



Loss of flockmates weakens winter site fidelity in golden-crowned sparrows (*Zonotrichia atricapilla*)

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Animal social interactions have an intrinsic spatial basis as many of these interactions occur in spatial proximity. This presents a dilemma when determining causality: Do individuals interact socially because they happen to share space, or do they share space because they are socially linked? We present a method that uses demographic turnover events as a natural experiment to investigate the links between social associations and space use in the context of interannual winter site fidelity in a migratory bird. We previously found that golden-crowned sparrows (*Zonotrichia atricapilla*) show consistent flocking relationships across years, and that familiarity between individuals influences the dynamics of social competition over resources. Using long-term data on winter social and spatial behavior across 10 y, we show that i) sparrows exhibit interannual fidelity to winter home ranges on the scale of tens of meters and ii) the precision of interannual site fidelity increases with the number of winters spent, but iii) this fidelity is weakened when sparrows lose close flockmates from the previous year. Furthermore, the effect of flockmate loss on site fidelity was higher for birds that had returned in more than 2 winters, suggesting that social fidelity may play an increasingly important role on spatial behavior across the lifetime of this migratory bird. Our study provides evidence that social relationships can influence site fidelity, and shows the potential of long-term studies for disentangling the relationship between social and spatial behavior.

migration | social networks | social affiliations | site fidelity | winter ecology

Site fidelity, the tendency to repeatedly return to the same location, is a feature of many animal populations (1, 2). Site fidelity can involve remarkable abilities of spatial memory and navigation and is an influential component of habitat selection, with important implications for population-level processes (3, 4). Site fidelity may range from returning to the same general region to returning to a specific home range or territory (1, 5). As an extreme example of site fidelity, many migratory animals travel thousands of miles between winter and breeding sites and often return to the same location (5). Breeding site fidelity in particular is common among birds. For example, 70% of returning male red-winged blackbirds maintain the same breeding territories across years (6), and over 70% of eastern bluebirds return to the same nesting cavity (7).

Wintering site fidelity is also often recognized as a feature of migratory populations (8–10), yet we know comparatively little about the factors that influence the degree of winter site fidelity. Migratory animals may exhibit high site fidelity if familiarity with a location provides benefits. For example, songbirds return to familiar winter sites to leverage their local knowledge of resources (e.g., Kirtland's warblers, 11). Site fidelity may also be influenced by social benefits, such as reduced aggression between familiar territorial neighbors ["dear-enemy effect" (12, 13)] or flockmates (14), and increased efficiency of social foraging with familiar partners (15, 16). Social influences on foraging behavior may result in high spatial overlap between social group members and low overlap with nongroup members (17, 18), or in extreme cases, may result in group territory defense (19, 20). While shared space use could result from sharing high-quality locations, benefits of long-term social relationships could potentially drive site fidelity because social partners might be reliably found at a given location.

Disentangling the role of social versus nonsocial benefits on site fidelity is complicated by the fundamental relationship between sociality and space (21). That is, social interactions must occur in space, whether individuals come into direct contact or interact over relatively longer distances with signals (22, 23). This creates a causal conundrum for investigating spatial and nonsocial influences on social behaviors because causality could come from either spatial or social processes. Site fidelity can drive social interactions when individuals incidentally interact with others simply because they are in close spatial proximity due to use of a shared resource or area (24–26). In this case, the

Significance

Animals may be faithful to specific locations (site fidelity) due to the benefits of finding resources in familiar spaces or due to maintaining familiar flockmates. However, separating social fidelity and site fidelity remains challenging. To test if social relationships can drive high site fidelity, we examined natural turnover events in a long-term winter study population of migratory golden-crowned sparrows. This population maintains stable flocking partnerships across years, and we show that returning individuals generally increase winter site fidelity with each subsequent winter. However, we found that losing previous flockmates reduces otherwise extraordinary winter site fidelity, particularly among older birds. Our results demonstrate the close connection between social and spatial dynamics, and provide evidence that social fidelity can promote site fidelity.

