Animal social networks are robust to changing association definitions.

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Abstract

The interconnecting links (edges) between individuals (nodes) in an animal social network are often defined by discrete, directed behaviours (interactions). However, where interactions are difficult to observe, a network edge is instead defined as individuals sharing space or overlapping in time (an association). Despite an increasingly accessible toolkit to assemble and analyse animal social networks, defining associations remains a challenge in behavioural ecology. While different study systems have used different ways to validate the definition of an association, an empirical comparison of how these different methods compare is lacking. Here, we apply three methods to define social associations, by 1) strict time-window, 2) co-occurrence in a group, and 3) arrival-time, in four bird systems. We first test the ability of each method to detect individually repeatable social traits. Then we describe the structure of each network using Jaccard similarity and Mantel tests, and finally, we test the sensitivity of network structure to changing parameters within the three definitions. We found that the network structure was largely robust to changing how associations were defined, with subtle differences. We suggest that these differences are the result of an inappropriate definition of association in the context of experimental design and system ecology. Researchers in ecology and evolution should carefully consider the biological relevance of association definition prior to starting research into animal social behaviour.

Keywords - Animal Behaviour, Gambit of the Group, Sociality, Social Network, RFID

Background

Sociality - one's propensity to socialise with others - has important consequences for life history and evolutionary processes (Wey et al. 2008; Maldonado-Chaparro et al. 2018). For example, sociable individuals experience increased survival or reproductive success (Silk et al. 2009; Oh and Badyaev 2010; Stanton and Mann 2012; Maldonado-Chaparro et al. 2018; Dunning et al. 2023) and better access to resources (Aplin et al. 2012), than less sociable individuals. These links have been demonstrated across systems (in birds: Covas et al. 2006; McDonald 2007; Oh and Badyaev 2010; Firth, Sheldon, and Farine 2016, and mammals: reviewed in Silk 2007), commonly using social network analysis to capture connections between individual animals (Croft, James, and Krause 2008; Way et al 2008). Likewise, social network structure can have implications for a range of biological processes, from disease transmission to population ecology (Keeling and Eames 2005; McDonald et al. 2013; Kurvers et al. 2014; Albery et al, 2020; Albery et al 2021).

Despite research interest, the terminology used to describe animal sociality varies. Throughout this manuscript, we use *association* to refer to any link between animals inferred from an overlap of two individuals in space and time (James, and Krause 2008; Wey et al. 2008). The properties of an association may vary in their intentionality, intensity and duration – e.g., moths gathering around a light are not intending to socialize (Tinbergen 1952), or in mixed-species groups (Hinde 1952; Morse 1970, but also see Goodale, Beauchamp, and Ruxton 2017). We refer to non-social associations as *aggregations* (Krause and Ruxton 2002). Researchers often refer to social associations (defined above) as *relationships* when individuals repeatably associate through relevant behaviours, e.g., grooming (Siracusa et al. 2023) or eye-poking (Perry 2011). However, where interactions are difficult to observe (e.g. in passerine birds; Iserbyt et al. 2018), associations are often used as proxies for relationships. Thus, throughout this manuscript we use association in its social context, distinct from aggregation.

The importance of distinguishing association from aggregation is dependent on the research objectives. For example, group sizes may be more relevant than the strength and identity of associations in diluting predation risk (e.g. Cresswell 1994; Krause and Ruxton 2002; Sorato et al. 2012; Voelkl, Firth, and Sheldon 2016). Whereas for other questions, e.g. on mate choice or information transmission, the identity of the associating individuals may be more important (Oh and Badyaev 2010; Beck, Wascher et al. 2015; Farine, and Kempenaers 2021; Dunning et al.

2023). Hence, whether the distinction is important, and if so, how this distinction is made depends on the research question and study system.

The most common method of building social networks in small birds (Aplin et al. 2012; Sánchez-Tójar et al. 2017) and mammals that feed and shelter communally (Godsall, Coulson and Malo 2014; Evans, Lindholm, and König 2021; Raulo et al 2021), is using the identity of PIT-tagged (Passive Integrated Transponder) animals visiting a static RFID antenna (Radio-frequency identification; Ringsby et al. 2009; Mariette et al. 2011; Farine 2017A; Sánchez-Tójar et al. 2017; Bandivadekar et al. 2018; Firth et al 2018; Broughton, Maziarz, and Hinsley 2019; Hillemann et al. 2020). This approach builds a data stream of temporal presence/absence at one location, from which associations can be inferred using different methods.

Most recent methodological advances (Farine 2017A; Iserbyt et al. 2018; Bridge et al. 2019; Youngblood 2019; Hart et al 2021; Hart, Franks and Brent 2022) seek to define social associations through membership of discrete social groups – the gambit of the group method (Whitehead and Dufault 1999; Franks, Ruxton, and James 2010). This method assumes that individuals that overlap in space and time interact with each other, are socially associated. The first common approach is to use a *time-window* (**Δ**t; Figure 1Aa) within which all individuals co-occurring at the same location and time are defined as socially associating. For example, associations have been defined between PIT-tagged house sparrows *Passer domesticus* foraging at the same RFID feeder within three seconds of each other (Plaza et al. 2019). However, if the time-window is too short, individuals that are socially associated may not be detected as belonging to the same group, yet, if the time-window is too long, associations are defined between aggregating individuals (Croft, James, and Krause 2008; Psorakis et al. 2015). This creates a problem in defining association between individuals, and the social network created will depend on how researchers define the time-window parameter.

