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LETTER

Across-year social stability shapes network structure in wintering migrant sparrows

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Abstract

Migratory birds often form flocks on their wintering grounds, but important details of social structure such as the patterns of association between individuals are virtually unknown. We analysed networks of co-membership in short-term flocks for wintering golden-crowned sparrows (*Zonotrichia atricapilla*) across three years and discovered social complexity unsuspected for migratory songbirds. The population was consistently clustered into distinct social communities within a relatively small area (~ 7 ha). Birds returned to the same community across years, with mortality and recruitment leading to some degree of turnover in membership. These spatiotemporal patterns were explained by the combination of space use and social preference – birds that flocked together in one year flocked together again in the subsequent year more often than were expected based on degrees of home range overlap. Our results suggest that a surprising level of social fidelity across years leads to repeatable patterns of social network structure in migratory populations.

Keywords

Flocks, group living, MRQAP, social networks, spatial communities, temporal stability, winter ecology.

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INTRODUCTION

The social structure of animal populations – e.g. the size, composition and stability of social groups – is a fundamental aspect of social evolution (Alexander 1974). In birds, studies of breeding systems have shown that ecological conditions can favour different social structures ranging from simple pairs to cooperative breeding groups (Emlen 1982). The winter social structure of year-round resident birds has also been investigated, but to a lesser degree than for the breeding season (Ekman 1989; Kraaijeveld & Dickinson 2001; Aplin *et al.* 2012). In migratory birds, the most basic aspect of winter social structure is known for many species – e.g. territoriality versus flocking in social groups. However, in species that form flocks (defined here as temporary aggregations of individuals in the same place at the same time), we know almost nothing about dynamics of flock membership over space and time (see Myers 1983; Piper & Wiley 1990; Conklin & Colwell 2008 for notable exceptions).

Our lack of understanding of the winter societies of small-bodied birds is particularly surprising because these taxa were so crucial to the development of important theories in ecology. A large body of influential research on small-bodied birds in winter explored how food, predation and sociality interact to affect the evolution of optimal foraging (Stephens & Krebs 1986), sociality and optimal group size (Pulliam & Caraco 1984), energy management (Cuthill & Houston 1997),

predator–prey interactions (Bertram 1978) and status signals (Rohwer 1975; Rohwer & Ewald 1981). For many of these topics, the pattern of group stability and the specific identities of group members matter. For example, the degree to which individuals form long-term associations could alter the dynamics of anti-predator behaviours and the form of cooperation involved (Croft *et al.* 2006; Micheletta *et al.* 2012). In addition, the pattern of social structure also has critical implications for the mechanisms by which intragroup competition is mediated by signals (Rohwer 1975).

In theory, the social structure of wintering birds could range from the small, highly stable groups observed in a variety of year-round resident birds (e.g. Ekman 1989) to short-term random associations with little or no structure (Myers 1983; Conklin & Colwell 2008). Between these two extremes, winter bird societies could also involve a complex mix of social stability and change in both space and time – often termed fission–fusion dynamics (Aureli *et al.* 2008). Migration poses an added challenge to across-year stability because individuals that winter together do not necessarily breed together (Ryder *et al.* 2011; Seavy *et al.* 2012), and thus long-term social bonds must bridge a break in contact between winter seasons. However, high levels of site fidelity and long-term memory of individuals can promote social stability between neighbours in the breeding season (Godard 1991), and the same type of stability could exist on the wintering grounds. Even in birds that switch flocks over short time scales (e.g. min, h), social

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stability can occur over longer time spans (e.g. days, seasons) if certain sets of birds tend to join flocks together more often than expected by chance. The challenge for researchers is to use observations of short-term dynamics to detect the underlying patterns of social associations as well as changes in social structure across time – a task that has become more tractable with recent advances in social network analysis (Wey *et al.* 2007; Croft *et al.* 2008; Pinter-Wollman 2014).

Social network analysis has recently emerged as a quantitative framework for understanding patterns of social structure in animals, and the number of studies documenting non-random social structure has exploded. Many of these studies have used network theoretical methods to detect social communities – clusters of individuals that associate with each other more often than expected by chance (Newman 2006) – in populations of animals such as fish, birds and mammals (e.g. Wolf *et al.* 2007; Oh & Badyaev 2010; Mourier *et al.* 2012). Here, we use social network analysis to determine the social structure of a wintering population of a migrant species, the golden-crowned sparrow (*Zonotrichia atricapilla*). Our goal was to determine whether flocks represent aggregations that arise from discrete social communities within the population, and whether long-term social preferences play a role in structuring such social communities.

We constructed networks of flock co-membership in three sequential non-breeding seasons. We show for the first time that the social lives of migrant birds in winter are characterised by complex community structure and that these social communities are remarkably stable across years despite the potentially destabilising effects of recruitment, mortality and long-distance migration. We demonstrate that stable social associations among birds returning across years help shape these patterns of network structure.

