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Over-Wintering Grounds Social Behavior of White-Crowned Sparrows

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Table of Contents Page Number

Abstract

White-Crowned Sparrows (WCSP), *Zonotrichia leucophrys gambelii*, are small, migrating passerine birds whose over-wintering ground social behavior is poorly researched. Suitable wintering grounds must balance climate preference and migration length, are affected by territory size and habitat competition, and have long-term effects on bird fitness. A study observed Golden-Crowned Sparrows (*Zonotrichia atricapilla*) returning every year to the same wintering ground and forming strong social communities during those winter months. We predicted that WCSPs exhibit wintering ground fixation and form stable flock structure at the Bernard Field Station (BFS) in Southern California during the winter months of October to February. To test this prediction, we studied WCSPs that forage in the BFS (BFS) in Claremont, CA as a continuation of a three-year study that started in 2019. We used motion-censored cameras to capture WCSPs to observe site fidelity and flock size and strength. To assess WCSPs level of fixation to the BFS, we found that nearly one out of four WCSPs returned season 2021-22 from season 2020-21. To assess the strength of the WCSP social communities, a modularity optimization network analysis identified significantly non-random WCSP flock structures within the BFS over season 2021-22. Future research must be conducted to observe if WCSP flock structures remain the same over several winter seasons, and our research can serve as a baseline for those future studies.

Introduction

Migratory birds make up nearly half of the world's bird species—around 4,000 total—with North America being home to over 350 of those (Dokter, 2018). These migrating birds vary from swallows to waxwings, and they spend the summer months in their breeding ground and the winter months in their wintering grounds. During migration, birds typically travel from the harsh, cold weather regions near the Earth's poles to more temperate equatorial regions during the winter months.

The wintering grounds—the location picked by the bird to settle down during the winter—depends upon the length of migration and the optimal climate of the bird species (Toews, 2017). While not a breeding location, wintering grounds have been hypothesized to affect the fitness of birds because the location of wintering grounds can directly influence where and when birds choose to breed. If a bird chooses a wintering ground far away from the typical breeding grounds for that species, the bird may either arrive late to the breeding season or never make it to the breeding area at all. When selecting wintering grounds, birds must balance the need for warmer climates with the need to return to breeding ground in the spring and summer months. Some species have evolved over the centuries to allow for long-distance migration, such as the Blackpoll Warbler (*Setophaga striata*) which conducts a transoceanic migration from South America to Alaska and back again every year (DeLuca et al., 2015). However, long-distance migrating birds must balance the cost of energy and time constraints with finding better habitats and reduced predation significantly more than short-term migrants (Anderson et al., 2019). Birds must learn where the best breeding grounds are, where the best wintering grounds, and how to migrate between these two locations.

Selecting a specific wintering ground that will be the suitable climate and habitat during the winter months and the reasonable migration distance from the breeding grounds is essential to the bird's fitness. Therefore, returning to the same wintering grounds, which the bird's personal experience can confirm to be a proper balance between climate preference and migration length, allows birds to spare energy and time looking for suitable wintering grounds (Toews, 2017). Spare time and energy can be used to establish territory, food competition, and social status in their selected wintering grounds. Territory refers to an area of land occupied and defended by a bird because of its geographical advantage and resource abundance. Territory and habitat competition are some of the most significant factors in selecting a wintering ground because limited space due to high population densities leads to some birds spending their wintering months in less preferred places (Sherry & Holmes, 1996). These contributing factors on a bird's success during the winter months affect whether the bird is prepared for migration, mating, and general survival while in their breeding grounds (Harrison et al., 2011). However, limited research has been conducted on whether birds return to the same wintering ground—wintering ground fixation—and whether birds develop and maintain social interactions with specific other birds who also return to the same wintering ground every year. When Palm Warblers (*Setophaga palmarum*) were captured at their wintering grounds on Eleuthera Island and transplanted to a new site 22.5 km away, not a single one of the captured Palm Warblers were observed staying at the new release site (Stewart & Connor, 1980). When the researchers looked for where the birds had gone after being released, it was discovered that nearly a third of the transplanted birds had returned to the original capture site (Stewart & Connor, 1980). The study articulates that the reason the Palm Warbler returned was because they had fixated to that specific capture sites during their winter months. The study only provided research on Palm Warblers, and therefore more research needs to be conducted to determine what bird species fixate to wintering grounds and whether it is more beneficial for birds to do so.

Many bird species form groups, or flocks, in the wintering grounds, during migration, and at the breeding grounds to increase their survival and fitness throughout the year. Birds that migrate in flocks save substantial energy during their travels. Great-White Pelicans (*pelecanus onocrotalus*) save between 11 and 14% of energy when they travel in a flock V-formation (Portugal, 2020). In addition to migration benefits, flocks provide safety and security to birds through prey detection and information sharing especially during foraging behaviors and in places with high predatory risk. On information sharing, researchers explored how flocks of House Sparrows (*Passer domesticus*) relay food availability to each other in their habitat by exposing select individuals from each flock to hidden food sites and then releasing the rest of the flock into the test environment. Researchers found significant information sharing occurring between the prior-exposed birds and the rest of the flock during foraging (Toth et al., 2017). On prey detection behavior, communities of Tufted Titmouse (*Baeolophus bicolor*) were observed utilizing their bird song to inform fellow individuals in their flocks of nearby predators (Sieving et al., 2010). One key disadvantage to birds that flock in large communities is that an increased density of birds in one area can result in increased competition for food and mating. However, the benefits for flocking often outweigh the costs, especially for small, foraging birds that have increased flock propensity and flock size during wintering months in comparison to larger birds (Martinez et al., 2016). Thus, it appears that social structure can be an important determinant of an individual's success on the wintering grounds.

Complementing the advantages of forming flocks, forming flocks with the same individuals every year could also be beneficial to birds. Familiarity of foraging behavior, song dialect, and territory can increase the general survivability of a flock. A study conducted on Golden-Crowned Sparrows (GCSP; *Zonotrichia atricapilla*) explored the bird's foraging behaviors and flock structures in their wintering grounds (Shizuka et al., 2014). The studied GCSP migrated from their breeding grounds in Alaska to wintering grounds in Santa Cruz similar to the WCSP. The study observed 26% of GCSP returning to the same study site from season 1 to season 3; and, of those returning GCSP, the birds displayed significantly non-random affiliation to social communities (Shizuka et al., 2014). With a significant amount of the returning GCSP interacting with the same individuals every year in their select wintering grounds, the study supported the hypothesis that GCSP develop stable flock structures and fixate to specific wintering grounds (Shizuka et al., 2014). With GCSP being from the same genus as White-Crowned Sparrows, *Zonotrichia leucophrys gambelii*, (WCSP), it begs to question if the behaviors observed in GCSPs—flock social structures and fixation at their wintering grounds—are also observed in WCSPs.

