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Using individual capture data to reveal large-scale patterns of social association in birds

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Abstract

Studying social behavior has traditionally been labor-intensive, limiting the scale of datasets and therefore the questions that can be asked. We explore the potential for large individual capture datasets, which arise from population monitoring projects such as bird banding stations, to fill this gap. Using a 23-year dataset from San Jose, CA, comprised of six passerine bird species from four families, we constructed social networks to investigate whether age-, sex-, and taxon-related patterns of social association could be detected. We found support for age-related patterns in social behavior and patterns of overall species differences that agreed with past work. We then explored interactions between species and patterns in social behavior over time, two questions that have historically been difficult to address. We detected positive assortment by taxon, and we observed a significant multi-decade decrease in mean degree. Using an agent-based simulation to allow us to independently vary behavior and aspects of the capture dataset, we found that sample size and capture probability affected the metrics that were intended to only measure social behavior, but that these confounding effects could be effectively managed in many cases. We conclude that while analysis of individual capture datasets should not replace more intensive studies of social behavior, the utilization of these data could considerably expand the scope of our knowledge of social behavior, particularly at large temporal scales and for species that are difficult to observe.

Keywords Age · Agent-based model · Bird banding · Passerellidae · Social behavior · Social network

Zusammenfassung

Verwendung individueller Fangdaten zur Aufdeckung von Langzeitmustern in sozialen Verbänden bei Vögeln

Die Untersuchung des Sozialverhaltens ist traditionell sehr arbeitsintensiv, was den Umfang von Datensätzen und somit die Fragen einschränkt, die gestellt werden können. Wir untersuchten das Potential großer, individueller Fangdatensätze, welche aus dem Populationsmonitoring wie z. B. an Vogelberingungsstationen stammen, um derartige Wissenslücken zu schließen. Anhand eines Datensatzes über 23 Jahre aus San José, Kalifornien, der sechs Singvogelarten aus vier Familien umfasst, erstellten wir ein Netzwerk der Sozialstruktur, um zu untersuchen, ob es alters-, geschlechts- und taxonbezogene Muster bei Sozialverbänden gibt. Wir fanden Hinweise auf ein altersbedingtes Muster im Sozialverhalten sowie auf ein Muster allgemeiner artspezifischer Unterschiede, die mit früheren Studien übereinstimmen. Wir untersuchten weiterhin Interaktionen zwischen Arten und Mustern im Sozialverhalten über die Zeit, zwei Aspekte, die in der Vergangenheit nur schwer zu beantworten waren. Wir fanden eine positive assortative Gruppierung nach Taxa und beobachteten eine signifikante jahrzehntelange Abnahme des mittleren Grades der sozialen Vernetzung. Durch die Verwendung einer agentenbasierten

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Simulation, die es uns ermöglichte, das Verhalten und die Aspekte des Fangdatensatzes unabhängig voneinander zu variieren, fanden wir heraus, dass die Stichprobengröße und die Fangwahrscheinlichkeit die Maße beeinflussten, die nur zur Messung des Sozialverhaltens gedacht waren. Doch mit diesen störenden Auswirkungen konnte in vielen Fällen effektiv umgegangen werden. Zusammenfassend lässt sich sagen, dass die Analysen der individuellen Fangdatensätze zwar keine intensiveren Studien des Sozialverhaltens ersetzen sollten, die Verwendung dieser Daten jedoch den Umfang unseres Wissens über das Sozialverhalten erheblich erweitern können, vor allem über große Zeiträume und für Arten, die schwierig zu beobachten sindDie Untersuchung des Sozialverhaltens ist traditionell sehr arbeitsintensiv, was den Umfang von Datensätzen und somit die Fragen einschränkt, die gestellt werden können. Wir untersuchten das Potential großer, individueller Fangdatensätze, welche aus dem Populationsmonitoring wie z. B. an Vogelberingungsstationen stammen, um derartige Wissenslücken zu schließen. Anhand eines Datensatzes über 23 Jahre aus San José, Kalifornien, der sechs Singvogelarten aus vier Familien umfasst, erstellten wir ein Netzwerk der Sozialstruktur, um zu untersuchen, ob es alters-, geschlechts- und taxonbezogene Muster bei Sozialverbänden gibt. Wir fanden Hinweise auf ein altersbedingtes Muster im Sozialverhalten sowie auf ein Muster allgemeiner artspezifischer Unterschiede, die mit früheren Studien übereinstimmen. Wir untersuchten weiterhin Interaktionen zwischen Arten und Mustern im Sozialverhalten über die Zeit, zwei Aspekte, die in der Vergangenheit nur schwer zu beantworten waren. Wir fanden eine positive assortative Gruppierung nach Taxa und beobachteten eine signifikante jahrzehntelange Abnahme des mittleren Grades der sozialen Vernetzung. Durch die Verwendung einer agentenbasierten
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Introduction

Social associations can have large impacts on fitness. Aggregations of individuals reduce the risk of predation on any one through the dilution and confusion effects (Seghers 1974; Foster & Treherne 1981; Roberts 1996) and through increased vigilance, while also reducing the vigilance load on any one individual (Roberts 1996; Favreau 2018). Foraging in groups can improve the chances of locating food (Baker et al. 1981; Smolla et al. 2016). Socially-associated juveniles may become reproductive pairs when they mature (Teitelbaum et al. 2017). Crucial behavioral skills such as courtship signaling, breeding site selection, migration routes, foraging techniques, and predator identification are learned through observation of, and interaction with, conspecifics (Griffin 2004; McDonald 2007; Cornell et al. 2012; White et al. 2012; Mueller et al. 2013; Griesser andd Suzuki 2017; Rivera-Cáceres et al. 2018). On the negative side, proximity to others can increase competition for resources, including food, territories, and mates (Baker et al. 1981; Schoepf & Schradin 2012), and increase the risk of disease (Nunn et al. 2015). Patterns of individual social association can therefore yield insights into any of these potential selective pressures, and understanding what drives variation in social association among individuals, between species, and over time is an important goal in behavioral ecology (Farine andd Whitehead 2015).

A dearth of basic data on social associations remains a major hurdle for the achievement of this goal (Shizuka et al. 2014). Collecting data on individual social associations has traditionally been labor-intensive, requiring individuals to be uniquely marked and then monitored. Active monitoring by human observers requires training and the investment of many man-hours (e.g. > 9000 h in McDonald 2007), while passive monitoring using technology (e.g. Aplin et al. 2015) is costly. Due to these limitations, multi-year, multi-species, and large-sample-size social datasets are extremely rare. This restricts our knowledge of social association patterns, and therefore our ability to understand what drives their variation.

Yet while large-scale social behavior datasets are rare, large-scale individual capture datasets—such as those generated by bird banding stations, long-term traplines, and sometimes camera traps—are comparatively common. These datasets may span decades and contain tens of thousands of marked individuals belonging to dozens of species. In this paper we explore whether such individual capture datasets can be effectively employed in social behavior analysis, with the potential to dramatically expand the scale of questions that can be asked. For our exemplar we employ a dataset from a single banding station in California, consisting of 23 years of capture data for six bird species distributed across four families. We focus on two widely used social network metrics (Farine and Whitehead 2015; Fig. 1), one individual-centered (degree, a measure of the number and strength of an individual's associations), and one network-wide (transitivity, the propensity of individuals in a network to cluster, reflecting the broad-scale shape of the social

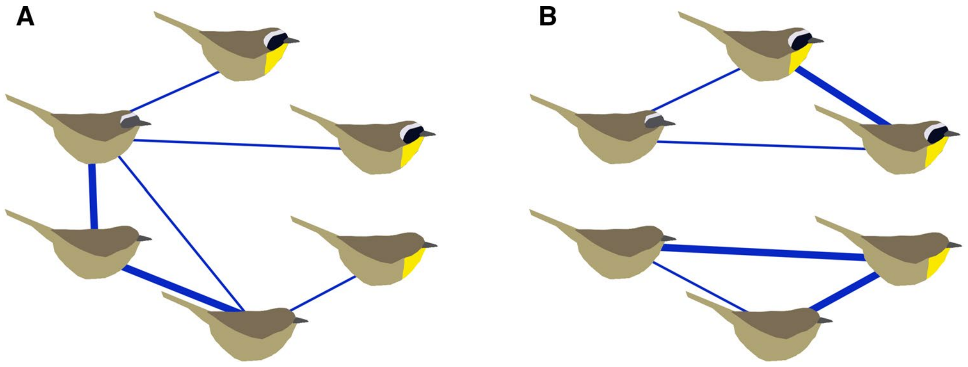

Fig. 1 In social networks, individuals are represent by nodes, and associations between individuals are represented by lines ("edges") connecting the two individuals. Nodes may have attributes, such as sex (in this figure, males have masks) and age (adults have yellow throats). Line weight represents association strength. The degree of a node is the number of edges connecting to it, usually (as in this study) weighted by edge weight. Mean degree of a network is the mean of the degrees of all constituent nodes. Network transitivity is the propensity of the network to "cluster," to form closed three-node triangles; network (**a**) has a lower transitivity than network (**b**). We predicted that young birds would have more associations than older birds, as depicted in network (**a**); and that sex would influence associations, for example by individuals preferentially associating with others of the same sex, as depicted in network (**b**)

community). We test whether the individual capture dataset is informative for questions of social behavior by comparing the social patterns therein to those found in other, more traditionally-studied systems. Then, we demonstrate the further potential of this approach by exploring patterns of social association at a scale that traditional social behavior datasets are rarely able to address. We finally employ agent-based modelling to investigate the potential for data structure to bias results from individual capture datasets.

