
33 learn their vocal signals. Vocal learning has been found only in humans, songbirds (oscine passerines),
34 cetaceans, bats and two other orders of birds (parrots and hummingbirds) (Baptista & Schuchmann,
35 1990; Boughman, 1998; Pepperberg, 1994; Reiss & McCowan, 1993; Todt, 1975). Aside from human
36 language, songbirds have provided the main model system for studying social learning of communicative
37 signals (Brainard & Doupe, 2002; Doupe & Kuhl, 1999).

38 In most songbirds, particularly in close-ended learners, the young bird learns its songs after it
39 has dispersed from its natal area and is prospecting for and establishing a breeding territory in a new
40 area (Beecher, Campbell, & Stoddard, 1994; DeWolfe, Baptista, & Petrinovich, 1989). Indeed, in most
41 species of songbirds where song learning has been studied in the field, the learning process results in
42 the young bird having learned their songs from their eventual neighbors (Beecher et al., 1994; Liu &
43 Kroodsma, 2006; Nelson & Poesel, 2009; Payne, 1983; Wheelwright et al., 2008).

44 If the function of a song learning strategy is to learn songs of your eventual neighbors, the
45 timing of learning should evolve such that the bird memorizes songs and actively shapes its song
46 repertoire while establishing a territory amongst its tutor-neighbors. But early laboratory studies found
47 that song memorization is usually limited to a short period early in the natal summer (Marler & Peters,
48 1977, 1987, 1988). This poses a dilemma for species that are close-ended learners (birds that learn their
49 repertoire of songs in their first year of life and subsequently don't modify it): the young bird will need
50 to learn the songs of its eventual neighbors, but will have to learn these songs in advance of knowing
51 exactly who these neighbors and what their songs will be.

52 A partial solution to this dilemma was proposed by Nelson and Marler (1994). According to their
53 selective attrition model, a young bird memorizes songs only in its natal summer. The following spring,

54 however, when the young birds are singing and trying to establish their territories, they produce more
55 songs than they will eventually keep. During this time of overproduction, they interact with older,
56 territorial birds, and prune their song repertoire down to just those songs that best match those of
57 these older birds who will be their neighbors. Field and laboratory studies have provided some support
58 for the over-production and selective attrition model in several species (Nelson, 1992; Nelson & Marler,
59 1994; Nelson, Marler, & Morton, 1996; Nelson & Poesel, 2009; Nordby, Campbell, & Beecher, 2007).

60 Another solution to the dilemma is flexibility in the timing of the memorization phase depending
61 on the young bird's social experience. Evidence for such flexibility comes from studies on marsh wrens
62 (*Cistothorus palustris*) (Kroodsma & Pickert, 1980, 1984). Young male marsh wrens who hatch early in
63 the summer and are exposed to recorded marsh wren songs in the laboratory in the summer and
64 following spring will complete their song learning in the first 60-80 days of life (Kroodsma, 1978). In a
65 laboratory study using recorded song, Kroodsma and Pickert (1980) compared the tendency of marsh
66 wrens to memorize new songs in the spring as a function of whether they had been raised on a
67 photoperiod simulating early hatching (June) or late hatching (August). Both groups received the same
68 regimes of song tutoring in the natal year, but when exposed to new songs the following spring, only the
69 late (August) birds added some of these new songs to their repertoires. This suggests that late hatching
70 and under-exposure to song may extend the period in which a bird is capable of memorizing new songs
71 into the following spring.

72 In this paper we examine the relationship of song learning and the timing of territory
73 establishment in a resident population of song sparrows (*Melospiza melodia*). Song sparrows are a
74 temperate songbird species in which only males sing; female song is very rare (Arcese, Stoddard, &
75 Hiebert, 1988; Beecher, Campbell et al. unpublished observations). Male song sparrows are close-ended
76 learners that develop a repertoire of about 9 songs (range: 5-13 songs) in their first year of life, which
77 they do not modify in subsequent years (Nordby, Campbell, & Beecher, 2002).

