

Original Article

# Spatial movements and social networks in juvenile male song sparrows

Christopher N. Templeton,<sup>a</sup> Veronica A. Reed,<sup>a</sup> S. Elizabeth Campbell,<sup>b</sup> and Michael D. Beecher<sup>a,b</sup>

<sup>a</sup>Department of Biology, University of Washington, Seattle, WA 98195-1800, USA and <sup>b</sup>Department of Psychology, University of Washington, Seattle, WA 98195-1525, USA

The time between fledging and breeding is a critical period in songbird ontogeny, but the behavior of young songbirds in the wild is relatively unstudied. The types of social relationships juveniles form with other individuals can provide insight into the process through which they learn complex behaviors crucial for survival, territory establishment, and mate attraction. We used radio telemetry to observe social associations of young male song sparrows (*Melospiza melodia*) from May to November. Juvenile song sparrows were frequently observed in social flocks and generally associated with more birds in the summer than in the autumn months. Most juvenile subjects formed stable social relationships with other birds and were seen with the same individual on up to 60% of the days observed. The strongest associations occurred with other juvenile males, and these individuals were often seen <1 m from the subject, even when the subject moved large distances between tracking observations. Associations also had long-term behavioral consequences as subjects were more likely to establish territories near their associates and learn shared song types. Our results indicate that male song sparrows spend a large percentage of the juvenile life stage forming social relationships and suggest that these associations may be important for the ecology of young birds and the ontogeny of their behaviors. [*Behav Ecol* 23:141–152 (2012)]

## INTRODUCTION

The juvenile life stage is a formative and perilous time for young animals. Juveniles must learn to navigate complex environments, find suitable breeding territories and mates, and develop the behaviors necessary for maintaining social relationships with breeding partners or social groups (Slater 1983; Pearce 2008). At the same time, juveniles can face tremendous challenges in finding food and often must also learn to avoid predators (Caro 2005).

In addition to these challenges, juvenile songbirds (males only in most temperate zone species) must also learn their song repertoires in this period. Song learning is often concentrated at the beginning of the juvenile life stage but can last throughout the juvenile period (typically, the first year of life in most temperate songbirds) (Catchpole and Slater 2008). Learning appropriate and well-formed songs are critical for establishing a territory or attracting a mate (Catchpole and Slater 2008), and the quality of a male's songs may be a good indicator of his ability to divert resources into brain development while still finding food and avoiding predators (Nowicki, Searcy, and Peters 2002; MacDonald et al. 2006). Songbird fledglings face extremely high rates of predation, with only a small fraction of individuals surviving to breed in their first year (Snow 1958; Sullivan 1989; Naef-Daenzer et al. 2001; Arcese et al. 2002). Juvenile songbirds typically have drab plumage and are generally behaviorally inconspicuous as well, presumably to reduce the chances of predation (Graber 1955), though dull plumage may also help juveniles avoid confrontations

with territorial adults (Rohwer et al. 1980; Ligon and Hill 2009; Templeton CN, Campbell SE, Beecher MD, manuscript in review). Although these adaptations may help minimize predation, they also make observing juvenile birds extremely difficult in the wild. Thus, despite the importance of songbirds as model systems in behavior and ecology, very little is known about what takes place during their less conspicuous juvenile life stage (between fledging and the first breeding season). This is precisely the stage when many key behaviors develop, and thus, understanding more about juvenile ontogeny is critical for our understanding of adult behaviors (West et al. 2003).

Recent miniaturization of radio transmitter technology (Naef-Daenzer et al. 2005) has made it possible to track even relatively small birds. With this technology, it is now feasible to intensively study juvenile songbirds, even when they remain inconspicuous and lack site fidelity. Numerous recent studies have capitalized on this technology and used radio telemetry to study dispersal, spatial movements, and survival in songbirds during the postfledging period (Anders et al. 1998; Adams et al. 2001; Naef-Daenzer et al. 2001; Cohen and Lindell 2004; Kershner et al. 2004; White et al. 2005; King et al. 2006; Berkeley et al. 2007; White and Faaborg 2008; Whittaker and Marzluff 2009). These studies have increased our understanding of the ecology of young birds, but they have been confined mainly to studying movements and demographic patterns. To better understand the juvenile life stage, we need to know not just where birds travel but what they do along the way. Only a few studies have examined the behavior of juvenile birds. Arcese and Smith (1985) observed juvenile interactions at feeders and in aviaries and found that a bird's dominance status as a juvenile was correlated with his future success establishing an adult breeding territory. Using social network methods to analyze a long-term data set for a tropical suboscine bird, McDonald (2007) demonstrated that the social interactions of young manikins in the subadult

Address correspondence to C.N. Templeton, who is now at School of Biology, St Andrews University, St Andrews, Fife, KY16 9TS, UK. E-mail: christopher.templeton@st-andrews.ac.uk.

Received 17 February 2011; revised 18 July 2011; accepted 27 July 2011.

© The Author 2011. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

period (up to 8 years of age) have long-term effects on their future success. We know of no study that has examined the social interactions of wild juvenile songbirds under natural conditions.

In this study, we focus on the social relationships of juvenile song sparrows (*Melospiza melodia*). Song sparrows are small songbirds that are widely distributed throughout North America (Arcese et al. 2002). After fledging from the nest, juveniles remain with their parents for a few weeks, after which they disperse to another area. Sometime in the late summer (late July to early September), juveniles undergo a prebasic molt into breeding plumage nearly identical to that of adults (Arcese et al. 2002). After they complete their molt, some juveniles may attempt to establish a territory as early as August (Nice 1937; Arcese 1989a, 1989b; Wingfield and Hahn 1994). However, many of these juveniles are later evicted by the resident adult after he recovers from his own molt (Nice 1937). Aside from the relatively conspicuous territorial juveniles, most juveniles go unobserved by researchers as they inconspicuously "float" through different adult territories throughout the first year of life (Arcese 1989a, 1989b).

In the present study, we employ radio telemetry and aspects of social network theory to begin examining the social behavior of wild juvenile song sparrows. We systematically followed radio-tagged males and observed their interactions with other song sparrows. We describe the number and types of individuals that juvenile males associated with at different distances and in different seasons and suggest how the observed patterns in social relationships may affect the development of biologically important behaviors.

## MATERIALS AND METHODS

### Study site

Our research was conducted in Discovery Park, a large (1.2 km<sup>2</sup>), mostly undeveloped city park in Seattle, WA (lat 47°39'N, long 122°24'W). Song sparrows are year-round residents and are common in Discovery Park, with about 200 pairs breeding in the park every year (Beecher 2008). In the spring and early summer of 2004, we marked most of the adult males and many of the adult females holding territories in our core study area of approximately 60 territories. By color banding each bird with an individually distinct combination of 3 plastic leg bands and a numbered aluminum band, we could accurately identify individuals from a distance using binoculars.

### Subjects

We banded approximately 80 juvenile song sparrows, evenly split between males and females, in each of 2004 and 2005. Because juveniles do not typically respond to song playback, we captured young birds primarily by "herding" them into mist nets. We banded each juvenile with uniquely colored leg bands (as above) and measured his or her wing chord, tail length, and mass. This population of song sparrows has been heavily studied for the past 20 years (Beecher 2008), and the wing chord is a good, though not perfect, predictor of a bird's sex. In adults, males and females differentiate at around 65 mm (Beecher MD, unpublished data). Because juveniles typically have somewhat shorter wing feathers than adults (Alatalo et al. 1984), we assigned sex using the following rules originally proposed by Nice (1937): Wing chord less than 64 mm were females, equal to 64 mm were "unknown," and 65 mm or larger were males. This classification was confirmed for birds surviving into late summer, autumn, or early winter when males began producing subsong (Beecher 2008) or by

breeding observations the next spring. Overall, this system it is quite accurate, with those birds classified as males and females correctly classified >95% of the time (Nice 1937). Rare males and females can be misclassified (especially large females), and one such subject, "tram," who had a wing chord of 66 but turned out to be a female, is discussed below. Juveniles banded in the nest or before independence (noted by the presence of their parents or by particularly short retrices) were also sexed as unknown.

In addition to color banding, we tagged 24 different juveniles (i.e., our subjects) with radio transmitters. Because our particular interest was in juvenile behavior and movements as they relate to song learning, and only males sing in this species, we chose to focus on males for the radio-tagging sample. To be certain that we tagged only males, we used a somewhat more conservative cutoff for these individuals: Only birds with wing chords larger than 66 mm were tagged.