Age- and sex-related patterns of social behavior

Because the costs and benefits of social association may vary depending on individual attributes, we expect that social behavior itself will similarly vary. Age has been shown to affect social behavior, with younger individuals being more social in birds (White-crowned Sparrows *Zonotrichia leucophrys*, King et al. 1965; Royal Terns *Sterna maxima*, Buckley & Buckley 1974) and other vertebrates (humans *Homo sapiens* and bottlenose dolphins *Tursiops* spp., Lusseau & Newman 2004; rhesus macaques *Macaca mulatta*, Liao et al. 2018). If our individual capture dataset accurately reflects patterns of social association, we expect that it will support a pattern of greater sociality of juveniles compared with adults (hypothesis 1; Fig. 1).

Sex also influences social associations, but patterns vary among study systems and over time (e.g. Lusseau andd Newman 2004; Croft et al. 2004; Spiegel et al. 2018). Birds have been observed to associate assortatively by sex (Ketterson and Nolan 1979; Kohn et al. 2011; Whiteside et al. 2017) and dissassortatively (Hunt and Flaspohler 1998; Guzy andd Ritchison 1999). Based on patterns observed in other socially monogamous species (Ketterson and Nolan 1979; Farine 2014), we expect to find dissassortative association by sex in the breeding season and assortment by sex in the non-breeding season (hypothesis 2; Fig. 1).

Interspecific and interannual variation in social behavior

Utilizing large individual capture datasets would permit the study of questions in social behavior that have historically been difficult to address. Understanding how social behavior differs among species is crucial to unraveling the relationships between social behavior and ecology (Ekman 1989), yet quantitative comparisons of social behavior among species have been limited by methodological variation among studies, which can preclude comparison. The consistency of methods across species in our dataset allows interspecific comparison. We predict that social network metrics will reflect previously documented differences in species sociality in our six species (hypothesis 3). We also demonstrate the potential of individual capture datasets for examining interspecific interactions by examining the interactions between individuals of three species of passerellid sparrow.

Knowledge of multiyear patterns in social behavior is important in elucidating the drivers of plastic change in behavior, as well as discriminating such plastic change from evolutionary change (Clutton-Brock and Sheldon 2010); but such patterns have rarely been characterized, due to the difficulties of building long-term social datasets. Individual capture datasets could contribute findings in both of these topics, as they are commonly long-term and document multiple species with consistent methods. We use our long-term multispecies dataset to demonstrate this potential.

Social affiliation or simply location?

Capture data present the challenge that true social association cannot be distinguished from geographic co-occurrence. This difficulty applies to many social behavior studies (e.g., all those that employ the "gambit of the group" [Whitehead and Dufault 1999]), but is especially pronounced here because individual capture datasets record only presence in a place and time, whereas direct observation permits other information to be gathered (e.g. duration of presence, social interaction). However, even if findings from individual capture datasets are interpreted most conservatively as patterns of spatial structure rather than social structure, these patterns may be relevant to questions of behavioral ecology such as competition, predation risk, and habitat selection. Additionally, geographic co-occurrence is a prerequisite for social association: any structure in space will constrain the potential for structure in social association. Therefore, at minimum, results from individual capture datasets reflect the potential for social association.

Robustness to sampling artefacts

Because individual capture datasets are unlikely to have been collected with social analysis in mind, and will likely contain the complexity expected of observational data, it is important to consider the potential for artefacts resulting from the structure of the data itself to influence results. For example, datasets with more captures per individual might yield higher estimates of individual degree, confounding the estimation of degree unless this relationship is taken into account. We investigated whether there is evidence of such confounds in our focal dataset. Further, we constructed an agent-based model to simulate birds with variable behavior being captured and recorded in an artificial individual capture dataset, and used this model to explore potential confounds in an environment where aspects of biology and data structure could be varied independently. We conclude with practical recommendations for minimizing the effect of confounding factors on analyses of individual capture data.

Methods

Study location

The San Francisco Bay Bird Observatory's Coyote Creek Field Station (CCFS), in San Jose, CA, has been operating year-round since 1983, except for multi-week closures in 1999 and 2002. The net lanes run through remnant and restored riverine habitat as well as grassland that is mowed annually in late summer or fall. CCFS operates 48 nets, all of which are 30 mm mesh and 12 m × 2 m in dimension, except for one 6 m × 2 m net. Two of the net locations have double-high nets, one net stacked above the other, in effect forming a 12-m long by 4-m high net. Banding starts 30 min before sunrise and runs for five hours, barring inclement weather, on Wednesdays, Saturdays, and Sundays, with each weekday operating a different, non-overlapping set of nets. Nets are operated passively; i.e., no song or other inducement is presented to lure birds into the nets. Capture times are recorded in 30-min intervals. Captured birds are banded with a US Fish and Wildlife metal band with a unique number on it for individual identification, and are examined and measured following standard bird banding data collection protocols. Sex and age is determined following Pyle (1997). The birds are handled according to federal and state guidelines and those of the North American Banding Council. This study did not involve any deviation from standard operating procedure at CCFS.

In analysis, we use the age categories "first-year," "after-first-year," or unknown. These deviate from standard age categorization in bird banding, wherein a bird is considered a second-year as soon as the calendar year changes on 01 January; by that system, a bird hatched in August may be a nominal second-year at < 4 months old. Instead, we considered a bird to be a "first-year" from the day it hatched through 29 February the following year. In other words, a "first-year" bird by our system has never experienced the breeding season as an adult, which we considered to be a more biologically relevant approach to age categorization.

Study species

We studied the six species with the highest number of captures (including both new captures and recaptures) at CCFS, which belong to four families within the order Passeriformes. These species range from 5 to over 30 g in mass, from solitary to highly social, and from year-round residents to annual migrants that winter at CCFS (Table 1).

Generating social networks

The initial dataset included all captures of the six focal species at CCFS from 01 January 1996–31 December 2018. Data prior to 1996 were excluded because data collection protocols were standardized in 1995.

We generated single-species subsets of the data for each focal species. We considered individuals to be associated if they were captured during the same 30-min "net run" and within the same 12-m mist net. This represents the most stringent criteria possible given the dataset, which records the timing of the net run in 30-min intervals and the net of capture. This is a "gambit of the group" approach to assigning associations, in which all individuals observed within

Table 1 Description of each species studied, timing of presence, captures (including recaptures of the same individual), and individuals captured from 1996 through 2018 at Coyote Creek Field Station, near San Jose, CA. Br = Apr–Sep, the breeding season; non-br = Oct–Mar, the non-breeding season; parentheses indicate reduced presence during that time period

Family	Species	Mass	Diet	Sociality	Presence at CCFS	Captures	Individuals	References
Aegithalidae	Bushtit (*Psaltriparus minimus*)	4–6 g	Arthropods	High	br, non-br	5018	1974	Sloane (2001)
Turdidae	Hermit Thrush (*Catharus guttatus*)	25–34 g	Arthropods, fruit	Low	non-br	6215	3486	Dellinger et al. (2012), Brown et al. (2000)
Passerellidae	Song Sparrow (*Melospiza melodia*)	20–28 g	Generalist	Low	br, (non-br)	12,396	4096	Arcese et al. (2002), Goodson et al. (2012)
	Golden-crowned Sparrow (*Zonotrichia atricapilla*)	30–33 g	Seeds	Moderate	non-br	3437	1735	Norment et al. (1998), Shizuka et al. (2014)
	White-crowned Sparrow (*Zonotrichia leucophrys*)	25–28 g	Seeds	High	non-br	5086	3631	King et al. (1965), Chilton et al. (1995)
Parulidae	Common Yellowthroat (*Geothlypis trichas*)	9–10 g	Arthropods	Moderate	br, (non-br)	6489	3391	Guzy and Ritchison (1999)

a group are considered associated with each other (Whitehead and Dufault 1999). This method equates geographical and temporal co-occurrence with association, an assumption that should be considered when evaluating results from such analyses. Because some species were present at CCFS only in the non-breeding season, while others are resident year-round (Table 1), we split the datasets of the year-round residents by season, with October through March designated "non-breeding" and April through September, "breeding." To prevent the non-breeding season from being split by the change of the calendar year at December/January, we named non-breeding seasons according to the year of their beginning; e.g., the season of October 2017–March 2018 is "non-breeding season 2017".

We constructed individual networks for each year and season within each species. We used the package *asnipe* (Farine 2013) and custom code in R v. 3.4.4 (R Core Team 2018) to create networks, incorporating sampling period and occurrence data and employing the "simple ratio index" metric of association as recommended by Hoppitt and Farine (2018) for cases where observation probabilities are not known. Any combination of year and season with < 50 captures of the focal species was excluded for insufficient sample size.

To explore differences between species and changes in social network structure over time, we calculated the mean degree and the transitivity of each social network using packages *sna* (Butts 2008b) and *network* (Butts 2008a), respectively. Mean degree measures the average number of connections per individual, weighted by the strength of those connections. Transitivity, a.k.a. clustering coefficient, measures the propensity of connections in the network to cluster (specifically, to form a three-node triangle motif or closed triad), with higher values indicating greater clustering (Farine and Whitehead 2015). Because transitivity is calculated as a ratio of closed triads to total triads (including open triads, which are triangle motifs missing one edge), a minimum sample size of edges is required for the measure to be meaningful; therefore we did not calculate transitivity for any networks with < 20 edges. We also did not perform any further analyses (described below) on networks with < 20 edges.