The White-Crowned Sparrows are a small foraging species of passerine bird native to North America known to reside in low brush. They are easily identified by their yellow bill and the black-and-white stripes on the crown of their head. The WCSP spends its winter months of October to March along the southern coast of California and its breeding months of April to August in Alaska migrating back and forth along the Pacific Coast (Jones, 2008).

The purpose of this study is to determine if the White-Crowned Sparrow fixates to specific wintering grounds and forms stable winter flocks. With substantial evidence of wintering ground fixation, flock propensity, and social interactions between small foraging birds, WCSPs are hypothesized to exhibit behaviors similar to that of GCSPs. Specifically, we predict that WCSPs exhibit wintering ground fixation and form stable flock structure at the Bernard Field Station (BFS) in Southern California during the winter months of October to February. My study uses motion-detecting cameras to capture photos of WCSPs which were then analyzed to identify developed flock structures of WCSP at the BFS. The data collected from the cameras will help develop theories about WCSP social behaviors involving wintering ground and flock structures which can be used to predict the behavior of other small, foraging bird species in future research.

Methods

The Study Site

The study is conducted at the Robert J. Bernard Field Station (BFS) located in Claremont, CA. The BFS is situated on an outwash of the San Gabriel Mountains and is approximately 86 acres primarily composed of native coastal sage scrub species—such as Coastal Sage Brush (*Artemisia californica*), White Sage (*Salvia apiana*), and Flat-top Buckwheat Brush (*Erigonum fasciculatum*)—native evergreen species—such as Laurel Sumac (*Rhus laurina*), Redberry

(*Rhamnus crocea*), and Coffeeberry (*Rhamnus californica*)—, and non-native shrub in the Southeast corner of the BFS. WCSPs are commonly observed foraging among the short brush in the BFS. The WCSPs arrive at their wintering grounds in the BFS in October and leave in February-March for the breeding grounds in Alaska.

Data Collection

We collected data over five months from October 2021 through February 2022 at 24 sites in the BFS (Figure 1). Each location was photographed for one week a month for five months using motion-sensor Bushnell cameras. We placed 12 Bushnell cameras at 12 sites for one week and then moved the cameras to the other 12 sites for another week. This procedure built upon the previous years of data collection. The first round of data collection occurred during the 2019-2020 winter season over 12 locations and camera data from October through January of that winter (Drea, 2020). During the 2020-2021 winter season, data was collected at all 24 locations form Oct-Jan of that year (Clague, 2021). During the 2021-2022 winter season, trapping occurred at all 24 sites, and camera data was collected from Oct-Feb (an additional month compared to previous years).

The data collection of this experiment comes from the analysis of photos taken at the BFS. The catching of WCSP via cage traps is referred to as "trapping," the photographic observation of a WCSP is a "capture," and a flock is the capturing of two or more WCSPs in a single photo. In this study, other bird species do not count toward total number of captured birds or flock size.

Figure 1: Trap Locations at the Robert J. Bernard Field Station located in Claremont, California. The map shows the camera and cage trap locations (yellow boxes; 1-12, 30-35, 40-45). Seed was placed at every location during the months of October and February. Cameras captured each location for one week per month over the period of five months from October to February.

Bird trapping occured in the months of October and February during which seed—a mixture of millet, sunflower seeds, and cracked corn (baked at 200°F for 30 minutes)—was placed at each cage trap. During the trapping, which takes place in the early morning for a total of 20-24 hours total in October and February, we checked the cage traps every 15 minutes and carefully secured any birds caught in the traps to obtain blood samples, body fat scores, age (adults or juvenile based on head plumage), identification numbers (if banded), and wing lengths of WCSP located in the BFS. Banded birds have a metal USGS-issued band located on their leg. For all trapped un-banded WCSPs, we attached a metal USGS-issued band and a unique combination of colored, plastic leg bands for future identification in the photos. The banding of WCSPs began in 2017 and has continued all the way to February 2022.

For camera placement, we set the cameras in open areas with short brush at ground level. During the photo analysis, we sorted all photos containing WCSPs during the daytime (all night-time and blurry photos removed from the analysis) into a folder. From the sorted WCSP photos, we obtained the total number of WCSPs (banded) captured by cameras, the identity of the WCSPs (banded) captured, and the flock size of WCSPs captured.

Data Analysis

The analysis of the sorted WCSP photos was conducted using Camera Base 1.7 software created by Mathias Tobler from the Atrium biodiversity information system. We imported the presorted photos onto Camera Base to record the age of the birds, the color and placement of the leg bands, the time of the photo, and the location of the photo.

All data analysis was conducted using R . For overall data analysis, we calculated the total number of WCSPs captured, the total number of banded and unbanded WCSPs, the total number of WCSP flocks captured, and the average number of WCSPs captured in a flock. For individual camera sites, we calculated the total number of WCSPs captured, the total number of banded WCSPs, and the total number of flocks at each specific camera location. We then compared each site's WCSP capture frequency with a Chi-Squared Test of Independence ($\alpha = 0.05$) to study whether all the camera sites experienced the same level of WCSP activity. We used a contingency table analysis to determine differenced in WCSP captures per individual camera site between season of 2020-2021 and season of 2021-2022. The assumptions for the Chi-Squared Test of Independence that all expected values are greater than zero, no more than 20% of the expected values are less than five, and the sample was random and independent were all met.

A network analysis of banded WCSPs captured during season 2020-21 was conducted in continuation of the limited network analysis conducted for the 2020-2021 season (Clague, 2021). The network analysis used a modularity optimization package from R to detect bird flocks within the data (RCoreTeam, 2021). The fast greedy modularity optimization algorithm then identifies the modularity of these communities by first treating the flock separately and then all together in the complete data set (Shizuka, 2014). The network analysis graphs the community structure of WCSP via nodes—circle—that indicate individual WCSPs, node colors that indicate a WCSPs membership in the community structure based off where the photo was captured, and edge weight—line between nodes—that represents a relationship between WCSPs. The distribution of nodes and the edges between them represent the communities of banded WCSP captured at the BFS. The algorithm then calculates the optimized modularity—the measure of the structure and division of communities within a network. Networks with high modularity values have strong edge weight within isolated communities and weak edge weight between different communities in the network. To assess whether or not the detected community strength was due to chance, we used a "Random Flock Null Model" that simulated a network analysis but assumed that all flock interactions were random (Shizuka, 2014). Controlled for all observed flock size and total number of unique banded birds captured, the Random Flock Null Model works to simulate random flock interactions of individual birds over specific time points restrained by the actual dataset of banded WCSPs. In addition, we re-sampled the season 2021-22 data via a bootstrapping technique to minimize sampling error and generate a more accurate modularity values for our empirical data (Lusseau, 2008). During the bootstrapping procedure, we resampled the observed flocks and recalculated each flocks' modularity value 100 times to create a bootstrapped network from the original data (Shizuka et al., 2014). Visualized in a boxplot with bootstrap confidence intervals, we compared the "Random Flock Null Model" to the bootstrapped network. The null hypothesis is that the season 2021-20 flocks are random and will not be significantly different than the Random Flock Null Model. We conducted an ANOVA to compare the mean modularity values of the two different models.