78 Several field studies (Nordby et al 1999; Akçay et al 2014) have identified key features of song
79 learning in our study population of song sparrows. (1) Each young bird (hereafter tutee) learns from
80 several older males (hereafter tutors). (2) The final repertoire of the tutee is biased towards a single,
81 primary tutor who on average accounts for about half of the tutee's song repertoire, although this
82 proportion varies from 0.3 to 1. This primary tutor is usually an immediate neighbor (Nordby, Campbell,
83 & Beecher, 1999). (3) Song learning begins in the natal summer, but ultimately the bird learns (or
84 retains) more songs from tutors who survive into the next spring than from tutors who don't. (4) Song
85 sharing with neighbors is important in territorial interactions in this population as the birds use shared
86 songs in a hierarchical, graded signaling system (Akçay, Tom, Campbell, & Beecher, 2013; Beecher,
87 Stoddard, Campbell, & Horning, 1996; Burt, Campbell, & Beecher, 2001; Stoddard, Beecher, Campbell, &
88 Horning, 1992). (5) Although it is not completely clear how song sharing benefits a bird, the degree of
89 song sharing with neighbors in the young bird's first breeding season is positively correlated with the
90 number of years the bird survives on territory (Beecher, Campbell, & Nordby, 2000; P. L. Wilson,
91 Towner, & Vehrencamp, 2000). In contrast, repertoire size is unrelated to a bird's territory tenure
92 (Beecher et al., 2000).

93 Early laboratory studies of song learning in male song sparrows in an eastern population (*M.*
94 *melodia melodia* subspecies) revealed a sensitive period mostly limited to the first summer (Marler &
95 Peters, 1987). Subsequent laboratory studies of our resident population (*morphna* subspecies) have
96 found that learning of new songs can occur in the fall and following spring as well (Nordby, Campbell, &
97 Beecher, 2001; Nulty et al., 2010; Templeton, Burt, et al., 2012) although how common this 'late
98 learning' is in nature is still unknown, and generalizing to natural conditions from laboratory studies is
99 difficult).

100 In our field site and nearby resident populations, young song sparrows are observed to 'float'
101 over a wide area until they manage to find a territory (Arcese, 1987, 1989; J. N. M. Smith & Arcese,

102 1989; Templeton, Reed, Campbell, & Beecher, 2012), which can happen from as early as July (at about 2-
103 3 months of age) to as late as April of the following spring. As suggested above, this individual variation
104 in territory establishment might have consequences for song learning, especially given that song
105 sparrows in our population sing throughout the late summer and fall (though at a reduced rate) which
106 means that potentially tutees can overhear singing interactions among territorial adult males as well as
107 directly interact with them.

108 An early establishing male, particularly those establishing territories in the summer (July and
109 August) would likely have more opportunities earlier to interact with their primary tutors, leading
110 potentially to more song learning to them. However such an advantage would only materialize if the
111 primary tutor also survived into the breeding season, given our finding that birds learn (or retain) more
112 songs from tutors that survive the winter (past January 1) than from tutors who do not (Akçay,
113 Campbell, Reed, & Beecher, 2014; Nordby et al., 1999). Depending on the year, about 30 to 40% of the
114 older birds do not survive over winter. Thus, we might expect that the effect of early territory
115 establishment would only be seen in cases where the primary tutor has also survived into the breeding
116 season.

117 In contrast, a late establisher may be at a disadvantage in terms of learning the neighbors'
118 songs. Our earlier studies suggest that in at least some cases, young birds establish their territories late
119 because they have been shut out of the area where they learned songs in their natal summer, as can
120 happen, for example, when none of the tutor-neighbors die over winter (Nordby et al., 1999). In this
121 case the songs the young bird memorized in his natal year will generally be poor matches to the songs of
122 their new neighborhood, leaving the young bird with the alternatives of learning a new set of songs in
123 short order or of just retaining, through selective attrition, the best-matching of his early-memorized
124 songs. Other late establishers may simply have hatched late and will not have heard enough song in
125 their natal summer, in which case they would have to do much of their song learning in the fall or

126 following spring, which might lead to sub-optimal repertoires. A late establisher may have fewer
127 opportunities to engage in direct interactions or overhear interactions between neighboring males, and
128 these are thought to have an important role in the attrition process (Nelson & Marler, 1994). Another
129 potential handicap for late establishers is that even young song sparrows singing non-crystallized song
130 are treated more aggressively by territorial adults in the spring than they are in the fall, and more
131 aggressively in the fall than they are in the summer (Templeton, Campbell, & Beecher, 2012). Moreover,
132 while young song sparrows are seen associating closely with older males in the summer, they are not
133 seen doing so in the spring (Templeton, Reed, et al., 2012).