To explore interactions between species, additional matrices that included the three sparrow (Passerellidae) species were constructed as described above. These matrices included only the non-breeding season, because two of the three sparrow species were not captured in the breeding season.

Statistical analysis

All analyses were performed in R v. 3.4.4 (R Core Team 2018). To test for species differences in the mean degree and transitivity of the yearly social networks and for long-term patterns in those metrics, we ran linear models with mean degree or transitivity as the response variable. The full models included the following as fixed effects: species, year, season, a species*year interaction, a species*season interaction, the number of captures per individual in the dataset used in constructing the network, and standardized sampling effort (number of hours the nets were open) for that year. The model of network transitivity additionally included the number of edges in the network as a fixed effect, because this can affect transitivity. We then compared the full model to three reduced models using ANOVA; two of the reduced models omitted one of the two interaction terms in the full model, and the third reduced model omitted both interaction terms. If the models did not significantly differ in explanatory power, then the interaction term(s) omitted in the reduced model was also omitted from the final model. If the full and reduced models did significantly differ, suggesting that the omitted interaction term contributed to the model's explanatory power, then the interaction term omitted in the reduced model was not omitted from the final model.

To test for sex- and age-related differences in degree within species, we followed the approach recommended by Farine (2013) of calculating the effect of the variable on degree in the network, then comparing that effect to similarly calculated effects from randomly permutated networks to derive a p-value. This approach is recommended because social network data rarely conform to the assumptions of standard statistical distributions (Bejder et al. 1998; Farine 2017). We ran a linear model for each network with degree as the response variable and sex or age as a fixed effect, producing an estimated effect size of age or sex on degree. We then used the "network_permutation()" function of *asnipe* (Farine 2013) to calculate 1000 pre-network permutations of the original association data (Bejder et al. 1998; Farine 2017), with each permutation separated by five "swaps" of association between individuals, and swaps restricted to occurring within the same day. These permutated networks share attributes of the true dataset (sample size, number of associations, temporal distribution of associations, etc.) but should not exhibit any relationship between the variable of interest and degree, since the swaps occur without reference to any individual attribute. For each permutation, we ran a linear model to calculate the effect of age or sex on degree. We were then able to compare the observed effect size to 1000 permutated effect sizes to calculate the likelihood of observing that effect size in a dataset with the same attributes but with no true relationship between age or sex and degree.

To test for assortment by age and sex within species, we used the package *assortnet* (Farine 2014) to calculate the assortativity coefficient r and its standard error. Although Farine (2014) found these two values to be generally reliable for determining significance, to be conservative we additionally calculated significance by running 1000 random permutations of the attribute data (sex or age) and comparing our observed r to the distribution of randomly permutated rs. This measure corresponds to P_n in Farine 2014.

We additionally investigated subspecies- and species-related patterns. Our captured White-crowned Sparrows belong to the subspecies Puget Sound White-crowned Sparrow *Zonotrichia leucophrys pugetensis* and Gambel's White-crowned Sparrow *Z. l. gambelii*. We tested for assortativity by subspecies in White-crowned Sparrows, and for assortativity by species in our multi-species passerellid sparrow networks, as described above for age and sex.

When determining the significance of patterns in our analyses, we used the Holm-Bonferroni correction for multiple comparisons to control the family-wise error rate at 0.05 (Holm 1979). We considered networks of the same species (or mix of species, in the case of the multi-species sparrow analysis) and season to belong to the same statistical family.

Simulation

To evaluate the potential effects of confounding factors on patterns derived from capture data, we built an agent-based model in NetLogo v. 6.1.1 (Wilensky 1999) simulating the processes that produce individual capture data (code in Supplementary Material; Fig S1). This simulation enabled us to independently vary aspects of "behavior" and aspects of the collected dataset (e.g. sample size). Briefly, the simulation included agents—simulated birds—that moved through space, some ("loners") moving randomly and some ("flock members") following other agents to form six-agent flocks. When an agent happened to occupy a location that was also occupied by a simulated mist net, that agent was "captured"—its ID and the time recorded—with some probability. This capture probability could be varied, as could the rate of agent movement ("vagility") and how closely coordinated flockmates were in their movements ("affinity"). Output data consisted only of agent IDs, net locations, and time stamps; these data were turned into networks from which network metrics could be calculated in the same manner as the non-simulated bird capture data. We then tested the relationship between those metrics and variables of interest using linear models.

We tested whether relative sample size (specifically, the mean number of capture records per individual) affected mean degree or transitivity by running simulations for different numbers of "days." (Each simulated day included the same number of time periods as a real banding day from our banding dataset, and agent locations were re-set after each day to simulate diel patterns in movement.) We tested whether capture probability, which can be influenced by factors such as mist net quality and species size, affected mean degree or transitivity by running simulations at different capture probabilities. In all cases we simulated two different levels of sociality, to increase the likelihood that our results are generalizable and to test whether mean degree and transitivity captured those differences in behavior. For degree, an individual metric, we included "loners" and "flock members" in the same simulation, to recreate the natural situation of birds with different degrees of sociality existing in the same space, and calculated different mean degree values for the two categories. For transitivity, a whole-network measure, we ran separate simulations of flocks with high and low affinity.

To assess the potential for complex effects of variation in several factors simultaneously, we also calculated mean degree and transitivity for multiple combinations of sample size, capture probability, vagility, and affinity. Note that an ideal metric of social behavior would be affected by vagility and affinity because these are aspects of social behavior, but would not be affected by sample size and capture probability. To assess the effects of these factors, we ran linear models with mean degree or transitivity as the response variable. The full models included as fixed effects a vagility*affinity interaction and a captures-per-individual*capture probability interaction. We then compared the full model to three reduced models using ANOVA; two of the reduced models omitted one of the two interaction terms in the full model, and the third reduced model omitted both interaction terms. If the models did not significantly differ in explanatory power, then the interaction term(s) omitted in the reduced model was also omitted from the final model. If the full and reduced models did significantly differ, suggesting that the omitted interaction term contributed to the model's explanatory power, then the interaction term omitted in the reduced model was not omitted from the final model.

To mimic a real-world analysis scenario, we additionally ran "field" analyses of the multivariate simulation data in which we did not include capture probability, because capture probability is unlikely to be known for non-simulated data. The results of these analyses therefore better represent results that might be obtained from actual individual capture datasets.

Results

Age and sex

There was evidence of positive assortment by age in at least one half-year network for every species except the White-crowned Sparrow (Fig. 2). Support for age assortment was strongest in the Common Yellowthroat (significant in seven of ten half-year networks) and Song Sparrow (significant in 13 of 16 half-year networks) in the breeding season. Age differences in degree were significant only for the Bushtit, with first-year birds having higher degree than older birds in six of twenty-three half-year networks in the breeding season, and first-year birds having lower degree than older birds in the non-breeding season of 2012–2013.

There was no significant support for sex-related assortment or differences in degree (Fig. 2).

Multi-taxon association

White-crowned Sparrows showed evidence of positive assortment by subspecies, with significant results in ten of eighteen half-year networks. In the multi-species analysis, Golden-crowned, Song, and White-crowned Sparrows assorted positively by species, with significant results in 18 of 22 half-year networks.

Species differences and long-term patterns in network metrics

The final model of mean degree included no interaction terms (ANOVA comparing full and most-reduced models: df = –7, F = 1.03, *p* = 0.414). The final model of network transitivity also included no interaction terms (ANOVA comparing full and most-reduced models: df = –6, F = 0.933, *p* = 0.476).

The Bushtit, Golden-crowned Sparrow, and White-crowned Sparrow had significantly higher mean degree than the Song Sparrow (Table 2; Fig. 3). The Golden-crowned Sparrow and White-crowned Sparrow also had significantly greater network transitivity than the Song Sparrow (Table 3; Fig. 4).

Mean degree decreased over the 23 years sampled (Table 2).

Simulation results

Both mean degree and transitivity were significantly related to simulated social behavior in the form of loner vs. flock member (for mean degree) or of low vs. high affinity (for transitivity) (Table 4; Figs. 5 and 6), as would be expected of metrics designed to reflect social behavior. However, both mean degree and transitivity were also related to at least one of the two tested variables that do not represent social behavior: transitivity was significantly affected by the number of captures per individual, and both mean degree and transitivity were significantly affected by capture probability.