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architecture of the environment and heterogeneity in resource density across a landscape can create nonrandom social structure (26–29). Conversely, factors that promote social associations will necessarily affect individual patterns of space use. For example, collective movement of social group mates (16), matching foraging activity with close social partners (15, 30), and foraging in areas with familiar individuals to decrease aggression (31) all show social influences on individual space use. Thus, it is often unclear what drives site fidelity: Are individuals faithful to a location, or are they faithful to social partners at a location?

Separating the effects of social preferences versus shared spatial preferences has relied on a number of techniques. Myriad studies have developed statistical frameworks to either control for or quantify the spatial basis of social structure (32–35). However, such methods cannot determine the causal relationship between social affiliations and shared space use. Experiments manipulating the presence or absence of individuals (e.g., removal, translocation) or resource distributions have addressed these questions directly by asking whether social changes result in space use changes and vice versa (30, 36–38). However, such experimental studies are logistically challenging, often impractical, and may induce different responses than natural losses such as death or emigration (39, 40). Here, we use an approach leveraging long-term observations of a wild population to disentangle the effects of sociality on site fidelity. Long-term demographic data contain information on natural turnover of individuals in a population—e.g., deaths, births, emigration, and immigration. These demographic processes interact with social structure by adding and removing individuals, thereby changing the density, identities, and strengths of connections in flocks over time (39). We show that tracking changes in site fidelity along with changes in flockmates across lifetimes of individuals provides evidence for how social relationships drive site fidelity.

We examined the magnitude of site fidelity in a long-term study of golden-crowned sparrows (*Zonotrichia atricapilla*), and used naturally occurring turnover of individuals to ask whether winter site fidelity was affected by the loss of flockmates from the previous year. Golden-crowned sparrows are long-distance migrant birds that breed in Alaska and western Canada and winter along the western United States (41, 42). During the winter, these sparrows do not defend territories, instead forming foraging flocks with dynamic memberships that change on the order of minutes. However, flock comembership measured across a season reveals “social community” structures in the social network, in which socially and spatially discrete clusters of birds flock together more often than with others (35). These flocking associations are not driven by kinship (43). Among birds that return to the wintering population across years, social associations bridge sequential winter seasons: While all birds migrate to breeding grounds hundreds

or thousands of kilometers away each spring, returning birds flock with the same individuals between years more often than expected by their degree of overlap in home ranges (35). As a result, the community structure of this winter social network can show similar spatial signatures between years (35). Stable flockmate relationships may have several potential benefits in this species. For example, prior experiments showed that familiarity among flockmates reduces aggressive interactions (14) and individuals that are more dominant are more likely to return in the following year (44). However, whether these stable social relationships are based on fidelity to flockmates or fidelity to a specific home range is unknown.

Here, we used 10 y of flock observations and demographic censuses to track winter space use and social associations for individual sparrows, comparing these associations between consecutive years. We first determined the spatial fidelity of individual birds to their wintering site, as measured by the shift in the centroids of home ranges between years. Next, we asked whether individual attributes such as the number of winters spent on the study site, sex and dominance status affected the precision of interannual site fidelity. Finally, we asked whether loss of close flockmates (i.e., frequent flockmates from the previous year) affected site fidelity.

Results

Long-Term Site Fidelity. On average, 46.8% of individuals [average $N = 111.6 \pm 13.1$ (SEM) per year over 10 y] returned to our small study site (approx. 6 ha). Returning individuals exhibited extreme fidelity to their winter home ranges, with an average interannual shift in home range centroid of 27.3 ± 1.5 (SEM) m from 2009 to 2019 (*SI Appendix, Fig. S2A*). There was some annual variation in the shift of home range centroids, with the winter of 2018 to 2019 showing the largest shift in home range centroids [40.4 ± 1.5 (SEM) m]. This increase in home range shift for the 2018 to 2019 winter season is likely attributed to habitat loss in the spring/summer of 2018, when vegetation was removed from a contiguous patch of habitat comprising approximately 13% of the study site (*SI Appendix, Fig. S1*).