Results

The 24 cameras in the BFS captured 12369 photos of WCSPs over the 2021-2022 season from October through February (Table S1). Out of the total number of WCSP captures, 2336 birds were banded, and 9933 birds were not banded (Table S1). Out of the identified banded WCSPs, 93.07% percent of the photos had one WCSPs, 6.20% percent of the photos had two WCSPs and 0.73% percent of the photos had three or more WCSPs. Including banded and not banded WCSPs captured, the average flock size in each photo capture was 1.185 ± 0.566 (mean $\pm$ SD, n = 12369) with a range of 1 to 5 WCSPs in the photo (Table S1).

We assessed the occurrence of WCSPs at each trap via a X^2 Goodness of Fit Test. The null hypothesis of the X^2 Goodness of Fit test was that all traps have the same capture frequency (0.04167); the alternative hypothesis of the X^2 Goodness of Fit test was that all traps do not have the same capture frequencies. The observed capture frequency significantly differed from the expected known frequency at each trap ($X^2 = 21937$, $p < 0.001$). Favoring several traps over others, nearly 50 percent of all captures occurred at Traps 2, 3, 31, and 34; Trap 34 had the highest percentage of captures at 19.07% (Figure 2) (Table S1). Traps 2, 3, 31, and 34 are all relatively close to each other being in the more Northern area of the BFS (Figure 1). On the other hand, Traps 10 and 30 had less than 100 capture and Traps 4, 5, 6, 7, 8, 9, 40, and 45 all had less than 50 captures of WCSPs over the five months (Figure 2) (Table S1). Across the 24 traps at the BFS, there was an average capture count of 511.208 $\pm$ 698.271 (mean $\pm$ SD, n = 24) with the high volume of captures at Trap 34 resulting in the large standard deviation (Figure 2) (Table S1).

The banding of WCSPs allowed us to track where each bird frequented over the five months (Figure 2). Trap 30 had the largest percentage of banded birds (47.917%) (Table S1). However, Trap 30 had less than 100 WCSP captures total and had only captured 12 uniquely banded WCSP (Figure 2). In comparison, Trap 31 captured 36 unique banded birds out of the 1501 total captures (Figure 2). On average, the unique banded WCSP was captured at 2.41 $\pm$ 1.39 trap locations over the season (mean $\pm$ SD, n = 166) with the range of 1 to 9 traps (Figure 3). Of the unique banded birds, 43% were capture at only one trap location, 22% at two locations, 12% at three locations, 7% at four locations, 8% at five locations, and 8% at six or more locations (Figure 3). Despite the few birds that were captured at several traps, the low average points to WCSPs routinely foraging in small area habitats at the BFS. And for birds that were captured at more than six trap locations, the majority were captured by Traps 31-35 which are near each other. For example, the most captured WCSP—273106432—was connected to nine trap locations which included Traps 31-35 (Figure 3). And the next two highest captured birds—273106430 and 273106412—were connected to seven trap locations including Traps 31-35 (Figure 3). The banded WCSPs appear to forage in small areas as highlighted by the average WCSP being captured by less than three traps during the winter season.

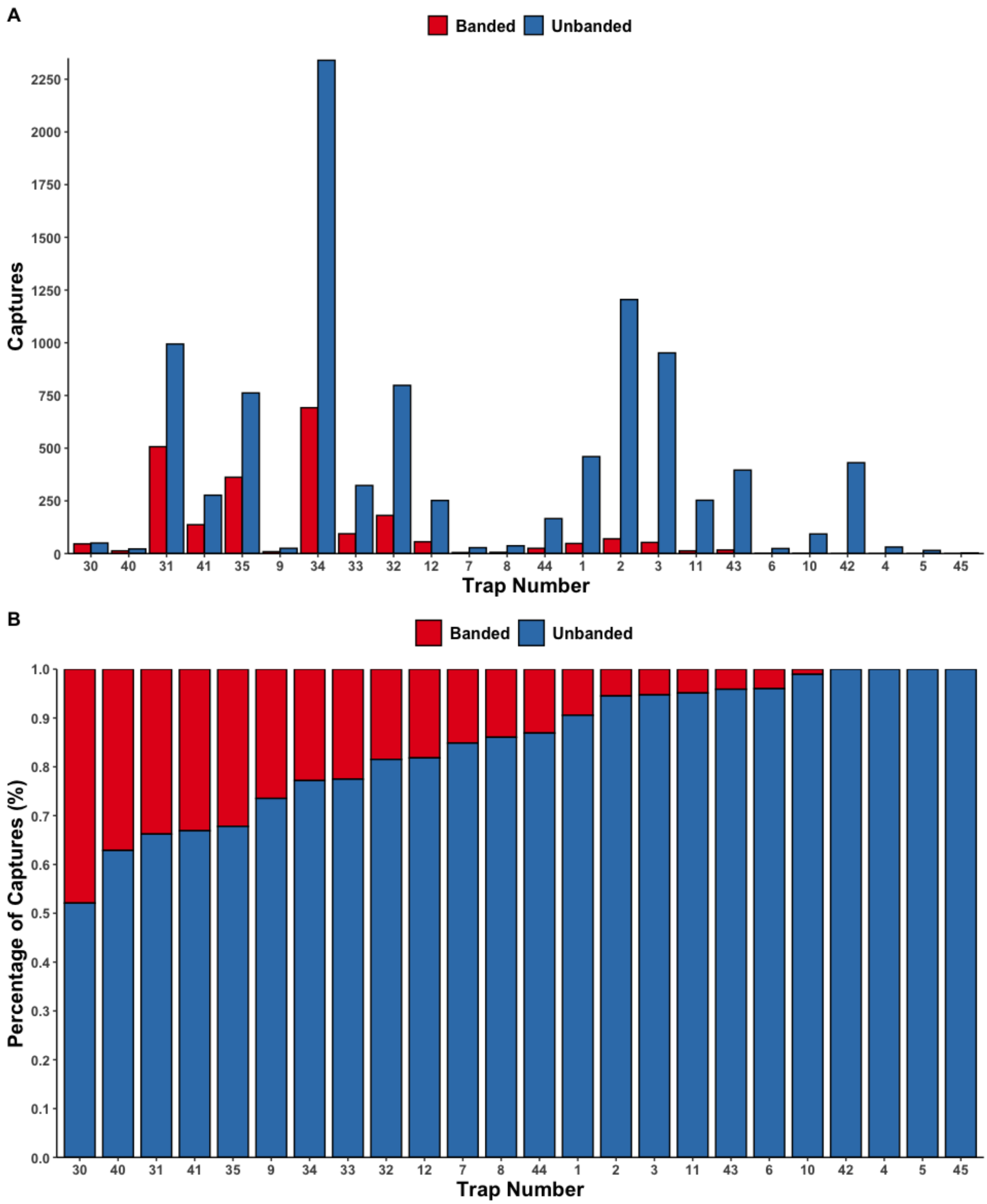

Figure 2. Count and Percent of Banded WCSPs per Trap. A) The number of captures (total count) of banded (red) and unbanded (blue) WCSPs across all the trap locations at the BFS from October 2021 to February 2022; B) The percentage of captures (%) of banded (red) and unbanded (blue) WCSPs across all the trap locations at the BFS from October 2021 to February 2022.

