PNAS COMMENTARY

Social, not spatial, fidelity underlies between-year winter site fidelity in a migratory bird

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Site fidelity is one remarkable aspect of migration, with animals returning to the same general regions, or even specific territories, year after year. Site fidelity may be driven by site familiarity when an animal benefits from prior knowledge of the local landscape and resources. Site fidelity may also stem from long-term social relationships, with individuals repeatedly returning to the same location because of the social benefits of associating with familiar individuals, such as reduced aggression and increased feeding (1). Disentangling the relationship between spatial fidelity and social fidelity has been a long-standing chicken-and-egg dilemma in the field of animal social networks: Do two individuals associate incidentally because they are drawn to the same location or do two individuals share space because they are drawn to each other? Additionally, much of what we know about spatial and social fidelity comes from mated pairs in the breeding range; mechanisms of winter site fidelity are less well understood. In the current issue of PNAS, Madsen et al. (2) elegantly apply network modeling techniques to long-term resighting data from a wild population of golden-crowned sparrows to demonstrate that social fidelity underlies winter site fidelity in this migratory population.

Madsen et al. (2) monitored a population of golden-crowned sparrows (*Zonotrichia atricapilla*) in a 6-ha arboretum in California over a 10-y period, during the winters of 2009 to 2019. Using color bands to identify and resight individual birds each winter, the researchers delineated each individual's home range and changes in space use over time. Remarkably, after completing migrations of hundreds or thousands of kilometers, sparrows returned to the field site and occupied home ranges within tens of meters of the previous year. This scale of winter site fidelity has been observed before (e.g., ref. 3), but the combination of fine-scale repeatability in home range locations between years and remarkable consistency of social relationships at this site (4) set the stage for a meaningful analysis of the effect of social relationships on site fidelity.

The researchers leveraged the individual fidelity with natural demographic turnover (year-to-year changes in the population due to births, deaths, immigration, and emigration) to test the relationship between social and spatial fidelity. This approach is a unique strength of the study. Previous methods for disentangling social fidelity from spatial fidelity include statistical analytical tools that are unable to determine causality (5) or simulated and experimental manipulations that may not always recreate natural conditions (6). Instead, by quantifying the spatial effect of natural turnover in social partners, the researchers solved the "causal conundrum" between site fidelity and social fidelity under natural conditions.

Madsen et al. (2) used long-term data of individual space use and social relationships, in the context of year-to-year demographic changes, to test whether social or spatial fidelity underlies between-year winter site fidelity. If sparrows continued to use the same home ranges despite the loss of flockmates between years, this result would suggest the sparrows were faithful to a particular location and that site fidelity did not depend on social relationships. However, if sparrows altered their space use after losing close flockmates, this result would suggest that maintaining stable social relationships was the primary driver of habitat selection the previous year. Madsen et al. (2) found support for the latter prediction. Sparrows that lost more close flockmates from the previous year (either due to death or emigration) showed the greatest shifts in home range location. A sparrow's home range was concentrated in a particular area because of the presence of other individuals there, and the loss of social relationships eroded site fidelity. While the influence of year-to-year changes in habitat was not evaluated, Madsen et al. (2) provide strong evidence that fidelity to a given site is at least partially driven by social associations. This key result demonstrates that social factors can play an important role in shaping animal behavior and movement (7). Furthermore, this study demonstrates the utility of longitudinal, observational studies to address long-standing and impactful research questions in ecology (6).

Madsen et al. (2) found that both spatial and social fidelity changed over time. Sparrows' spatial fidelity increased the more winters they spent at the site. That is, the centroid of their home range shifted less with each subsequent year. While other studies have shown sparrow return rates are greater among older birds (8), Madsen et al. (2) show that the precision of site fidelity—on the scale of tens of meters—increases across an animal's lifetime. The authors propose that site fidelity precision may increase with age because the benefits of interacting with the same individuals increase over time. For instance, Madsen et al. (2) found that the loss of close flockmates only shifted the home range centroid of

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sparrows that had already spent at least two winters at the site; second-winter sparrows were unaffected by flockmate loss. Thus, social relationships are important for older birds but not necessarily for those returning for their second winter. It is possible—though not explored in the current paper—that the length of the social relationship plays a key role here. Birds returning to the site across multiple winters may have established multiyear relationships and were more affected by the loss of these flockmates than the second-winter birds with their single-year relationships.

Madsen et al. elegantly apply network modeling techniques to long-term resighting data from a wild population of golden-crowned sparrows to demonstrate that social fidelity underlies winter site fidelity in this migratory population.

Site fidelity has critical implications for population-level processes. Strong site fidelity may isolate migratory populations and limit gene flow. Populations faithful to a particular location may also be less likely to change locations under adverse conditions, making them more susceptible to the effects of habitat degradation, loss, or change. Thus, understanding the mechanisms underlying site fidelity—that is, whether it is determined by features of the location itself or the social relationships found there—could improve predictions of population-level responses to habitat alterations. Notably, in their supporting information, Madsen et al. (2) describe habitat loss before the final winter of their study, when a parking lot was built on part of the field site. As a result, sparrows in the 2018 to 2019 winter demonstrated the largest shifts in home range centroids and one of the largest average losses of close flockmates of the study's duration. The authors suggest that sparrows likely emigrated from the field site in response to habitat disturbance. This result demonstrates that habitat quality likely still contributes to winter site fidelity because there was greater flockmate loss after the habitat disturbance. Further, this result shows how habitat disturbances can impact social networks by altering rates of demographic turnover (6). Therefore, it is important to consider how habitat disturbances not only disrupt an individual's physical space, but also the potential benefits of an individual's social relationships. Understanding the effect of ecological changes on social systems will help predict the resilience of social populations to anthropogenic change (6).

The lives of migratory birds may be far more socially influenced than previously thought. In this paper, golden-crowned sparrows return from breeding in Alaska and Canada to the same social communities in California year after year and these social associations influence site fidelity at the scale of the home range. Further, the individual relationships formed and maintained on the wintering grounds are not a function of relatedness (9) and do not carry over to the breeding season, with winter flockmates breeding in distant locations (10). This elegant analysis of sparrows at a long-term field site demonstrates that social associations persist across years and that the loss of a close social relationship alters space use, providing evidence that social fidelity can influence site fidelity. These results amplify how little is known generally about the role of social interactions in the individual movement decisions that underlie full annual cycle distributions. At the same time, there is a growing recognition that migration itself may be far more of a social behavior than previously considered (11, 12).

Social interactions among migratory animals are poorly understood (11), but they likely shape movement decisions throughout the annual cycle during migration (11, 12), breeding (13), and wintering periods, as Madsen et al. (2) now demonstrate. Big-picture, and truly fascinating, questions about the social relationships of most migratory species remain open: How do they affect space use, and vice versa? How common and impactful are they? Are they more impactful during certain stages of the annual cycle? How do they impact migratory routes, timing, or success (11)? Do they influence, or are they influenced by, the migratory connectivity of populations (3, 10)? What are their functions and consequences? Do they persist between seasons and years? Do they vary with age or between sexes? How resilient or sensitive are they to ecological change? How are they influenced by demographic processes and how do they influence demography (6)? Is it important to consider social relationships for effective conservation and management (13)? By describing the influence of social relationships on a migratory bird's winter site fidelity, Madsen et al. (2) reveal the need for and importance of further research on the social relationships of migratory animals. Finally, if social relationships are an important component of habitat selection throughout the annual cycle, even outweighing environmental features, then work is urgently needed to inform habitat restoration and management during non-breeding as well as breeding periods.

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