In the multi-variable analyses, the final models of mean degree and of transitivity both included an interaction between number of captures per individual and capture probability, but no interaction between vagility and affinity (mean degree: ANOVA comparing full model to reduced model lacking affinity*vagility interaction, df = –1, F = 0.69, *p* = 0.414; ANOVA comparing full model to reduced model lacking captures-per-individual*capture probability interaction, df = –1, F = 6.97, *p* = 0.008*; transitivity: ANOVA comparing full model to reduced model lacking affinity*vagility interaction, df = –1, F = 1.58, *p* = 0.208; ANOVA comparing full model to reduced model lacking

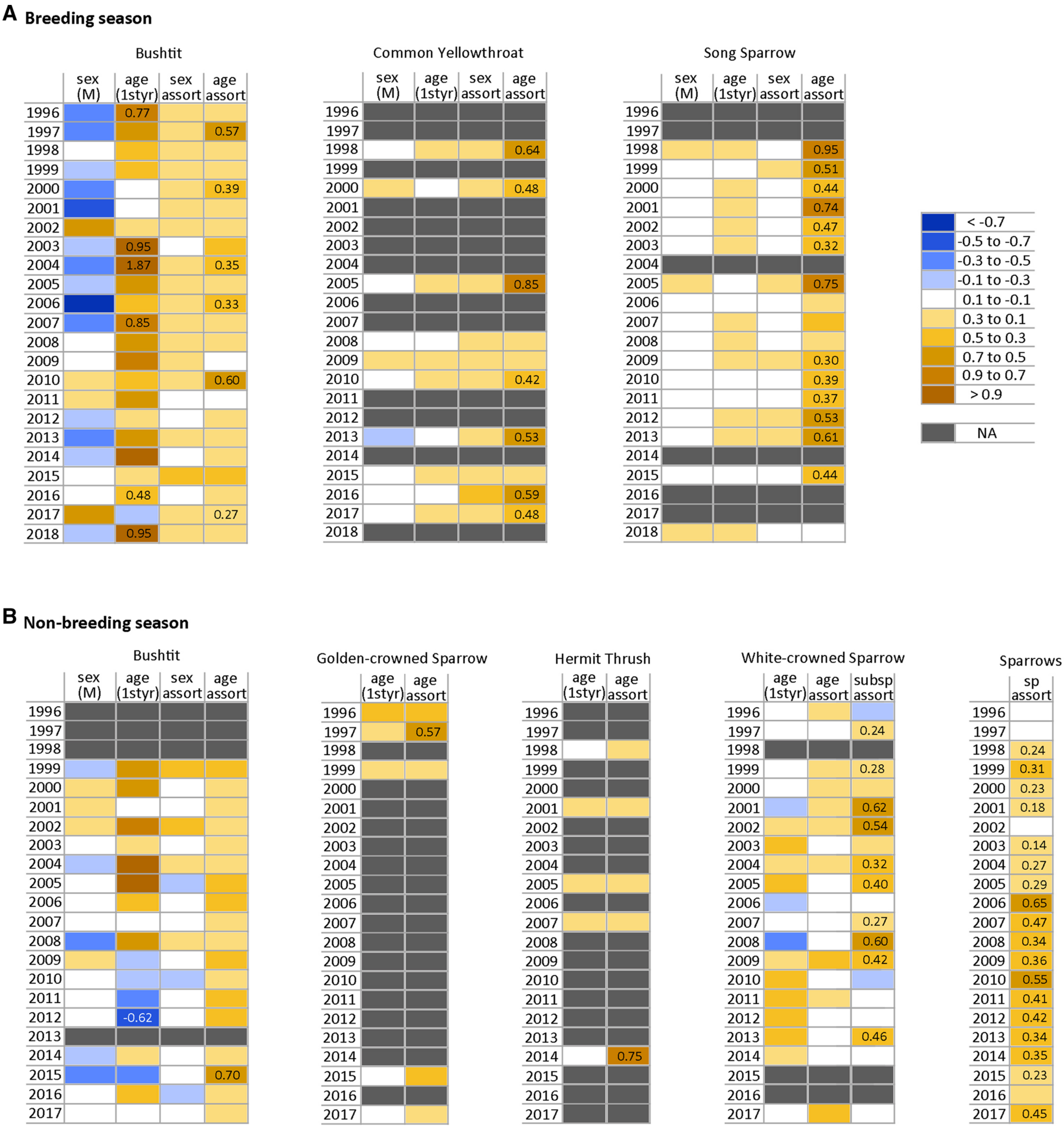

Fig. 2 Sex-, age-, and taxon-related patterns of apparent social association in each year and season in the six species. Columns labeled with a specific variable category (M = male, 1styr = first-year) show the coefficient for that category in comparison with the other, reference category (female for sex, after-first-year for age) in a linear model of degree. Columns labeled "assort" show the assortativity coefficient r for that variable, with higher values indicating greater assortativity. Colors indicate the approximate value for all results, but specific values are shown only for coefficients that were significant based upon p-values calculated from permutations and after Holm-Bonferroni correction for multiple comparisons (Holm 1979). Years in dark grey had insufficient sample size to run analyses. Not shown is non-breeding Song Sparrow, which had only one year of sufficient sample size for analyses and no significant results. "Sparrows" includes Golden-crowned, Song, and White-crowned Sparrows. Subsp = subspecies; sp = species

captures-per-individual*capture probability interaction, df = −1, F = 54.15, $p < 0.001$*). Mean degree and transitivity were significantly related to vagility and to the interaction between number of captures per individual and capture probability (Table 5; Figs. 7 and 8).

In "field" models omitting capture probability, results were broadly the same as those from the full models, with vagility and captures per individual significantly affecting network metrics while affinity did not (Table 5).

Discussion

We used an individual capture dataset to uncover patterns in social association at a multi-species, multiyear scale that is, to our knowledge, among the largest studies of individual social behavior. In testing hypotheses that have been previously supported in the literature, we found evidence supporting age differences in social associations (hypothesis 1) and species-level differences in sociality (hypothesis 3). This suggests that patterns observed in studies with more intensive observational methods may also be found in individual capture datasets. We found no support for effects of sex on social associations (hypothesis 2). We detected long-term changes in social network shape, specifically degree, supporting the potential utility of individual capture datasets in documenting changes in social behavior over time. Using simulated individual capture data, we found that analyses should explicitly incorporate aspects of data structure when possible, and also that social patterns may be accurately estimated even if some confounding aspects of data structure are not accounted for.

Association by age and sex

The prediction that younger individuals would be more social than older individuals was supported only for the Bushtit in the breeding season (Fig. 2). The lack of more widespread evidence of greater juvenile sociality is inconsistent with the general pattern of younger individuals being more social in vertebrates (King et al. 1965; Lusseau and Newman 2004; Liao et al. 2018) and the expectation that greater juvenile sociality would be favored by the fitness benefits of social learning (McDonald 2007; Griesser and Suzuki 2017). However, we did find broad support for age-structured associations in the form of positive assortment by age, particularly in the breeding season.

There was no evidence of effects of sex on social association in any of the three species that could be reliably sexed. This is surprising as it conflicts with the results of numerous previous studies (Lusseau and Newman 2004; Whiteside et al. 2017; Spiegel et al. 2018). Indeed, even if our data reflect space use more than social affiliation, we would expect sex differences because the sexes often differ in habitat utilization (e.g., Ketterson and Nolan 1979; Jormalainen and Tuomi 1989; Pagani-Núñez et al. 2019). This discrepancy merits further investigation.

Species patterns in social association

Both of the species considered to be highly social in the literature (Bushtit and White-crowned Sparrow), and one of the two species considered to be moderately social (Golden-crowned Sparrow, but not Common Yellowthroat), had more associations than the Song Sparrow, a species considered to have low sociality (Tables 1 and 2). The other species with

Table 2 Mean degree was higher for the Bushtit, Golden-crowned Sparrow, and White-crowned Sparrow than it was for the Song Sparrow

Family	Variable	Effect ± SE	*t*	*p*
Aegithalidae	Sp: Bushtit	0.775 ± 0.045	17.19	< 0.001*
Turdidae	Sp: Hermit Thrush	0.097 ± 0.057	1.70	0.092
Passerellidae	Sp: Song Sparrow	NA	NA	NA
	Sp: Golden-crowned Sparrow	0.134 ± 0.059	2.26	0.025*
	Sp: White-crowned Sparrow	0.447 ± 0.057	7.90	< 0.001*
Parulidae	Sp: Common Yellowthroat	−0.062 ± 0.052	−1.18	0.238
–	Season: non-breeding	−0.136 ± 0.036	−3.82	< 0.001*
–	Mean no. of captures per individual	−0.103 ± 0.079	−1.31	0.194
–	Sampling effort	0.064 ± 0.132	0.48	0.628
–	Year	−0.006 ± 0.002	−2.55	0.012*

Mean degree decreased over time, and was lower in the non-breeding season than the breeding season. Higher mean degree indicates more associations among individuals. Effect sizes were calculated using Song Sparrow as the reference level for species, and using the breeding season as the reference level for season. Asterisks indicate statistical significance after Holm-Bonferroni correction for multiple comparisons (Holm 1979).