Ontogeny of Site Fidelity. We found that site fidelity increased across an individual’s lifetime. Returning birds decreased centroid shifts as they returned over multiple subsequent winters (Fig. 1*B* and Table 1). We did not detect any significant differences in centroid shifts with sex or dominance score (Table 1).

Effect of Flockmate Loss on Site Fidelity. To explore the effect of flockmate relationships on winter site fidelity, we first identified “strong flockmates” for each bird as those within the 90th percentile of an individual’s association strengths in each year (see threshold

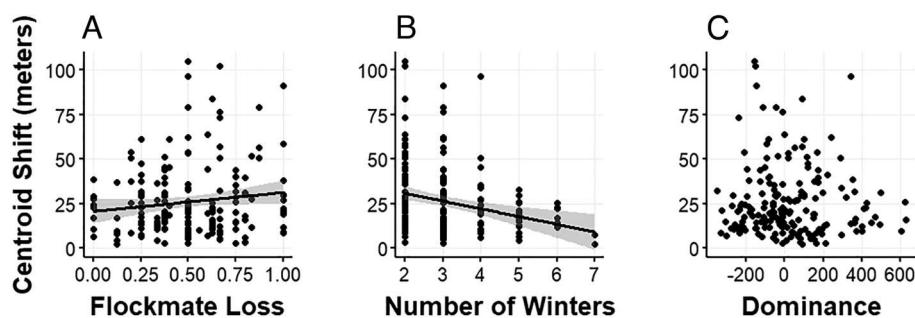


Fig. 1. Home range centroid shift from the previous year by (A) flockmate loss index, (B) number of winters, and (C) dominance. Shaded regions represent 95% CIs. $N = 181$.

Table 1. Factors affecting the degree of home range centroid shift of a) all individual golden-crowned sparrows between subsequent winters ($N = 181$), b) golden-crowned sparrows returning in their 3rd or greater winter ($N = 114$), and c) golden-crowned sparrows returning in their second winter ($N = 67$)

a) All sparrows ($N = 181$)					
Fixed Effects	Estimate	Lower CI	Upper CI	P	
Intercept	28.55	17.35	40.61	<0.001	
Flockmate loss	20.62	5.19	34.49	0.0060	
Number of winters	-4.19	-6.66	-1.59	0.00090	
Sex	1.14	-5.14	7.74	0.76	
Dominance	0.0017	-0.014	0.018	0.83	
b) Sparrows in 3rd+ winter ($N = 114$)					
Fixed Effects	Estimate	Lower CI	Upper CI	P	
Intercept	9.58	1.31	18.95	0.030	
Flockmate loss	28.66	12.80	45.73	0.0013	
Sex	-2.34	-10.99	6.06	0.58	
Dominance	-0.00028	-0.022	0.019	0.97	
c) Sparrows in 2nd winter ($N = 67$)					
Fixed Effects	Estimate	Lower CI	Upper CI	P	
Intercept	22.89	6.65	40.16	0.007	
Flockmate loss	12.86	-17.66	43.80	0.39	
Sex	6.35	-5.35	18.05	0.28	
Dominance	0.0033	-0.027	0.034	0.83	

selection, *SI Appendix, Fig. S3*). This resulted in a network where each individual was connected to an average of 10.5 ± 0.2 (SEM) flockmates. We then quantified social flockmate loss as the proportion of an individual's flockmates present in 1 y that were not seen in the population in the next year. Birds lost an annual average of 52.4 ± 1.5 (SEM)% of close flockmates over the entire study period (Fig. 1*B*). One of the largest average losses of close flockmates occurred in 2018 to 2019 [72.1 ± 2.9 (SEM)%], likely due to individuals moving off our study site due to the habitat alteration (*SI Appendix, Fig. S2B*). Excluding this year did not substantially change our results (*SI Appendix, Table S1*). In the last year they were sighted, lost flockmates did not differ in demographic characteristics from the remaining birds (*SI Appendix*).