### Radio telemetry

Each subject was fitted with a small radio transmitter (BD-2 model from Holohil Systems Ltd., Carp, Canada) using elastic thread to make a backpack-style harness (Rappole and Tipton 1991). In 2004, half of the subjects received radio tags with 3-week batteries (transmitter mass = 0.62 g or <3% of the bird's body mass), and the other subjects received tags with 6-week batteries (mass = 0.9–1.0 g or ~4% of the bird's body mass). Each subject was weighed prior to tag attachment, so that we could be sure that the transmitter was never more than 4% of the subject's body mass (Kenward 2001). Because the 0.9–1.0 g tags did not appear to inhibit any aspects of the subject's behavior during our observations and we observed no difference in survival between the 2 groups (overall recruitment, the next spring was also fairly high [~50%] compared with expected first year survival for song sparrows [~20%; Arcese et al. 2002]), we used only the larger tags on all birds in 2005.

### Sampling protocol

In 2004, we radio-tagged 7 individuals between 21 July and 17 September and 4 individuals between 2 October and 10 November. One of these individuals was tracked in both the late summer and autumn periods. In 2005, we radio-tagged 8 individuals between 20 May and 26 July and 9 birds between 10 September and 2 November. Of the 2005 birds, 3 individuals were tracked in both periods. One subject (tram) tracked in early summer of 2005 was later discovered to be a female, and data from this individual are reported separately. The time periods were chosen to roughly correspond with different behavioral phases of our population of song sparrows: May to mid July represents the breeding season, when pairs are nesting, adult males have the highest singing rates, and juveniles are fledging and dispersing; mid July to mid September coincides with juvenile independence and adult prebasic molt; and mid September to November is a post breeding period, when many adults are active and some juveniles attempt to establish territories. For analysis purposes, we collapse these data to correspond with these biologically relevant seasons: early summer (2005), late summer (2004), and autumn (2004 and 2005 combined). We combined autumn data because our initial analyses indicated that which year a subject was tracked (2004 or 2005) did not greatly affect the number of birds he associated with where we had overlapping tracking months ( $P > 0.15$ ), though subjects generally tended to associate with fewer birds in 2005. Because the specific individuals sampled varied both with season and year, it is possible that either of these factors works in combination with season to affect the observed association patterns. We

discuss individual variation below but do not have data to address interyear variation. Birds were tracked every day until the subject disappeared, died, or the transmitter batteries were scheduled to run out. We recaptured each subject to remove the radio transmitter just prior to the transmitter batteries dying; in the 4 subjects mentioned above, we replaced the transmitter with a fresh one before releasing the bird. Within a given season/year tracking period, each bird was observed between 5 and 49 days (up to 75 days total for the 4 birds tracked in 2 seasons), with a mean ( $\pm$  standard error [SE]) number of samples being  $25 \pm 2$  days per bird.

On each day, we located each subject and followed him for 1 h. Subjects were tracked at times ranging from 06:00 to 21:00 h in an effort to survey behavioral patterns throughout different times of the day. The sampling start time for each bird was balanced, so that if a bird was tracked in the morning on 1 day, he was tracked in the afternoon or evening the next day and vice versa. Once a subject was located, we observed all other song sparrows near him at 10-min interval. We tallied the total number of birds seen near the focal bird and also noted the age of any unbanded birds (juveniles have distinctive plumage and are easily distinguished from adults until they molt in September; Pyle 1997) and the specific color combinations for all banded birds, so that we could keep track of associates' age, sex, and identity. We sampled all birds seen within 1, 3, 5, and 10 m of our focal subject but focus primarily on 2 levels of association here:  $<1$  m (individuals with which a subject was almost certainly visually and behaviorally interacting at that time) and  $<10$  m (individuals who likely were acoustically interacting, through song or contact calls, and who also had the potential to visually or behaviorally interact). Although we attempted to keep track of specific behavioral interactions (chasing, following, etc.), we observed few interaction events of this sort. Thus, for the purposes of this study, we limit our analyses to proximity measures and use these to infer social associations (Whitehead and Dufault 1999). Though rare interactions might also be important for learning, we expect strength of association to be generally indicative of some type of social relationship, especially when birds are found  $<1$  m from each other. Because of our sampling design (following radio-tagged individuals) and the fact that nontracked individuals are inconspicuous and are not likely to be observed when not in association with focal birds, we report associations as the percent of focal observations where the subject was seen with each other individual associate. Although this measure is nearly equivalent to the "simple ratio" and other association indices (Whitehead 2008) because associates were only very rarely observed without the focal bird and the probability of observing an associate without the focal bird approaches zero, simple proportions most accurately portray the relationships of our focal subjects.

### Data analysis and statistics

We analyzed association data at 3 different levels. First, we measured the average number of individuals (banded and nonbanded) observed near each subject (level 1). Second, we considered only banded birds near the subject to evaluate whether the subject interacted with the same birds repeatedly (level 2). Third, we evaluated whether age/sex category influenced these interactions (level 3). To illustrate, suppose the subject was observed near 3 banded birds and 2 unbanded birds on each of 2 days. We would then say that he was with 5 individuals each day (level 1). Examining the specific color-band combinations tells us further, for example, that he was with 1 particular banded bird on both days and 4 different banded individuals, 2 on each of the 2 days, for a total of 5 unique known individuals (level 2), but we cannot and thus

do not say whether the 2 unbanded birds represent 2, 3, or 4 different birds over the 2 days. Finally, consulting our banding records tells us, for example, that the subject was with 1 particular (banded) juvenile male both days, 2 different male juveniles on 1 day, and 2 different female juveniles on the other day (level 3).

### Number of individuals seen with the subject

To estimate the total number of birds ("total individuals") observed near the focal subject in a particular observation period, we counted the total number of birds, banded or unbanded, observed within 10 m. We tallied the number of song sparrows near the subject for each 10-min observation period within the full 60-min sampling period. Although subjects often moved considerable distances and flock composition often changed over the course of an hour, there is the potential that the 10-min data points within the hour are autocorrelated (Cairns and Schwager 1987). To reduce these potential biases, we based all of our analyses on 1 point per bird per day, which were much less autocorrelated. Because all birds near a subject were not always visible during the entire sampling period, we used the maximum number of birds we observed during a 10-min sampling period each day to estimate the number of birds with which a subject associated during a given sample. When we were not focused on more detailed within-season patterns, we then averaged these daily maxima within subjects to obtain a single estimate per subject per season. Thus, the sampling unit for statistical comparisons was an individual subject either per day or per season. To determine what factors determined the number of total birds near the subject, we used a general linear model (GLM) with season (early summer 2005, late summer 2004, and autumn 2004 and 2005 combined), time of day (by hour sampled) as explanatory variables and subject identity as a random factor. We then conducted further analyses of each of these variables using linear regression analysis with sampling date and time to examine how the number of associates (defined below) changed across seasons and time of day and GLM to examine how subject identity influenced the average number of associates observed per day. All statistics reported throughout this study are 2 tailed and were computed in JMP v. 7.0.1 (SAS Institute, Cary, NC).

### Numbers of age/sex class of associations

To examine subjects' association patterns with individuals of different age and sex classes and with specific individuals, we conducted a second analysis focusing on birds near the subject who could be identified based on their colored leg bands ("unique individuals"). We used techniques from social network theory to examine the number and types of associations for each of our juvenile subjects. Social network analysis examines the relationships ("links") among different individuals ("nodes") and has long been used in the social sciences (Wasserman and Faust 1994). Recently, social network analysis has become popular in behavioral and ecological research because of its ability to help us understand complex social relationships (e.g., Croft et al. 2008; Miller et al. 2008; Wey et al. 2008; Sih et al. 2009). We used the spring-embedding function in NetDraw (Borgatti 2002) to visualize the overall social network for each juvenile subject and the specific links connecting them with other individuals. One measure of social network analysis that is compatible with our sampling design is the "degree" of connectedness for each subject (the number of connections or number of unique individuals observed with each subject). We calculated the overall degree of connectedness (total number of unique individuals with whom each subject associated) at 2 different spatial scales:  $<10$  and  $<1$  m. We designated individuals within 10 m of



the focal bird “associates” and those within 1 m “close associates.” At each of these distance classes, we examined how the total number of individuals changed by season (early summer, late summer, and autumn). We were conservative in our use of partial band observations and only included those observations where it was clear that they could not be explained by other known individuals (e.g., if we saw green and red on one leg but did not see the other leg, we would include this individual only if no other associates had green and red on the same leg).