SE standard error

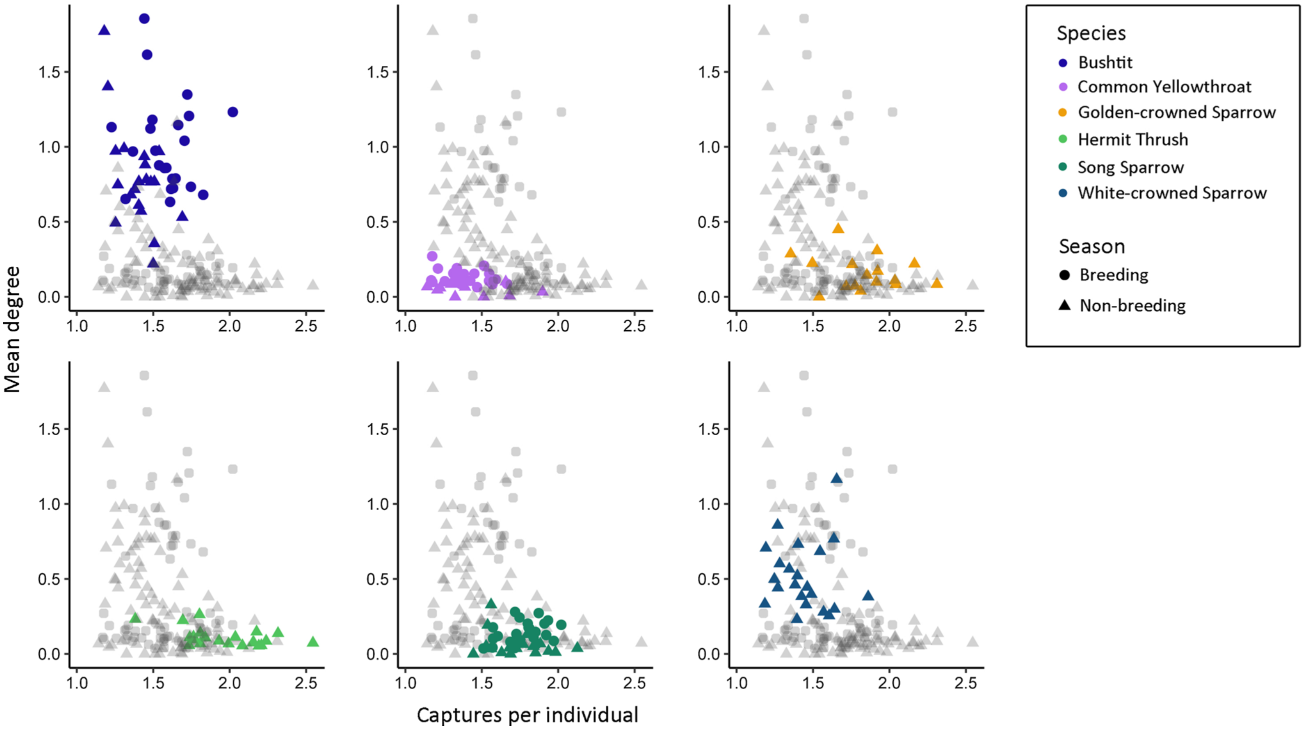

Fig. 3 Mean degree of each half-year network calculated from banding station capture data for the six focal species, with each panel showing colored datapoints for one species and those for the other species in grey

Table 3 Network transitivity was higher for the Golden-crowned Sparrow and the White-crowned Sparrow than the Song Sparrow

Family	Variable	Effect ± SE	*t*	*p*
Aegithalidae	Sp: Bushtit	0.065 ± 0.042	1.56	0.123
Turdidae	Sp: Hermit Thrush	0.115 ± 0.073	1.57	0.119
Passerellidae	Sp: Song Sparrow	NA	NA	NA
	Sp: Golden-crowned Sparrow	0.212 ± 0.070	3.01	0.003*
	Sp: White-crowned Sparrow	0.165 ± 0.055	3.00	0.004*
Parulidae	Sp: Common Yellowthroat	−0.027 ± 0.056	−0.49	0.623
–	Season: non-breeding	−0.035 ± 0.039	−0.90	0.371
–	Mean no. of captures per individual	−0.398 ± 0.080	−4.95	< 0.001*
–	Sampling effort	0.211 ± 0.129	1.64	0.104
–	Year	$-9.2*10^{-4} \pm 2.0*10^{-3}$	−0.45	0.655
–	No. of network edges	$1.2*10^{-4} \pm 3.5*10^{-4}$	0.36	0.719

The structure of the data also influenced transitivity, with transitivity values negatively related to the number of captures per individual. Higher transitivity indicates greater clustering in the social network. Effect sizes were calculated using Song Sparrow as the reference level for species, and using the breeding season as the reference level for season. Asterisks indicate statistical significance after Holm-Bonferroni correction for multiple comparisons (Holm 1979). *SE* standard error

low sociality, the Hermit Thrush, did not differ from the Song Sparrow in mean degree. Network transitivity exhibited a similar pattern, with the Golden- and White-crowned Sparrows exhibiting higher transitivity than the Song Sparrow (Table 3).

This overall agreement of mean degree with the literature suggests that individual capture datasets have the potential to discriminate differences in sociality using mean degree as a metric. Using individual capture datasets to quantify broad patterns of species sociality could be a viable approach in

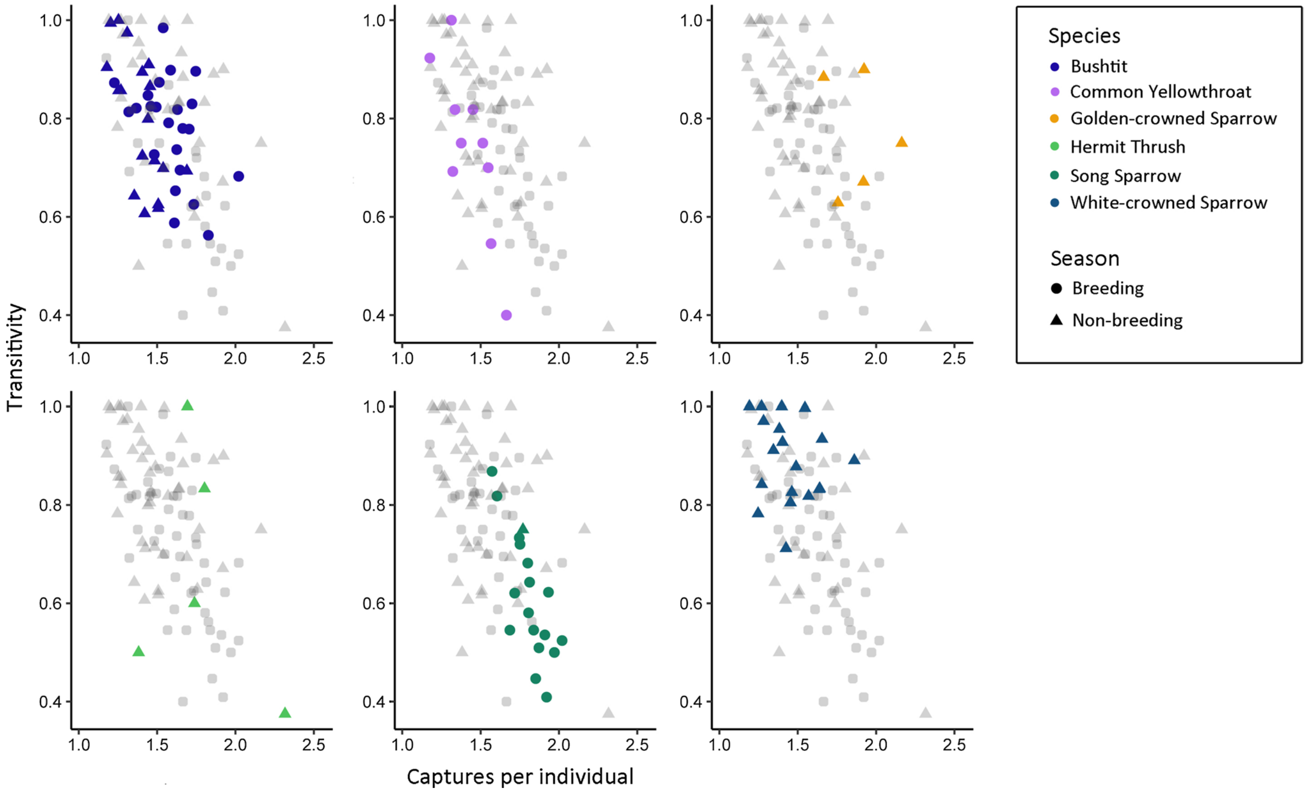

Fig. 4 Transitivity of each half-year network calculated from banding station capture data for the six focal species, with each panel coloring the datapoints for one species and showing those for the other species in grey

cases where differences in sociality are expected to be large or where other types of data are not available.

Multi-taxon social association

We found strong support for assortment by taxon in the White-crowned Sparrow (comprised in this study of two subspecies, *Z. l. gambelii* and *Z. l. pugetensis*) and in the combined analysis of the three sparrow species. This positive assortment was not driven by association among active breeding pairs or recently dependent offspring, since both analyses concerned only the non-breeding season, but may have reflected species differences in foraging niche or in their role in anti-predator behavior (Sridhar and Shanker 2014). Golden-crowned Sparrows can have stable associations over multiple years with winter flockmates (Shizuka et al. 2014); if such long-term relationships form among conspecifics but not heterospecifics, they might drive a pattern of assortment by species within the larger mixed-flock matrix. More in-depth analysis of multi-species flocks with individual capture data, for example looking at repeated associations among individuals, would improve our understanding of behavior among heterospecifics.

Long-term patterns in social association

We found a significant decrease in mean degree over 23 years in these six species. This long-term change could be the result of ongoing habitat restoration at our study site, of increasing urban development of the larger San Francisco Bay Area, or of factors such as climate change. Analysis of long-term individual capture data from other banding stations could shed light on this by testing whether our observed changes are local to our focal study site or are occurring more broadly. While more study is necessary to clarify the mechanisms behind this result, it demonstrates the potential value of using long-term individual capture datasets.

