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Male's return rate, rather than territory fidelity and breeding dispersal, explains geographic variation in song sharing in two populations of an oscine passerine (*Oreothlypis celata*)

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Abstract Males of some oscine passerines learn and share songs of neighboring males. This process can lead to the formation of song pattern neighborhoods or microhabitat song dialects. The degree to which song sharing occurs between populations and the spatial scale over which neighboring males share songs, however, can vary widely, and interpopulation comparisons have suggested that song sharing is more common in residents than in migrants. Here, we examine two populations of the orange-crowned warbler (*Oreothlypis celata*) to quantify patterns of song sharing at the northern (long-distance migrant) and southern (short-distance migrant) edges of the breeding distribution and to test if return rate, territory fidelity, and breeding dispersal explain the patterns found in the two populations. The southern population (*O. celata sordida* breeding on Santa Catalina Island, California; 33°N) had a higher annual return rate to their territories and exhibited higher song sharing in neighborhoods than their counterparts (*O. celata celata* breeding in Fairbanks, Alaska; 64°N). Year-to-year patterns of territory fidelity and breeding dispersal distances were similar between populations. Our results suggest that if migratory distance generally covaries with the proportion of returning males, this could explain different levels of song sharing between the short- and long-distance migrants.

Keywords Breeding dispersal · Geographic variation · Migratory behavior · Return rate · Song sharing · Territory fidelity

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Introduction

Songs of oscine passerines are used as a primary communication tool in social interactions and can be shared among neighboring males (Kroodsma and Miller 1996; Catchpole and Slater 2008). Song copying and sharing appear to be beneficial for acquiring territories near resident males (Payne 1981, 1982; Rohwer 1982) or for advertizing the quality and/or competitive ability of territory holders (Vehrencamp 2001; Wilson and Vehrencamp 2001). Males learn and share songs of individuals that they interact with socially, and such cultural transmission can lead to the maintenance of song components in an area for multiple generations (Goodale and Podos 2010). However, the processes of song learning in relation to spatial patterns of song sharing both vary between populations and species, leading to calls for more comparative studies (Beecher and Brenowitz 2005). Several hypotheses, reviewed by Slater (1989), have been proposed to explain how migratory behavior, breeding phenology, and/or competition on acoustic

communication could explain geographic variation in the patterns of song sharing among territorial males.

Resident populations or species tend to exhibit more song sharing than migrants (Kroodsma 1996; Kroodsma et al. 1999). For example, male rufous-sided towhees (*Pipilo erythrophthalmus*) in a resident Florida population exhibited more shared song types with immediate neighbors compared to a migratory population in New York (Ewert and Kroodsma 1994). However, comparisons of resident and migratory song sparrows (*Melospiza melodia*) from western and eastern North America suggest that migratory behavior alone may not predict the extent of song sharing between geographically separated subspecies (Hill et al. 1999). Handley and Nelson (2005) found that within the family Fringillidae, sedentary populations breeding at lower latitudes and with longer breeding seasons were more likely to exhibit a higher degree of song sharing compared to their migratory counterparts. Yet, sedentary populations may also be at higher densities (e.g., Hill et al. 1999), such that males may exhibit more song sharing because of the benefits for territory acquisition in more competitive environments. The relative lack of comparative studies on song sharing and potential covariation between multiple environmental factors, such as migratory behavior, duration of the breeding season, and latitude (e.g., Handley and Nelson 2005), has left unresolved the causes of geographic variation in the extent of song sharing.

