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Social connections across migration: Do Golden-crowned Sparrows (*Zonotrichia atricapilla*) that socialize in winter also breed together?

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ABSTRACT—Many birds that are territorial in the breeding season live in groups during the nonbreeding season, thereby gaining benefits such as protection from predators and increased access to resources. However, how the social connections in group life change across seasons in migratory animals is mostly unknown. We ask whether winter social connections continue during the breeding season in a migratory songbird. Golden-crowned Sparrows (*Zonotrichia atricapilla*) have distinct, stable winter communities that include both site and group fidelity across years: birds almost always rejoin the same social community each year after migration. If these birds have social connectivity across migration, we would expect individuals that associate in winter would also associate together on their breeding grounds. Our small-scale GPS tagging study combined with intensive social behavior data indicates that sparrows in the same tightly knit winter community migrate to highly disparate locations during summer, and therefore, social connections in winter do not continue in summer. This suggests that Golden-crowned Sparrows have entirely separate social structures across seasons and that long-term social memory allows them to reform stable groups each winter. *Received 21 February 2023. Accepted 25 November 2023.*

Key words: animal communities, GPS tags, migration, social networks, social structure, winter groups.

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Conexiones sociales a través de la migración: ¿los gorriones *Zonotrichia atricapilla* que socializan en invierno también se reproducen juntos?

RESUMEN (Spanish)—Muchas aves que son territoriales durante la temporada reproductiva viven en grupos en temporada no reproductiva, ganando así beneficios como protección ante depredadores y mayor acceso a recursos. Sin embargo, cómo las conexiones en la vida de grupo cambia a través de las estaciones en animales migratorios es mayormente desconocido. Nos preguntamos si las conexiones sociales de invierno continúan en temporada reproductiva en un ave canora migratoria. El gorrión *Zonotrichia atricapilla* tiene comunidades de invierno discretas y estables que tienen fidelidad de sitio y de grupo a través de los años: las aves casi siempre se unen a la misma comunidad cada año después de la migración. Si esas aves tienen conectividad social a través de la migración, esperaríamos que individuos que se asocian en invierno también se asociarín en sitios reproductivos. Nuestro estudio de pequeña escala con marcación GPS combinado con datos de comportamiento social intensivo indica que los gorriones de la misma comunidad altamente relacionada durante el invierno migra a sitios muy diferentes durante el verano por lo que las conexiones sociales de invierno no continúan durante el verano. Esto sugiere que el gorrión *Zonotrichia atricapilla* tiene estructuras sociales completamente separadas a través de las estaciones y que la memoria a largo plazo le permite volver a formar grupos estables cada invierno.

Palabras clave: comunidades animales, estructura social, grupos de invierno, marcas GPS, migración, redes sociales.

Social connections across migration could fundamentally affect how social relationships are formed and maintained in migratory animals. Social carry-over effects between seasons are seen in year-round resident birds where connections in winter predict associations in the breeding season, nesting proximity, or even increased extra-pair paternity (Firth and Sheldon 2016, Beck et al. 2020). Such social carry-over effects could exist in migratory birds as well. New tracking technologies enabling trans-seasonal tracking of individual migrants have provided recent evidence that social interactions can influence migration patterns, although evidence for such social migration remains rare in songbirds (Aikens et al. 2022). However, in one remarkable case, lightweight multisensor loggers provided evidence that migratory European Bee-eaters (*Merops apiaster*) maintain cohesive social relationships across seasons by migrating together (Dhanjal-Adams et al. 2018). Such seasonal continuity in social relationships could potentially explain how season-specific social relationships are maintained across years in some migratory birds (e.g., "dear-enemy" effects among territorial neighbors in breeding season: Godard 1991; flock mate relationships in winter: Shizuka et al. 2014). Alternatively, such within-season social relationships may be maintained across years despite breaking apart during the intervening seasons.