DISENTANGLING THE EFFECTS OF SPACE USE AND SOCIALITY

A major difficulty in analyses of social networks is to understand whether social communities arise as a consequence of shared spatial preferences, preferential social associations between some individuals or both (Pinter-Wollman *et al.* 2014). By definition, associations among individuals are determined on the basis of close spatial proximity, so the key question is whether an association reflects shared preference for the same space, or whether the animals use the same space because they prefer to associate with each other. One approach to teasing apart some of the influences of spatial preference from social preference is to compare empirical networks against spatially explicit null models, e.g. by building simulated networks that randomly group individuals into short-term flocks based on the overlap in their broader patterns of use of space (Ramos-Fernández *et al.* 2006; Best *et al.* 2014). This null model approach is conservative for testing the effects of social preferences because it cannot account for the fact that space use patterns themselves can reflect social preferences. For example, a lack of difference in structure between an empirical network and networks generated by a spatially explicit null model cannot reject the possibility that social processes were important in determining individual home ranges

in the first place. However, demonstrating that empirical networks exhibit significantly more structure than predicted from a spatially explicit null model can provide evidence that social preferences among certain individuals plays some role in structuring the community. Thus, this approach identifies the *minimum* contribution of social preferences above and beyond their role in determining the patterns of overlapping home ranges of individuals. A complimentary approach is to use network regression methods to determine whether specific social attributes (e.g. familiarity) predict patterns of associations in flocks independently of space use patterns. While this approach still suffers from the potential influence of social preference on space use, it can help identify specific social factors that influence network structure. In this study, we employ both null model and network regression approaches to determine how social preference shapes social network structure across time.

METHODS

Constructing social networks

Sparrows arrive at our study site (The University of California, Santa Cruz Arboretum) in October–November and depart for their breeding grounds, likely in disparate areas along the Alaskan coast (Seavy *et al.* 2012), in March–April each year. Our study spanned three non-breeding seasons: January–March 2010 (Season 1), October 2010–February 2011 (Season 2) and October 2011–April 2012 (Season 3). Each year, we captured birds using baited traps and attached individually unique combinations of colour bands. In Season 2, we did not band any birds between October–December 2010. We censused short-term flocks (defined as a group of individuals found within a single 5 m radius) by identifying the colour-banded individuals in each flock. Most censuses were conducted while the flock was foraging in short grass and more rarely when they were foraging on shrubs and trees. The birds are habituated to people and we typically observed birds from a distance of about 10 m. In most cases, we left the flock once all individuals were identified before we lost sight of the flock. We also noted the location where the flock was first observed, using an aerial photograph with 10 × 10 m grids (Fig. 1) as a map. To ensure independence of our data points, our samples included flocks censused at least 20 min apart, as preliminary analysis suggested that flock membership often changes within this time frame. We also included flocks censused less than 20 min apart as independent data points if they contained no more than one individual in common. We only included flock observations that occurred away from feeders used for trapping. A minority of observations ($\leq 10\%$) in Seasons 2 and 3 were conducted on days when feeders were placed elsewhere within our study site at some point during the day and excluding these observations did not affect our results.

We included in our analysis only birds with confirmed band combinations and those banded prior to the beginning of the census period for each season. Thus, birds banded early in the season (October–December) were included in Season 1 because flock censuses began in January, but early-banded birds were excluded in other seasons when flock observations began in October. Inclusion of individuals banded later in the