The orange-crowned warbler (*Oreothlypis celata*) is a territorial and socially monogamous New World warbler, and its breeding range includes four subspecies (*O. celata celata*, *O. celata orestera*, *O. celata lutescens*, and *O. celata sordida*) that cover the western and northern parts of North America (Gilbert et al. 2010). The subspecies *O. celata celata* is a long-distance migrant with a breeding range that extends from central Alaska, throughout boreal Canada, to the northeastern USA; it winters along the Gulf Coast of the USA and northern Mexico (Gilbert et al. 2010). In contrast, *O. celata sordida* has a breeding range largely confined to the California Channel Islands, and most make a short-distance migration to spend the nonbreeding season in the adjacent mainland (Gilbert et al. 2010). Such life history differences lead to the prediction that the California population should exhibit more song sharing solely due to variation in migratory behavior, yet little is known about geographic variation in orange-crowned warbler song. Gilbert (1986) reports personal observations describing the vocal characteristics of a population of *O. celata lutescens* breeding in central and inner-coastal California (37°N). He noted that individually marked males commonly had one song type and were closed-ended song learners that did not modify selected songs during their lifetime. He also found that adjacent males often formed "song pattern neighborhoods," where one song type was shared by several neighboring males and persisted in one area for nearly a decade. The lack of studies examining interpopulation variation in song sharing motivated

us to pursue the generality of these observations between the populations breeding in Alaska and California.

The objectives of this study were to examine if patterns of song sharing among neighboring territory holders differed between the Alaska and California populations and to determine if return rate and breeding dispersal distance (movements involving a change of territory between years) could explain geographic variation in song sharing. Because population differences could alter the number of song tutors, the process of song learning, and the benefits of song sharing, we also examined how these variables explained patterns of song sharing in Alaska and California. Specifically, we tested three hypotheses: (1) short-distance migration is associated with a high annual return rate (see below), resulting in relatively high song sharing compared to long-distance migrants with low return rates; (2) territory fidelity predicts song sharing, with low song sharing expected in a population with low territory fidelity; and (3) breeding dispersal explains song sharing, resulting in low song sharing in a population with relatively large breeding dispersal distances.

Methods

Study areas and populations

We studied song sharing in two populations of orange-crowned warblers breeding at the northern and southern edges of their breeding distribution. The study site for *O. celata celata* was located near Fairbanks, Alaska (64°47′41″N, 147°53′45″W); habitat was dominated by spruce (*Picea* spp.), birch (*Betula* spp.), and willow (*Salix* spp.). The study site for *O. celata sordida* was located in Bulrush Canyon on Santa Catalina Island, one of the California Channel Islands (33°20′56″N, 118°26′59″W), which was characterized by oak (*Quercus* spp.)-dominated habitat. Our previous studies suggested that the two populations had distinct life histories and were exposed to very different ecological conditions (Horton et al. 2010; Yoon et al. 2012; Sofaer et al. 2013): the annual survival rate (proportion of males) was higher in California warblers (65±2 %) than in Alaska warblers (40±16 %), breeding density was higher in the California population (3.42–5.28 territories/ha) than in the Alaska population (0.46–0.49 territories/ha), and breeding season length was shorter in Alaska (50–60 days, mid-May to early July) compared to California (100–120 days, late February to mid-May).

Male territory fidelity, return rate, and breeding dispersal

We applied standard methods for mapping territories by marking and tracking individuals and by monitoring active nests and measuring the patterns of return rate and territory settlement in both study plots. The area of the study plot

required to monitor a similar number of territories was larger in Alaska (88 ha) than in California (14 ha) due to the differences in breeding density and territory size. The difference in study plots likely increased the detection probability of returning males that moved off their breeding territories within and between years in the Alaska population. Like other warblers, males exhibited high territory fidelity, but some breeding dispersal did occur in consecutive seasons in the two populations. We measured breeding dispersal behavior (the distance between the territories of the same male that did not exhibit territory fidelity between years) of returning males in both study sites. Warblers in both study plots were captured with mist nets, individually banded with a unique combination of three-color leg bands and a U.S. Geological Survey aluminum leg band, then classified by sex and age based on plumage and morphological characters as described by Pyle (1997). We mapped all territories in the Alaska (2006–2008) and California (2003–2009) study areas. All territory boundaries were determined by observing territorial disputes and movements of banded males and females throughout the season (from 4:00 a.m. to 12:00 p.m. AKDT in Alaska and from 6:00 a.m. to 12:00 p.m. PDT in California). To facilitate individual identification and territory mapping, our study plots were divided into 25×25-m grids with flagging, which were recorded in ArcGIS version 9.1 (ESRI Inc., 2005, Redlands, CA). We recorded locations (waypoints) of banded individuals using a GPS unit and also marked the locations of individual warblers on an aerial photograph marked with waypoints of grid locations, which all were then transferred and updated in ArcGIS once every 2 weeks. Final territory boundaries were determined using a minimum convex polygon (Ford and Myers 1981) in ArcGIS.