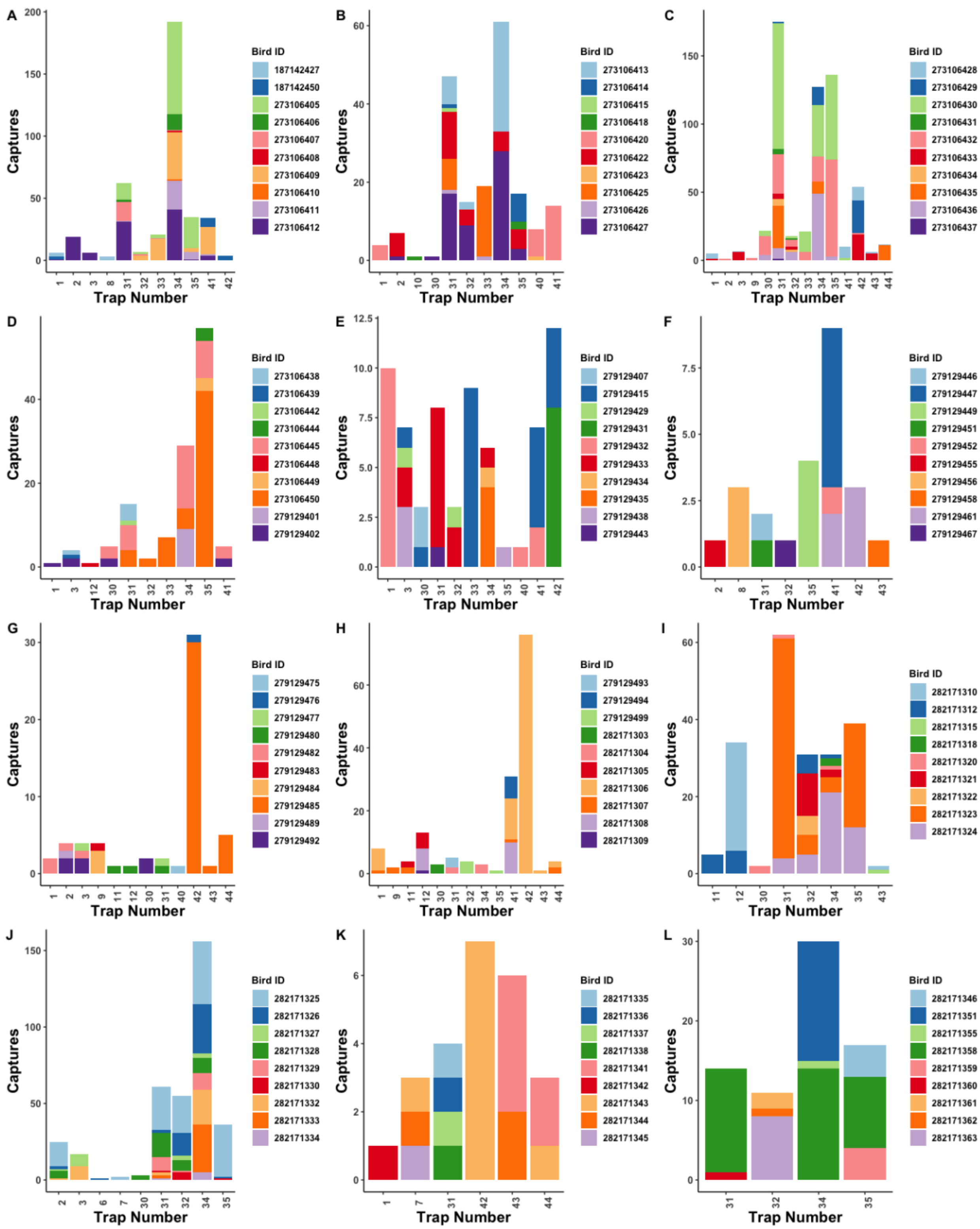

Figure 3. Banded WCSP Trap Frequencies. A-L) The number of captures each unique WCSP (identified by a number combination and color) had at the 24 trap locations. To visualize trap frequency per unique bird, "A-H" have 10 WCSPs per graph and "I-L" have 9 birds per graph for a total of 116 uniquely banded birds captured at the BFS between October 2021 and February 2022.

Several WCSPs were observed to return for season 2021-2021. Of the 40 unique captured WCSPs in season 2020-2021, 57.5% of the birds returned for the 2021-2022 season (Table 1) (Clague, 2021). Compared to 2020-2021, the 2021-2022 winter season had almost three times as many unique banded WCSPs that were captured between the months of October and February (Table 1) (Clague, 2021). Of the unique WCSPs captured in season 2019-20, nearly half of the banded WCSPs returned to the BFS for season 2020-22 (Table 1) (Clague, 2021). And, of the unique WCSPs captured in season 2020-21, nearly 20% of the banded WCSPs returned to the BFS for season 2021-22 (Table 1; Table S2). The large number of recaptured WCSPs over the three seasons points to wintering ground fixation rather than coincidence. In significance, seven WCSPs—273106428, 279129446, 279129458, 279129475, 279129483, 279129485, and 279129492—were captured during season 2019-20, season 2020-21, and season 2021-22 (Table S2) (Drea, 2020; Clague, 2021). Overall, we observed an increase in captured unique banded WCSPs and an increase in returning banded WCSPs over the three season of data collection.

Table 1. Unique Banded WCSPs Captured over Three Seasons. The number of unique banded WCSPs that were captured over the last three seasons of 2019-20, 2020-21, and 2021-22 at the BFS. Season 2019-20 data was only collected at 12 trap sites (Drea, 2020). Season 2020-21 data encompassed only the months of October to January (Clague, 2021). Season 2021-22 data encompassed the months of October to February.

Season	Unique Banded WCSPs (Count)	Recaptured WSCPs	Number of Flocks	Mean WCSPs in Flock	Individuals per Flock
2019-20	23	N/A	1	2	2
2020-21	40	10	5	5	2, 2, 2, 2, 7
2021-22	116	25	9	4.89	2, 3, 6, 6, 4, 12, 2, 7, 2

The network analysis using the fast greedy modularity optimization algorithm identified several communities of WCSP within the BFS from October 2021 to February 2022 (Figure 4).