We tracked Golden-crowned Sparrows (*Zonotrichia atricapilla*) across seasons to ask whether winter social relationships in flocks carry over to the breeding season. Golden-crowned Sparrows are small long-distance migratory birds that form foraging flocks in winter. They exhibit high winter site fidelity and their social relationships can be extremely stable across years (Shizuka et al. 2014, Madsen et al. 2023). One hypothesis for across-year stability in flock relationships is that flock-mates maintain year-round social interactions across seasons despite long-distance migration. Golden-crowned Sparrows form socially monogamous pairs in the breeding season but interact with adjacent territory holders, often through vocal communication (Hudson et al. 2020). Golden-crowned Sparrows have broad-scale migratory connectivity, as birds wintering in coastal California tended to go to coastal areas in Alaska while more inland birds went to more inland areas in the north of Alaska to breed (Seavy et al. 2012, Cormier et al. 2016, Iverson et al. 2023). We used archival global positioning system (GPS) tags to determine if Golden-crowned Sparrows maintain their close social connections from the nonbreeding season to the breeding season. This hypothesis would be supported if Golden-crowned Sparrows from the same winter social communities also breed in close proximity. While we report a small sample size due to low tag recovery, we have detailed data on individual social interactions prior to migration and follow birds from the same winter social group.

Methods

As part of an ongoing larger study at the University of California Santa Cruz (UCSC) Arboretum in Santa Cruz, California (36.98230, −122.05987) (e.g., Chaine et al. 2011, Shizuka et al. 2014), we gathered behavioral data and caught, measured, and banded Golden-crowned Sparrows during the nonbreeding season (Sep–Mar). We also collected blood from each bird for genetic sex determination following methods from Chaine et al. (2011) and

Griffiths et al. (1998). Each bird received a U.S. Geological Survey uniquely numbered metal band and unique combinations of color bands for individual identification in the field.

GPS methods

We programmed archival GPS tags (1g PinPoint 10 Swift GPS tags; Lotek Wireless, Newmarket, Ontario, Canada) to record up to 100 locations (every 2–5 d during migration and breeding seasons). The precision of GPS coordinates (~10 m; Supplemental Fig. S4), was sufficient to determine whether birds had neighboring breeding territories. In the spring of 2017, we attached 30 GPS tags to previously banded Golden-crowned Sparrows using a leg-loop attachment method (Rappole and Tipton 1991) with 0.7 mm stretchy jewelry cord. In the spring of 2018, we attached 40 GPS tags to a different sample of sparrows. We focused on tagging sparrows that had been at our study site for at least 1 previous winter as these age classes are more likely to return across winters. After attaching the GPS tags, we monitored the tagged sparrows at the winter site prior to migration to ensure that the birds maintained their normal behavior and could move, fly, and feed unhindered (Supplemental Fig. S1–S3).

Archival GPS tags store data on the tag and must be recovered to retrieve the data. From 30 GPS tags in 2017, we recovered 5 the next field season. The low return rate of tags for this season was partially due to problems with the GPS harness attachment. Of the 5 that returned with tags, 2 tags malfunctioned and gathered incomplete data, leaving us with data for 3 birds. From 40 tags attached to sparrows in January 2018, we recovered 1 tag in Fall 2018. In March 2018, a substantial portion of our study site was converted to a parking lot (0.54 ha) within a month of tag-deployment, in the precise location where we had focused our tagging effort. This likely caused the very low return rates of tagged birds in the fall. The 4 tags with full data recorded 75 GPS points for bird 77968, 68 points for bird 81319, 85 points for bird 81324, and 49 points for bird 19388 (Block et al. 2023).

We determined the location of the Golden-crowned Sparrows' breeding territories by searching for highly localized clusters of more than 5 GPS points at the farthest northern location of a bird's migration route. The breeding locations for all 4 birds had a high density of GPS points over a small area (<0.4 km^2), and we used these locations to determine the start and end date of the time each sparrow spent on its putative breeding territory. We determined the mean breeding territory location by calculating a centroid location from the clustered points using the package *geosphere* (Hijmans 2019). To calculate the distance of spring migration, we used the great-circle-distance between 2 points from the Vincenty ellipsoid method (Hijmans 2019). We excluded 2 outlier GPS points during the breeding season (1 for bird 77968, 1 for bird 81324) that were deemed erroneous due to their extreme distance from other points clumped on the breeding grounds (327 and 615 km away) and a reduced number of satellites for those GPS fixes (3 satellites, compared to 5 or more for most other points). Maps were made in ArcMap 10.7.1.