134 In the present study we analyze a three-year dataset on the timing of territory establishment by
135 young birds in our resident population of song sparrows. In three consecutive years starting with 2009,
136 we banded and recorded young males during the period of their song learning and attempted to track
137 their time of territory establishment through systematic surveys. We then compared their song
138 repertoires to those of all adult males in the population in the bird's first year of life, and attempted to
139 correlate the characteristics of song learning in birds establishing their territories in the natal summer,
140 fall or following spring. We also compared the tutees subsequent survival on territory to test whether
141 early establishing birds were either somehow of better quality and therefore survived for longer on
142 territory. This pattern may be expected if timing in territory establishment is correlated with
143 competitive ability of the young bird as has been proposed for migratory birds (Kokko, 1999). If that is
144 the case earlier establishing birds should survive more years on territory than later establishing birds.
145 Alternatively, establishing your territory early be provide an advantage in itself, which would also lead to
146 early establishing birds surviving longer on territory.

147 **2. METHODS**

148 **2.1. Study site and subjects**

149 This study is part of a long-term study of song sparrows located in Discovery Park, Seattle, Washington,
150 USA, that started in 1986 (Beecher et al., 1994). More information on the specifics of the site can be
151 found in Beecher (2008). This population is resident year-round and males generally defend their
152 territories all year, with the exception of during molting (August) and cold weather periods in
153 November-December, when birds show reduced territoriality (but often are still on their territory).
154 Breeding usually starts in March or April depending on the weather conditions, particularly the El Nino
155 cycle (S. Wilson & Arcese, 2003), although song sparrows start becoming territorial again and singing
156 immediately after the winter solstice when days start to lengthen (G. T. Smith, Brenowitz, Beecher, &
157 Wingfield, 1997). We therefore considered January 1 as the starting point of Spring. Each year between
158 120 and 150 adult males hold territories in the portion of the park under study. Males were caught with
159 mist nets or Potter traps and each male was fitted with a US Fish and Wildlife Service metal band and
160 three color bands for visual identification. Often multiple juveniles were caught in the same net by
161 herding them into the net as a flock (Templeton, Reed, et al., 2012).

162 **2.2 Surveying**

163 During the study, we kept track of the arrival and disappearance of males on territory by visiting
164 territories every two weeks throughout the year, with the exceptions noted above of August (molting)
165 and November and December (inclement weather) when we surveyed the study area opportunistically
166 and banded new birds whenever we could. We used either playbacks or observation of singing males to
167 determine whether a territory holder was still present or had been replaced by a new bird.

168 We counted a bird as territorial if he was observed singing on a territory and approached
169 playback of conspecific song. We took the date of territory establishment of the young bird to be the

170 date of first such observation on a territory if the same area was known to have been held by another
171 bird recently (within a few weeks) and the young bird kept the territory into the spring. In our study site,
172 all suitable areas for song sparrow territories are occupied at any given point in time, and we have rarely
173 observed song sparrows expanding into "no-man's land" areas where there were no song sparrows
174 previously, except for cases where habitat had been significantly changed (e.g. planting or growth of
175 new shrubbery). We classified territory establishment dates into three categories: the summer of the
176 hatch year (before September), fall of hatch year (September to January) and next spring (January to
177 April, the majority of these birds established their territories in January and February).

178 In total we determined territory establishment dates and song learning for 71 young birds who
179 hatched in the years 2009 (n=30), 2010 (n=22) and 2011 (n=19) and established territories in our study
180 site sometime between the summer of their hatch year and the subsequent spring. The majority of the
181 subjects (44 out of 71, 61.9%) were banded either in the summer with juvenile plumage or in the fall
182 with breeding plumage but singing plastic song. The rest of the subjects were banded after January 1st of
183 their second calendar year with breeding plumage but were identified as second year birds from their
184 songs which still showed plastic elements (see Figure 1 for examples of song development at different
185 stages in the first year).