Two isolated communities with significant interactions between bird pairs are identified by heavy edge weight between nodes. One community, orange node color, was between birds 273106439 and 282171363 captured by Trap 32, and the second community, grey node color, was between birds 278106435 and 273106428 (Figure 4). Another isolated community with heavy edge weight was between three birds—279129480, 282171307, and 279129482—captured by Trap 1 and Trap 11 (Pink node; Figure 4). The biggest community contained five significant members—282171358, 282171326, 282171351, 282171333, and 282171321—and was captured by Traps 31 and 35 (Dark blue node; Figure 4). In addition to the communities with heavy edge weight, the algorithm outlined edges with low weight that connected 38 total banded WCSPs to each other in distant communities. These low edge weight interactions were captured by nearly every trap, and most of the captures occurred over the month of February.

There was an increase in social communities at the BFS from season 2020-21 to season 2021-22 (Figure 5). Within season 2020-21, a large proportion of banded WCSPs—seen in the figure as nodes—were not connected to another node which depicts low interactions between a large amount of captured, banded WCSPs in that season. However, in season 2021-22, all nodes were connected in the figure and significant edge weight can be observed between certain communities of banded WCSPs. While season 20-21 had some observed communities linked by low weight edges, season 21-22 has visibly more edges and heavier weighted edges connecting nodes together. The WCSPs exhibited strong community structures in both seasons as shown by the relatively high modularity values (season 2020-21, Q = 0.6; season 2021-22, Q = 0.45) (Figure 5). Season 2020-21 likely has a higher modularity level because, while there are less communities outlined, those identified communities are more isolated from the rest of the network than the communities from season 2021-22 (Figure 5). To assess that season 2021-22 community strength was not due to chance, we compared the “Random Flock Null Model” to the bootstrapped network derived from the season 2021-22. The bootstrapped network modularity was significantly different than the Random Flock Null model, and therefore season 2021-22 community structure and flock formation was not random (ANOVA: $p < 0.0001$) (Figure S2).

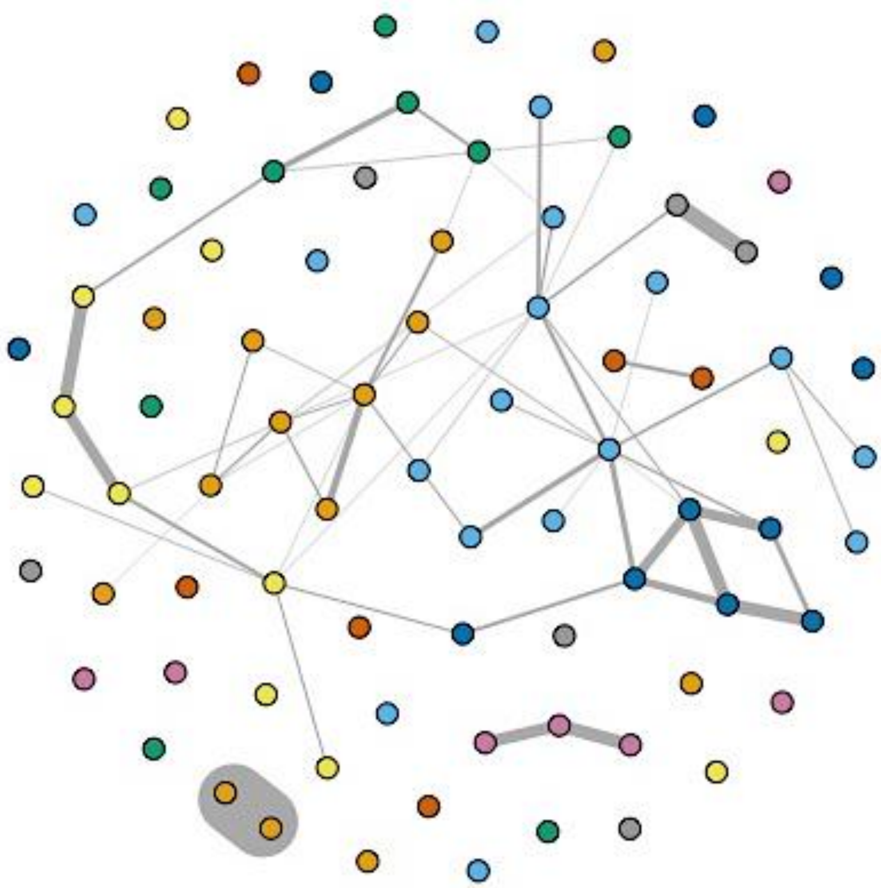

Figure 4. WCSP Network Analysis. The network analysis of the WCSP community structures and interactions at the BFS was created by the fast greedy modularity optimization algorithm. Each node—circle—indicates an individual WCSP, and the node color indicates a WCSPs membership in the community structure based off where the photo was captured. Each edge—line between nodes—represents a relationship between WCSPs. Only birds that were captured three or more times were included in the figure. Figure S1 displays banded WCSP ID number of graph (found in Supplemental Figures and Table section). Nodes not connected by edges were randomly assigned a community color by the algorithm and are not a part of mapped communities in the figure.

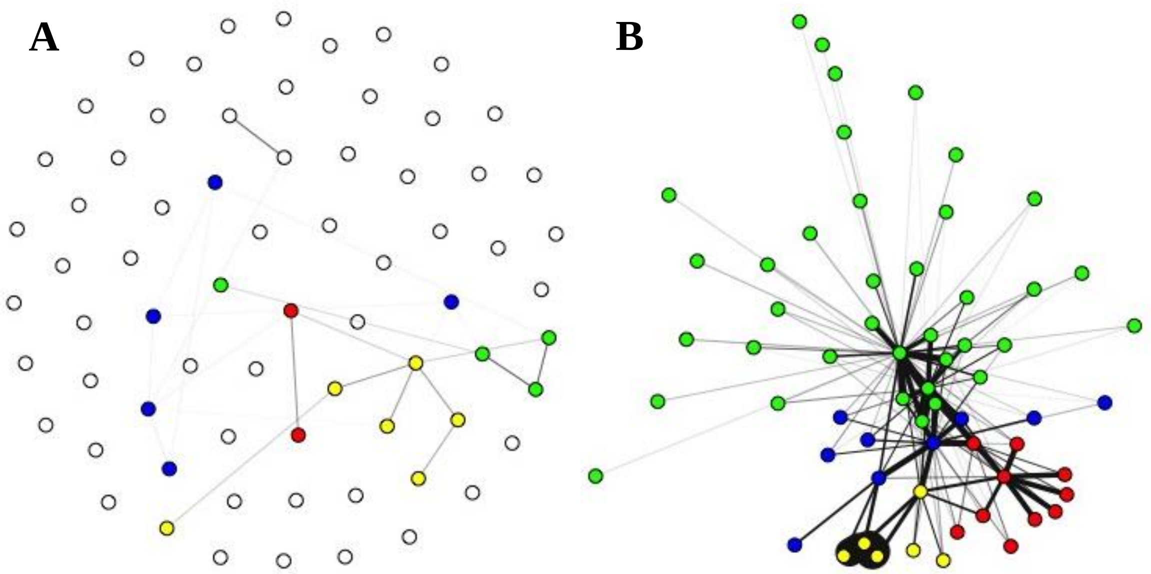

Figure 5. Season 2020-21 and 2021-2022 WCSP Network Analysis. The modularity optimization network analysis of the WCSP community structures and interactions of A) season 2020-21 and B) season 2021-22 at the BFS. Each node—circle—indicates an individual WCSP, and each edge—line between nodes—represents a relationship between WCSPs. Only birds that were captured three or more times were included in the figure. Season 2020-21 data encompasses only the months of October to January (Clague, 2021). Season 2020-22 data encompassed the months of October to February. The modularity value of flock structures in season 2020-21 and season 2021-22 was calculated from the modularity optimization network analysis (season 2020-21, 0.6; season 2021-22, 0.45).