We first calculated degree (number of links) of connectedness for each node (subject) and then used these tallies for further statistical tests, so that each subject was treated as the sampling unit. Although we expected to find a relationship between the sampling effort (number of days a subject was tracked) and the total number of different individuals with whom a subject was seen, we did not find such a relationship (linear regression:  $R^2 = 0.003$ ,  $P = 0.77$ ), and thus, we did not control for sampling effort in subsequent analyses. We used GLM with season and associate age/sex class as factors and subject identity as a random factor to assess overall differences. We used post hoc Tukey Honestly Significant Difference tests (overall  $\alpha = 0.05$ ) to examine specific relationships between different factors.

#### *Identity and age/sex class of associates*

In addition to patterns in the total number of unique associates, we also assessed whether subjects selectively associated with individuals of different age (juvenile or adult) and sex (male or female) categories. Again, using each subject as the sampling unit, we tallied the total number of unique individuals the focal juvenile male associated with in each age/sex class. To determine how the associate- and close associate-level associations with different types of individuals changed through the seasons, we used GLM with age/sex class and season as fixed factors and subject ID as a random factor for both distance categories (<10 and <1 m, respectively). These were again followed by post hoc Tukey tests (overall  $\alpha = 0.05$ ) to examine the specific relationships between levels of each category.

It is possible that the observed patterns in association data could be due to variation in the abundance of individuals in each age/sex category or the likelihood of interacting with birds in each category. We banded roughly equal numbers of male and female juveniles each year (ca. 40 of each sex in each year) but more adult males (ca. 60 per year) than adult females (ca. 20 per year). Although the opportunity for subjects to interact with male and female juveniles should have been about the same, it is difficult to predict their expected encounter levels with adults because adults are territorial, whereas juveniles are not. In addition, adult females are generally less conspicuous than adult males. For these reasons, we do not attempt to correct our association data by the probability of encounter.

#### *Extent of associations*

To evaluate the extent to which a subject associated with specific individuals, we calculated the proportion of days that each of our radio-tagged subjects was observed near particular birds. For each subject, we noted the individual with whom he spent the most time to assess whether juvenile song sparrows formed stable relationships with other birds. We examined the amount of time spent with this individual at both distance categories—associates (<10 m) and close associates (<1 m)—to determine if subjects associated more closely with the individuals with whom they associated more frequently. We noted the age and sex of each associate to determine with which types of individuals juveniles repeatedly spent time. Finally, for birds

surviving until the next spring, we tested whether juveniles who had formed close associations with one another were also likely to settle near one another. We mapped the breeding territories for all first-year birds banded as juveniles (i.e., in the same cohort as our radio-tagged subjects) and measured the distance from the territories of these birds to the territories of our subjects. We compared the subject's distance from his nearest surviving close associate with the subject's average distance from all other previously banded first-year birds using a paired *t*-test.

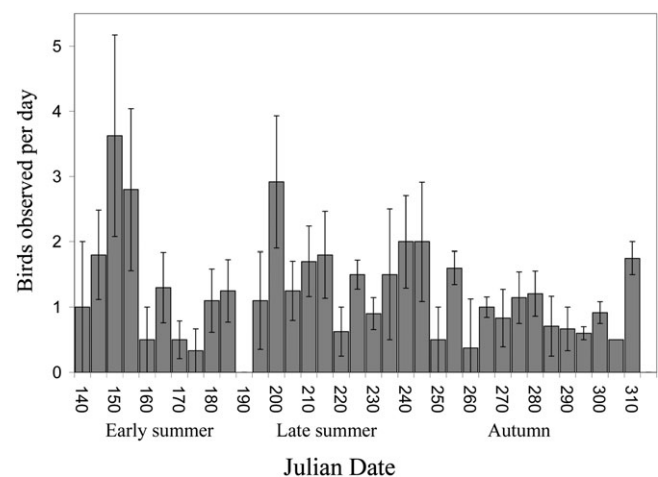
#### *Home range analysis*

To determine whether movement patterns influenced the number of associates, we calculated the kernel estimates for the home range of each subject in each season following Kertson and Marzluff (2009). We used Animal Space Use 1.3 Beta (Horne and Garton 2007) to estimate the smoothing parameter (*h*). We compared *h* values calculated by methods including likelihood cross-validation, least squares cross-validation, and the reference method (HREF). We choose to use HREF derived values because they provided the most reliable and best-fitting distributions of the 3 methods (other methods frequently produced 95% contours, which isolated many single points and were thus judged to be too narrow). To estimate home ranges or utilization distributions (UD), we calculated fixed kernel estimates for each subject using the Hawth's Tool Extension for ArcMap 9.2 (Beyer 2004). We used a raster cell size of 0.3 (m) based on the pixel size in the raster images of our study site. We calculated the 95 percent volume contours of each home range polygon and used Hawth's Tools to calculate the area (m<sup>2</sup>) of these contours. We used these UD to examine how home range sizes changed across seasons, and whether they were correlated with the number of associates for each subject.

## RESULTS

### Number of individuals seen with the subject

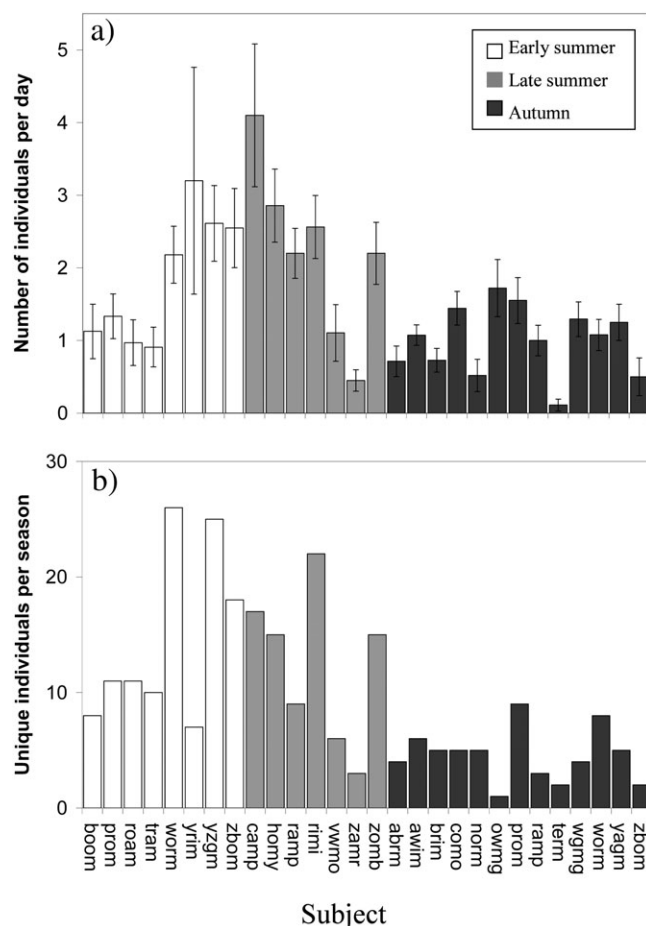
Juvenile song sparrows were frequently observed with other individuals (Figure 1). On most days of tracking, radio-tagged



**Figure 1**

The total number of other song sparrows (banded and unbanded) observed within 10 m of focal juvenile subjects varied by date. Data are compiled into 5-day time bins, represented by Julian date (June 1 = 152, for reference). These data represent the mean ( $\pm$ SE) number of total individuals, not just unique (banded) individuals, observed with the focal birds. Means are derived from 28 subjects (8 early summer, 8 late summer, and 15 autumn). Data from 2004 to 2005 are combined in the few time bins where they overlap.

subjects were observed with associates (<10 m), although there was considerable variation in the number of birds observed among days and among subjects. Overall, juveniles associated with an average of 1.5 birds per day (range = 0–12 birds, per focal observation period). The large variation can be explained by both tracking season ( $F_{2,89} = 8.66$ ,  $P = 0.0004$ ) and time of the day in which the subject was observed ( $F_{1,257} = 6.02$ ,  $P = 0.015$ ) (Overall GLM:  $F_{25,257} = 9.13$ ,  $P < 0.0001$ ). Further analysis showed that effects of time of day were confounded by season (due to decreased day length in the autumn), and within a given season, time of day did not affect the number of associates ( $P > 0.2$  for all). In general, subjects associated with significantly more birds per day in the early summer (mean  $\pm$  SE =  $1.86 \pm 0.31$ ) and late summer ( $1.90 \pm 0.49$ ) than in the autumn ( $1.40 \pm 0.31$ ; Tukey post hoc tests). Juveniles spent time with fewer birds as time progressed from May to November, although date alone explained little of the overall variation in the data (GLM:  $F_{1,265} = 48.03$ ;  $R^2 = 0.065$ ,  $P < 0.001$ ). Finally, some individuals associated with more birds than others (GLM:  $F_{24,435} = 3.82$ ,  $P < 0.0001$ ), with subjects varying between 0 and 4 birds observed per point on average (range 0–10; Figure 2a). We also saw substantial individual variation among subjects ( $F_{25,257} = 3.16$ ,  $P < 0.0001$ ).