Accounting for sampling artefacts

Variability in aspects of data structure, such as sample size and the mechanisms underlying data generation, can bias conclusions drawn from those data. Understanding the extent of that potential bias allows the researcher to take countermeasures where possible, and to appropriately contextualize results where the potential for bias cannot be removed.

Table 4 In simulations holding all other variables constant, both mean degree and transitivity were affected by sociality, as respectively indicated by individual type (loner vs. flock member) or by affinity (low at 0 or high at 10)

Network metric	Variable	Effect ± SE	*t*	*p*
Mean degree	Individual type: loner	− 1.291 ± 0.088	− 14.59	< 0.001*
	Mean no. of captures per individual	0.007 ± 0.041	0.17	0.868
Transitivity	Affinity: high	0.102 ± 0.026	3.92	< 0.001*
	Mean no. of captures per individual	− 0.057 ± 0.007	− 8.36	< 0.001*
Mean degree	Individual type: loner	− 2.198 ± 0.129	− 17.04	< 0.001*
	Capture probability	0.024 ± 0.002	10.71	< 0.001*
Transitivity	Affinity: high	0.058 ± 0.011	5.27	< 0.001*
	Capture probability	$1.8*10^{-3} \pm 2.0*10^{-4}$	8.98	< 0.001*

Both network metrics were also affected by capture probability, but only transitivity was affected by the number of captures per individual. Effect sizes were calculated using flock member as the reference level for individual type, and using low affinity as the reference level for affinity. Asterisks indicate statistical significance. *SE* standard error

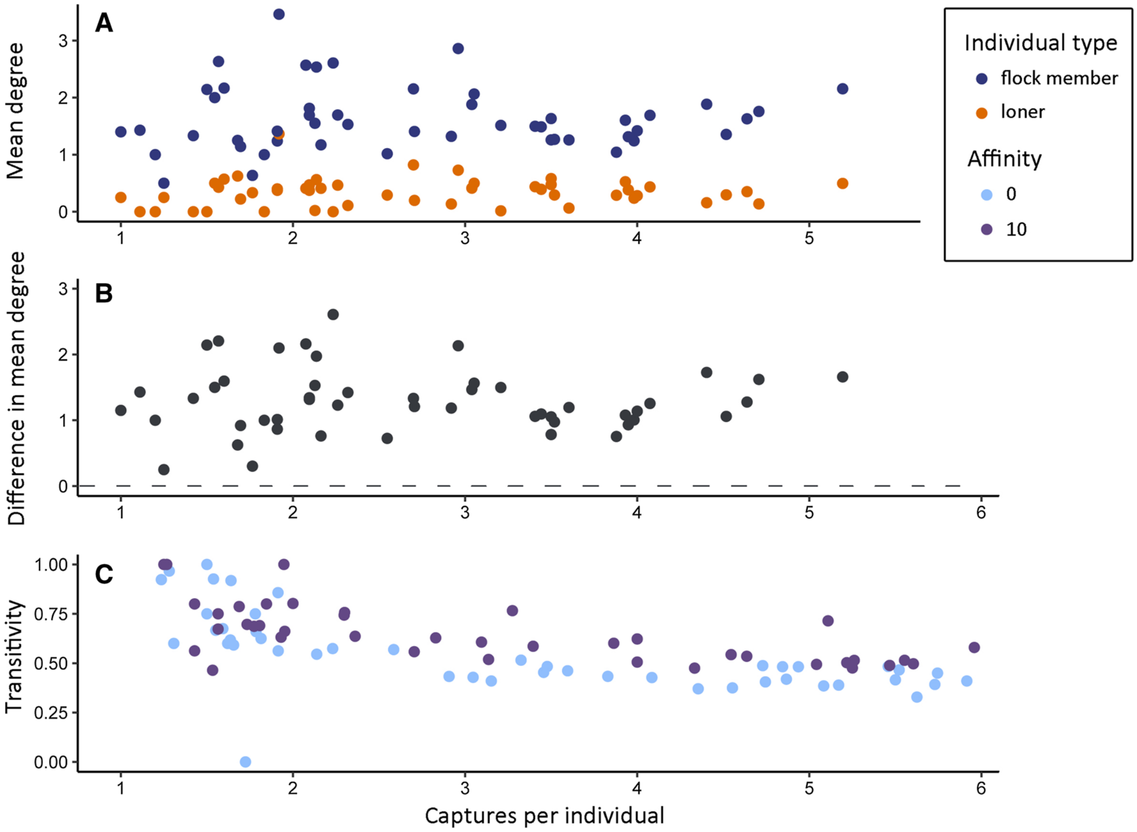

Fig. 5 In simulations in which only the amount of data collected was varied, there was no evidence that sample size affected mean degree (**a**, **b**); however, transitivity was negatively related to greater sample sizes (**c**). In simulations with both social ("flock member") and non-social ("loner") individuals, the non-social individuals always had a lower mean degree than the social individuals (**a**, **b**). Simulations of social individuals with high affinity for each other generally had greater transitivity than those with low affinity (**c**)

In our focal dataset, sample size (in the form of the number of captures per individual) did not affect mean degree but did negatively affect transitivity (Tables 2 and 3; Figs. 3 and 4). The same pattern was seen in the simulated data when sample size was varied and all else was held constant, with captures per individual negatively related to transitivity but not to mean degree (Table 4; Fig. 5). This suggests that mean degree may be reliable across a range of sample sizes. The simulated data further suggest that despite transitivity's relationship with sample size, transitivity can reflect social behavior as long as sample size is included as a variable in the model of transitivity, as demonstrated by the fact that the two simulated social phenotypes (low vs. high affinity) could be differentiated by transitivity (Table 4). However, it is worth noting that this simulated

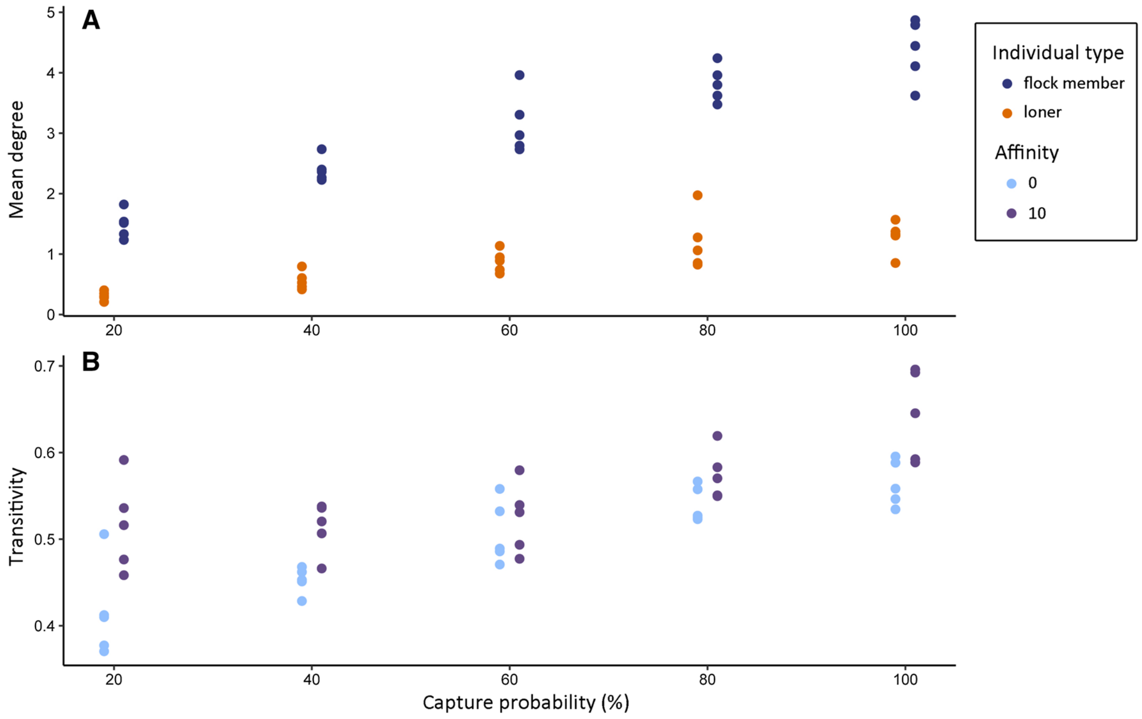

Fig. 6 Simulated data showed a positive relationship between capture probability and both (**a**) calculated mean degree, and (**b**) transitivity. In simulations with both social ("flock member") and non-social ("loner") individuals, the non-social individuals always had a lower mean degree than the social individuals (**a**). Simulations of social individuals with high affinity for each other generally had greater transitivity than those with low affinity (**b**)

Table 5 In simulations, both mean degree and transitivity were affected by vagility, an indicator of individual travel speed, but not by affinity, an indicator of the propensity of flockmates to move together