Discussion

The purpose of the study was to determine if the White-Crowned Sparrow fixates to specific wintering grounds and forms stable winter flocks. With substantial evidence of wintering ground fixation, flock propensity, and social interactions between small foraging birds, we hypothesized that WCSPs will exhibit wintering ground fixation and form stable flock structure at the Bernard Field Station (BFS) in Southern California during the winter months of October to February. We observed banded WCSPs—captured during season 2021-22—who returned to the BFS from last year's season (season 2020-21) supporting our hypothesis that WCSPs fixate to wintering grounds (Table 1; Figure 3-5; Clague, 2021). And from season 2020-21 to season 2021-22, we observed an increase of community interaction and community size among WCSPs at the BFS (Table 1; Figures 4-5). While limited data from season 2020-21 prevented season to season data analysis, season 2021-22 displayed high clusters of WCSPs that formed strong community structures at the BFS (Figure 4).

The extent of banded WCSPs that returned for the winter season of 2021-22 supports our predication that WCSPs exhibit wintering ground fixation to the BFS. These results are comparable to those observed in the study of Golden Crowned Sparrows (GCSPs) (Shizuka et al., 2014). A significant number of GCSPs were observed to return every year to the study site in Santa Cruz, California over the three-year research period (Shizuka et al., 2014). While a greater percentage of GCSPs were observed returning in the other study, we still had a 25% return rate over the three winter seasons from 2019 to 2022 (Table 1). Overall, nearly three out of five GCSPs returned from season to season at Santa Cruz, and nearly one out of four WCSPs were returned to the BFS. Considering the large number of birds observed at both research sites, that data support the prediction that a large population of sparrows are nonrandomly selecting to return to their respective wintering grounds. And similar to the large distance that displaced Palm Warblers traveled in order to return to their original habitat, both WCSPs and GCSPs travel long distances from their breeding grounds to return to their wintering grounds at the BFS and the Santa Cruz study site respectfully (Stewart & Connor, 1980). And with a low probability that birds randomly return to the same wintering grounds every year, the study on GCSPs paired with our research strengthens the theory that small, foraging birds are likely to exhibit wintering ground fixation.

The network analysis identified several strong communities of WCSPs over the 2021-22 winter season (Figure 4). The significantly non-random flock structure of WCSPs during the 2021-22 winter season supports our predication that WCSPs form stable flocks in the BFS (Figure 4). The observed WCSP flock structures in the BFS, while not as numerous or well-defined, are a similar result to the observed flock structures of GCSP communities in Santa Cruz (Shizuka et al., 2014). While both studies detected isolated flocks of birds at their respective study sites, we were unable to observe specific flocks returning year to year at the BFS. Several GCSP flocks return season after season in Santa Cruz supporting the combined theory that birds not only fixate to a specific wintering ground but also fixate to specific flocks within those wintering grounds (Shizuka et al., 2014). And while the season 2020-21 study did not analyze any February photos, several flocks were identified among the WCSP population at the BFS (Clague, 2021). The season 2021-22 data builds on the previous year's research by utilizing the same modularity optimization network analysis to allow season to season data analysis. The season 2021-22 had significant modularity value which is an improvement from last year's insignificant results. Taken together, our study paired with the GCSP research and season 2020-

21 research paves the way to understanding the social flocking behavior of WCSPs in Southern California.

With the network analysis of season 2021-22 WCSPs provide substantial evidence toward community structure, flock development, and wintering ground fixation at the BFS, we can now look to future studies to examine flocking behaviors over years instead of just over a season. Overall, more research must be conducted to map birds to specific areas of the BFS. Strong evidence of site fidelity within the WCSP community can produce an accurate and complete flock pattern because otherwise it is hard to determine whether the WCSPs are forming flocks or just prefer the same locations as other WCSPs. While the fast greedy algorithm observed several strong community structures within the captured WCSPs, there was not enough data in previous seasons to compare inter-seasonal date (season 21-22 to season 2019-20 or season 2020-21 to season 2021-22). In addition, we did not observe any returning flocks' season to season due to less data being collected in season 2019-20 (only 12 total camera sites were captured) and less data being analyzed in season 2020-21 (February 2021 photos were not analyzed) (Drea, 2020: Clague, 2021). The continuation of this research in the future could potentially map any returning flocks' season to season along with the development and fixation of new ones at the BFS. With season 2021-22 as the baseline, future research can verify the preliminary evidence collected over several years of data on the WCSP social behavior at the BFS.

The purpose of this study lies in crafting a complete understanding of the social behavior of WCSPs. The wintering behavior of WCSPs takes up five to six months of the birds' year and very little research has been conducted on their behavior during those months. If WCSPs fixate to specific wintering grounds, then land development and city growth is likely very harmful to the birds. In addition, climate change likely affects where birds will stay during the winter months by shortening migration distances and displacing birds from their typical wintering grounds (Visser, 2009). Studying how WCSPs behave in their wintering grounds can provide researchers with ways to protect birds from population decline, habitat decline, and in the extreme, potential extinction. But while the large number of returning banded WCSPs supports the hypothesis of wintering ground fixation at the BFS, future research must be conducted to verify these results. With similar or even more data output in future seasons, season 2021-22 can provide a strong baseline for comparison in forthcoming research. Continuation of this research far in the future can produce a map of WCSP social behavior over the bird's entire life span rather than just a couple years. The study can evolve from studying wintering behavior within given years to studying wintering behavior development over a bird's lifetime. In addition, for future studies past the analysis of flock structure and wintering ground fixation, researchers can explore if the increase in land development around the BFS and/or rising global temperatures caused by climate change affects WCSPs fixation to the BFS.

Supplemental Figures and Tables

Table S1. Count and Percent of Banded and Unbanded WCSPs. The number of banded and unbanded WCSPs captured for all 24 traps at the BFS during the 2021-22 winter season months of October to February.