**Figure 2**  
Individual subjects varied in the number of birds with whom they associated. (a) Mean  $\pm$  SE number of birds (marked and unmarked) observed per day <10 m of each subject. (b) Total number of unique (marked) individuals each subject associated with (<10 m) during the entire tracking season. Subjects are grouped by season: early summer (white), late summer (gray), and autumn (black). Subjects tracked in 2 seasons are shown in both seasons.

## Unique individuals

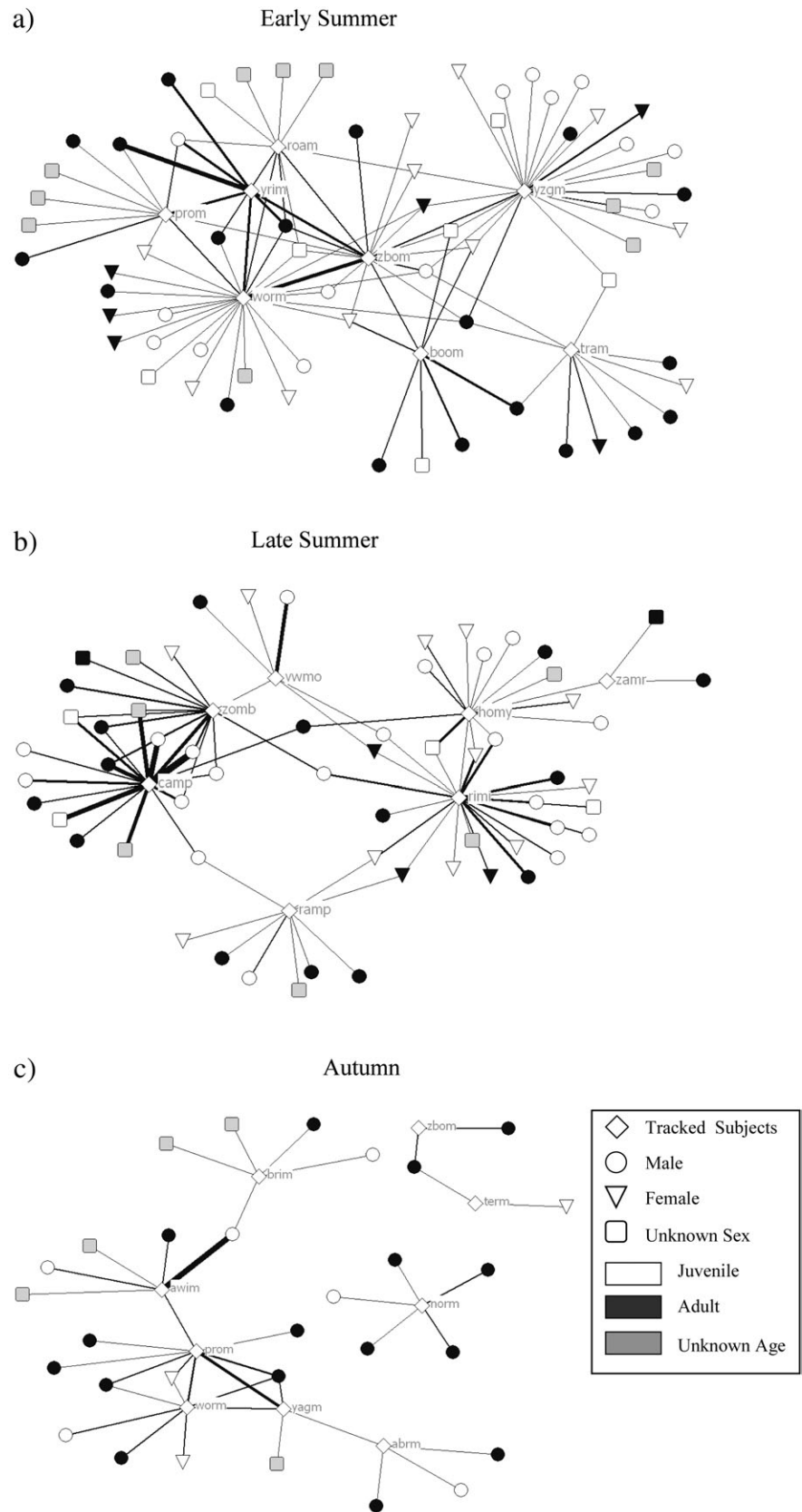
In addition to calculating the average number of individuals near a subject during each observation, we used a social network visualization to examine the number of unique individuals that a subject was observed with across all days he was tracked (Figure 3). Numbers reported are underestimates because they do not include unbanded individuals observed near our subjects. These analyses include both individuals observed within 10 m (associates) and those observed within 1 m (close associates). Juveniles associated (<10 m) with  $10.8 \pm 1.71$  different individuals on average (mean  $\pm$  SE; range = 1–28; different seasons are treated separately for the few subjects tracked in multiple seasons; Figure 2b). The total number of unique birds a subject associated with was affected by the season (GLM:  $F_{2,74} = 15.16$ ,  $P < 0.0001$ ) and the age and sex category of the observed individual ( $F_{3,94} = 23.85$ ,  $P < 0.0001$ ; overall GLM:  $F_{27,119} = 6.58$ ,  $P < 0.0001$ ). Again, juveniles associated with more unique individuals in the early summer (mean  $\pm$  SE:  $13.22 \pm 1.78$ ) and late summer ( $14.0 \pm 2.18$ ) than in the autumn ( $4.42 \pm 1.43$ ) (GLM:  $F_{2,26} = 7.44$ ,  $P = 0.0028$ ; Tukey post hoc test), and there was substantial individual variation (GLM:  $F_{22,92} = 2.51$ ,  $P = 0.001$ ). For close associates, subjects interacted with more unique individuals in the late summer (mean  $\pm$  SE:  $2.86 \pm 0.74$ ), than autumn ( $0.86 \pm 0.25$ ), with the early summer ( $1.78 \pm 0.52$ ) being intermediate and not statistically different from either group (Tukey test). Networks were generally star-like, with high degree hubs connected to pendants. This may indicate that associates of focal juveniles were generally not associates to each other or it may be an artifact of focusing data collection on radio-tracked individuals.

## Age/sex classes of unique associates

In each season, juveniles interacted with more unique males than females (paired *t*-tests;  $P < 0.02$  in all seasons and at both distances). The types of individuals with whom juveniles primarily interacted depended both on the season and the scale of the interactions. For associates (<10 m; Figures 3a and 4a), subjects generally interacted most with juvenile males, followed by adult males, juvenile females, and finally adult females. The significance of these differences varied slightly by season (Appendix I). Patterns also varied somewhat by season when we examined only close associates (seen <1 m from the subject; Appendix II). The overall trend for close associates was that focal birds were observed with adult and juvenile males in the early summer but primarily with juvenile males in the late summer and autumn (Figures 3b,c and 4b). Although we did not band equal numbers of birds in each age/sex class, our banding bias if anything predicts a different pattern: More associations should be observed with adult males, followed by juvenile females and males and then adult females. The subject that was later discovered to be female had a rather different pattern of associations, with most associations being with adult males (tram, Figure 3a) and the only close association (<1 m) being with an adult female.