186 We tracked the survival of birds through 2016 by surveying the area as indicated above. Song
187 sparrows don't move significant distances once they establish a territory, moving at most a few
188 territories over (Hughes & Hyman, 2011). We therefore considered birds to have lost territory if they
189 were not observed on their prior territory, any of the nearby territories or anywhere else in our study
190 area, and if their original territory was being defended by another male (Akçay, Campbell, & Beecher,
191 2015).

192 **2.3 Song recording and song learning analyses**

193 We recorded the repertoire of young males and their potential tutors with a digital recorder and a
194 shotgun microphone (Marantz PMD 660 and Sennheiser ME66/K6). We considered the repertoire fully
195 recorded after at least 16 switches in a continuous recording, which has been shown to be a large
196 enough sample to capture the entire repertoire (Nordby et al., 2002). From these recordings we carried
197 out song analyses as in our previous studies (Akçay et al., 2014; Beecher et al., 1994; Nordby et al.,
198 1999). Briefly, we made spectrograms of each song in the repertoire of each tutee and potential tutor
199 using Syrinx (John Burt, www.syrinxpc.com). We considered each adult male that held a territory in June
200 of the tutee's hatch year as a potential tutor. Three judges independently compared the visual match
201 between the songs of the tutee and potential tutors. After this stage, the three judges compared their
202 matches and arrived at a consensus sheet where all judges agreed upon the matches.

203 If a male was implicated as having the sole best match to a tutee song, he was given a score of 1
204 (full credit) for that song. For songs where more than one male was judged to have the best match, the
205 score was split among these males (e.g. if there were two males, each received 0.5, etc.). Split-credit
206 songs like these happen because of high levels of song sharing within neighborhoods in our population
207 (Hill, Campbell, Nordby, Burt, & Beecher, 1999). For about half of the songs, tutorship was shared in this
208 way (46.5% in 2009 cohort; Akçay et al., 2014). For each tutee, the tutor with the highest tutoring score
209 was defined as the primary tutor. For this primary tutor, we noted whether he survived past January 1st
210 of the second calendar year of the tutee.

211 **2.4. Data analyses**

212 From the dates of territory establishment, we classified each tutee as having established a territory in
213 the natal summer, natal fall, or spring (after January 1st of their second year). Our dependent variables
214 were repertoire size, proportion of songs learned from the primary tutor and number of tutors that

215 accounted for the entire repertoire. We analyzed these dependent variables with linear mixed models
216 with territory establishment season, tutor survival into spring and their interaction as the predictor
217 variables and cohort as a random factor. We analyzed survival of the tutees with a general linear mixed
218 model with Poisson distribution and log-link, adding cohort as a random factor and territory
219 establishment season as a fixed factor. The analyses were carried out in R (R Core Team, 2012).

220 **3. RESULTS**

221 Fourteen (15.6%) and 32 (35.6%) of the tutees were first observed to be territorial in the natal summer
222 and fall respectively, while 44 tutees (48.9%) were first observed to be territorial in spring after January
223 1st(11 of these established their territories in March and April while the rest established their territories
224 in January and February). The season in which the tutees established their territory did not have a
225 significant effect on either the proportion of songs learned from the primary tutor, the number of
226 tutors, or the overall repertoire size (Table 1, Figure 2). Whether the primary tutor survived into the first
227 spring of the tutee had a significant effect on proportion of the repertoire this tutor accounted for:
228 tutees whose primary tutors survived past January 1st learned a higher proportion of their repertoire
229 from them than did tutees whose primary tutor did not, and had a smaller number of tutors, replicating
230 earlier findings in our population. There also was no interaction effect of territory establishment season
231 and whether the primary tutor survived into spring. Finally, there was no difference in survival
232 depending on the timing of first territory establishment ($\chi^2=1.70$, $p=0.43$, Figure 3).

233 **4. DISCUSSION**

234 We tested whether the timing of territory establishment has any influence on song learning strategies of
235 male song sparrows. While we replicated our earlier finding that tutor survival into spring increases the
236 tutoring influence of that bird, we found that whether the young bird established his territory in the
237 summer, fall or spring did not affect either proportion of the song repertoire learned from that tutor,

238 the number of tutors or the final repertoire size of the tutee. We also found no support that early
239 establishing birds experienced a fitness benefit in the long-term as survival on territory did not
240 significantly differ between birds establishing their territories in different seasons.