The multiple-year list of territorial males and territory maps allowed us to summarize each returning male's year-to-year breeding dispersal behavior and to create an adjusted neighborhood scale for song-sharing analysis using a nearest neighbor distance (NND). First, we calculated mean NND for each population, using territory maps in ArcGIS with the extension of Hawth's Analysis Tools (Beyer 2004). Mean NND was significantly greater in the Alaska population (92.6 ± 3.5 m, 2007–2008) than in the California population (33.3 ± 0.7 m, 2003–2009; two-tailed t test: $t_{101.3}=16.60$, $P<0.001$). Second, to measure the distance of breeding dispersal between the two populations, we defined territory fidelity as when the distance between the centers of a territory in 1 year and a territory of the same male in the following year being shorter than the average of NND (hereafter 1NND). Third, this circular area with the radius of 1NND that intercepted an immediate neighbor's territory was also used for analyzing song sharing in neighborhoods (see below). Based on this standardized scale, the adjusted number of territories neighboring from a target territory did not differ between the two populations (1.52 ± 0.16 territories/male in
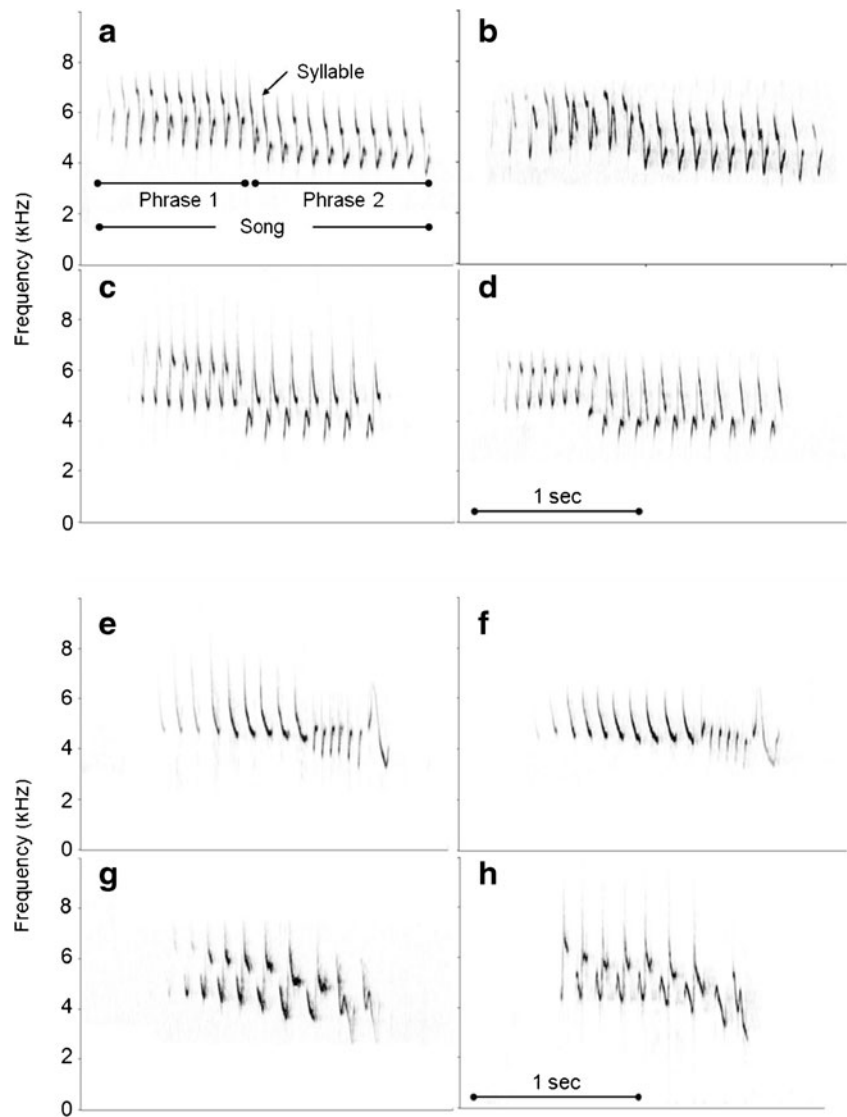
Alaska vs. 1.69 ± 0.15 territories/male in California; two-tailed t test: $t_{154}=-0.79$, $P=0.43$).