Social network methods

We censused sparrows multiple times per week during winter at the UCSC Arboretum by identifying all color-banded sparrows and marking their location from a gridded map with 100 m^2 cells. We counted birds as associating with each other if they were in the same flock in approximately a 100 m^2 cell. From these data, we built a social network for a given season, following methods from Shizuka et al. (2014). We modified these methods to include all birds seen more than 5 times in the focal field season. We used flocking data from before 1 April of each year because social behavior changes prior to spring migration. With the flocking data, we built undirected social networks with edge weights representing an association index (Simple Ratio Index: Cairns and Schwager 1987). We detected social communities in the network using the Louvain method (Csardi and Nepusz 2006). Our past work on this population suggests that co-membership in the same social community suggests high probability of across-year social relationships (Shizuka et al. 2014). All analyses were performed in R 4.2.0 (R Core Team 2022).

Results

There were 96 Golden-crowned Sparrows in the 2016–2017 social network, with 4 different social communities (community size range = 17–30: Fig. 1). All 4 tagged birds had summer

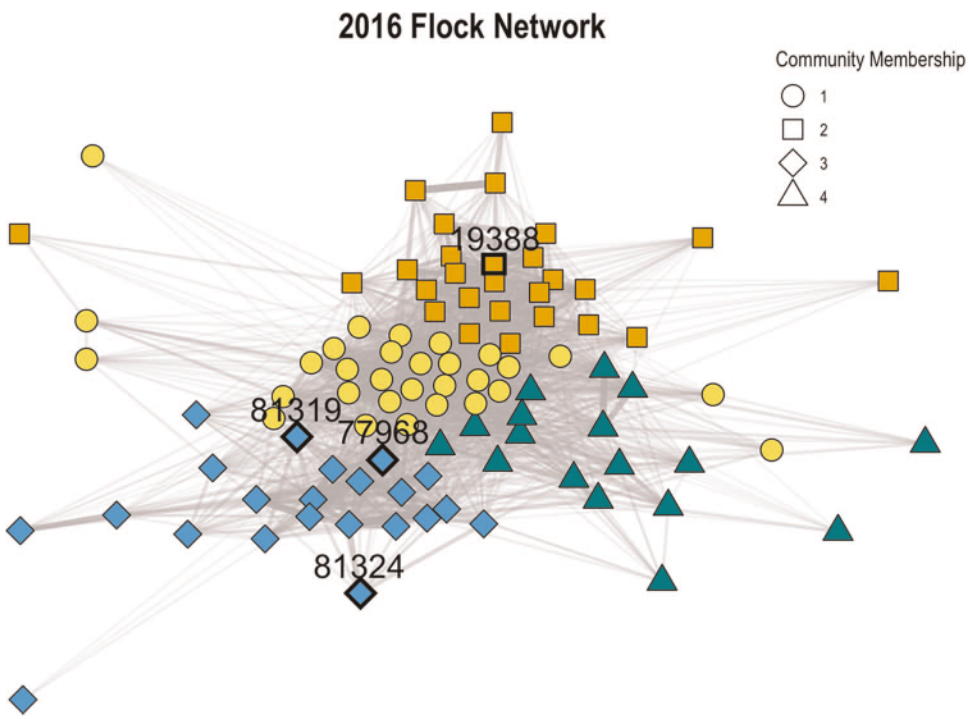

Figure 1. The Golden-crowned Sparrow social network at the UCSC Arboretum, Santa Cruz, California, for the winter of 2016–2017 (representation is not spatially explicit). The 4 communities are shown in different symbols, and each shape represents an individual. The thickness of the lines connecting individuals is proportional to how frequently birds associated with each other weighted by the number of times each bird was seen in total (a Simple Ratio Index). The 4 individuals with GPS tag data are highlighted in black edging with their band IDs. Birds 81324, 77968, and 81319 have GPS data corresponding with this year, but GPS data for bird 19388 is from the following year (2018).