Network metric	Model	Variable	Effect ± SE	*t*	*p*
Mean degree	Full	Affinity	-0.005 ± 0.011	−0.44	0.662
		Vagility	0.260 ± 0.018	14.46	< 0.001*
		Mean no. of captures per individual	-0.025 ± 0.020	−1.24	0.215
		Capture probability	0.050 ± 0.002	24.27	< 0.001*
		Mean no. of captures per individual * capture probability	$5.9*10^{-4} \pm 2.2*10^{-4}$	2.64	0.008*
	Field	Affinity	-0.004 ± 0.019	−0.25	0.805
		Vagility	0.108 ± 0.028	3.87	< 0.001*
		Mean no. of captures per individual	0.134 ± 0.008	15.99	< 0.001*
Transitivity	Full	Affinity	$-3.6*10^{-4} \pm 1.1*10^{-3}$	−0.32	0.752
		Vagility	-0.044 ± 0.002	−25.45	< 0.001*
		Mean no. of captures per individual	-0.013 ± 0.002	−6.89	< 0.001*
		Capture probability	$3.8*10^{-4} \pm 2.0*10^{-4}$	1.94	0.053
		Mean no. of captures per individual * capture probability	$1.6*10^{-4} \pm 2.2*10^{-5}$	7.36	< 0.001*
	Field	Affinity	$-4.1*10^{-4} \pm 1.2*10^{-3}$	−0.33	0.738
		Vagility	-0.050 ± 0.002	−27.55	< 0.001*
		Mean no. of captures per individual	$2.8*10^{-3} \pm 5.4*10^{-4}$	5.19	< 0.001*

Both network metrics were also affected by the interaction between the number of captures per individual and the capture probability. In "field" models, which imitate a real-world data scenario by omitting capture probability, vagility and number of captures per individual are still detected as influencing the network metrics. Asterisks indicate statistical significance. *SE standard error*

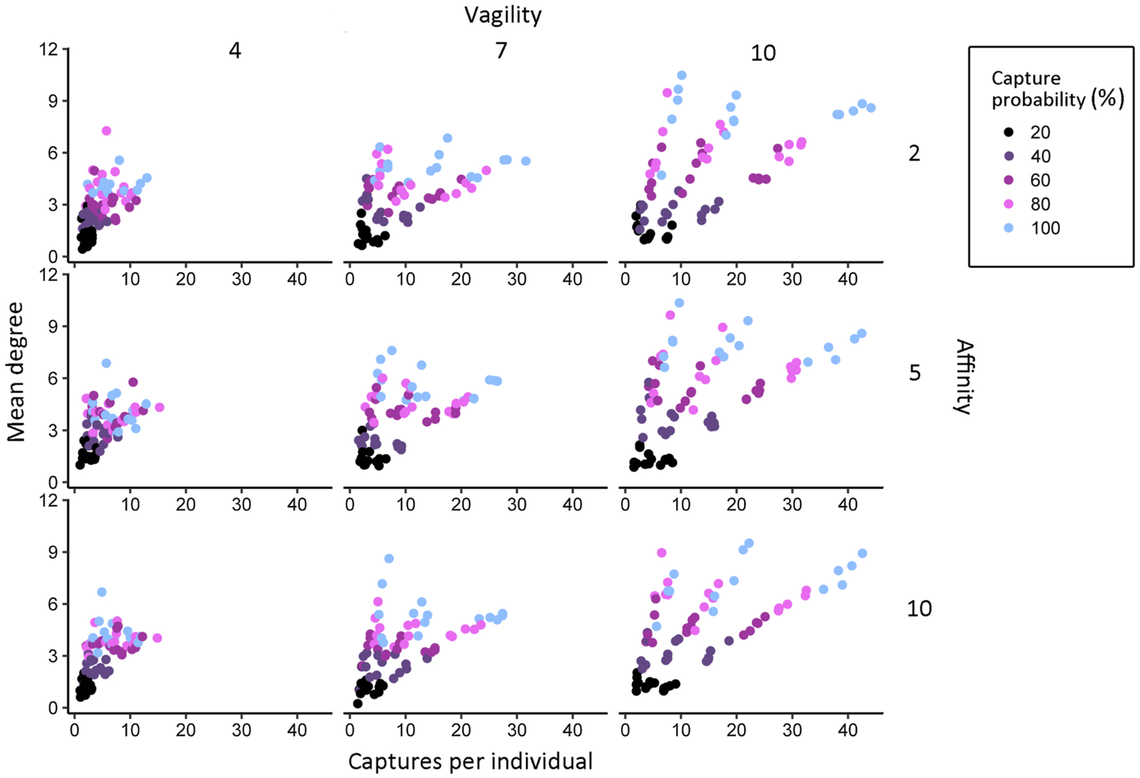

Fig. 7 Mean degree of social individuals was influenced by vagility and by an interaction between sample size and capture probability, but not significantly by affinity. Shown here are the results of five iterations of every vagility*affinity*capture probability combination, run for lengths simulating two, five, and ten banding days of data. The three groups apparent in some panels correspond to those three sample size categories

case was particularly well-suited to distinguishing confounding effects on transitivity, as the dataset sampled a broad range of sample sizes for both social phenotypes. In a dataset where the categories of interest did not have overlapping ranges of sample size—for example, comparing the Common Yellowthroat (captures per individual range 1.18–1.66) to the Golden-crowned Sparrow (captures per individual range 1.67–2.16)—testing for differences in transitivity between those categories is likely not advisable.

Simulated data also suggested that when all else was held constant, both mean degree and transitivity were positively affected by capture probability, the probability of an individual in the capture location actually being captured (or recorded, or otherwise entered into the dataset). This is concerning because, unlike sample size, capture probability will not be known for real-world datasets, so its effect will be difficult to estimate. Capture probability cannot simply be assumed to be invariable; for birds captured by passive mist netting, for example, capture probability may be affected by space use, which may vary by sex and age (Bonter et al. 2008), and by an interaction between body size and net mesh size (Pardieck and Waide 1992).

The multivariate simulations, in which sample size, capture probability, vagility, and affinity were all varied, further elaborate on the risks of comparing network metrics without careful consideration of confounds (Table 5; Figs. 7 and 8). Capture probability not only affected mean degree and transitivity, but affected them while interacting significantly with sample size, suggesting that the latter cannot be discounted as a potential influence on mean degree despite the reassurance of previous analyses. Differences in vagility were effectively detected by mean degree and transitivity in models that included the confounding variables, but differences in affinity were not, suggesting that relatively subtle differences in social behavior are likely to be lost in complex datasets.

These simulations also yield reassurance with regards to the use of individual capture datasets. In models that mimicked a real-world data situation by omitting capture probability—which would presumably be unknown—as a variable, vagility was still detected as significantly affecting

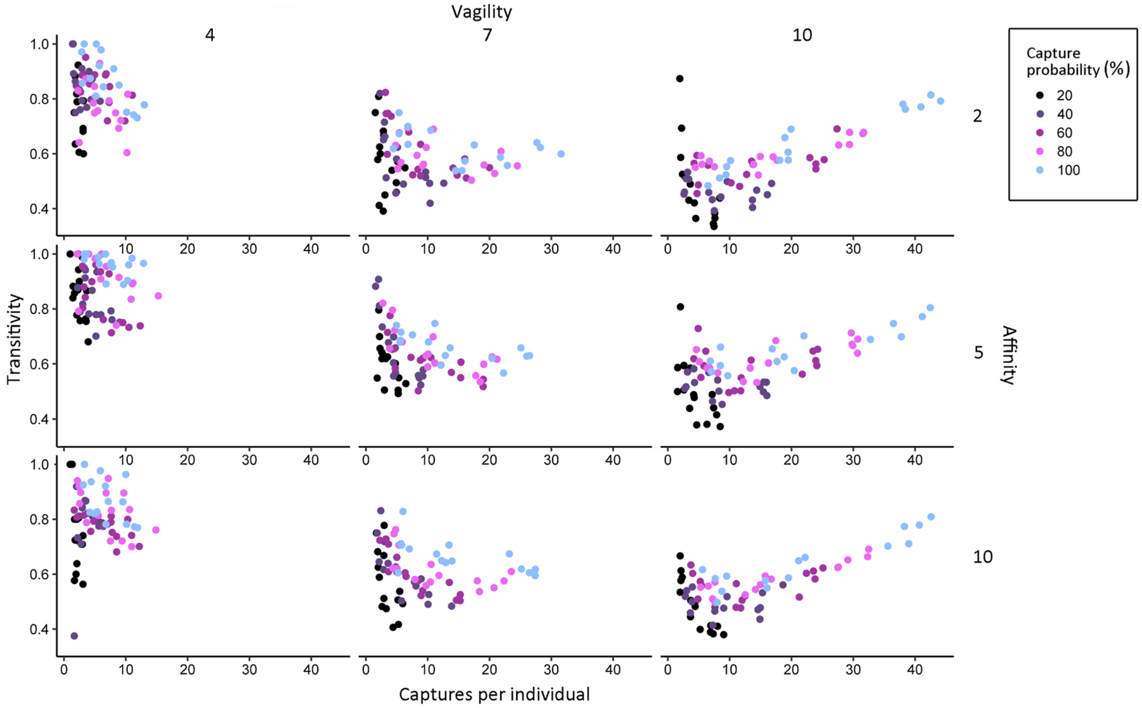

Fig. 8 Transitivity of networks formed of social individuals was influenced by vagility and by an interaction between sample size and capture probability, but not significantly by affinity. Shown here are the results of five iterations of every vagility*affinity*capture probability combination, run for lengths simulating two, five, and ten banding days of data

both network metrics (Table 5), with approximately half the estimate detected by the full model for mean degree and nearly an equal estimate to that in the full model for transitivity. This suggests that although capture probability impacts network metrics, it does not fully obscure the effects of social behavior, even when varying with such extreme ranges as 20–100%; and in some cases, such as for transitivity in this analysis, capture probability may have very little influence on the estimated effects of the focal variable.