## Extent of associations

Although some juvenile subjects ( $N = 5$ ) never had repeated interactions with other individuals, most subjects ( $N = 23$ ) reassociated with specific birds on multiple occasions (Figure 3). We found that the amount of time subjects spent with specific individuals varied from 8% of the time (only 2 days) to over 60% (up to 11 different days) (mean  $\pm$  SE:  $25 \pm 4\%$ ). Most subjects interacted primarily with another juvenile male ( $N = 16$ , 70%), but several spent the majority of their time with an adult male ( $N = 7$ , 30%). For none of the subjects was

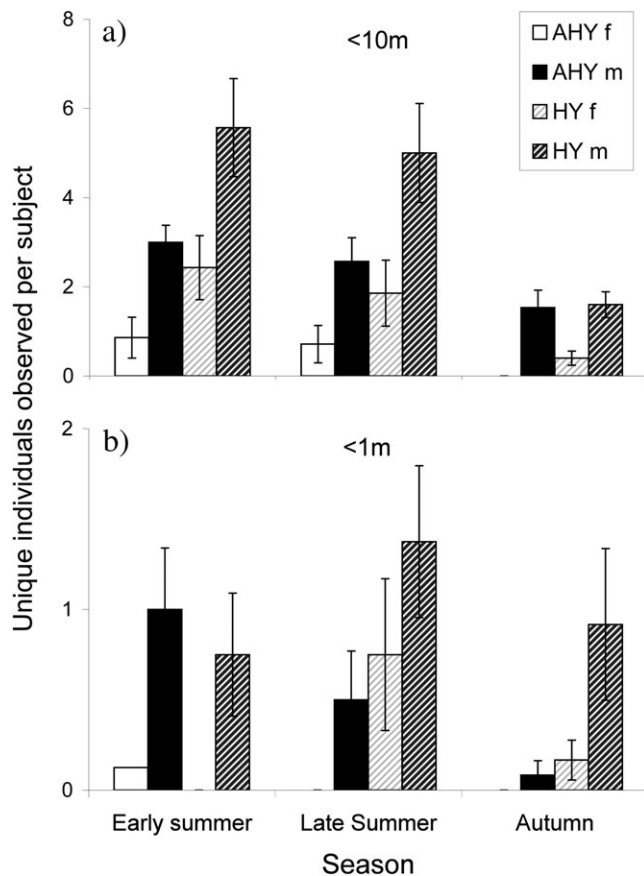


**Figure 3**  
Subjects were most commonly observed with other juvenile male song sparrows. Ego-based social networks are shown for radio-tagged subjects and their associate-level ( $<10$  m) interactions in (a) early summer, 2005, (b) late summer, 2004, and (c) autumn, 2005 (autumn 2004 network was similar and is not depicted here). In these social networks, symbols represent individual banded birds. Symbol color designates age: white symbols represent juveniles, black symbols represent adults, and gray symbols represent birds of unknown age. Symbol shape indicates a bird's sex:  $\circ$  are males,  $\nabla$  are females, and  $\square$  are birds of unknown sex. Juvenile subjects are indicated by  $\diamond$ . Birds connected by lines were observed together, and line thickness represents the strength of the association, with birds observed together more frequently connected by thicker lines (thinnest lines indicate  $<10\%$ , whereas the thickest lines indicate birds observed together on  $\sim 60\%$  of tracking days). Nodes are arranged in space for clarity, and only line thickness (not internode distance) indicates the strength of connections. One early summer subject (tram) turned out to be a female, and it is intriguing that, unlike most male subjects, her associations tended to be primarily with adults.

the primary associate a female (juvenile or adult). Subjects interacting with other juvenile males were typically observed as close associates, spending time at close range (10 of 16

individuals were observed  $<1$  m and 15 of 16  $<3$  m), whereas subjects primarily interacting with adult males were only rarely observed at close range (only 2 of 7 individuals were ever





**Figure 4**

The number of different (marked) individuals each radio-tagged subject associated with varied by age/sex class and season, with the most common interactions being with other juvenile males. Mean  $\pm$  SE number of unique individuals observed within (a) 10 m and (b) 1 m of each radio-tagged subject in each season. Each bar represents data for a different age/sex class of associates: females (f), males (m), adults (AHY or after hatch year), and juveniles (HY or hatch year).

observed <1 m; 3 of 7 <3 m). In a few cases, the closest associate happened to be another tagged bird. In these cases, the radioed subjects were frequently observed together in certain areas and alone in other areas (Figure 5). However, we also observed one radio-tagged subject traveling very close (<1 m) to another juvenile male over large distances (up to 1 km) during a single observation period. Although we have only one example where 2 radioed subjects did this together (Figure 6), we have several (>5) observations of our subjects traveling closely with other banded individuals. These close associates were often seen with the subjects again on other tracking days (up to 60% of days tracked) and were almost always the strongest associations in the social network (Figure 3). Subjects also tended to establish territories near other juveniles with whom they associated earlier in life. Two subjects who were frequently seen together (up to 60% of the time) established neighboring territories (Figure 6), and several other individuals who had previously interacted established territories in the same neighborhood. Overall, when juveniles and associates survived to establish territories ( $N = 8$  pairs), subjects established territories closer to the individual with whom they had primarily interacted the previous summer/autumn when compared with the mean distance from other first-year birds ( $147 \pm 30$  vs.  $298 \pm 23$  m paired  $t$ -test;  $t_7 = 3.29$ ,  $P = 0.0134$ ). Birds who spent more time together also established territories nearer to each other the

next spring (Linear regression,  $R^2 = 0.57$ ,  $F_{1,7} = 7.85$ ,  $P = 0.031$ ). The area where birds associated was usually in the same neighborhood (though not always the same exact territories) where they later set up their territories.

### Home range sizes and associations

Juvenile males varied considerably in their movements across the landscape. Subject home ranges varied between 935 and 156 838 m<sup>2</sup> (for reference, the average adult territory size in our population is 2750 m<sup>2</sup>), with a mean home range size of  $49\,291 \pm 8633$  m<sup>2</sup> (or ca. 18 $\times$  the size of an adult territory). Home-range size was not related to the duration a bird was tracked (Linear regression:  $R^2 = 0.001$ ,  $P = 0.87$ ). Season had a strong effect on home-range size (Wilcoxon signed ranks,  $\chi^2_2 = 7.05$ ,  $P = 0.029$ ), with birds occupying larger home ranges in the late (mean  $\pm$  SE:  $74\,407 \pm 16\,957$  m<sup>2</sup>,  $N = 7$ ) and early summer ( $56\,790 \pm 17\,709$  m<sup>2</sup>,  $N = 7$ ) than in autumn ( $31\,729 \pm 10\,818$  m<sup>2</sup>,  $N = 13$ ). There was an overall positive relationship between a subject's home-range size and the number of associates he had (Linear regression:  $R^2 = 0.144$ ,  $P = 0.050$ ; Figure 7). However, season also affected patterns of juvenile association (above) and when both parameters were examined together, season was a much stronger factor than home-range size in determining the number of individuals with whom a subject associated (Home-range size:  $F_1 = 1.14$ ,  $P = 0.295$ ; Season:  $F_2 = 8.74$ ,  $P = 0.0015$ ). Thus, it appears that both spatial movement patterns and associations vary together by season.

### DISCUSSION

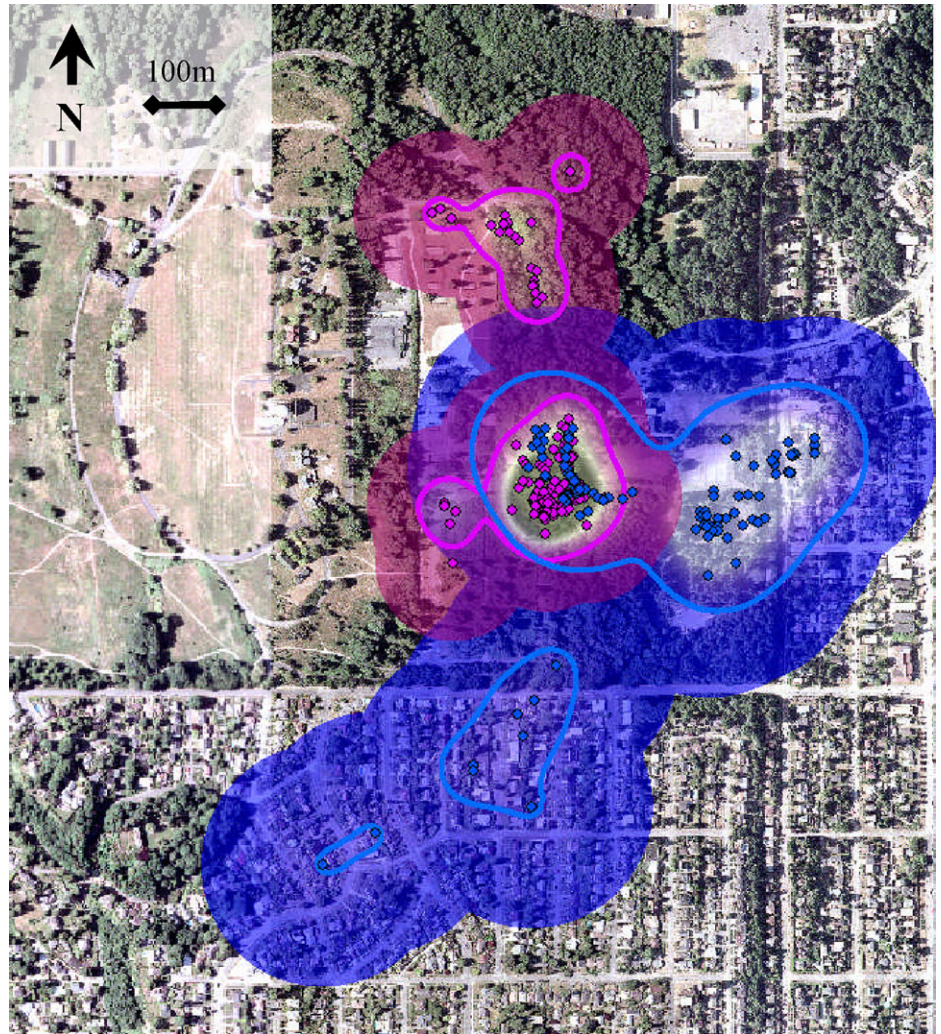
Radio-tracking juvenile male song sparrows and recording the individuals with whom they associated revealed a number of interesting patterns. First, juvenile males most commonly interacted with other males rather than females, and these individuals were typically other juveniles rather than adults. Moreover, their associations with juveniles were typically closer than they were with adults. This observation sharply contrasts with the behavior of territorial adult males, who generally associate only with females (their mate). Second, subjects formed social flocks and tended to establish consistent relationships with specific individuals. Third, subjects established territories in the same neighborhood as their associates. Last, there was substantial individual and seasonal variation in association patterns. We consider each of these observations below.