locations far away from each other, with the closest 698 km apart and the most distant 1,837 km apart (Fig. 2; Table 1). A video summary of migration routes is available online (https://doi.org/10.6084/m9.figshare.24502465.v1). The 3 birds in 2017, all from the same social community (Fig. 1), had very distant breeding territories, showing no evidence that winter social relationships were associated with proximity of summer breeding territories. Note that the scale on which birds overlap during the winter is tens of meters, while in the summer all sparrows were many hundreds of kilometers apart. Bird 19388, which we tracked in 2018, was also present on the wintering grounds at the Arboretum the previous year with the 3 other birds (2017) but belonged to a separate social group (Fig. 1). With the precision from the GPS data, we could even see potential nesting locations from the density of points in 1 location (Supplemental Fig. S4).

Discussion

The GPS-tagged Golden-crowned Sparrows used breeding grounds that were widely separated from each other, showing entirely different social connections on winter versus summer grounds. In this species, migratory connectivity appears to exist at broad regional scales (Seavy et al. 2012, Cormier et al. 2016, Iverson et al. 2023) but not at the level of social groups. While we have a limited sample size for the location of the sparrows' breeding territories, the social affiliations from winter are comprehensive. If birds in the same winter community went to similar breeding grounds, we should have seen some indication with breeding locations closer to each other, rather than hundreds of kilometers apart.

Our findings increase the understanding of causes behind across-year social stability in wintering passerine birds. Shizuka et al. (2014) and

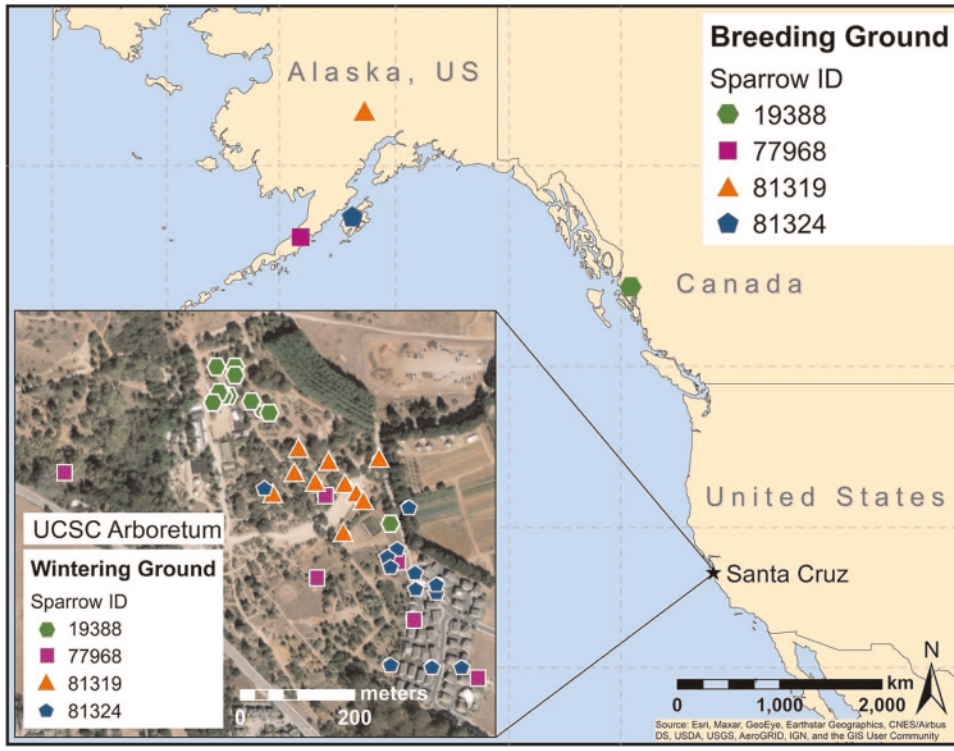

Figure 2. Breeding (main map) and wintering (inset map) locations for each bird. Tag data for bird 19388 was from 1 year after (2018) the other 3 birds (2017), but all birds were present in winter 2017. Symbol representation of each point is not to scale, and breeding ground areas are vastly smaller than each symbol. The points shown at the UCSC Arboretum (36.98230, −122.05987) were from the GPS tags shortly before the birds left for spring migration, not the birds' home ranges for the winter season. To see the stable winter communities detected with social network analysis, see Fig. 1. For mean breeding season GPS coordinates, see Table 1. Dashed lines represent major latitude and longitude lines.