To solve this problem, an alternative approach was developed. Here, the second method for defining groups is to use a gaussian mixture model to identify discrete grouping events (GMM; Psorakis et al. 2012, 2015; Figure 1Ab). This GMM approach considers dynamically changing time-windows determined based on periods of increased activity automatically (Psorakis et al. 2012) and was developed for the great tit (*Parus major)* study system. The publication of the associated R package “asnipe” (Farine 2013; Farine 2017A) has led to popular use across many bird (see, Madsen, Vander Meiden and Shizuka 2021; Moyers et al. 2018; Broughton, Maziarz, and Hinsley 2019; Evans and Morand-Ferron 2019; Whiteside et al. 2019; Taff, Zimmer and Vitousek 2019; Brandl et al. 2021; Beltrão, Gomes and Cardoso 2022), and non-bird systems (Findlay et al. 2016; Poirier and Festa-Bianchet 2018; Zeus, Reusch and Kerth 2018; Skinner and Miller 2020).

Yet, the biological validity of the associations extracted using the GMM approach heavily depends on the biology and experimental design of the species and study system. E.g., great tits form small fission-fusion flocks of loose social groups over the non-breeding season. In contrast, house sparrows form very large nomadic, gregarious flocks with loose group-level social preferences, and aggregate at a feeder (Tóth et al. 2009; Havlíček, Riegert, and Fuchs 2022; Dunning et al. 2023). In such gregarious systems, the power of the GMM approach may not be appropriate, because meaningful association is difficult to separate from random aggregation (e.g. to feed, rather than socialise; Dunning et al. 2022). In such systems, a third definition of association may be considered, based on variation in individual arrival time to a feeder (hereafter Arrival-time; Dunning et al 2022; Chan and Dunning 2023; Figure 1Ac). This approach assumes that strongly associated individuals are more likely to arrive together at a resource than those who are not (Atton et al. 2012; Hilleman et al. 2020).

Evidently, different methodologies were developed for different study systems to collect similar data, and are often presented without validation. The definition of an association (a network edge) therefore poses a methodological challenge to behavioural ecologists interested in quantifying animal social networks (Carter, Lee, and Marshall 2015, Castles et al. 2014; Farine 2015; Farine and Whitehead 2015). Some studies have used randomizations (Farine 2014, 2017), or other biological observations to validate association definitions (Farine 2014; Boogert, Farine and Spencer 2014), e.g. when demography or familial ties inform social structures (Haddadi et al. 2011; Davis, Crofoot and Farine et al. 2018; Ferreira et al. 2020; Gomes et al. 2021). However, in most studies where this is not possible, an association must be defined *a priori*, and in the context of the study species. Thus, the observed behaviour, and distinguishing intentional association from aggregation presents a challenge (Croft et al. 2008; 2011; Gomes et al. 2021).

When direct observations are not possible, an alternative biological measure to validate association definition can be the repeatability of individual network traits. Individual social network metrics are an aspect of an individual's animal personality and have been shown to be consistent across various study systems (Bell, Hankison, and Laskowski 2009; Aplin et al. 2015; Hillemann et al. 2019; Tkaczynski et al. 2020; Proops et al. 2021). Thus, we assume an appropriate definition of association should find repeatability of social traits over time.

Here, we set out to empirically test how different definitions of associations affect the structure of social networks across four study systems, each with differing ecologies and experimental design. We compare the robustness of the global social network and individual network metrics, using three association definitions (1. time-window, 2. GMM, and 3. arrival-time). First, we compared the repeatability of individual social network metrics between definitions to describe the ability of each method to capture repeatable social behaviours. Next, we describe the similarity of the global social networks built using different association definitions. Finally, we explored the sensitivity of the parameterisation on the network structure. We hope our results will assist behavioural ecologists when making methodological choices for animal social behavioural studies.

Materials and Methods

Systems

We collected data from wild PIT-tagged birds at four systems: Two house sparrow populations, at Broken Hill, Australia, and Lundy Island, UK; one sociable weaver population at Benfontein Nature reserve, South Africa; and a great tit population at Wytham woods, UK. In all four systems, RFID antennas were mounted at a bird feeder to record PIT tagged individuals (Figure 1B). Detailed experimental design and system ecology can be found in the supplementary methods.

Social network construction using different association definitions.

We built three networks for each system, one for each association definition (Figure 1), 1) time-window (Figure 1Aa); 2) GMM (Psorakis et al. 2012, 2015; Farine 2017; Figure 1Ab); 3) arrival-time definitions (Dunning et al 2022; Figure 1Ac). We build weighted, i.e. scaled using the simple ratio index (Farine and Whitehead, 2015) and undirected networks in R (R Core Team 2023). We applied these general parameters between systems:

1) Strict time-window (Figure 1Aa): The time-window approach has a single overlap parameter (**Δ**t), where two individuals visiting a feeder within **Δ**t were defined as associates. In the current study, we hope to compare other methods with the strictest definition for association, so we defined **Δ**t as one second to capture absolute physical and temporal proximity at the feeder (for example McCully and Rose 2023; Farine 2015).

2) GMM (Figure 1Ab): We used the GMM function in the asnipe R package (Farine 2013; Farine 2017A) to detect groups. The GMM function detects the start and end point of gathering events and associates all individuals (Psorakis et al. 2012; 2015). We combined the date and location parameters within each system into a unique location to reduce processing time (Farine 2017A).
3) Arrival-time (Figure 1Ac): We build arrival networks using a series of functions, (see Chan and Dunning 2023). We defined two parameters: 1) A time overlap to define two or more birds arriving and recorded at the RFID antenna for the first time (**Δ**t). 2) A period of inactivity, after which a bird is considered to have left the feeder (**Δ**i). We defined **Δ**t as 150 seconds and **Δ**i as 300 seconds following Dunning et. al. (2022).