Song recordings and song type classification

We recorded songs of 30–40 focal males per study site during two breeding seasons (2007–2008) to obtain a catalogue of song types in relation to males and locations of their territories. Individual male's songs were recorded for 2–5 min (approximately 10 songs/individual, two to three times per season) at a distance range of 5–10 m between the microphone and the male, using a MiniDisc recorder (Sony MZ-NH1) with a Dan Gibson Electronic Parabolic Microphone (P-650). We saved songs in an uncompressed format (PCM format, 16 bits at 44.1 kHz) to minimize loss of high-frequency sounds and converted them to the Waveform Audio File Format (.wav) using a digital sound program (Sonic Stage version 4.0, Sony Inc.). While some high-frequency sounds may have been lost during this process, the same approach was used in both study sites. The recording period was limited to 4:00 a.m.–8:00 a.m. AKDT in Alaska and 7:00 a.m.–11:00 a.m. PDT in California. We recorded songs from 66 males in Alaska (36 males in 2007, 30 males in 2008) and 90 males in California (46 males in 2007, 44 males in 2008).

Individual song types in spectrograms (FFT size, 512; window type, Blackman) were visualized using the program Syrinx (John Burt, http://www.syrinxpc.com/index.html), and the identified song types were assigned to territories in ArcGIS. Males sang slightly different songs between the two populations: Alaska males sang a thin, fast trill, and California males sang a slower, lower-pitched trill (Fig. 1). Orange-crowned warblers have only one song type that is usually sung with little variation, which makes the classification of song types relatively easy. Moreover, the fact that males do not have a repertoire of several song types is also advantageous when measuring song sharing between individuals (Koetz et al. 2007). We used a visual examination of spectrograms of individual songs to calculate the degree of song sharing while keeping the spatial proximity of songs unknown (see Fig. 1 for examples). Our song sharing criteria were adapted from Beecher et al. (2000). A complete song that contained syllables in two phrases from an individual was considered to be an individual song type. Male orange-crowned warblers used a single song type within seasons and did not change their song types between seasons in both Alaska ($n=9$ males) and California ($n=18$ males, see also Gilbert et al. 2010). Deletion or addition of the same syllables within phrases was not considered to be different. We could not determine the frequency of addition or deletion of syllables within and between individuals because the number of syllables in song spectrograms was visually variable, depending upon the level of attenuation of song amplitude in the starting and ending phrases. Two songs from different