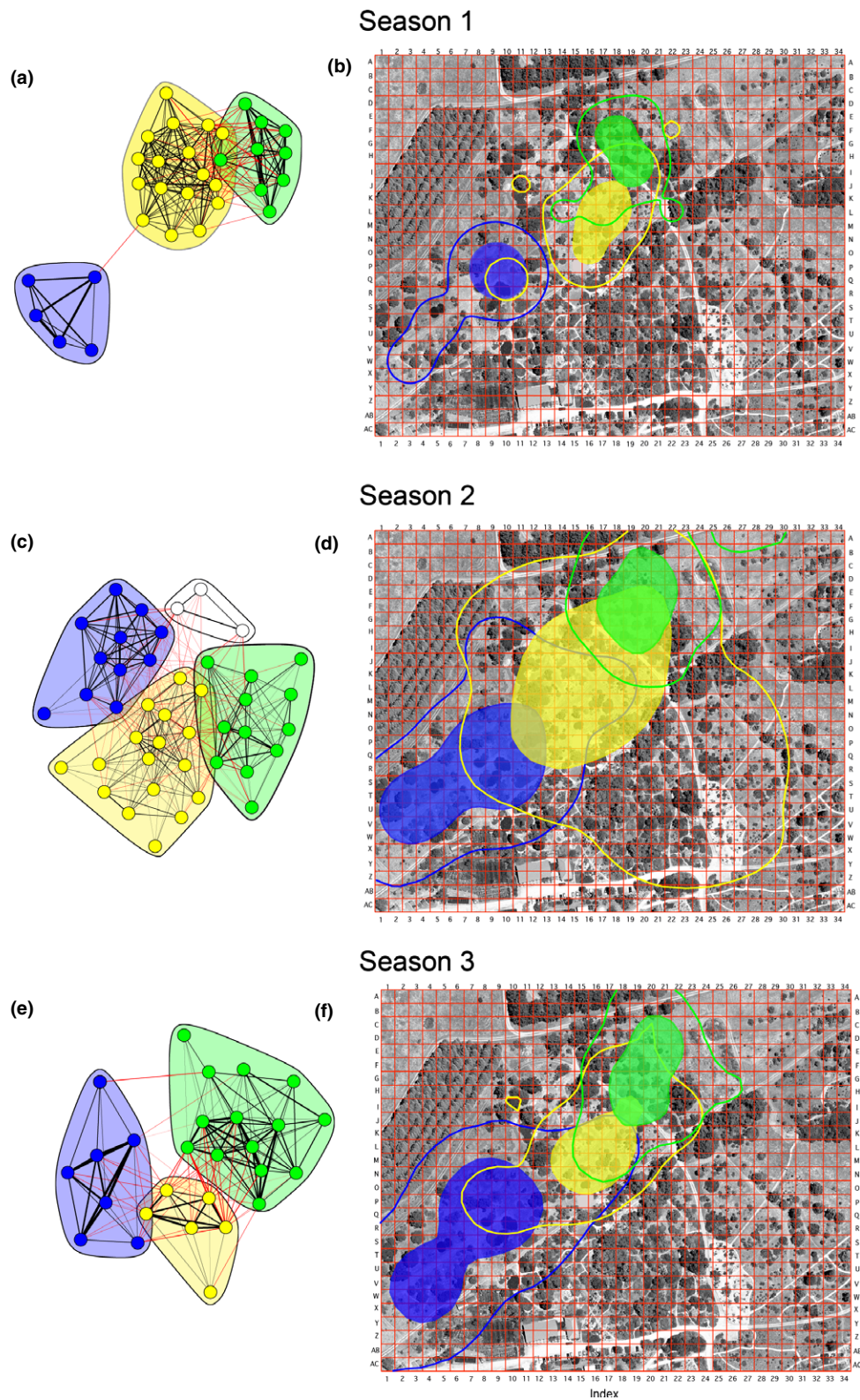


Figure 1 Social communities and their spatial distribution across years. (a, c, e) Social networks of flock co-membership in each season. Each node, representing an individual bird, is assigned to a social community, denoted by node colour and coloured bubbles. Edge widths are proportional to the association index. Edges connecting nodes in different social communities are drawn in red. Node placement is determined by a force-directed algorithm from the *igraph* package (Csárdi & Nepusz 2006), which tends to place strongly associated nodes closer together. (b, d, f) Social community home ranges for each season overlaid on an aerial photo and grid of the study area. The filled areas and outlines represent 50% and 90% utilisation density estimates respectively (see Appendix S2 for methods). Each cell of the study grid is 10 × 10 m. (d) For visual clarity, we excluded the minor community of three individuals in Season 2 (shown in white) from the home range plot.

season would cause us to underestimate the strength of their network relationships as prior to banding they would not be identified even if present in a flock. We also omitted from the network analysis transient individuals that were observed fewer than three times, but the major results are not affected by their removal. For each season, we calculated the Simple Ratio association index (Cairns & Schwager 1987) for each pair of individuals, which ranges from 0 for pairs never seen in the same flock and 1 for pairs always seen in the same flock. We then constructed social networks using the individuals as nodes and association index as edge weights. The flock composition data are available on the Dryad Digital Repository (doi: 10.5061/dryad.d3m85).

Detecting social communities in empirical and simulated networks

We used a modularity-optimisation community detection approach to detect social communities (Newman 2006) – groups of individuals that are tightly connected with each other through flock co-membership. Modularity (Q) refers to the weighted proportion of edges that occur within a pre-defined group, minus the expected proportion of such edges if edges were distributed randomly in the network. Modularity-optimisation community detection refers to a class of methods to search for the groupings of nodes that result in the maximum modularity value (Q_{max}). The value of Q_{max} is used as a metric of how discretely a network is divided into distinct clusters, and we later statistically compare empirical Q_{max} values to those of null models. We tried several different community detection algorithms using the R package ‘igraph’ (Csárdi & Nepusz 2006). We used the method of Clauset *et al.* (2004) for our final analysis because it consistently yielded the highest Q_{max} value (i.e. the optimal community division) among these community detection methods. This method allowed us to assign each individual to a social community for each season.

We used a bootstrapping technique to account for sampling error in our observed networks (Lusseau *et al.* 2008). We re-sampled flocks with replacement up to the number of flocks observed (Table 1) to create a re-sampled network. We calculated Q_{max} for 1000 re-sampled networks to generate bootstrapped confidence interval for our empirical measure of modularity. We used the same bootstrap procedure to calculate a novel index of the robustness of community assignment, $r_{community}$, whose value is 1 when all bootstrap replicates result in the exact same community assignment as the empirical result, and 0 when community assignments in bootstrap replicates are random with respect to empirical network (see Appendix S1).