We used the iGraph package in R (Csardi and Nepusz 2006) to extract three node-based network measures from the three association dataset for each of the four systems: degree, the number of unique associates connected to a focal individual; strength, the total number of associations between a focal individual and all associates; and betweenness, the number of geodesics (shortest paths between any nodes) that pass through a focal individual. We removed all individuals from networks who had a degree of 0, thus the number of individual vertices in each did not represent the number of individual birds recorded.

Analysis

Within-system comparisons in social network structure

a) Repeatability of social traits

We first constructed weekly sub-graphs across each recording period for each of our four systems. We extracted three network measures from each subgraph for each week, then z-transformed to normalise the measures due to differences in network structure across weeks.

We ran repeatability models using the R package MCMCglmm (Hadfield 2010), using default model parameters. We modelled each social trait as a response variable against the model intercept and with individual ID as a random effect. Repeatability was defined as the variance explained by individual ID over the total variance (Nakagawa and Schielzeth 2010). We interpreted repeatability in the context of three levels, low (< 0.3), medium (< 0.5) and high (> 0.5; following Bell, Hankison, and Laskowski 2009; Winney et al. 2018). Using these subgraphs, we also explored the correlation between individual network measures extracted using each association definition, by running Pearson’s correlation tests for each association definition pair for all bird individuals across all weeks.

To test if our analyses could yield similar results from randomised data, we ran network permutations for the repeatability analysis (Farine 2017A). We created 1000 random networks by shuffling individual IDs within each weekly sub-graph, while maintaining network structure (Aplin et. al, 2014; Farine 2017A). We constructed a null distribution and extracted p-value for each repeatability estimate by calculating the proportion of data more extreme than the actual estimate.

b) Similarity in network structures

We described the cardinality of for each network for each association definition, i.e. the number of individuals (Vertices; V), and the number of associations (Edges, E), as well as the network density (D). The density of a network is defined by the number of observed edges over the maximum potential edges. Then, we used three Jaccard similarity indices to compare global network structures between all possible pairs of association definitions, within systems using the multinet R package (Magnani, Rossi, and Vega 2021). Following (Bródka et al. 2018; but see Emmert-Streib, Dehmer and Shi 2016): 1) Jaccard actors to compare the identity of individuals; 2) Jaccard edges to compare common edges; and 3) Jaccard triangles as a measure of common clusters of individuals between networks. All Jaccard similarities range between 0 and 1, where 0 denotes no overlap between networks, and 1 when networks are identical. We further interpret Jaccard similarities using equivalent qualitative terms to the repeatability analyses.

Finally, we ran Mantel tests to account for similarity in network edge weights (Mantel 1967; Croft, James, and Krause 2008). Mantel tests account for network edge weights by comparing correlation of values between two matrices. We extracted the weighted adjacency matrices for each network and computed the Mantel coefficient using the Pearson correlation method and 999 matrix permutations with the 'Vegan' R package (Dixon 2003). The results produce a correlation between network layers that varies between -1 and 1, representing matrices being negatively and positively correlated respectively. The p-value and 95% confidence intervals are computed using the null distribution obtained by the permutations.

c) Sensitivity Analyses

Finally, to test for how parameterisation affects resulting biological validity of networks constructed, we computed repeatability measures again but varying the Δt parameter from 1 to 300 seconds for both the arrival and strict time-window methods. For arrival network, we maintained Δi at 300 seconds. We did not do this for GMM networks, since associations defined by GMM automatically set parameters within the detection algorithm.

Results

We built social networks using 286,669 RFID detections comprising of 118 individuals visiting feeders on Lundy Island, 27,456 detections of 66 individuals at Broken Hill, 402,255 detections of 219 individuals at Wytham Woods and 197,857 detections of 62 individuals at Benfontein. The number of individuals (network nodes) and association (edges) and their centrality varied with association definition (Table 2).

a) Repeatability of social traits

We calculated repeatability over nine weeks at Broken Hill, Australia, fourteen weeks on Lundy Island (see Dunning et al. 2023), thirteen weeks at Benfontein Nature Reserve, South Africa; and fourteen weeks at Wytham woods (see Aplin et al. 2015). We found that three social traits, degree, strength and betweenness, are repeatable in all four systems, with little variation between association definitions (Figure 2). All three definitions displayed low repeatability in the Lundy systems; low-moderate repeatability in the Wytham system; and high repeatability for degree and strength, but low – moderate repeatability for betweenness in Broken Hill and Benfontein systems. We found significantly lower repeatability of degree and strength in the Wytham system when associations were defined by the strict time-window definition (Figure 2C). The arrival-time and GMM definitions performed equally across systems (Figure 2). All repeatability measures were statistically significant, except for betweenness in arrival definition in Benfontein (Table 1).

b) Similarity in network structures

Using the network metrics extracted from each weekly sub-graph, we show that degree and strength is strongly correlated across all systems, with weaker correlations for betweenness (Figure 3). Other than the house sparrows on Lundy Island (Figure 3A), the correlation coefficient between arrival and GMM were always highest for all the traits.