#### Associations with adults

Subjects were more likely to associate with adults in the early summer (May to June) than in other seasons, although close associations were generally less common with adults than with juveniles. One hypothesis is that juveniles may associate with adults in order to solicit food during the period when adults are feeding their own offspring. However, this interpretation suggests that subjects should associate equally with adult males and females. Instead, juvenile subjects only rarely associated with adult females. Moreover, we witnessed no feedings of tagged juveniles by these adult males, indicating that juvenile males preferentially seek out adult males for other reasons. Associating with adult males may allow juveniles to collect information important for their future reproductive success, such as territory boundaries and habitat quality or adult dominance status, health, or aggression levels. Early summer also marks the critical period for song learning (Marler and Peters 1987), so juveniles may spend more time associating with adults during this season to facilitate song memorization or to

**Figure 5**

Subjects typically ranged between 2 locations, and these 2 subjects overlapped in one of these neighborhoods. Movement patterns and home range estimates are shown for 2 subjects tracked both in late summer and autumn 2004. This map shows a small portion of Discovery Park and the surrounding neighborhood. Tracking observations are designated by points, with each subject represented by a different color (worm = dark gray, zbom = light gray). UD (shaded contours reflecting probability of occurrence) and 95% contours (solid lines) are indicated for each bird. Although the most frequent associate for most subjects was not another subject, these 2 individuals were observed <10 m from each other during approximately 60% of tracking points.



determine which song types are shared among residents of a given neighborhood. We have previously shown that juveniles are attracted to countersinging adults (Templeton et al. 2010) and also that they can approach adults closely without eliciting aggression (Templeton CN, Campbell SE, Beecher MD, manuscript in review) during the early summer months. Here, we have shown that some juveniles do associate with adult males in the early summer; these associations may be critical for juveniles to learn songs and other important behaviors.

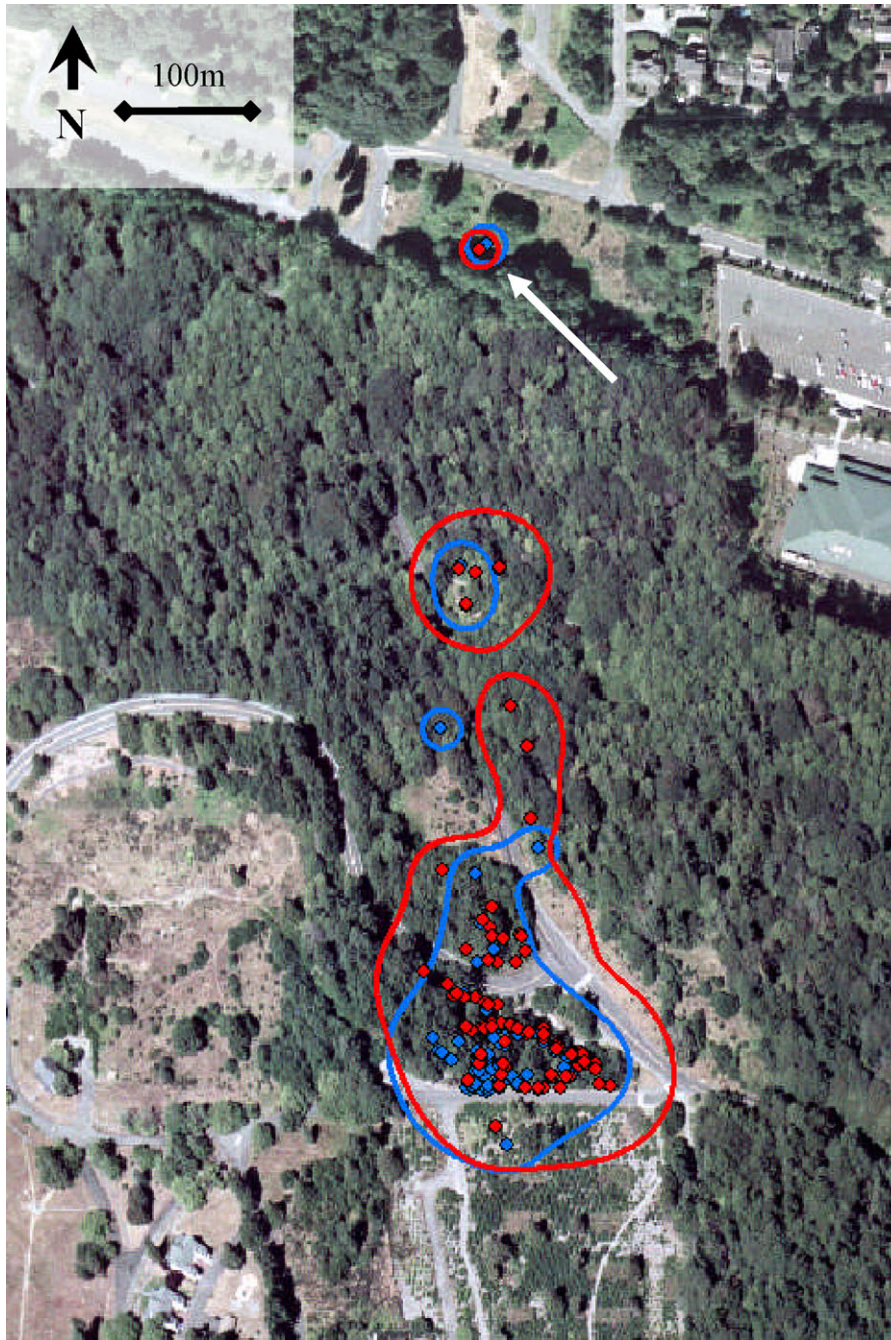
Although some juvenile subjects associated with adults in the early summer, we observed very few associations with adults later in the year. The lack of associations by juveniles with adults beyond the early summer suggests that juveniles are not tolerated by adults after early summer or that they gain less by interacting with adults during other seasons. The tolerance that adults display toward young individuals in the early summer is probably mediated in part by the drab plumage possessed by juveniles (Rohwer et al. 1980; Ligon and Hill 2009). Because juvenile song sparrows molt into adult plumage in August (Pyle 1997), young birds could be seen as potential competitors in the autumn. However, adults do not respond aggressively to juvenile mounts during simulated territorial intrusions in late summer and respond only moderately aggressively in the autumn (Templeton CN, Campbell SE, Beecher MD, manuscript in review), so the lack of interactions with adults at these times is probably not driven solely

by adult intolerance. It seems more likely that juveniles actively direct their social interactions toward other juveniles during this time period. Regardless of the mechanisms, juveniles do not tend to associate with adults in the late summer or autumn and instead appear to form stronger and more consistent bonds with other juvenile males.