We tested whether the observed community structure was greater than expected by chance using two null models. The first null model (hereafter ‘Random Flock Model’) assumed that flock associations were random, but controlled for the observed sizes of flocks and number of times each bird was seen. In effect, this model simulated flocks as random aggregations of individuals occurring at separate time points such that any individual could join any flock, but with several constraints: the total number of flocks, number of individuals in each flock and the number of flocks an individual joined all matched the empirical dataset. We conducted this randomisation using the ‘Swap’ algorithm (Bejder *et al.* 1998; Whitehead *et al.* 2005) with $2*v$ ‘swaps’ for each run of the randomisation procedure (v = total sum of individuals across all flocks). Preliminary analysis indicated that this was sufficient to ensure that the flock matrix had been randomised. We then applied the community detection methods as described above to measure the modularity (Q_{max}) of each network generated from a randomised flock matrix and then repeated this process 1000 times to produce a null distribution for comparing the empirically observed modularity measures.

Our second null model, the ‘Spatial Flock Model’, incorporated information about home ranges under the assumption that birds flock randomly with those that share the same space. First, we estimated the home range of each bird using minimum convex polygons based on whether the individual had been recorded in each 10×10 m grid cell on the map. In each iteration of the simulation, we constructed flocks using the observed flock sizes and grid cell locations from the empirical data, and drew flock members at random from among all individuals for which that grid cell location was part of their home range. Flocks were simulated to occur at separate times such that each individual could join any flock within their home range. We then used this flock membership matrix to construct social networks and measure modularity as above. We repeated this procedure 1000 times to produce a distribution of modularity values.

We compared the modularity values generated by the Random Flock Model and the Spatial Flock Model with the empirical modularity value with bootstrap confidence intervals for each year.

Testing for effects of prior social associations on network structure

Having found that the observed social networks exhibited more discrete community structure than predicted by our null models, we tested whether a specific form of social preference – social stability across years – could explain how social com-

Table 1 Basic statistics for social networks

| Season | # Flocks observed | Mean # banded individuals per flock (SD) | N | # Communities (# indiv. per community) | Q_{max} | R |
|--------|-------------------|--|-----|--|-----------|------|
| 1 | 77 | 3.3 (1.9) | 31 | 3 (17, 9, 5) | 0.43 | 0.15 |
| 2 | 340 | 2.2 (1.7) | 43 | 4 (17, 12, 11, 3) | 0.49 | 0.19 |
| 3 | 430 | 2.0 (1.4) | 27 | 3 (14, 7, 6) | 0.43 | 0.17 |

N = Total number of individuals in the network; Q_{max} = modularity; R = The proportion of total edge weights that links nodes in different communities (denoted in red in Fig. 1).

munities arise. For each of three comparisons (Season 1 vs. Season 2, Season 2 vs. Season 3, Season 1 vs. Season 3), we constructed matrices of association indices between all possible dyads of individuals that were present in both years. We then conducted Mantel Tests to determine whether social associations were consistent across years.

While significant correlations in association matrices would suggest social preference for familiar individuals, this could simply reflect spatial fidelity to home ranges and not to familiar flock mates. To determine if social preferences based on past social experience could be detected after controlling for the degree of home range overlap, we used a network regression approach called MRQAP (multiple regression quadratic assignment procedure) in which a dependent matrix is regressed against multiple independent matrices of the same size (Krackhardt 1988). Here, we use the matrix of association indices between each pair of focal individuals (all individuals observed across two consecutive years) as the dependent matrix, and the two independent matrices consisted of the association indices in the previous year and home range overlap between each pair of focal individuals. We calculated the degree of home range overlap for each of these pairs of birds as $2C/(A+B)$, where A and B are number of 10×10 m grid cells included in the home range of each individual bird (estimated by minimum convex polygons), and C is the number of grid cells included in both home ranges. This analysis was conducted using the package 'statnet' in R (Handcock *et al.* 2003).

Having shown that individuals flock with the same birds across years, we were interested in whether these long-term social ties play a role in shaping the community structure of the social network. For example, strong ties between individuals that return to the same social community across years could generate community clusters in the network. To test this idea, we measured how well-connected an individual was within its own social community using a normalised score of within-community node strength (Z_i ; Guimerà & Amaral 2005). If K_i is the sum of association indices of individual i to other individuals in its own social community, s_i , $\overline{K_{s_i}}$ is the average of K_i over all the nodes in s_i , and $\sigma_{K_{s_i}}$ is the standard deviation of K in s_i , then:

$$z_i = \frac{K_i - \overline{K_{s_i}}}{\sigma_{K_{s_i}}}$$

We used an ANOVA to compare the within-community strength of individuals that returned across years with those that were included in the network for the first time. Note that in Seasons 2 and 3, we only included birds that were previously banded (see above). Thus, we are comparing the within-community strength of individuals that returned to the population for a second year with those that returned three times or more.