Using Jaccard similarity indices and Mantel tests to compare similarities between networks, we show that network structures are robust to changing association definition (Table 2). Although, where the number (vertices; cardinality V) and identity (Jaccard actors, range 0.86 – 1) of individuals detected are similar between network pairs, metrics to capture clustering (Jaccard triangles; 0.01 – 0.77), dyad identity (Edges, cardinality E) and associated edge weights (Mantel coefficient; 0.46 – 0.92) varied more. We found the highest similarity scores between the GMM and arrival-time definitions (15 high/ 1 medium/ 0 low similarity scores), followed by GMM and strict time-window definitions (11 high/ 2 medium/ 3 low similarity scores), then strict time-window and arrival definitions (10 high/ 3 medium/ 3 low similarity scores). All definitions identified a similar number of individuals between networks, but the number of edges differed. Specifically, networks based on strict time-windows produced less dense networks, while using the arrival-time definition resulted in denser networks.

c) Sensitivity Analyses

Finally, we explored how altering the time parameter (**Δ**t) affected network structure within the arrival-time and strict time-window methods. For the arrival-time definition, our results show that social traits have low repeatability with a low **Δ**t, but increased as **Δ**t increases, and finally plateaued. We report a similar plateau for the time-window method, without the initial increase in repeatability. The repeatability of betweenness was more sensitive to changes for both methods, especially in Broken Hill and Benfontein (Figure 4).

Discussion

In this study, we compared three association definitions applied to avian social networks in four study systems. These were strict time-window (Farine 2015), GMM (Psorakis et al. 2012, 2015), and arrival-time (Chan and Dunning 2023; Dunning et al. 2023). Our results suggest that association definitions were robust to the noise of visitations when applied to individuals attending a resource, with subtle differences. Hence before constructing animal social networks, it is important to consider which social association definition is appropriate for the study species, system and research question (Croft, James, and Krause 2008; Farine and Whitehead 2015) at hand.

We found statistically significant and similar levels of repeatability, high level of correlation between traits, similar similarity indices and mantel coefficients within systems, between association definitions. We found that some association definitions resulted in more similar networks between systems with more similar ecologies, for example in the highly gregarious and open-access antenna systems at Lundy and Benfontein. Altering the arrival-time overlap (**Δ**t) within arrival and time-window networks was also generally robust to the definition of **Δ**t across systems. No single association definition we used resulted in significant change in network size, except for the use of strict time-window at Broken Hill. The similarity was expected, because each association method is trying to capture meaningful social associations from the same temporal data-stream. However, we show that methodological decisions can result in subtle differences explained by a mismatch between an appropriate association definition in the context of system ecology. Alternatively, association definitions may also capture subtly different behaviours, e.g. the propensity to aggregation or exploration of novel food patches.

Our results also suggest that the design of RFID feeders can influence the obtained social networks using different association methods. When using the strict time-window definition, we observed lower repeatability of individual social traits in Wytham woods, but increased repeatability in Broken Hill and Benfontein. Since we used a strict threshold of 1 second to define the time-window, the method was likely not appropriate for RFID feeders in Wytham woods because birds can only visit feeders one or two birds at a time, in which case meaningful associates would have been lost. Similarly, the strict time-window definition in Broken Hill also resulted in smaller network sizes, since sparrows were only detected as they entered and left a feeding chamber, making detection of groups difficult. In the Broken Hill sparrows, a higher **Δ**t value (e.g 5-10 s) might be more appropriate to capture physical and temporal proximity. On the other hand, shorter time-windows can be more appropriate for open RFID systems like in Benfontein and Lundy Island (Figure 1A), where multiple individuals can access the food resource at one time. Overall, GMM and arrival definitions captured more similar networks compared to strict time-window, probably because the latter is capturing physical and temporal proximity, while the two former are based on a the gambit of the group approach. Surprisingly, the pattern was not observed for house sparrows on Lundy Island, with more similar networks between GMM and strict-time window. This may reflect the inability of the GMM approach to identify group structures in large flocks visiting a feeder at one time.

From our sensitivity analysis, we show that both approaches are robust against changes in parameters, where the values increase then plateau consistently across study systems. We also confirm that the choice of Δt =150 in the arrival-time method used in the current study was appropriate and can be a reasonable starting threshold for future researchers.

A core limitation of our study is the inability to know the true social associations between individuals, because sociality measures are only ever a sample of a wider underlying behaviour, and there is often no directly observable social interaction between passerine birds, as opposed to other species like primates. The similarity in the networks observed may be attributed to the inherent noise of aggregation present in social data, but visitation rates of individuals can also be influenced by several factors beyond a necessity to socialise, such as dominance (Oh and

Badyaev 2010; Evans, Jones, and Morand-Ferron 2018) and behavioural preference (Aplin et al. 2013, 2014, 2015; Culina, Firth, and Hinde 2020). For example, for individuals attending a resource and linked using time-window and GMM definitions, network edges (associations) may also capture a propensity to monopolise a resource.

We suggest that future studies should define associations based on the specific ecology of their study system and sampling methodology. Key considerations are: 1) The gregariousness of the study system, or their propensity to aggregate (Krause and Ruxton 2002) at a resource. For example, where a social association is equivalent to group membership, the gambit of the group definitions is appropriate (Farine 2017; Psorakis et al. 2012, 2015). Whereas in highly gregarious systems, where social associations are masked by aggregation of individuals at a resource, time-window or arrival-time are likely more appropriate (Ferreira et al. 2020; Dunning et al. 2023); 2) Sampling methodology, for example, in open-access systems where multiple individuals can access an RFID antenna at one time, gambit of the group definitions may be less appropriate, than in systems which limited access to the antenna. Where the concepts of social association are unclear, it may be beneficial to compare different definitions before hypothesis testing. Furthermore, we encourage researchers to report justification of association definition in published research, providing a biological justification on the choice when conducting animal social network studies. These could be empirically tested against another variable (e.g Ferreria 2020) or based on observation of the study species (e.g Dunning et. al, 2023). While we show here that differing association definitions are generally robust and produces broadly similar networks, decisions that researchers make would nevertheless result in different network structures and may influence research outcomes.