Flockmate loss was a significant predictor of home range centroid shift ($P = 0.006$); i.e., individuals that lost more flockmates had a greater home range centroid shift (Fig. 1*A* and Table 1). This effect of flockmate loss could be modulated by the establishment of long-term social relationships. If so, birds in their second winters should be less affected by the loss of their flockmates from the previous year compared to birds that have returned for multiple winters. To assess this, we conducted separate analyses for birds returning in their 3rd winter or greater and birds returning for their second winter. This revealed that the effect of flockmate loss on home range centroid shift is strong for birds returning in their 3rd winter and on ($P = 0.001$, Table 1*b* and Fig. 2*A*), but birds returning for their second winter showed no significant relationship between centroid shift and flockmate loss ($P = 0.39$, Table 1*c* and Fig. 2*B*). There was a difference in sample sizes between these models ($N = 114$ 3rd+ winter, $N = 67$ 2nd winter) that may have an effect on the difference in significance between these models.

Discussion

Many migratory birds show high site fidelity, both during the breeding season (5, 45) and nonbreeding season (46, 47). However, it remains unclear if such precise fidelity is a result of an attachment to a specific location or to the social relationships that occur there.

Previous studies have shown that spatial and ecological factors such as shifts in local resource availability influences the degree of site fidelity (1). In contrast, our findings provide strong evidence that sociality can promote site fidelity—birds that lost close flockmates were more likely to shift their space use from previous years (Fig. 1*A*). Importantly, this effect appears to be driven by birds that returned in 3 or more winters (Fig. 2). A limitation of our analysis is that we cannot rule out that birds in their second year might show a significant relationship between flockmate loss and centroid shift given a larger sample. However, the pattern we see for multi-year returners is consistent with previous work at our study site showing that birds flock with the same individuals across years, even after statistically controlling for the degree of spatial overlap in home range (35). In this study, we leveraged natural patterns of changes in social environment of an individual through patterns of flockmate loss caused by demographic processes to understand social effects on spatial behavior. Thus, while this study remains observational, it provides robust evidence that social fidelity influences spatial behavior.

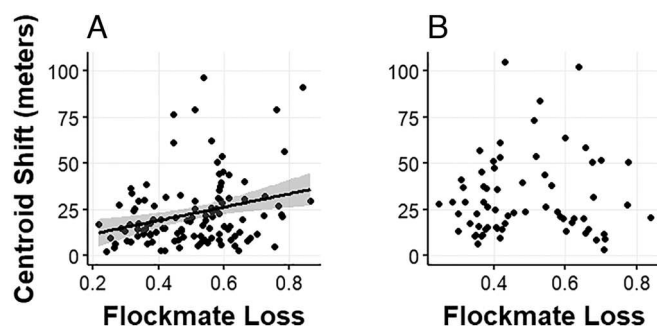


Fig. 2. Home range centroid shift from previous year in (A) birds returning for 3rd or greater winters ($N = 114$) and (B) birds returning for their second winter ($N = 67$). GLMM showed that (A) the relationship between centroid shift and flockmate loss was significant for birds returning in 3+ winters, but (B) not birds returning for their second winter. Shaded regions around regression lines represent 95% CIs.

Golden-crowned sparrows in our study population maintain remarkable site fidelity to their winter site: The baseline shift in home range centroids averaged only 27.3 ± 1.5 (SEM) m between years. This degree of within-site fidelity aligns with other nonbreeding studies that quantified across-year site fidelity shifts in a long-distance migrant (46, 48) and may be a more general pattern than previously appreciated. This precision is striking compared to the thousands of kilometers that these birds travel between winter and breeding grounds (49, 50). We also found that the precision of winter site fidelity increased substantially with the number of winters a bird has spent at the winter site (Figs. 1*B* and 2*A*). This observation is consistent with prior displacement experiments from other *Zonotrichia* winter populations in California, which reported birds returning to wintering sites from as far as Maryland, USA (51–53). In those experiments, return rates to winter sites were highly dependent on age—return rates increased substantially for birds that were displaced during or after their second winter at the site (51–53). However, while the previous golden-crowned sparrow studies quantified site fidelity at the level of the study plot, our work tracks site fidelity at the scale of the home range and shows that precision of site fidelity increases across years. This increase in the degree of site fidelity as a bird returns across multiple winters suggests that the benefits of returning to the same location, and especially interacting with the same flockmates, likely accumulates across an individual's lifetime (54).