Fig. 1 Examples of shared song types in both phrases between male orange-crowned warblers breeding in Fairbanks, Alaska [*O. celata celata*: (*A*) shared with (*B*), (*C*) shared with (*D*)] and on Santa Catalina Island, California [*O. celata sordida*: (*E*) shared with (*F*), (*G*) shared with (*H*)]. The term "syllable" is used to refer to the smallest temporal unit of sound in a song. The group of syllables refers to the term "phrase." One song contains two phrases

males were considered to be shared if at least one phrase of a song type (i.e., the majority of song types with two phrases) was shared. To determine the degree of song sharing, one observer (J. Yoon) first generated and classified song spectrograms and then three judges (H. J. Yoon, E. J. Joo, and J. S. Jung), who were uninformed about the hypotheses being tested, scored all individual song types for the degree of sharing. A Cronbach's alpha test (Cronbach 1951) of interobserver reliability yielded a high score for classification agreement (AK=0.81, CA=0.87), indicating that song types were being classified according to the same criteria.

Ring buffer analysis

We examined the proportion of song sharing as a function of neighborhood distance through a ring buffer analysis (i.e., song sharing with a target male's song in four ringed zones defined by their proximity to the target male's territory). We used a standardized scale for territory distances because breeding density and territory size differed between Alaska and California. To measure the percentage of song sharing of a target territory over the distance to other territories, we generated four ring buffer areas from the center of a target territory in ArcGIS (Fig. 2), with a mean buffer width of 93 m in Alaska vs. 33 m in California. For example, the four circular zones (1NND, 2NND, 3NND, and 4NND) in Alaska covered an area within 93, 93–186, 186–279, and 279–372 m, from the center of a target territory. These ring buffers intercepted adjacent territories in a series of concentric rings. Individual song types that intercepted each ring buffer zone were compared to the song type of target males to assess the proportion of song sharing between each target male and his neighbors (see Fig. 2 for a calculation example for proportional song sharing).
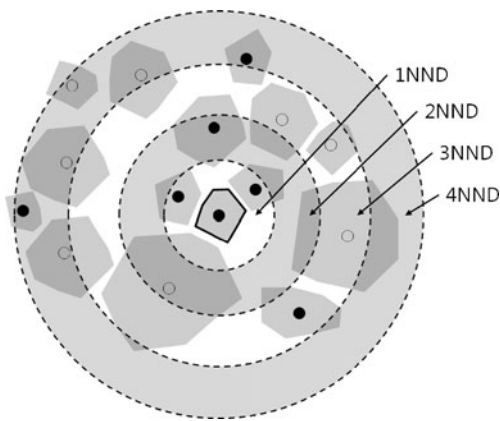
Fig. 2 A visual representation of the spatial scale over which song sharing was calculated. The proportion of song sharing (i.e., the number of territories with shared songs/total number of territories) over four ring buffer areas, which were determined by averaged nearest neighbor distance, NND, from a target male. *Gray polygons* indicate individual territories. Centers of territories show a *filled* (song shared with the target male) or *unfilled circle* (song unshared)

Statistical analyses

The means of return rate, uncorrected for detection probability, territory fidelity, and breeding dispersal distance between the two populations were compared using a two-tailed *t* test. A generalized linear mixed model with a Poisson error distribution (PROC GLIMMIX of SAS 9.2, SAS Institute Inc.) was used to analyze song sharing in neighborhoods as a function of site (Alaska vs. California), four neighborhood distances (1NND, 2NND, 3NND, and 4NND), and the two-way interaction (distance × site). In the model, each territory number (i.e., male) was also treated as a random effect because of repeated sampling of the song-sharing percentage over distance per territory. We then conducted a second mixed model without the site effect to analyze the relationship between song sharing and territory proximity. We did not need to transform any variables to meet model assumptions. All means are presented with±1 standard error (SE).