Recommendations and conclusions

Our results support several recommendations for researchers interested in using individual capture datasets to investigate social behavior. Statistical models should include any likely confounds, such as number of captures per individual, number of network edges, and sampling effort. As is the case with any variable, the confounding effects will be more effectively distinguished when sample sizes are large (Forstmeier and Schielzeth 2011). Happily, large sample size is usually a strength of individual capture datasets.

Potential confounds that cannot be included because they are unknown, such as capture probability, should be considered qualitatively and discussed. For example, our finding that the Bushtit had a higher mean degree than the Song Sparrow could be related to the positive association between capture probability and degree: the Bushtit's smaller size may cause it to be more securely enmeshed and less likely to "bounce" out of the net than the Song Sparrow, yielding a higher capture probability. In this case, we know from natural history data that the Bushtit is a highly social species (Sloane 2001), lending support to the interpretation that the observed high degree is substantially driven by behavior. For less well-known species, a similar potentially-confounded result might favor an adjustement in analytical approach, such as including body size in the model as a proxy for capture probability or comparing degree only between species of similar body size; or further investigation, such as direct observation of behavior.

Long-term individual capture datasets represent several opportunities in the study of social behavior. One is a matter of power: a dataset comprising many years of observation can furnish large sample sizes, and therefore permit powerful tests of hypotheses. Perhaps more important, however, is the matter of time: a long-term dataset allows researchers to investigate change. While power may alternatively be achieved in a short-term study with a large sample size, there is no substitute for long-term temporal data when the subject of inquiry is change over time. Understanding social association variation over larger temporal scales will be crucial as the pace of change in the natural world increases (Clutton-Brock and Sheldon 2010). Such questions can best be addressed with long-term data. Yet the perennial challenge of long-term studies is that by the time the researcher knows one is necessary, the opportunity is past: you cannot travel back in time to start the long-term study you wish you had done. Because many individual capture projects have been ongoing for decades, however, long-term data is available right now for those who will use it.

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Author contributions KL and JCS designed the study and collected and managed the data; KL carried out analyses and wrote the manuscript; KL and JCS edited the manuscript.

Data availability All banding data have been deposited with the United States Fish and Wildlife Service Bird Banding Lab in accordance with bird banding regulations. Code for the simulation is available in the supplementary material.

Ethics statement

Birds were handled under the San Francisco Bay Bird Observatory's Coyote Creek banding station permit and according to the banding station's protocols, which prioritize the welfare of the birds. All data collection complied with the laws of the United States of America, where this study was performed.

References

Aplin LM, Firth JA, Farine DR, Voelki B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd LR, Psorakis I, Milligan ND, Radersma R, Verhelst BL, Sheldon BC (2015) Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. Anim Behav 108:117–127

Arcese P, Sogge MK, Marr AB, Patten MA. 2002. Song Sparrow (*Melospiza melodia*), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.704

Baker MC, Belcher CS, Deutsch LA, Sherman GL, Thompson DB (1981) Foraging success in junco flocks and the effects of social hierarchy. Anim Behav 29:137–142

Bejder L, Fletcher D, Bräger S (1998) A method for testing association patterns of social animals. Anim Behav 56(3):719–725

Bonter DN, Brooks EW, Donovan TM (2008) What are we missing with only ground-level mist nets? Using elevated nets at a migration stopover site. J Field Ornithol 79(3):314–320

Brown DR, Stouffer PC, Strong CM (2000) Movement and territoriality of wintering hermit thrushes in southeastern Louisiana. The Wilson Bulletin 112(3):347–353

Buckley FG, Buckley PA (1974) Comparative feeding ecology of wintering adult and juvenile royal terns (Aves: Laridae, Sterninae). Ecology 55(5):1053–1063

Butts CT (2008a) network: a Package for Managing Relational Data in R. J Stat Softw 24(2):1–36

Butts CT (2008b) Social network analysis with sna. J Stat Softw 24(6):1–51

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol Evol 25(10):562–573

Cornell HN, Marzluff JM, Pecoraro S (2012) Social learning spreads knowledge about dangerous humans among American crows. Proc Royal Soc B 279:499–508

Croft DP, Krause J, James R (2004) Social networks in the guppy (*Poecilia reticulata*). Proc Royal Soc London B 271:S516–S519

Dellinger R, Wood PB, Jones PW, Donovan TM. 2012. Hermit Thrush (*Catharus guttatus*), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.261

Ekman J (1989) Ecology of non-breeding social systems of *Parus*. Wilson Bulletin 101(2):263–288

Farine DR (2013) Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol 4(12):1187–1194

Farine DR (2014) Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. Anim Behav 89:141–153

Farine DR (2017) A guide to null models for animal social network analysis. Methods Ecol Evol 8(10):1309–1320

Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. J Anim Ecol 84:1144–1163

Favreau F, Goldizen AW, Fritz H, Pays O (2018) Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. Anim Behav 135:165–176

Forstmeier W, Schielzeth H (2011) Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol 65(1):47–55

Foster WA, Treherne JE (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293:466–467

Goodson JL, Wilson LC, Schrock SE (2012) To flock or fight: neurochemical signatures of divergent life histories in sparrows. Proc Nation Acad Sci 109(S1):10685–10692

Griesser M, Suzuki TN (2017) Naive juveniles are more likely to become breeders after witnessing predator mobbing. Am Nat 189(1):58–66

Griffin AS (2004) Social learning about predators: A review and prospectus. Learn Behav 32(1):131–140

Guzy MJ, Ritchison G. 1999. Common Yellowthroat (*Geothlypis trichas*), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.448

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6(2):65–70

Hoppitt WJ, Farine DR (2018) Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. Anim Behav 136:227–238

Hunt PD, Flaspohler DJ. 1998. Yellow-rumped Warbler (*Setophaga coronata*), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.376

Jormalainen V, Tuomi J (1989) Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. Anim Behav 38:576–585

Ketterson ED, Nolan V (1979) Seasonal, annual, and geographic variation in the sex ratio of wintering populations of dark-eyed juncos (*Junco hyemalis*). Auk 96(3):532–536

King JR, Farner DS, Mewaldt LR (1965) Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelii*. Condor 67:489–504

Kohn GM, King AP, Scherschel LL, West MJ (2011) Social niches and sex assortment: uncovering the developmental ecology of brown-headed cowbirds *Molothrus ater*. Anim Behav 82(5):1015–1022

Liao Z, Sosa S, Wu C, Zhang P (2018) The influence of age on wild rhesus macaques' affiliative social interactions. Am J Primatol 80:e22733

Lusseau D, Newman MEJ (2004) Identifying the role that animals play in their social networks. Proc Royal Soc B 271:S477–S481

McDonald DB (2007) Predicting fate from early connectivity in a social network. Proc Natl Acad Sci 104(26):10910–10914

Mueller T, O'Hara RB, Converse SJ, Urbanek RP, Fagan WF (2013) Social learning of migratory performance. Science 341:999–1002

Norment CJ, Hendricks P, Santonocito R. 1998. Golden-crowned Sparrow (Zonotrichia atricapilla), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.352

Nunn CL, Jordán F, McCabe CM, Verdolin JL, Fewell JH (2015) Infectious disease and group size: more than just a numbers game. Philosoph Trans Royal Soc B 370:20140111

Pagani-Núñez E, Barnett CRA, Senar JC (2019) Age and sex differences in niche use at molt and its effect on plumage coloration characteristics in a bird. Curr Zool 65:251–260

Pardieck K, Waide RB (1992) Mesh size as a factor in avian community studies using mist nets. J Field Ornithol 63:250–255

Pyle P (1997) Identification guide to North American birds: a compendium of information on identifying, ageing, and sexing "near-passerines" and passerines in the hand. Slate Creek Press, Bolinas, CA

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rivera-Cáceres KD, Quirós-Guerrero E, Araya-Salas M, Templeton CN, Searcy WA (2018) Early development of vocal interaction rules in a duetting songbird. Royal Soc Open Sci 5(2):171791

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51(5):1077–1086

Schoepf I, Schradin C (2012) Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). J Anim Ecol 81:649–656

Seghers BH (1974) Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution 28(3):486–489

Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE (2014) Across-year social stability shapes network structure in wintering migrant sparrows. Ecol Lett 17:998–1007

Sloane SA. 2001. Bushtit (*Psaltriparus minimus*), version 2.0. In The Birds of North America (Poole AF and Gill FB, Eds). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.598

Smolla M, Alem S, Chittka L, Shultz S (2016) Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. Biol Let 12:20160188

Spiegel O, Sih A, Leu ST, Bull CM (2018) Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. Anim Behav 136:207–215

Sridhar H, Shanker K (2014) Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. Behav Ecol Sociobiol 68(2):185–196

Teitelbaum CS, Converse SJ, Mueller T (2017) Birds choose long-term partners years before breeding. Anim Behav 134:147–154

White DJ, Gersick AS, Snyder-Mackler N (2012) Social networks and the development of social skills in cowbirds. Philsoph Trans Royal Soc B 367:1892–1900

Whitehead H, Dufault S (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Adv Study Behav 28:33–74

Whiteside MA, van Horik JO, Langley EJG, Beardworth CE, Laker PR, Madden JR (2017) Differences in social preference between the sexes during ontogeny drive segregation in a precocial species. Behav Ecol Sociobiol 71:103

Wilensky U. 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.