RESULTS

Microgeographical community structure

In this study, we defined *flocks* as temporary aggregations of individuals in the same place at the same time. In contrast, *social communities* are clusters of individuals that are tightly

connected within the social networks constructed from patterns of flock co-membership throughout the season. Thus, each social network represents the cumulative pattern of flock associations over the course of several months, and social community structure represents the partitioning of the population into clusters of individuals that flock more often with each other than expected. In each of three seasons, the network could be partitioned into three main social communities (Fig. 1, Table 1; Season 2 network has an additional 4th community of three individuals). The assignments of individuals to communities were generally robust to sampling error: pairs of individuals in the same community in the empirical network were usually in the same communities in bootstrap replicate networks (Appendix S1, Fig. S1 Fig. S2; Season 1 $r_{community} = 0.82$; Season 2 $r_{community} = 0.76$; Season 3 $r_{community} = 0.82$). The communities had spatially overlapping home ranges with relatively discrete core areas, though the degree of overlap varies among pairs of clusters and across years (Fig. 1).

Modularity differed significantly between the Random Flock Model, the Spatial Flock Model and the empirical network in each of the three years (Fig. 2; all ANOVA comparisons $P < 0.001$; statistical results shown in Table S1). The modularity of the empirical network was much greater than expected from the Random Flock Model, indicating that the observed network structure was highly non-random. The Spatial Flock Model, which incorporated information about individual home ranges, also was significantly more modular than the Random Flock Model, demonstrating that spatial segregation of home ranges per se leads to some level of community structure. However, empirical networks had still higher modularity values than the Spatial Flock Model; evidence that the population is more discretely divided into social communities than expected from the pattern of home range overlap. Thus, flocks are unlikely to be random aggregations of birds that share home ranges, and these observations suggest a role for social preferences above and beyond the role that sociality plays in determining home ranges. However, it remains unclear from these results alone whether the community structure arises from short-term preferences (e.g. preference to continue flocking with the same group over the course of a day) or long-term dynamics. We now show that these social preferences stem from long-term familiarity that persists across years.

Individuals prefer to flock with the same individuals across years

Patterns of social associations were strikingly consistent across years. Mantel tests revealed very high correlations in association indices between pairs of individuals that returned across consecutive years (Season 1 vs. Season 2: $n = 20$ birds, Mantel $r = 0.63$, $C.I. = 0.49-0.71$, $P < 0.001$; Season 2 vs. Season 3: $n = 15$ birds, Mantel $r = 0.73$, $C.I. = 0.63-0.84$, $P < 0.001$). The consistency in association patterns also continued across three winters (Season 1 vs. Season 3: $n = 8$ birds, Mantel $r = 0.72$, $C.I. = 0.50-0.84$, $P < 0.001$). Such consistent associations between individuals across years could be due to high fidelity to home ranges across years, social preferences that persist across years or both. Our network regression (MRQAP) analysis showed that associations between pairs of