Figures and tables

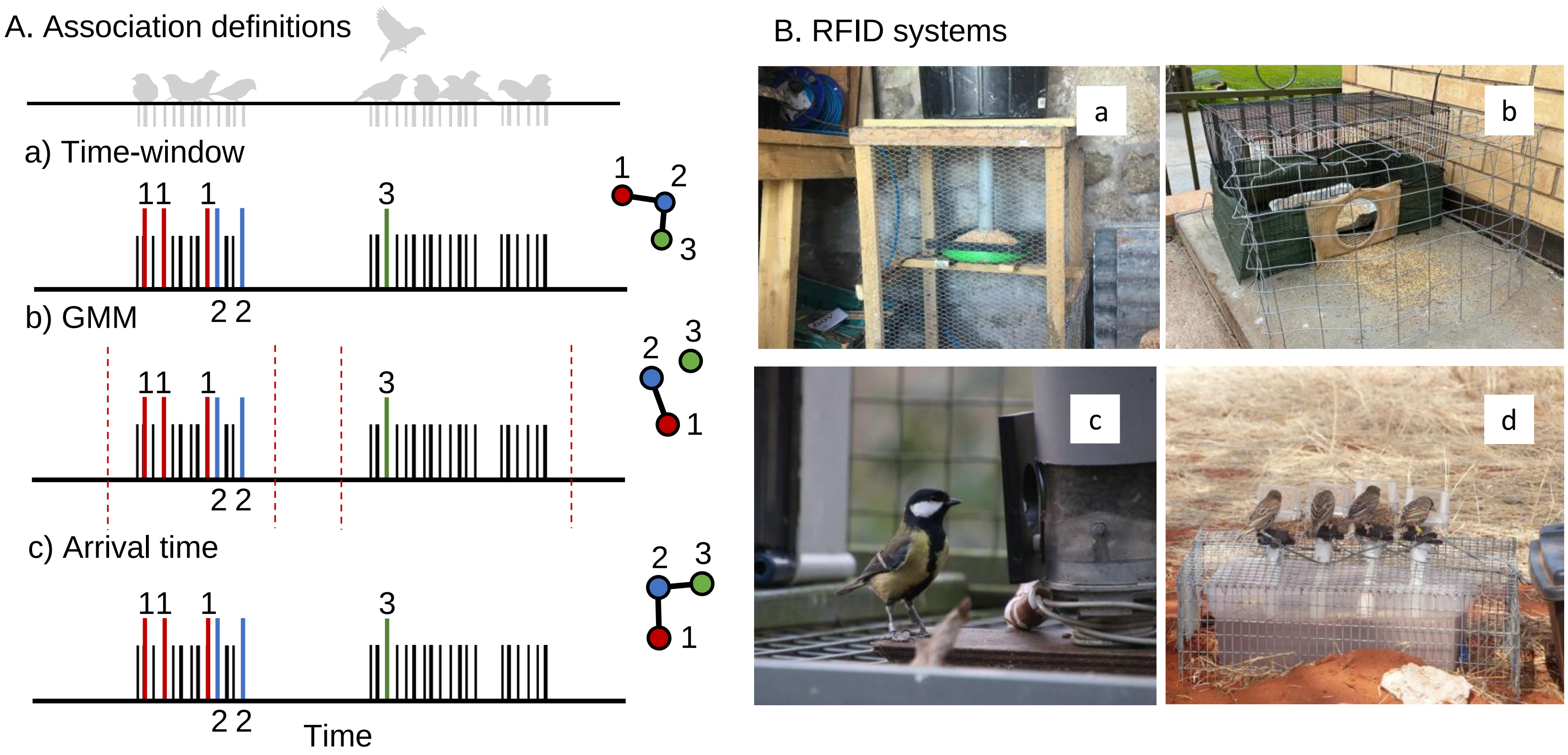

Figure 1A Three association definitions applied to sampled RFID data streams. Black lines denote individuals visiting a feeder where three are highlighted (one, two and three). The time-window definition (Aa) where individuals are considered associating when they overlap in space within (**Δ**t) of each other. The GMM (Ab) definition identifies the start and the end of gathering events, denoted here with red dotted lines. Finally, arrival-time (Ac) defines an association where individuals overlap by **Δ**t of their arrival (first detection) at the RFID antenna. An individual can only be recorded as arriving again after a period of absence defined by **Δ**i. **1B**. Radio Frequency Identification (RFID) experimental set-up in four systems: a) open RFID antenna on Lundy Island, UK; b) RFID antenna at the entrance to a feeding chamber at Broken Hill, Australia; c) Great tit *Parus major* interacting with a single RFID antenna at Wytham woods, UK; d) Sociable weaver *Philetairus socius* visiting four RFID antenna mounted at Benfontein Nature Reserve, South Africa.