Returning to the same social group can confer many benefits to individuals that have well-established social relationships. Golden-crowned sparrows have high social fidelity (35) and social recognition (14), which are hypothesized to decrease aggressive interactions and their associated costs. Because competitive interactions between strangers may be more costly than with group-mates (14), birds that have lost close flockmates may shift their home range to avoid previous foraging grounds where unfamiliar birds have replaced those flockmates. Interestingly, these shifts are not likely a result of being unable to defend a previously occupied area because dominance score did not affect interannual site fidelity. Notably, *Zonotrichia* sparrows are not known to defend territories on their wintering grounds although aggressive interactions alter foraging behaviors (14, 48). Instead, birds may spend more time close to their remaining flockmates to avoid aggressive interactions with strangers, which may contribute to higher home range shifts than usual. Even in the absence of effects of aggressive interactions, social loss may lead to centroid shifts if birds drift spatially after losing flockmates that “anchored” them to their previous range. In the absence of any social connections tying them to a particular area, they may simply be less loyal to that location—i.e., site fidelity is a byproduct of high social fidelity. These mechanisms are also not mutually exclusive—birds do clearly drift spatially after a social loss, and they do retain remaining flockmates from previous years after losing close flockmates—although the extent that each affects the resulting space use is not immediately clear. Spatial displacement following social disturbances suggests that the relative importance of associating with flockmates can outweigh the importance of occupying specific locations.

An important caveat to this discussion is that habitat may have additional effects on both space use and social associations. Our study site is remarkably stable between years in resource distribution as it is a cultivated arboretum. Nonetheless, there are potentially small changes in resource distribution and cover between years, but we cannot draw conclusions about long-term patterns of resource density because we have not systematically tracked habitat features over the 10-y study period. However, the final year of our study included an unusual habitat loss event that resulted in the removal of 15.4% of cover on the site (*SI Appendix*). This event resulted in both increased centroid shifts and increased

flockmate loss (*SI Appendix*, Fig. S2), highlighting the potential for the distribution of cover and resources to interact with social benefits of familiar flockmates and within-site space use.

Here, we showed that individual responses to flockmate loss can be extracted from long-term data on natural populations, providing insights into the inner workings of social and spatial dynamics. Social and spatial preferences overlap in many cases (55), and a central goal in socioecology is to understand the relative importance that each plays in the spatial structuring of populations. Social fidelity can arise in populations when there are benefits to retaining the same flockmates [e.g., shared information about resources (56, 57), increased vigilance (58), decreased stress (54)]. Site fidelity (i.e., returning to the same site) is beneficial for migratory birds when familiarity with a site allows them to exploit resources in a stable environment (5), but can also limit a population's ability to change space use to escape diminishing habitat quality (59) or newly unstable environments (60). Social-spatial dynamics are increasingly recognized as important drivers of ecological patterns such as disease spread (61), responses to climate change (62), and population dynamics (4). Our work shows that social losses can alter site fidelity, demonstrating one key way in which social environment can affect spatial processes such as dispersal and habitat choice (63, 64).