Results

Male's return rate, territory fidelity, and breeding dispersal

We found the return rate differed between the two populations, but territory fidelity and breeding dispersal did not. The between-season return rate in Alaska was 44.1±5.9 % ($n=26$ male over 2 years, 2006–2008) and was significantly lower than that of California (66.7±1.8 %; $n=113$ males over 6 years, 2003–2009) (*t* test: $t_6=-5.29$, $P<0.01$). Territory fidelity for returning males from the previous season, estimated as the percentage of males in which the distance between territory centers of two consecutive seasons was within the area

of 1NND, did not significantly differ between the two populations (*t* test: $t_{33.6}=-1.56$, $P=0.13$). Mean breeding dispersal distances were 98.8±15.7 m (range=8.0−360.7 m) in Alaska and 24.9±2.7 m (range=0.9−223.4 m) in California, which were near the range of 1NND of 93 m in Alaska and 33 m in California, respectively. Thus, year-to-year breeding dispersal in the two populations occurred at approximately the territory scale when adjusted by local breeding density and territory size.

Song-sharing patterns

Song sharing differed between the populations. We identified 25 song types in the Alaska population and 21 song types in the California population. The proportion of song sharing for the California population (28.6±2.1 %) was significantly higher than that for the Alaska population (7.9±2.5 %) (Poisson mixed model: site $F_{1, 422}=7.00$, $P<0.01$; distance $F_{1, 422}=0.95$, $P=0.33$; distance × site $F_{1, 422}=0.46$, $P=0.50$; Fig. 3). Within each population, the percentage of song sharing per territory did not change with territory proximity (i.e., four ring buffer zones) in the Alaska population (Poisson mixed model: distance $F_{1, 175}=0.03$, $P=0.87$), but it marginally declined with territory proximity in the California population (distance $F_{1, 247}=4.34$, $P=0.04$; Fig. 3).

Discussion

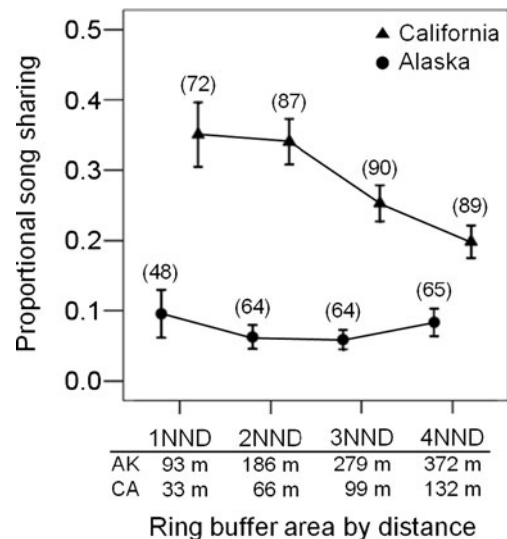Past research has shown that residents have greater song sharing compared to migrants (e.g., Ewert and Kroodsma 1994;

Fig. 3 Level and spatial patterns of song sharing of male orange-crowned warblers breeding in Fairbanks, Alaska and on Santa Catalina Island, California, 2007–2008. The percentage of song sharing for each male was measured in the four different ring buffer zones using the average of nearest neighbor distance (1NND) in the Alaska (i.e., mean=93 m) and California (i.e., mean=33 m) populations. *Error bars* denote means±1 SE with samples sizes

Kroodsma 1996; Kroodsma et al. 1999; Handley and Nelson 2005), but the degree to which return rates, territory fidelity, breeding dispersal, and other ecological or social factors correlated with migratory distance could influence song sharing has been largely unstudied. Here, we compared the patterns of song sharing in two populations of *O. celata* at the northern and southern latitudinal edges of their breeding distributions (i.e., *O. celata celata* at 67°N vs. *O. celata sordida* at 33°N) and found the predicted pattern of reduced song sharing in the long-distance migratory population in Alaska (7.9 %) compared to the short-distance migratory population in California (28.6 %). Furthermore, the California population showed a clear spatial pattern, with the degree of song sharing declining as a function of distance (Fig. 3). However, the differences in migratory behavior between these populations were also correlated with the return rate of territorial males, where the California population exhibited significantly higher return rates than the Alaska population. High return rates are likely to facilitate song sharing because more stable neighborhoods are formed and young birds can settle near song tutors. Other factors that could influence within and between year stability of song neighborhoods such as territory fidelity and breeding dispersal did not differ between the populations.