241 **4.1 Timing of Song Learning and Territory Establishment**

242 The fact that timing of territory establishment does not affect these aspects of song learning suggests at
243 least two possibilities. First, at least some birds that establish their territories late may have been
244 present all along. It is hard to detect juvenile song sparrows that are not territorial as they float around
245 and therefore while not territorial, the birds may have been present and listening in on the singing
246 interactions between adults. Given that eavesdropping in such a way is also a potent factor in song
247 learning (Beecher, Burt, O'Loughlen, Templeton, & Campbell, 2007; Templeton, Akçay, Campbell, &
248 Beecher, 2010), this may compensate for the lack of direct interactions with adults that they would have
249 if they were territorial. Relatedly, young song sparrows may be able to memorize a great number of
250 songs from many males during their floater period, such that even late-establishing birds are still able to
251 produce the songs of an older bird that becomes a primary tutor (instead of trying to reach a repertoire
252 that is composed of a single or few songs from many tutors). Radio-tracking studies of young birds in our
253 study population show that they sometimes cover a large amount of ground (Templeton, Reed, et al.,
254 2012), and during these movements they are likely to overhear many adults singing. Given laboratory
255 studies that failed to detect an upper limit in recognition memory for songs in song sparrows (Stoddard,
256 Beecher, Loesche, & Campbell, 1992), it is plausible that a bird is able to memorize a very large number
257 of songs during this floater phase. This hypothesis predicts that late establishers would be initially
258 singing larger repertoires which they would then winnow down to a repertoire that matches their
259 primary tutor and other neighbors. Note that this strategy of memorization and production of a large
260 repertoire may lead to a cost in terms of the quality of learning. For instance in Puget-Sound white-
261 crowned sparrows (*Zonotrichia leucophrys pugetensis*), young birds that sang large repertoires (e.g. 4

262 songs) imitated the local songs more poorly than young birds that sang the species-typical repertoire
263 size of a single song (Nelson & Poesel, 2014). Although we did not quantify the match between the tutee
264 and tutor version of the songs, it is possible that late establishers may match their primary tutor songs
265 less well compared to early establishers.

266 A second, non-exclusive possibility is that song sparrows can memorize new songs until at least
267 the time they establish their territories, whenever this happens. Estimates of the timing of
268 memorization phase comes from laboratory studies of hand-raised birds, typically tutored with recorded
269 songs played from speakers—the so-called “tape tutors” (Marler & Peters, 1987, 1988). Under more
270 naturalistic conditions involving either live birds or song presentation that represent naturalistic bouts of
271 singing, these estimates have proven to significantly underestimate the period of song memorization
272 which often extends into the first spring of the birds (Baptista & Petrinovich, 1984; Kroodsma & Pickert,
273 1980, 1984; Nordby et al., 2001; Nulty et al., 2010; Templeton, Burt, et al., 2012). Furthermore as
274 discussed above there is evidence that the memorization phase in some species, like marsh wrens and
275 white-crowned sparrows show flexibility with respect to hatching date and the presence of live tutors
276 (Baptista & Petrinovich, 1984, 1986; Kroodsma & Pickert, 1980, 1984; Petrinovich & Baptista, 1987).
277 Presumably, interactions with live tutors in the lab simulate territorial interactions in the field.
278 Therefore, the finding of flexibility in memorization phase suggests that the sensitive period for song
279 memorization would close in the summer for birds establishing at that time and close the following
280 spring for birds establishing at that time.

281 **4.2. Song learning in sedentary and migratory populations**

282 Our population of song sparrows are sedentary with birds singing year-round. This may result in the
283 evolution of a memorization phase that is longer. The situation would be different for migratory birds
284 which often travel to a wintering ground where they either don't hear conspecific song, or hear songs