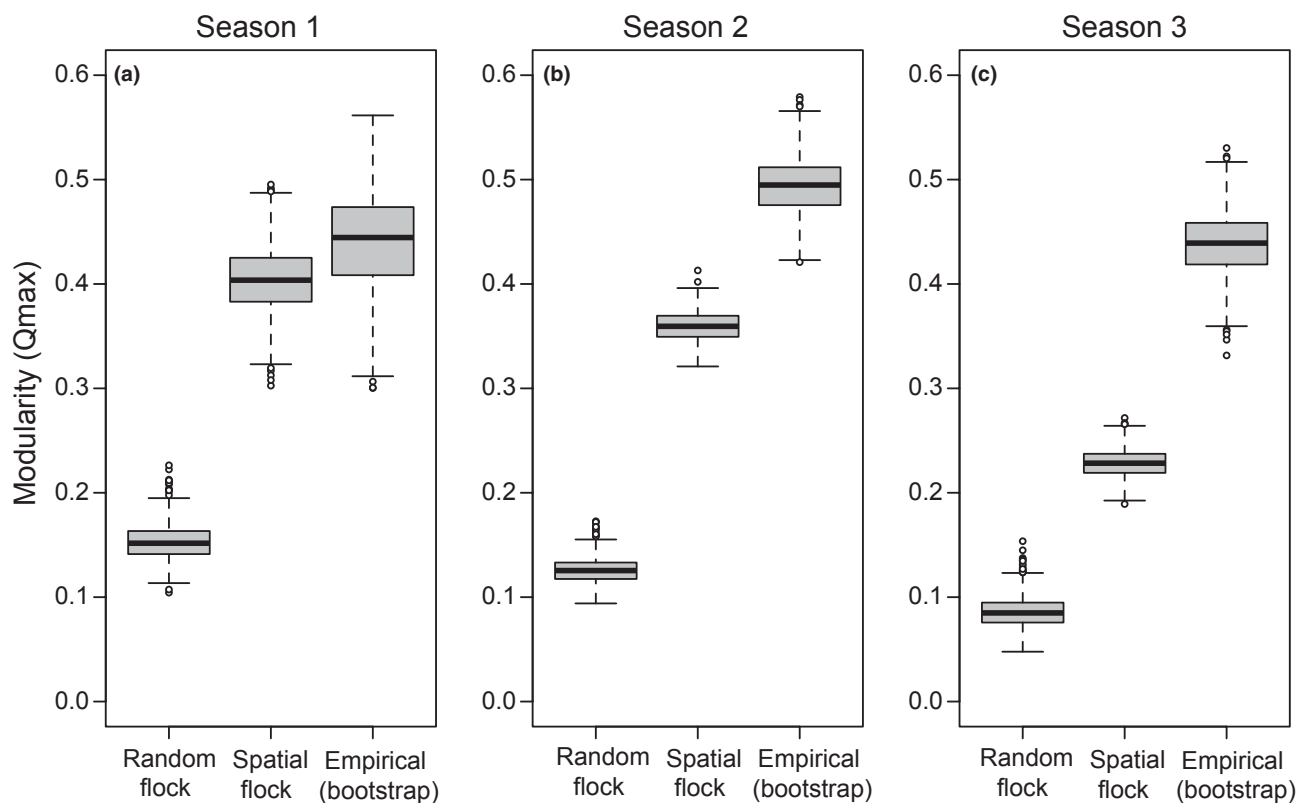


Figure 2 Empirical networks have greater community structure compared to null models. (a–c) For each season, we calculated modularity for an ensemble of Random Flock Null Model, Spatial Flock Null Model and Empirical Bootstrap networks. Box-and-whiskers plots are shown. For all ANOVA comparisons, $P < 0.001$. Statistical results are reported in Table S1.

individuals were significantly affected by both the degree of home range overlap and the association strength of that pair in the previous year (Table 2; see Fig. S1). However, the effect of previous association on predicting flocking patterns in subsequent years was approximately two to four times stronger than the effect of home range overlap (Table 2). Thus, sparrows clearly exhibit social preference for flocking with familiar individuals with whom they flocked in the previous season.

Re-assembly of same communities across years

The social community structure of the network remained stable across years despite the fact that a significant proportion of the individuals in the social network failed to return across years (36% from Season 1 to 2, 65% from Season 2 to 3, 74% from Season 1 to 3; Table 3). The consistent community structure across years was the result of social preferences that persisted across years between pairs of individuals that returned to the population. Individuals returning to the population across consecutive years were significantly more likely than not to re-join the social community located in the same area of the study site (Table 3: binomial test with expected probability = $1/N_{\text{communities}}$; Season 1 vs. Season 2: 18 of 20 returning birds, $P < 0.0001$; Season 2 vs. Season 3: 15 of 15 returning birds, $P < 0.0001$). Consistency in community membership also persisted across a two-year interval: 7 of the eight individuals that were in both the Season 1 and Season 3 net-

work also returned to the same social community (Table 3; $P = 0.003$). Birds that were observed in two consecutive seasons appear to have acted as the cores for social communities – they had stronger connections with other members of their social communities compared to other birds in the network (Fig. 3; ANOVA: Season 2, $F_{1,41} = 6.5$, $P = 0.015$; Season 3, $F_{1,25} = 13.2$, $P = 0.001$). Because these networks exclude birds that are banded for the first time during the observation period (i.e. birds likely in their first winter seasons), our analysis shows that birds continue to become more central in their communities even after three or more seasons.

DISCUSSION

We discovered previously unsuspected levels of social complexity for a wintering migrant songbird. Golden-crowned sparrows exhibit a highly non-random social structure in which three main communities occur within a small area (size of study site ~ 7 ha) each year. Short-term flocks were dynamic in composition but consisted of different subsets of a larger stable social community of individuals. Strikingly, we found that birds that flocked together often during one season were more likely to flock together again in the following year, above and beyond what would be expected by the extent of overlap in their home ranges. To our knowledge, this is the first evidence of such social stability across years in a wintering population of migratory birds. Across-

Table 2 Results of network regression (MRQAP) analysis comparing the effects of (1) previous year's association strength and (2) extent of home range overlap on the association strength between pairs of individuals in each of two seasons, seasons 2 and 3

| Season | Previous Year Association | | Home Range Overlap | | Full Model | | |
|--------|---------------------------|----------|--------------------|----------|-----------------------------------|-----------------------|----------|
| | Estimate | <i>P</i> | Estimate | <i>P</i> | <i>F</i> _(<i>d.f.</i>) | <i>R</i> ² | <i>P</i> |
| 2 | 0.24 | <0.001 | 0.13 | <0.001 | 476.8 _(2,1375) | 0.41 | <0.001 |
| 3 | 0.45 | <0.001 | 0.12 | <0.001 | 217.9 _(2,375) | 0.54 | <0.001 |