Trap Number	Captures				
	Banded		Unbanded		Total Count
	Count	Percent (%)	Count	Percent (%)	
1	48	9.52	456	90.48	504
2	70	5.49	1205	94.51	1275
3	53	5.27	952	94.73	1005
4	0	0	31	100	31
5	0	0	15	100	15
6	1	4	24	96	25
7	5	15.15	28	84.85	33
8	6	13.95	37	86.05	43
9	9	26.47	25	73.53	34
10	1	1.06	93	98.94	94
11	13	4.89	253	95.11	266
12	56	18.18	252	81.82	308
30	46	47.92	50	52.08	96
31	507	33.77	994	66.22	1501
32	181	18.48	798	81.51	979
33	94	22.54	323	77.46	417
34	692	22.82	2340	77.18	3032
35	362	32.21	762	67.79	1124
40	13	37.14	22	62.86	35
41	137	33.09	277	66.91	414
42	0	0	431	100	431
43	17	4.12	396	95.88	413
44	25	13.09	166	86.91	191
45	0	0	3	100	3
Total	2336		9933		12369

Table S2. Returning Unique Banded WCSPs Over Three Years. The identification numbers of all banded WCSPs that A) were captured during season 2019-20 and returned for season 2020-21, and B) were captured during season 2020-21 and returned for season 2021-22 at the BFS.

Banded WCSP Identification Numbers		
A) Returned for Season 2020-21	B) Returned for Season 2021-22	
273106428	273106402	279129431
279129446	273106405	279129433
279129458	273106409	279129435
279129466	273106410	279129446
279129475	273106414	279129458
279129483	273106415	279129459
279129485	273106418	279129475
279129491	273106420	279129476
279129492	273106428	279129482
279129500	273106437	279129483
	273106438	279129485
	279129415	279129492
	279129429	
10	25	

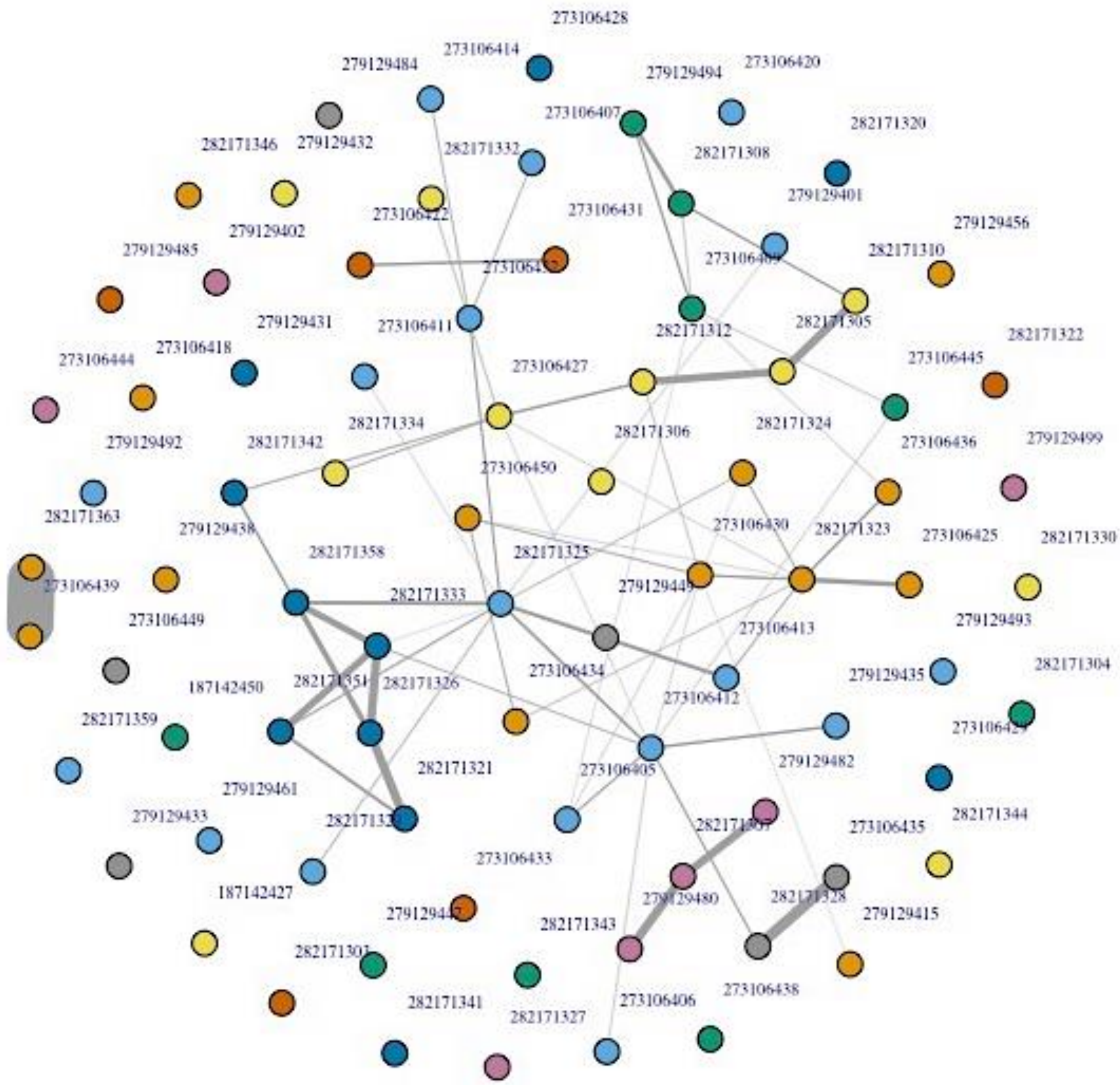

Figure S1. Season 2020-21 WCSP Network Analysis with Bird ID. The network analysis of the WCSP community structures and interactions at the BFS created by the fast greedy modularity optimization algorithm over season 2020-21. Each node—circle—indicates an individual WCSP with the unique ID above that node, and the node color indicates a WCSPs membership in the community structure based off where the photo was captured. Each edge—line between nodes—represents a relationship between WCSPs. Only birds that were captured three or more times were included in the figure. Nodes with no edge attached to them were assigned a random color that is not reflective of them being part of any community otherwise represented by nodes that are attached by edges.