285 that are not local to the areas to which they will return next spring. Thus, memorization of songs during
286 the first winter may not be adaptive, and birds should ignore or avoid memorizing these songs.
287 Nevertheless, song memorization phase might reopen the next spring. Some evidence on this point
288 comes from the previously-mentioned study of marsh wrens (Kroodsma and Pickert, 1980; 1984) and a
289 study of chaffinches (Thielcke & Krome, 1991). In the chaffinch study, the authors tutored juvenile birds
290 caught in late summer and early Fall with one song in the fall and winter and another song in the next
291 spring. Despite the fact that the birds had significant song exposure in the field before being caught,
292 they nevertheless learned the spring song from tape tutors. None of the birds copied the fall song
293 however, suggesting that chaffinches may be insensitive to song presented in this period. The Nulty et
294 al. study (2010) cited earlier also found evidence in our population that tutors that were heard in
295 summer and fall were less effective tutors compared to tutors heard in summer and spring, suggesting
296 that song sparrows too may be insensitive to fall song.

297 Although our population is sedentary, some nearby populations of song sparrows display
298 altitudinal migratory strategies in which the birds migrate from their high-altitude, snow covered
299 breeding grounds to lower altitudes where they would hear sedentary song sparrows singing that are
300 not necessarily local to their population. In a study of one such population Hill et al. (1999) found that
301 levels of song sharing was high and not different than the sedentary population that we studied here,
302 suggesting that song learning programs are not likely to be different in this migratory population. Given
303 that final territories in this population are not established until next spring, this suggest that
304 memorization phase either stays open throughout fall and spring or reopens in the spring. To distinguish
305 these possibilities, a common garden experiment comparing the memorization of songs presented in
306 different seasons to birds from these sedentary and migratory populations would be required.

307 **4.3. Timing of territory establishment and fitness**

308 We found no evidence that early establishing males experienced a long-term fitness benefit compared
309 to later establishing males. Given that in our population, almost all areas that is suitable for song
310 sparrows is occupied, the variation in timing of territory establishment is likely to be due to opening of
311 vacancies due to the disappearance of a prior territory owner or the presence of a large territory that
312 may be split into two territories enough to support two song sparrow pairs. The latter cases may arise
313 over spring: later in the spring, when breeding is ongoing, birds who are depredated often are not
314 replaced by new arrivals but their territories are taken over by their existing neighbors (Akçay et al.,
315 2012). This fact means by summer time, there are often territories that used to hold two territories but
316 are now defended by a single song sparrow, and juveniles may be able to insert themselves into these
317 territories more easily.

318 Most studies on timing of territorial behavior and subsequent fitness effects has been on
319 migratory species which arrive at their breeding territories from somewhere else (Brooke, 1979; Francis
320 & Cooke, 1986; Kokko, 1999; Lozano, Perreault, & Lemon, 1996). Variation in timing of territory
321 establishment has been studied in year-round resident species less often (Dixon, 1956; Matthysen,
322 1989). In one such study, Matthysen (1989) did not detect any differences in fitness (in terms of survival)
323 and eventual territory quality between early- and late-establishing males in the year round resident
324 European nuthatches (*Sitta europea*), consistent with our present findings.

325 Variation in the timing of territory establishment has been studied in a partially migratory
326 population of eastern song sparrows in rural Pennsylvania (Hughes & Hyman, 2011). In this population,
327 some males established their territories early in the Spring while about ¼ of males established territories
328 later (after the first nest has hatched). Hughes and Hyman (2011) found that timing of first-time territory
329 establishment did not relate to fitness in terms of survival. Indeed, late establishing males who

330 subsequently moved to a different, non-overlapping territory had the highest reproductive success in
331 terms of number of nests and young fledged. These results too suggest that late establishing males do
332 not necessarily consist of low-quality individuals, consistent with the present results.

333 **4.4 Conclusions**

334 In conclusion, in a large multi-year dataset we found no effect of timing of territory establishment on
335 song learning strategies as exemplified by the three main parameters that vary across individual song
336 sparrows: proportion of repertoire learned from the primary tutor, repertoire size and how many tutors
337 the tutee learned his songs from. These results indicate that song sparrows are able to match the songs
338 of their neighbors even if they establish their territories late, suggesting a versatile learning program
339 either due to a longer memorization phase, a large number of songs memorized or practicing singing
340 while not being territorial. We also found no evidence that late establishing males suffer a fitness cost,
341 consistent with earlier findings in year-round resident species. Future research can experimentally
342 manipulate song experience of birds in the field in realistic ways (e.g. Mennill et al., 2018) while keeping
343 track of their individual histories to dissociate the different hypotheses regarding how birds can
344 adaptively shape their learned song repertoire and territorial strategies.