The relationship between annual return rate, a proxy for annual survival probability, and migration distance raises new questions regarding the web of interacting factors underlying patterns of song sharing between neighboring males. Mortality in small migratory passerines appears to be concentrated during the migratory period (e.g., Sillett and Holmes 2002). This implies that annual survival should be greater in sedentary populations of the same species and suggests a mechanism for song sharing between neighbors (see Wilson et al. 2000): males that live longer and stay on their territories are able to influence other male's songs and/or repertoires by tutoring more of their own songs (Nordby et al. 1999). In contrast, when survival rates are low and high turnover exists for territory holders between years, such as we observed in our Alaska population, the probability of males learning and sharing songs from established tutors declines, and neighborhoods where adjacent males have similar songs fail to form. Our finding leads to general prediction that in populations with high survival rates and high stability of territory holders, we should observe greater song sharing and a greater spatial structuring of song pattern neighborhoods. This prediction assumes that a specific song type possessed by a territorial male remains fixed over multiple seasons. Moreover, the male should have a song that can be culturally transmitted to new breeders and could provide those males on nearby territories with a fitness-related advantage (Payne 1981; Rohwer 1982). In support of this prediction, we found that the level of song sharing increased with proximity between territories in the California population,

but not in the Alaska population (Fig. 3). This spatial pattern suggests that young males learn songs from song tutors on nearby territories in the relatively long-lived California population or, alternatively, that adult males are extending their sensitive period of song learning and incorporating specific song elements from nearby males (Gilbert et al. 2010).

Social interactions between territorial males are thought to be important in the development of song repertoire for young males (Nordby et al. 2000). For example, song sparrows tend to approach more frequently to simulated counter-singing than to simulated solo singing, suggesting that vocal interactions among adults might provide a better song-tutoring opportunity for young birds in neighborhoods (Templeton et al. 2010). Thus, spring tutoring, when males are most active in territory establishment and mate attraction, is likely more effective to the development of a final repertoire than the period of autumn tutoring (Nulty et al. 2010). In California, new male orange-crowned warblers were rarely born on the territories they later claimed, based on our multiple-year banding of nestlings and observations of banded individuals. Instead, nonterritorial males (i.e., floaters) were frequently caught in resident male territories, and these males later became resident males of those vacated territories in subsequent years (J. Yoon, personal observation), which might support song learning from established territory holders. Unfortunately, our study could not determine if nonterritorial males shared songs with resident males because these floaters rarely vocalized.

Comparative studies, like ours, provide opportunities to explore how patterns of song sharing change in relation to numerous potentially interconnected factors such as life histories, migratory behavior, and dispersal that can influence the process by which songs are learned. However, we acknowledge that because our study represents only a single contrast between an island population and a high latitude population, the results may not be broadly representative. First, the vocal traits of insular birds can be complicated by island-related factors (e.g., founder effect, sexual selection, and/or conspecific competition) compared to those of mainland birds (Baker et al. 2006; Baker 2012). Second, song-learning strategies of males breeding at high latitudes are likely to differ from those of their counterparts at low latitudes (Nelson et al. 2001). Specifically, shorter breeding seasons at high latitudes may limit the amount of time available for song learning relative to birds breeding at lower latitudes (Handley and Nelson 2005). Further, comparative study of song sharing between migrants and residents, short-lived and long-lived populations, and species breeding at high vs. low latitudes could provide key insights into which environmental factors are most correlated with the formation of song neighborhoods. Furthermore, we need intensive studies of the process by which young birds in natural populations learn their songs.

Ethical standards The present study involved marking individual warblers, mapping their territory boundaries, and song recording of breeding males. All research was conducted under ASAB/ABS guidelines and approved by the Institutional Animal Care and Use Committee of Colorado State University (08-342A-01).

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