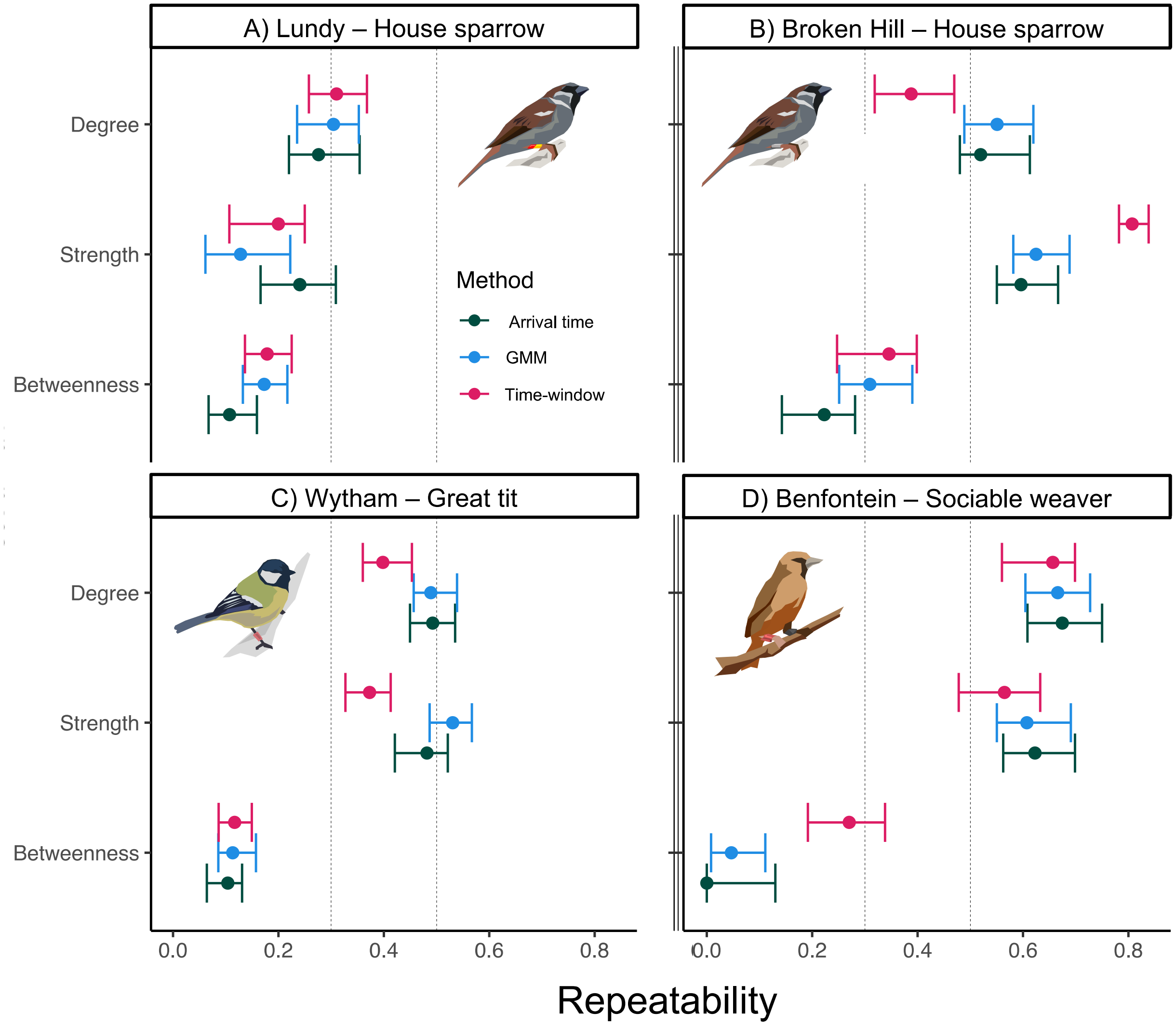
A) Lundy – House sparrow
B) Broken Hill – House sparrow
C) Wytham – Great tit
D) Benfontein – Sociable weaver
Degree
Strength
Betweenness
Method
Arrival time
GMM
Time-window
0.0
0.2
0.4
0.6
0.8
Repeatability

Figure 2. Between week repeatability for three individual social traits (degree, strength and betweenness), between three association definitions and in four systems: A) House sparrows from Lundy Island, UK, B) House sparrow data from Broken Hill, Australia; C) Great tits data from Wytham Woods, UK; and D) Sociable Weaver data from Benfontein National Park, South Africa. Points denote the mean repeatability, and error bars the 95% CIs. Dotted lines denote thresholds for low (< 0.3), medium (< 0.5) and high (> 0.5) repeatabilities (also see Table 2).