345

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489 **Table 1.** The results of linear mixed models with tutee territory establishment season, primary tutor's
490 survival into the first spring of the tutee and their interaction as fixed factors and cohort as a random
491 factor. The reported values are χ^2 values and the associated p-values from Wald tests.

	Proportion learned from primary tutor	Repertoire size	Number of tutors
Season of territory establishment	0.08 (0.96)	1.22 (0.54)	1.86 (0.39)
Primary tutor's survival into January	4.70 (0.026)	0.31 (0.58)	1.77 (0.18)
Interaction	0.34 (0.84)	0.04 (0.97)	1.19 (0.55)

492

493

494 **Figure Captions:**

495 Figure 1. Examples of song development in summer (top row), fall (middle row) and spring (bottom two
496 rows). The songs in panel a were recorded from a single male (hcmh) who was observed to be territorial
497 starting in late July, a few weeks after being banded in juvenile plumage. The two example songs in each
498 row were recorded in the same recording session on the indicated date and are meant to give the
499 reader a sense of the range in development of the songs. Note that by fall this bird had a rather well
500 developed repertoire in which song types could be distinguished although the songs still plastic as can
501 be seen by the non-consistent repetition of intro notes and the trill notes. By January, the bird sang
502 fairly crystallized songs where notes were repeated with high consistency and the overall song structure
503 did not vary from one rendition to the next (although occasionally he would sing plastic song). The two
504 songs in panel b were recorded from a different male (pgmy), also banded in the preceding July, but not
505 seen to be territorial until January. Note that the songs of this male are more plastic at this stage than
506 hcmh as indicated by the non-consistent repetition of the elements within and across song renditions.

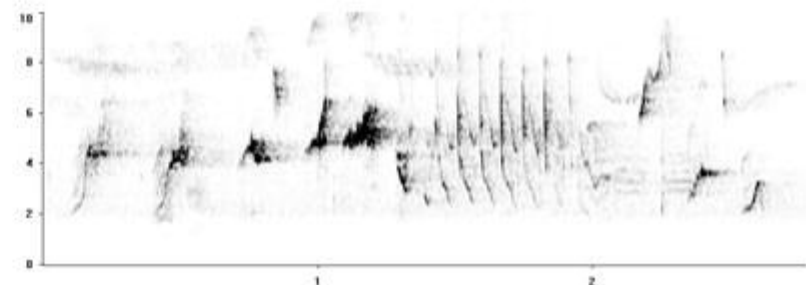
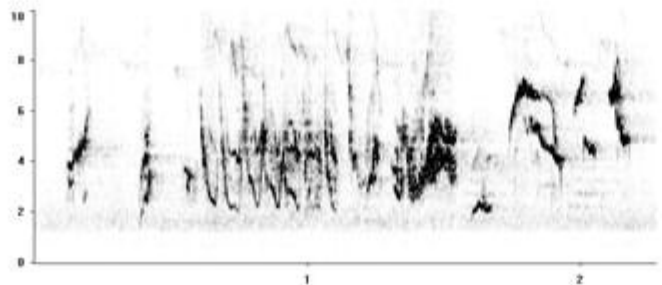
507 Figure 2. Proportion of songs learned from the primary tutor (a), repertoire size (b) and number of
508 tutors tutees had (c) depending on territory establishment date and whether the primary tutor survived
509 into the first spring of the tutee (white= tutor did not survive, gray= tutor survived).