Table 3 Comparisons of community membership across years to determine the number of individuals that returned to the same versus different communities

| Season 1 Membership | Season 2 Membership | | | | | Proportion Not Returning |
|---------------------|---------------------|--------|------|-------|----------------|--------------------------|
| | Green | Yellow | Blue | White | Did Not Return | |
| Green | 7 | 0 | 0 | 0 | 2 | 0.22 |
| Yellow | 1 | 8 | 0 | 1 | 7 | 0.41 |
| Blue | 0 | 0 | 3 | 0 | 2 | 0.40 |
| New* | 4 | 9 | 8 | 2 | | |
| Proportion New | 0.33 | 0.53 | 0.73 | 0.67 | | |

| Season 2 Membership | Season 3 Membership | | | Did Not Return | Proportion Not Returning |
|---------------------|---------------------|--------|------|----------------|--------------------------|
| | Green | Yellow | Blue | | |
| Green | 7 | 0 | 0 | 5 | 0.42 |
| Yellow | 0 | 4 | 0 | 13 | 0.76 |
| Blue | 0 | 0 | 4 | 7 | 0.64 |
| White | 0 | 0 | 0 | 3 | 1.00 |
| New* | 7 | 2 | 3 | | |
| Proportion New | 0.50 | 0.33 | 0.43 | | |

| Season 1 Membership | Season 3 Membership | | | Did Not Return | Proportion Not Returning |
|---------------------|---------------------|--------|------|----------------|--------------------------|
| | Green | Yellow | Blue | | |
| Green | 4 | 0 | 0 | 5 | 0.56 |
| Yellow | 1 | 2 | 0 | 14 | 0.82 |
| Blue | 0 | 0 | 1 | 4 | 0.80 |
| New* | 9 | 4 | 6 | | |
| Proportion New | 0.64 | 0.67 | 0.86 | | |

Community colours follow Fig. 1 for each community, we also note the number of individuals that did not return across seasons and the number of new immigrants that joined the community. *New denotes birds that are included in the network for the first time in Season 2 (top table) or Season 3 (bottom two tables).

year social stability between birds also leads to repeatable community structure of the population across years, even with large degrees of turnover in the population due to mortality and recruitment.

Our findings enrich our understanding of winter sociality of birds in the genus *Zonotrichia*, a particularly well-studied group with respect to social dynamics of non-breeding birds. One detailed longitudinal study (Piper & Wiley 1990) found that white-throated sparrows (*Zonotrichia albicollis*) tended to return to the same location across years, as we observed here, and that individuals also showed across year consistency in home range size. However, because the study did not explore the patterns of flock associations we do not yet know whether white-throated sparrows show the same patterns of network structure observed for golden-crowned sparrows. *Zonotrichia* sparrows, including golden-crowned sparrows, have also played a central role in the development

of the theory of 'badges of status' as a means of mediating social competition (Rohwer 1975; Rohwer & Ewald 1981; Watt 1986; Chaine *et al.* 2011, 2013). Much of this work assumed that these birds live in fluid flocks where individual recognition is not possible. Our findings suggest that the social context in which badges are used may be more nuanced than early theory assumed, a point we discuss more fully below.

Wintering golden-crowned sparrows show fission–fusion social dynamics that are similar to those found in some mammalian societies such as elephants (Wittemyer *et al.* 2005), equids (Sundaresan *et al.* 2006), sea lions (Wolf *et al.* 2007), dolphins (Connor *et al.* 2000), and some primates (Smuts *et al.* 1987). As with these systems, sparrow populations consist of social communities that subdivide to form temporary foraging flocks. Similar social dynamics have recently been described in a few systems that are generally not

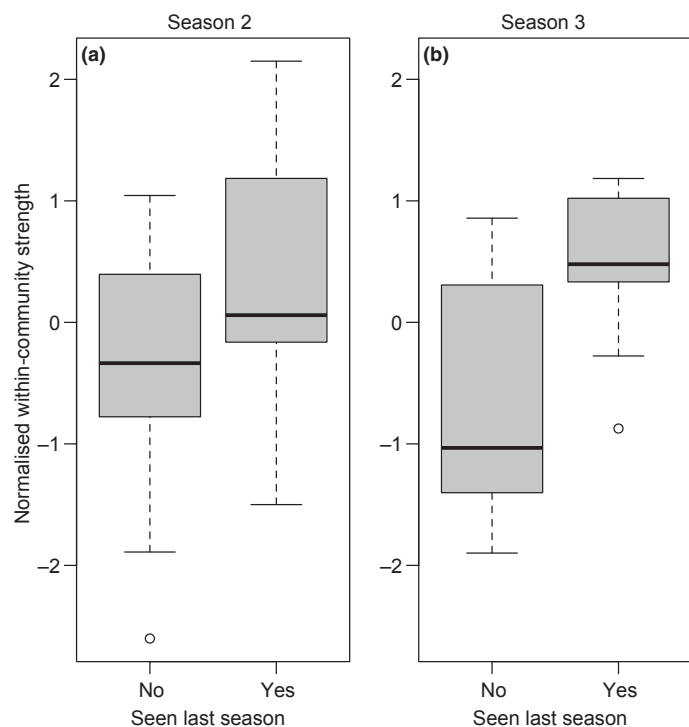


Figure 3 Birds that were seen in the previous year has stronger ties within their social communities than birds not previously seen in both (a) Season 2 and (b) Season 3. Shown are box-and-whiskers plots. Statistics are reported in the main text.

considered as highly social, such as sharks (Mourier *et al.* 2012). Our study adds to the growing evidence that fission–fusion dynamics are widespread across animal societies (Aureli *et al.* 2008).