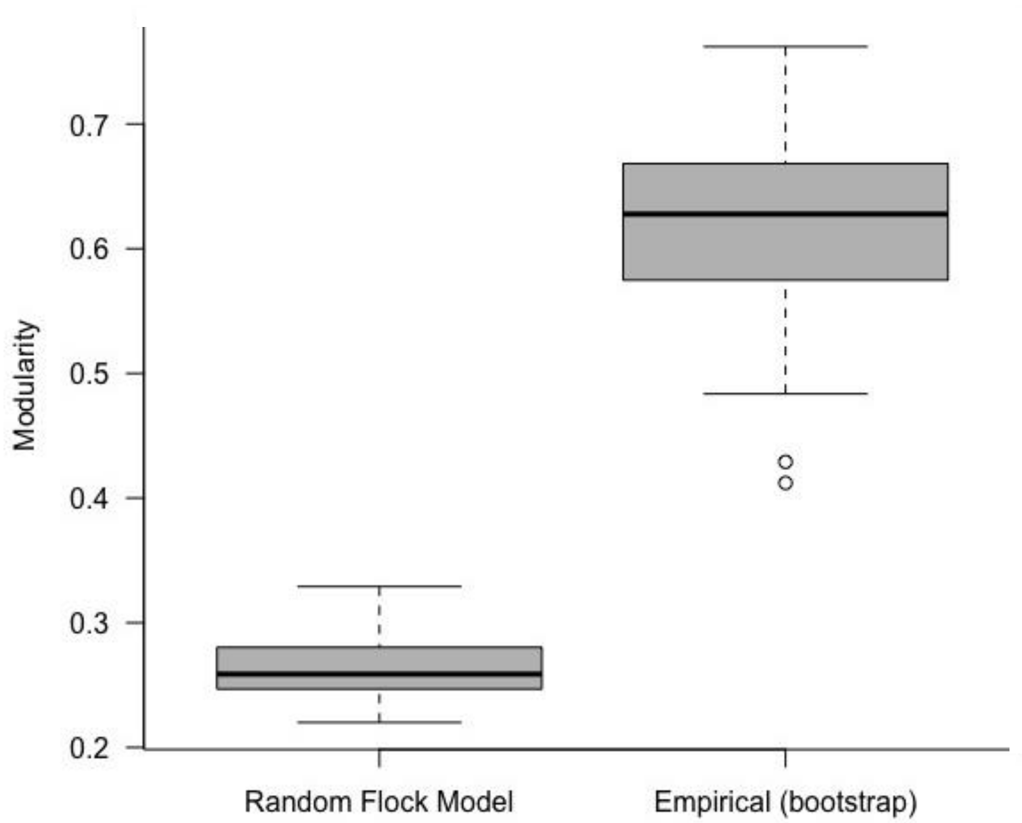

Figure S2: Modularity of Season 2021-22. The modularity of the resampled flocks from season 2021-22 (empirical (bootstrap)) compared to the Random Flock Null Model. The Random Flock Model simulated a random network analysis controlled for observed flock size and total number of unique banded birds captured. The empirical (bootstrap) re-sampled the season 2021-22 data 100 times via a bootstrapping technique (Lusseau, 2008). ANOVA: p value < 0.0001.

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Literature Cited

Anderson, A. M., S. Duijns, P. A. Smith, C. Friis, and E. Nol. "Migration Distance and Body Condition Influence Shorebird Migration Strategies and Stopover Decisions During Southbound Migration." [In English]. *Frontiers in Ecology and Evolution* 7 (Jul 9 2019). https://doi.org/ARTN.

Baas, P., and S. Carlquist. "A Comparison of the Ecological Wood Anatomy of the Floras of Southern-California and Israel." [In English]. *Iawa Bulletin* 6, no. 4 (1985): 349-53. https://doi.org/Doi 10.1163/22941932-90000961. <Go to ISI>://WOS:A1985AWF1500009.

Clague, S. Winter Flocking Behavior of Migratory White-Crowned Sparrows. 2021. Senior Thesis. Keck Science Department, Pitzer College, Claremont, CA.

DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. R. Norris. "Transoceanic Migration by a 12 G Songbird." *Biol Lett* 11, no. 4 (Apr 2015): 20141045. https://doi.org/10.1098/rsbl.2014.1045. https://www.ncbi.nlm.nih.gov/pubmed/25832815.

Drea, B. Alaskan White-Crowned Sparrows Wintering Flock Structure. 2020. Senior Thesis. Keck Science Department, Pitzer College, Claremont, CA.

Guz, S. S. "Terrestrial Vegetation of California." [In English]. *Library Journal* 132, no. 19 (Nov 15 2007): 82-82. <Go to ISI>://WOS:000251542700217.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. "Carry-over Effects as Drivers of Fitness Differences in Animals." [In English]. *Journal of Animal Ecology* 80, no. 1 (Jan 2011): 4-18. https://doi.org/10.1111/j.1365-2656.2010.01740.x. <Go to ISI>://WOS:000285110600002.

Jones, S., M. Pfister-Genskow, C. Cirelli, and R. M. Benca. "Changes in Brain Gene Expression During Migration in the White-crowned Sparrow." *Brain Research Bulletin* 76, no. 5 (2008): 536–44. doi:10.1016/j.brainresbull.2008.03.008.

Martinez, A. E., J. P. Gomez, J. M. Ponciano, and S. K. Robinson. "Functional Traits, Flocking Propensity, and Perceived Predation Risk in an Amazonian Understory Bird Community." *Am Nat* 187, no. 5 (May 2016): 607-19. https://doi.org/10.1086/685894. https://www.ncbi.nlm.nih.gov/pubmed/27104993.

Portugal, S. J. "Bird Flocks." [In English]. *Current Biology* 30, no. 5 (Mar 9 2020): R206-R10. <Go to ISI>://WOS:000518561000006.

RCoreTeam. R: A Language and Environment for Statistical Computing. 2021. R Foundation for Statistical Computing, Vienna, Austria.

Sherry, T. W., and R. T. Holmes. "Winter Habitat Quality, Population Limitation, and Conservation of Neotropical Nearctic Migrant Birds." [In English]. *Ecology* 77, no. 1 (Jan 1996): 36-48. https://doi.org/Doi 10.2307/2265652. <Go to ISI>://WOS:A1996TR07900005.

Shizuka, D., A. S. Chaine, J. Anderson, O. Johnson, I. M. Laursen, and B. E. Lyon. "Across-Year Social Stability Shapes Network Structure in Wintering Migrant Sparrows." [In English]. *Ecology Letters* 17, no. 8 (Aug 2014): 998-1007. https://doi.org/10.1111/ele.12304. <Go to ISI>://WOS:000339101100012.

Sieving, K. E., S. A. Hetrick, and M. L. Avery. "The Versatility of Graded Acoustic Measures in Classification of Predation Threats by the Tufted Titmouse Baeolophus Bicolor: Exploring a Mixed Framework for Threat Communication." [In English]. *Oikos* 119, no. 2 (Feb 2010): 264-76. https://doi.org/10.1111/j.1600-0706.2009.17682.x. <Go to ISI>://WOS:000275557500009.

Stewart, P. A., and H. A. Connor. "Fixation of Wintering Palm Warblers to a Specific Site." [In English]. *Journal of Field Ornithology* 51, no. 4 (1980): 365-67. <Go to ISI>://WOS:A1980LH60100008.

Tobler, M. Camera Base. V. 1.7. Atrium - Biodiversity Information System. PC. 2015.

Toews, D. P. L. "Habitat Suitability and the Constraints of Migration in New World Warblers." [In English]. *Journal of Avian Biology* 48, no. 12 (Dec 2017): 1614-23. https://doi.org/10.1111/jav.01157. <Go to ISI>://WOS:000418276300013.

Toth, Z., B. Tuliozi, D. Baldan, H. Hoi, and M. Griggio. "The Effect of Social Connections on the Discovery of Multiple Hidden Food Patches in a Bird Species." *Sci Rep* 7, no. 1 (Apr 11 2017): 816. https://doi.org/10.1038/s41598-017-00929-8. https://www.ncbi.nlm.nih.gov/pubmed/28400588.