510 Figure 3. Number of years survived on territory depending on the timing of territory establishment.

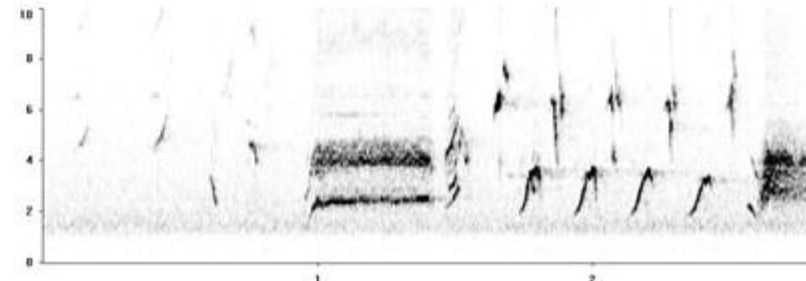
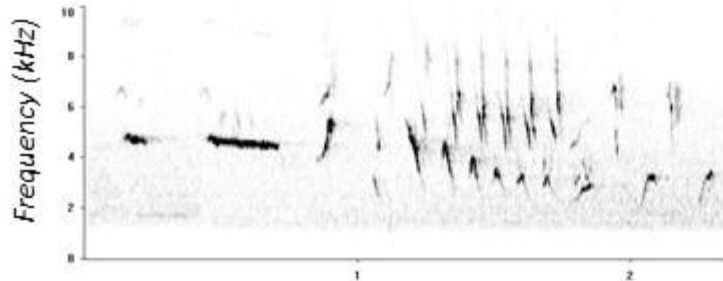
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a- hcmh

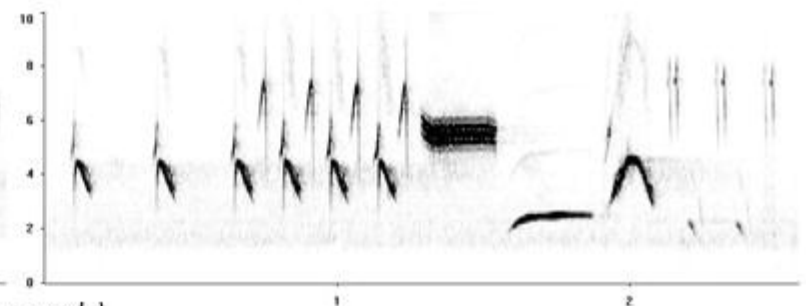
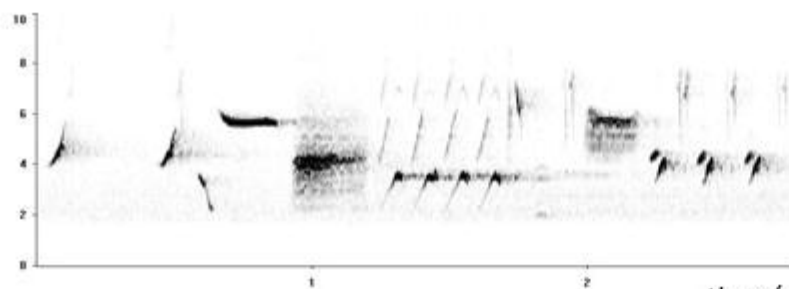
18 August
2009



16 September
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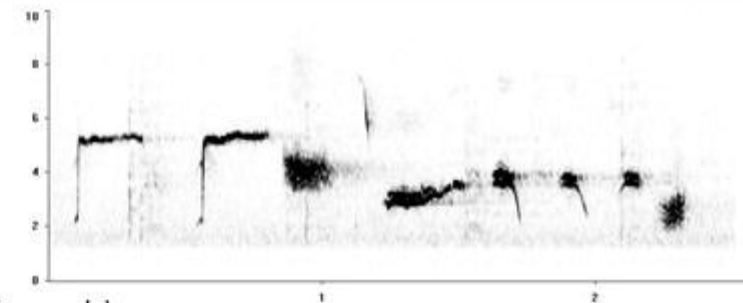
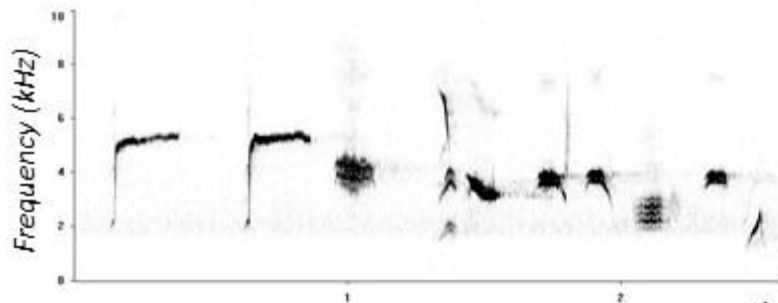
3 January
2010



time (seconds)

b- pgmy

29 January
2010



time (seconds)