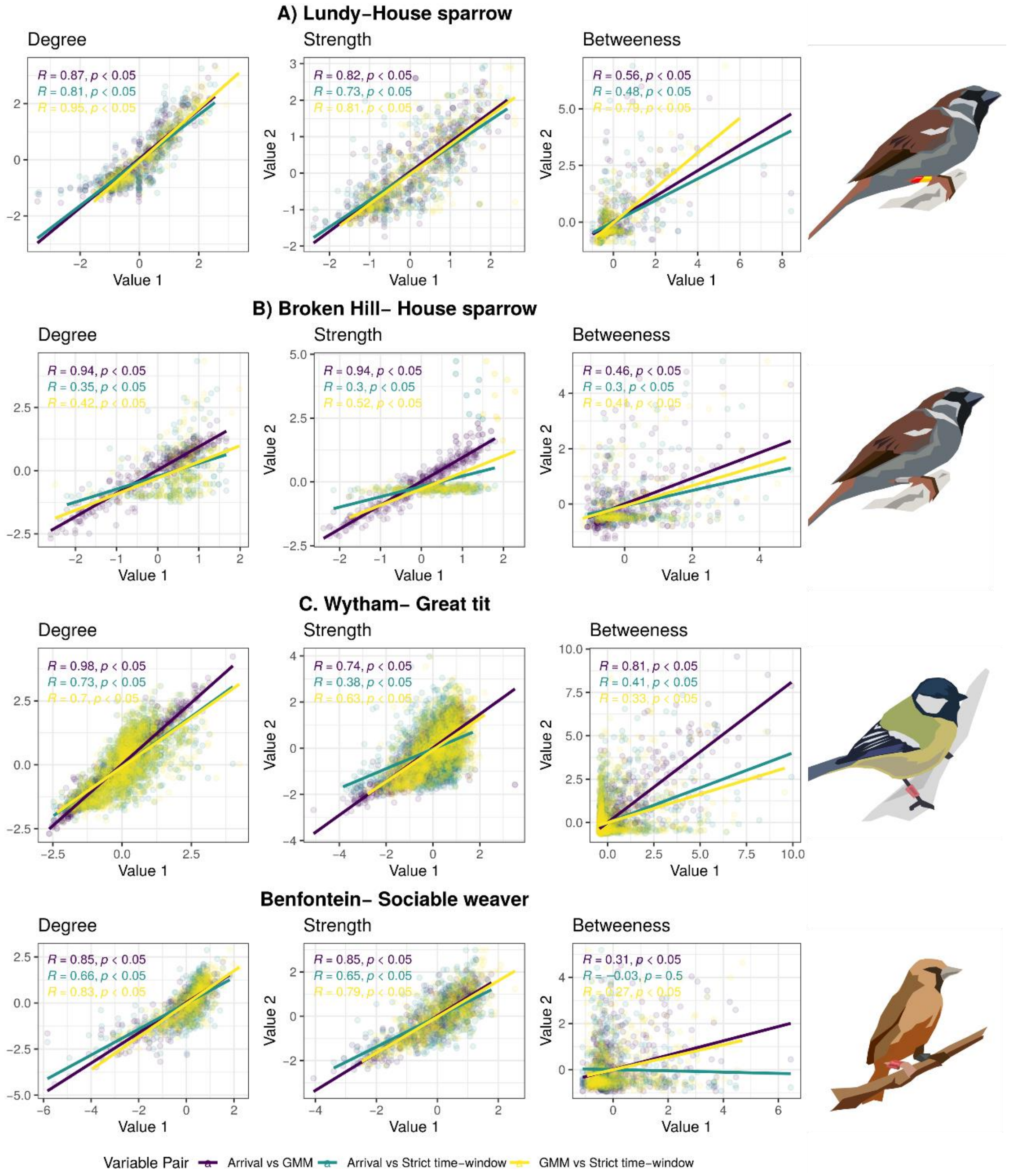
A) Lundy−House sparrow
Degree
R = 0.87, p < 0.05
R = 0.81, p < 0.05
R = 0.95, p < 0.05
Strength
R = 0.82, p < 0.05
R = 0.73, p < 0.05
R = 0.81, p < 0.05
Betweeness
R = 0.56, p < 0.05
R = 0.48, p < 0.05
R = 0.79, p < 0.05
Value 1
Value 2
B) Broken Hill− House sparrow
Degree
R = 0.94, p < 0.05
R = 0.35, p < 0.05
R = 0.42, p < 0.05
Strength
R = 0.94, p < 0.05
R = 0.3, p < 0.05
R = 0.52, p < 0.05
Betweeness
R = 0.46, p < 0.05
R = 0.3, p < 0.05
R = 0.41, p < 0.05
Value 1
Value 2
C. Wytham− Great tit
Degree
R = 0.98, p < 0.05
R = 0.73, p < 0.05
R = 0.7, p < 0.05
Strength
R = 0.74, p < 0.05
R = 0.38, p < 0.05
R = 0.63, p < 0.05
Betweeness
R = 0.81, p < 0.05
R = 0.41, p < 0.05
R = 0.33, p < 0.05
Value 1
Value 2
Benfontein− Sociable weaver
Degree
R = 0.85, p < 0.05
R = 0.66, p < 0.05
R = 0.83, p < 0.05
Strength
R = 0.85, p < 0.05
R = 0.65, p < 0.05
R = 0.79, p < 0.05
Betweeness
R = 0.31, p < 0.05
R = −0.03, p = 0.5
R = 0.27, p < 0.05
Value 1
Value 2
Variable Pair
Arrival vs GMM
Arrival vs Strict time−window
GMM vs Strict time−window

Figure 3: Correlations of three individual social network traits (z-transformed) extracted from weekly networks from four study systems using three association definitions. A) House sparrow data in Lundy Island, UK; B) House sparrow data in Broken Hill, Australia; C) Great tits data in Wytham Woods, UK; D) Sociable Weaver data in Benfontein National Park, South Africa. Correlations are denoted as value 1 vs. value 2: Arrival time vs. GMM (Purple), Arrival time vs. Strict time-window (Green) and GMM vs. Strict time-window (Yellow), with the value 1 on the x-axis and value 2 on the y-axis. R values represent the Pearson correlation coefficient, and p represents the p-value