### Juvenile social flocks

Young sparrows may form associations with other juveniles for several reasons. Social groups may provide basic ecological benefits, including higher foraging success (Giraldeau and Beauchamp 1999) or decreased predation rates (Lima and Dill 1990). Larger social groups may increase predator detection by providing higher overall vigilance rates or may reduce attack rates through the dilution effect or early warning alarm call systems (Lima and Dill 1990). Similarly to their antipredator advantages, juvenile social groups may provide reduced aggression from territorial adult song sparrows. Although adults are generally tolerant of juveniles, especially early in the season, they do sometimes show aggression and chase juveniles from their territories, and aggression levels increase throughout the seasons. A large flock may overwhelm a territorial adult or at least make it less likely that a single individual will bear the brunt of the adult's aggression. This advantage seems particularly important for





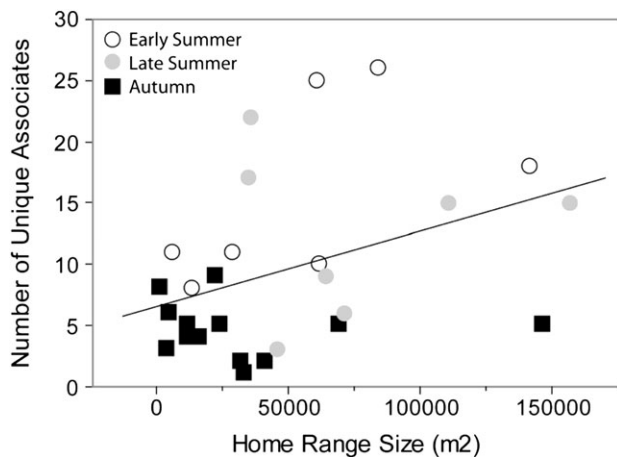
**Figure 6**

Birds who closely associated in the summer or autumn often established territories in the same neighborhood the following spring. Movements of 2 radio-tracked subjects during autumn 2004 are shown, 1 in each color (light gray = wgm, dark gray = como). Points show locations of tracking observations, solid lines indicate 95% contours for the home range estimate, and filled shapes indicate the territory boundary of each subject's territory the next spring. Several subjects were observed traveling together with their close associates to new areas and quickly returning as is shown here by the arrow.

songbirds like the song sparrows in our population, which maintain year-round territories and live at relatively high densities in fairly isolated populations. Under these conditions, even if a juvenile is not prospecting for a territory in the neighborhood, he must constantly intrude on adult territories, potentially stimulating aggressive responses from territorial adults. Finally, juvenile songbirds must learn a number of important things in the first several months of life, including how to find food, identify and avoid predators, evade aggressive adults, and visually and vocally communicate with rivals and potential mates. Close associations with other juveniles may facilitate the development of these behaviors through social learning (Valone 1989; Galef and Laland 2005).

### Social companions

Although there are reasons that young song sparrows might benefit from flocking with other juveniles in general, it is surprising that many of our subjects formed close and long-lasting associations with specific individuals. These close associates were nearly always other juvenile males rather than adults or juvenile females. Although juvenile males will pair with females, often females from their cohort, at some point during the first year, we witnessed few close social relationships between our juvenile male subjects and juvenile females. Thus, social relationships are formed for reasons other than establishing pair bonds. Another possibility is that the association patterns we observed were due simply to juveniles being repeatedly attracted to the same resource (food or bath site, etc.). Although these ecological factors are likely important



**Figure 7**

Home-range size varied among subjects but was positively correlated with the number of individuals with whom a subject associated. Different symbols represent subjects tracked in different seasons. Both home-range size and associate number varied by season, with both being higher in the summer than autumn tracking periods. Linear regression,  $y = 0.00006x + 6.49$ ;  $R^2 = 0.145$ ;  $P = 0.050$ .

in influencing where young birds are found, other studies with cowbirds (*Molothrus ater*) have similarly shown preferential social associations among juvenile males in their captive studies, where environmental influences are presumably absent (Freeberg 1999; Smith et al. 2002). Our field observations also argue against microhabitat features completely explaining juvenile social association patterns because we often observed pairs of juvenile close associates at very close distances (often <15 cm), and surprisingly, we also observed them traveling together on many occasions (e.g., Figure 6). In some of these trips, the birds moved to new areas where we had never tracked them, sometimes moving quickly up to a kilometer away and then back to the starting location within the hour-long sample. Some of these observations involved pairs of birds “exploring” areas or microhabitats where song sparrows are generally not found (e.g., prairies) and did not involve foraging. Thus, it appears that the close social relationships we observed between juveniles were not simply an artifact of their shared habitat use but rather reflect some type of important social strategy.

What adaptive value might be gained by forming stable social relationships with other juveniles? Establishing close relationships with other juvenile males may benefit young birds in establishing a territory. Arcese (1989b) noted that most juveniles obtain breeding territories by evicting older birds from their territories or by taking over a portion of an adult's territory. Adults presumably have many advantages in territorial disputes relative to juveniles, such as prior experience in resolving conflicts, dear-enemy relationships with current neighbors (Fisher 1954; Temeles 1994), and the important home territory advantage (Krebs 1982). Thus, juveniles unable to establish a territory on their own might benefit from “ganging up” to evict an adult and then sharing his territory. In several cases, juveniles who associated heavily during their first year established territories in the same neighborhood, sometimes even adjacent to one another (Figure 6). Although we did not witness the territory establishment to know if juveniles “teamed up” to evict adults, these observations suggest one way that young males might benefit from these close alliances established during the juvenile life stage.

Forming social relationships with other juvenile males may also be a mechanism that facilitates song learning by helping young song sparrows learn the appropriate neighborhood-specific song types. Juvenile song sparrows in the same cohort will often learn the same song types (Nordby et al. 2000). Although social reinforcement by cohort members can manifest itself problematically under unrealistic laboratory conditions, it is possible that it is an important factor in song learning in wild birds. Of the surviving subjects who frequently associated with another juvenile male during the summer months, close associates shared about 30% of their songs on average (unpublished data). This is comparable to sharing levels found among nearest neighbors at the study site (37% on average; Hill et al. 1999) and therefore higher than expected by chance given that our birds sometimes settled farther apart. Through their associations, these birds may have learned from each other or helped reinforce the learning of certain song types previously memorized from adults. The potentially important role that cohort members play in song learning is a topic deserving more study.

### Individual variation in association patterns

Although most subjects associated with other song sparrows, they varied greatly in the number of birds with whom they were usually seen, the number of unique individuals they associated with over the course of the tracking period, and how much time they spent with certain associates. Relatedness between individuals was not known, but it is possible that subjects preferentially associated with kin. Individual differences among subjects may reflect alternative life strategies or behavioral syndromes (Sih et al. 2004; Smith and Blumstein 2008). For example, some juveniles attempt to establish a territory in the autumn of their first year of life (Nice 1937; Arcese 1989a, 1989b; Wingfield and Hahn 1994), whereas others float until the next spring or longer (Arcese 1989b). Juveniles successful in establishing territories in the autumn months are typically hatched early in the year and often exhibit dominance over other juveniles (Arcese and Smith 1985); this trajectory and accompanying behavioral qualities may be expressed in the types and qualities of early associations. Juveniles preparing to establish a territory in the autumn might be expected to interact more with adults of a given neighborhood, so that they can learn appropriate songs types (Beecher et al. 1994) or gather information about aggression levels of territorial adults (Nowicki, Searcy, Krueger, et al. 2002; Hyman et al. 2004; Templeton CN, Campbell SE, Beecher MD, manuscript in review), whereas juveniles not likely to establish a territory until the next spring may investigate more neighborhoods for potential breeding territories and benefit from spending more time in social flocks with other juveniles. Thus, individual variation in social relationships may reflect both ecological and temporal factors and may have important consequences for future breeding behavior.

### FUNDING

National Science Foundation (to M.D.B.) and the University of Washington Biology Department Snyder Award (to C.N.T.). National Institutes of Health Auditory Neuroscience Training Grant and National Science Foundation International Research Fellowship during the analysis and writing of this work (C.N.T.).

Swift Optics donated binoculars. Elena Wager, Kyle Stewart, and Miles Bensky helped with fieldwork.