Materials and Methods

Golden-crowned sparrows were monitored at the University of California Santa Cruz Arboretum from 2009 to 2019 as part of a long-term research study on their winter social behavior. We conducted banding sessions each season, and birds were fitted with colored plastic and numbered metal leg bands in unique color combinations upon first capture. We were not able to reliably identify the age of the birds, but with intensive banding of the entire population, we are likely able to band most birds during their first winter at the site. However, we cannot completely rule out that some of the unbanded birds we capture are birds missed in the previous year or that moved to the study site from another area. Therefore, we used the year a bird was banded as an estimate of their first winter spent at the study site. We collected blood samples from the ulnar vein of the wing, and used sex-linked molecular markers [CHD-W/Z primers (65)] to determine the sex of each bird. Dominance interactions were recorded at seed piles, and we used the proportion of wins and losses to determine Elo scores, a measure of dominance rank that represents the likelihood an individual will win based on past performance (66–70). Foraging flocks were surveyed throughout the Arboretum by recording the identities of all banded birds in a flock (defined as all birds within a 5-m radius), and locations were determined using a reference map of 10 m × 10 m grid cells (35). Observations at seed piles could draw birds out of their social groups and home ranges, so we excluded them from our analysis of flocking relationships and home range centroids.

To ensure we were observing winter flocking behaviors rather than interactions between transitory individuals on migration, we limited observations to between November 1 (when most birds had arrived from breeding grounds) and March 1 [when winter flocks begin to break apart and birds begin migration (35)]. We further limited our sample to birds that had been sighted 3 or more times throughout this period to remove transient individuals and to increase accuracy of spatial statistics. We then inferred social associations from cooccurrences in foraging flocks and calculated the simple ratio index (SRI) to represent association strength (71). SRI is the likelihood that two individuals are sighted together out of all possible sightings, which ranges from 0, meaning a pair of birds were never in the same flock, to 1, meaning a pair of birds were always in the same flock.

Overall Site Fidelity. We used locations from our map of 10 m × 10 m grid cells to establish coordinates for each sighting of an individual, which we transformed into Euclidean space. For each year, we calculated individual home range centroids by taking the average Euclidean coordinates of sightings. We then calculated the interannual shift in home range centroid for each bird by calculating the Euclidean distance between the focal year centroid and the centroid from the previous year. Hereafter, this will be referred to as the centroid shift or spatial shift.

Quantifying Flockmate Loss. To quantify flockmate loss for each bird, we first identified their "close flockmates" as birds with which they shared an SRI (association strength) in the 90th percentile of that individual's associates for each year. This threshold was chosen to isolate the strongest flockmates while preserving as many focal individuals as possible (*SI Appendix*, Fig. S3). We then calculated the proportion of close flockmates that were lost from the previous year due to demographic turnover, giving us an index where 1 meant all close flockmates from the previous year were lost and 0 meant no close flockmates were lost.

Effect of Flockmate Loss on Site Fidelity. We used generalized linear mixed models (GLMM) to ask how losing flockmates affected interannual centroid shifts. Models were fitted using Markov chain Monte Carlo methods (R function *MCMCglmm*, 72). In the primary model, centroid shift was the dependent variable, the index of flockmate loss was the independent variable, number of winters, sex, and dominance were included as fixed effects, and year was included as a random effect to account for the degree of variation between years in sampling effort and habitat change (*SI Appendix*). Although it was possible for birds to be present in multiple years, it was not appropriate to include individual identity as a random effect because there were nearly as many unique individuals as there were observations in the final dataset. However, an alternative model including individual identity as a random effect is provided in *SI Appendix* and shows largely consistent results. To ask whether the effect of flockmate loss on centroid shift differed for older, more established birds, we further subset the data into two sets: birds that had returned for their second winter and birds that had returned

for 3 or more winters. We set this cutoff because birds returning after only 1 y at the wintering grounds had less time to establish a winter home range and form strong social bonds compared to birds who had spent a number of winters on site. For the two resulting GLMMs, centroid shift was the dependent variable, flockmate loss, sex, and Elo score were fixed effects, and year was a random effect.

Data, Materials, and Software Availability. Text files and R scripts' data have been deposited in Loss of Social Partners Weakens Winter Spatial Fidelity in Golden-Crowned Sparrows (*Z. atricapilla*) (<https://doi.org/10.5061/dryad.dv41ns22p>) (73).

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