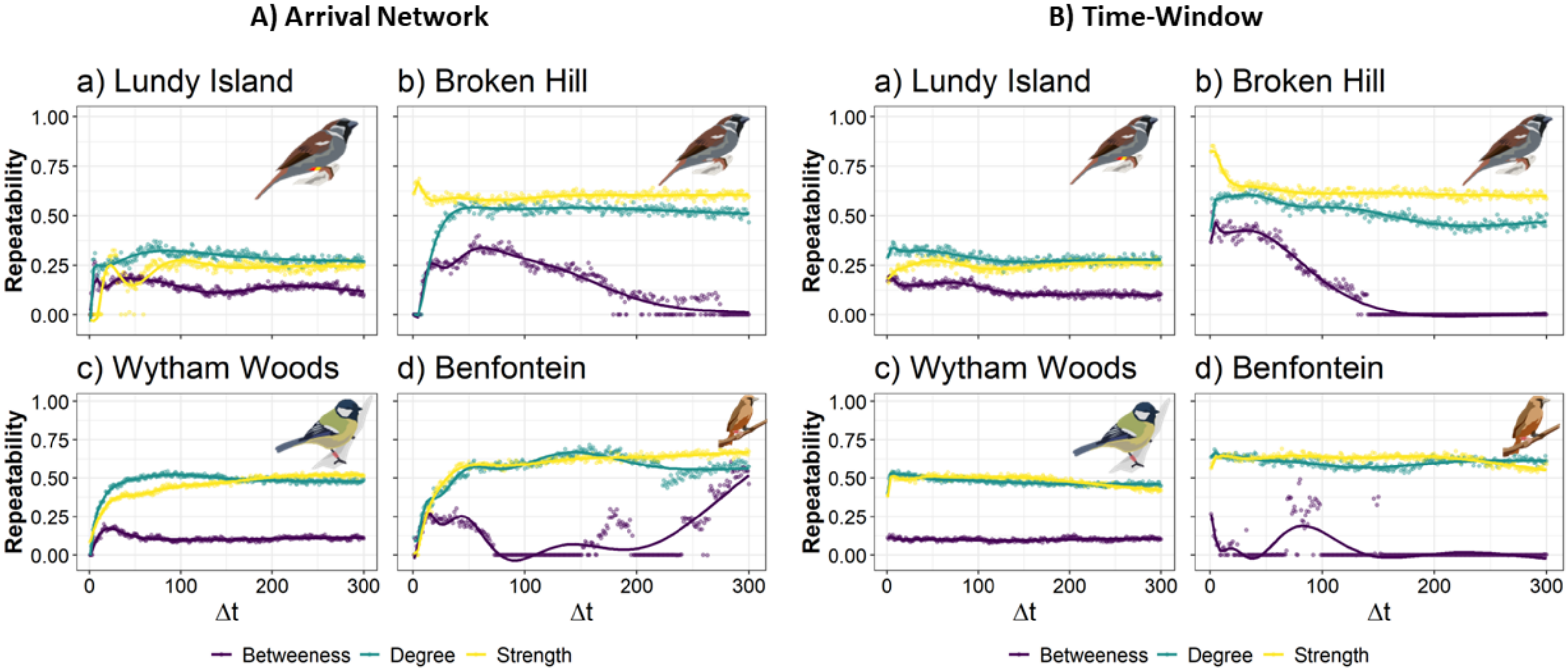

Figure 4. Sensitivity analysis of between week repeatability of individual metrics for arrival and time-window networks. For arrival time networks, we vary **Δ**t from 0 to 300 seconds, and fixed **Δ**i = 300s, and for time-window networks we varied **Δ**t from 0 to 300 seconds. For associations defined by A) arrival time and B) time window, across four systems: a) House sparrow data

in Lundy Island, UK; b) House sparrow data in Broken Hill, Australia; c) Great tits data in Wytham Woods, UK; d) Sociable Weaver data in Benfontein National Park, South Africa. Repeatability was calculated for degree (number of edges per node; green), strength (weighted degree; yellow) and betweenness (number of shortest paths passing through a node; purple).

Table 1: Repeatability and mean measures for three social network traits (Degree, Strength, Betweenness) across weeks in 4 study systems (Lundy Island House Sparrows, Broken Hill House Sparrows, Wytham Woods Great tits, and Benfontein Sociable Weavers) using three association definitions. We calculated for each metric across all weeks within study systems, with standard deviation provided in parenthesis. P-values were obtained by running 1000 random permutations and calculating repeatability in the same way, then computing the proportion of data that is more extreme than the observed value.

Table 2. We compared three network structures, built using three association definitions, for four systems: A) House sparrow on Lundy Island, UK. B) House sparrow in Broken Hill, Australia C) Great tits in Wytham Woods, UK: D) Sociable Weaver in Benfontein National Park, South Africa. 1) We report the cardinality of each network in the first row as vertices (V; individuals in each network), edges (E; associations between individuals) and network density (D; the number of edges over the total number of potential edges); 2) We described three Jaccard similarity measures between network layers (upper matrix A-D): Actors (common vertices); Edges (common dyadic edges); Triangles (common clusters of triads). Finally, we used Mantel coefficients (lower matrix A-D), given as the correlation between two networks. P-values and 95% CI of the null distribution (given in parentheses) denote the extent to which comparisons differ from 999 random matrix permutations (where $p < 0.05$ denotes a significant difference from random).

Author Contributions

AC & JD contributed equally to conception and development of project. All other authors contributed to data collection, writing and reviewing original text. AC & JD ran analyses, and prepared figures.

Data Availability

All code scripts used to generate arrival networks are available on the Zenodo repository (Chan and Dunning 2023). All data and code that can be used to reproduce results are available here: https://doi.org/10.5281/zenodo.7892571

Conflict of interest

We declare no conflict of interest.

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