## Appendix I

**Extent of loose associations (<10 m) with unique birds from different age and sex classes in each season. Mean values and SE are shown for each age/sex category. Different letters indicate statistically different groups within each season.**

Season	Age class	Sex class	Mean	SE	Statistical group
Early summer	Juvenile	Male	5.57	1.10	A
Early summer	Juvenile	Female	2.43	0.72	B,C
Early summer	Adult	Male	3.0	0.38	B
Early summer	Adult	Female	0.86	0.46	C
Late summer	Juvenile	Male	5.0	1.11	A
Late summer	Juvenile	Female	1.85	0.74	B
Late summer	Adult	Male	2.57	0.53	A,B
Late summer	Adult	Female	0.71	0.42	B
Autumn	Juvenile	Male	1.60	0.29	A
Autumn	Juvenile	Female	0.40	0.16	B
Autumn	Adult	Male	1.53	0.39	A
Autumn	Adult	Female	0.0	0.0	B

## Appendix II

**Extent of close associations (<1 m) with unique birds from different age and sex classes in each season. Mean values and SE are shown for each age/sex category. Different letters indicate statistically different groups within each season.**

Season	Age class	Sex class	Mean	SE	Statistical group
Early summer	Juvenile	Male	0.86	0.34	A,B
Early summer	Juvenile	Female	0	0	B
Early summer	Adult	Male	1.14	0.34	A
Early summer	Adult	Female	0	0	B
Late summer	Juvenile	Male	1.38	0.42	A
Late summer	Juvenile	Female	0.75	0.42	A,B
Late summer	Adult	Male	0.50	0.27	A,B
Late summer	Adult	Female	0	0	B
Autumn	Juvenile	Male	1.38	0.42	A
Autumn	Juvenile	Female	0.17	0.11	B
Autumn	Adult	Male	0.08	0.08	B
Autumn	Adult	Female	0	0	B

## REFERENCES

Adams AAY, Skagen SK, Adams RD. 2001. Movements and survival of lark bunting fledglings. *Condor*. 103:643–647.

Alatalo RV, Gustafsson L, Lundberg A. 1984. Why do young passerine birds have shorter wings than older birds? *Ibis*. 126:410–415.

Anders AD, Faaborg J, Thompson FR. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk*. 115:349–358.

Arcese P. 1989a. Intrasexual competition, mating system and natal dispersal in song sparrows. *Anim Behav*. 38:958–979.

Arcese P. 1989b. Territory acquisition and loss in male song sparrows. *Anim Behav*. 37:45–55.

Arcese P, Smith JNM. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *J Anim Ecol*. 54:817–830.

Arcese P, Mark K, Sogge, Marr AB, Patten MA. 2002. Song sparrow (*Melospiza melodia*). In: Poole A, editor. *The birds of North America online*. Ithaca (NY): Cornell Lab of Ornithology. Available from: <http://bna.birds.cornell.edu/bna/species/704>.

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

Beecher MD, Campbell SE, Stoddard PK. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proc Natl Acad Sci U S A*. 91:1450–1454.

Berkeley LI, McCarty JP, Wolfenbarger LL. 2007. Postfledging survival and movement in dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk*. 124:396–409.

Beyer HL. 2004. Hawth's analysis tools for ArcGIS. Available from: <http://www.spatial ecology.com/htools>.

Borgatti SP. 2002. NetDraw: graph visualization software. Harvard (IL): Analytic Technologies.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. *Anim Behav*. 35:1454–1469.

Caro TM. 2005. Antipredator defenses in birds and mammals. Chicago (IL): University of Chicago Press.

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

Cohen EB, Lindell CA. 2004. Survival, habitat use, and movements of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *Auk*. 121:404–414.

Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton (NJ): Princeton University Press.

Fisher J. 1954. Evolution and bird society. In: Huxley J, Hardy A, Ford E, editors. *Evolution as a process*. London: Allen & Unwin.

Freeberg TM. 1999. Spatial associations provide a context for social learning of courtship patterns in brown-headed cowbirds (*Molothrus ater*). *J Comp Psychol*. 113:327–332.

Galef BG, Laland KN. 2005. Social learning in animals: empirical studies and theoretical models. *Bioscience*. 55:489–499.

Giraldeau LA, Beauchamp G. 1999. Food exploitation: searching for the optimal joining policy. *Trends Ecol Evol*. 14:102–106.

Graber RR. 1955. Taxonomic and adaptive features of the juvenal plumage in North American sparrows. Norman (OK): University of Oklahoma.

Hill CE, Campbell SE, Nordby JC, Burt JM, Beecher MD. 1999. Song sharing in two populations of song sparrows (*Melospiza melodia*). *Behav Ecol Sociobiol*. 46:341–349.

Horne JS, Garton EO. 2007. Animal space use 1.2. Available from: [http://www.cnr.uidaho.edu/population\\_ecology/animal\\_space\\_use.htm](http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm).

Hyman J, Hughes M, Searcy WA, Nowicki S. 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour*. 141:15–27.

Kenward RE. 2001. A manual for wildlife radio tagging. San Diego (CA): Academic Press.

Kershner EL, Walk JW, Warner RE. 2004. Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. *Auk*. 121:1146–1154.

Kertson BN, Marzluff JM. 2009. Animal movement, home range, and resource utilization function (ruf) analysis in ArcMap 9.3. School of Forest Resources. Seattle (WA): University of Washington. p. 30.

King DI, Degraaf RM, Smith ML, Buonaccorsi JP. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J Zool*. 269:414–421.

Krebs JR. 1982. Territorial defense in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol*. 11:185–194.

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

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool*. 68:619–640.

MacDonald IF, Kempster B, Zanette L, MacDougall-Shackleton SA. 2006. Early nutritional stress impairs development of a song-control brain region in both male and female juvenile song sparrows (*Melospiza melodia*) at the onset of song learning. *Proc R Soc B Biol Sci*. 273:2559–2564.

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.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. *Proc Natl Acad Sci U S A*. 104:10910–10914.

Miller JL, King AP, West MJ. 2008. Female social networks influence male vocal development in brown-headed cowbirds, *Molothrus ater*. *Anim Behav*. 76:931–941.

Naef-Daenzer B, Fruh D, Stalder M, Wetli P, Weise E. 2005. Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters. *J Exp Biol*. 208:4063–4068.

Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J Anim Ecol*. 70:730–738.



- Nice MM. 1937. Studies in the life history of the song sparrow. *Trans Linn Soc N Y.* 4(Pt 1):1–247.
- 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.
- Nowicki S, Searcy WA, Krueger T, Hughes M. 2002. Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *J Avian Biol.* 33:253–259.
- Nowicki S, Searcy WA, Peters S. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol.* 188:1003–1014.
- Pearce JM. 2008. *Animal learning and cognition: an introduction.* 3rd ed. East Sussex (UK): Psychology Press.
- Pyle P. 1997. Identification guide to North American birds. Part I. Bolinas (CA): Slate Creek Press.
- Rappole JH, Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. *J Field Ornithol.* 62: 335–337.
- Rohwer S, Fretwell SD, Niles DM. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am Nat.* 115:400–437.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol.* 19:372–378.
- Sih A, Hanser SF, McHugh KA. 2009. Social network theory: new insights and issues for behavioral ecologists. *Behav Ecol Sociobiol.* 63:975–988.
- Slater PJB. 1983. The development of individual behaviour. In: Halliday TR, Slater PJB, editors. *Animal behaviour volume 3: genes, development and learning.* Oxford: Blackwell Scientific Publications. p. 82–113.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol.* 19:448–455.
- Smith VA, King AP, West MJ. 2002. The context of social learning: association patterns in a captive flock of brown-headed cowbirds. *Anim Behav.* 63:23–35.
- Snow DW. 1958. The breeding of the blackbird *Turdus merula* at Oxford. *Ibis.* 100:1–30.
- Sullivan KA. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *J Anim Ecol.* 58:275–286.
- Temeles EJ. 1994. The role of neighbors in territorial systems: when are they dear enemies? *Anim Behav.* 47:339–350.
- 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.
- Valone TJ. 1989. Group foraging, public information, and patch estimation. *Oikos.* 56:357–363.
- Wasserman S, Faust K. 1994. *Social network analysis: methods and application.* Cambridge: Cambridge University Press.
- West MJ, King AP, White DJ. 2003. The case for developmental ecology. *Anim Behav.* 66:617–622.
- Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav.* 75:333–344.
- White JD, Faaborg J. 2008. Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes. *Wilson J Ornithol.* 120:62–73.
- White JD, Gardali T, Thompson FR, Faaborg J. 2005. Resource selection by juvenile Swainson's Thrushes during the postfledging period. *Condor.* 107:388–401.
- Whitehead H. 2008. *Analyzing animal societies.* Chicago (IL): University of Chicago Press.
- Whitehead H, Dufault S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Adv Study Behav.* 28:33–74.
- Whittaker KA, Marzluff JM. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. *Auk.* 126:288–299.
- Wingfield JC, Hahn TP. 1994. Testosterone and territorial behavior in sedentary and migratory sparrows. *Anim Behav.* 47:77–89.