The structure of social networks is strongly influenced by both social preference among individuals and potentially non-social factors such as the spatial segregation of individuals in the population (Pinter-Wollman *et al.* 2014). For example, if habitat is heterogeneous and some home ranges cluster together, then social communities could arise as an emergent property of foraging patterns (Ramos-Fernández *et al.* 2006) – i.e. communities could consist of individuals that simply prefer to forage in the same locations without any benefits from being social. Similarly, individuals may form temporary social groups with other individuals with which they share space, even when the benefits of sociality do not depend on the identity of the individuals. Alternatively, network structure could be driven by purely social factors – individuals may seek out certain flock mates (e.g. familiar individuals or kin) because they gain additional benefits. In many cases, both social and spatial factors are likely to contribute to social structure. The challenge is to develop methods to tease apart the relative contributions of social versus non-social processes that lead to social network structure (Aureli *et al.* 2008; Pinter-Wollman *et al.* 2014).

In this study, we used two complimentary approaches to demonstrate social factors are involved in structuring the network: (1) comparing empirical networks with null models that

incorporate information on individual space use patterns (i.e. our Spatial Flock Model), and (2) using network regression (MRQAP) to test whether social factors (i.e. previous association) influence network structure independent of spatial patterns. The null model approach demonstrated that the empirical networks exhibit levels of community structure that cannot be explained by patterns of space use alone. The network regression tests showed that a large part of this unexplained variation in association patterns could be explained by previous social experience – birds prefer to flock with the same individuals across years.

While we detected a clear role of across-year social preference in social network structure in our sparrow population, it is important to note that social preferences could be even more important than our statistical tests indicate. This is because social factors could also influence the patterns of individual space use – birds may occupy a home range because they prefer to flock with other individuals that are found in that location. While the Spatial Flock Model captured the baseline level of community structure expected if flocks were composed of random sets of individuals that share home ranges, it did not account for the potential influence of social preference on home ranges. Development of more sophisticated models that incorporate changes in space use and social associations across finer temporal scales may help assess the influence of social preference on space use patterns. Statistical tests based on such spatiotemporal models may reveal that social preferences play an even bigger role in the social structure of wintering birds.

Across-year social preference could contribute to stability in social structure if returning individuals segregate into discrete groups based on past familiarity and form the cores of social communities in future years. Supporting this suggestion, we found that birds returned to the same social communities across years, and that birds observed in consecutive years had stronger ties within those communities. As a result, the overall social structure remained stable despite substantial turnover of individuals in the population due to mortality and recruitment: Comparing across three seasons, each community was composed of largely different individuals between Seasons 1 and 3 (64–86% new members; Table 3). In effect, social communities outlast the lives of their individual members. This type of turnover in community membership is known to promote the long-term stability human social networks (Palla *et al.* 2007), and it could explain the across-year stability of social communities in golden-crowned sparrows. Understanding the processes of formation and maintenance of social communities in golden-crowned sparrows will require more detailed data on behavioural and temporal aspects of flock associations and locations at finer time scales within seasons.

The existence of fission–fusion flock dynamics, stable social relationships and stable community structure in golden-crowned sparrows has important implications for sociality in non-breeding contexts. For example, forming stable groups with familiar individuals could provide a number of benefits through active food sharing (Carter & Wilkinson 2012) and improved coordination in anti-predator behaviour (Croft *et al.* 2006; Micheletta *et al.* 2012). The partitioning of the

population into small social communities can also facilitate cooperation via reciprocity (Trivers 1971; van Doorn & Taborsky 2011) and should favour the evolution of individual recognition as a means to identify flock-mates and prevent invasion of cheaters (Pagel & Dawkins 1997). While interactions between less familiar individuals are expected to involve conventional signals that mediate conflict [e.g. badges of status: (Rohwer 1975; Maynard Smith & Parker 1976)], individual recognition should help settle contests in small groups (Pagel & Dawkins 1997). We previously confirmed that badges of status influence the outcomes of competition between pairs of unfamiliar golden-crowned sparrows (Chaine *et al.* 2011, 2013). The existence of stable groups where individual recognition could be favoured would suggest that badges may be used in interactions during community formation or between communities, and that individual recognition might be more important within communities. A thorough exploration of the function and evolution of status signals will require a shift in perspective to context-dependent signalling directly tied to the dynamics of social organisation.

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STATEMENT OF AUTHORSHIP

All authors contributed to research design, AS, JA, OJ, IML and BL collected data, DS conducted analyses and wrote the first draft of the manuscript, and DS, AS and BL contributed substantially to revisions.

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