Madsen et al. (2023) established that Golden-crowned Sparrows maintain winter social connections across years and that these social preferences are not just based on space use. Our findings indicate these birds form and maintain long-term social relationships in the winter independent of social relationships in the breeding season. If birthplace on the breeding grounds was a strong influence for initial winter social connections, we would expect to have many highly related individuals in the population; yet, Arnberg et al. (2015) found kinship in Golden-crowned Sparrows was unrelated to social connections in our study population. This suggests across-year social stability involves long-term social memory bridging annual migration, rather than maintenance of social relationships constantly throughout the year. Thus, across-year social stability is not a byproduct of social carryover across seasons as demonstrated for some resident species (e.g., Firth and Sheldon 2016).

Our results add to ongoing research on whether and how migratory songbirds may maintain long-term social relationships despite long-distance seasonal movements: research that has been enabled by recent advances in miniaturized animal tracking technology. In some species, evidence suggests little maintenance of social associations during or after migration (e.g., Purple Martins, *Progne subis*: Stutchbury et al. 2016). When social associations are maintained across years despite long-distance migration, evidence has accumulated for 2 alternative mechanisms: (1) maintenance by proximity, and (2) maintenance by memory across years despite spatial separation during alternate seasons. The former is exemplified by European Bee-eaters that undergo transcontinental migration in social groups

Table 1. Migratory and breeding location parameters for 4 Golden-crowned Sparrows. We might expect that breeding locations closer to wintering sites would allow the birds to arrive more quickly. However, spring migration distance appeared unrelated to how many days it took the birds to migrate and even suggested a negative relationship. Due to similar migration departure dates in both spring and fall, time on the breeding territory appeared to be constrained by the duration of spring migration (for additional visualization, see Supplemental Fig. S5).

Bird ID	Sex	Mean mass (g)	Year	Spring migration start date	Migration distance (km)	Days on spring migration	Dates on breeding territory	Days on territory	Mean breeding location (lat, long)
77968	M	34.3	2017	23 Apr 2017	3,986	32	25 May 2017 – 8 Sep 2017	106	56.72763, −158.2483
81319	F	31.8	2017	3 May 2017	3,768	49	21 Jun 2017 – 9 Feb 2017	73	62.34368, −152.7031
81324	F	30	2017	23 Apr 2017	3,371	36	29 May 2017 – 5 Sep 2017	99	57.71666, −153.7152
19388	F	32.5	2018	5 Apr 2018	2,093	62	5 Jul 2018 – 5 Sep 2018[a]	62+	(54.25583, −129.2881)

(Dhanjal-Adams et al. 2018) and Barn Swallow (*Hirundo rustica*) pairs staying together throughout the year (Arizaga et al. 2015). Golden-crowned Sparrows provide an example of the latter, showing that across-year social stability is season-limited. The new era of lightweight tracking technologies opens avenues to learn when social cohesion in migratory birds may evolve to be maintained by continued spatial proximity or memory. To this end, it could be useful to collect data examining across-year social fidelity in species for which we have data on migratory connectivity. For the converse, it may be particularly fruitful to test for proximal migration in other migratory birds that have been shown to have social memory across years, such as species that retain long-term memory of neighbor songs (Hooded Warblers, *Setophaga citrina*: Godard 1991; Dusky Warbler, *Phylloscopus fuscatus*: Forstmeier and Balsby 2002). These complementary approaches would help us start to unravel how unusual or common it is for birds to rely on long-term memory to maintain social connections in disparate seasons.

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All methods complied with Federal and California State regulations under permits to B. Lyon and D. Shizuka and were approved by the UCSC Institute for Animal Care and Concern (IACUC; Animal Welfare Permit Number Lyonb1808) and University of Nebraska Lincoln IACUC (Animal Welfare Permit Number Shizuka1626).

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