LETTER

Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder

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Abstract

When the consequences of sociality differ depending on the state of individual animals and the experienced environment, individuals may benefit from altering their social behaviours in a context-dependent manner. Thus, to fully address the hypotheses about the role of social associations it is imperative to consider the multidimensional nature of sociality by explicitly examining social associations across multiple scales and contexts. We simultaneously recorded > 8000 associations from 85% of breeding individuals from a colony of Australasian gannets (*Morus serrator*) over a 2-week period, and examined gregariousness across four foraging states using multilayer social network analysis. We found that social associations varied in a context-dependent manner, highlighting that social associations are most prevalent during foraging (local enhancement) and in regions expected to provide clustered resources. We also provide evidence of individual consistency in gregariousness, but flexibility in social associates, demonstrating that individuals can adjust their social behaviours to match experienced conditions.

Keywords

Coloniality, consistency, group formation, individual behaviour, multiplex networks, social flexibility, social foraging, sociality, seabirds.

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INTRODUCTION

Animal sociality presents both costs and benefits to individuals living in groups. Thus, for social behaviours to evolve it is expected that the benefits will outweigh the costs of sociality (reviewed by Krause & Ruxton, 2005; Ward & Webster, 2016). For instance, social foraging strategies are expected to evolve when group behaviour increases individual foraging efficiency and the costs of competition are low (Giraldeau & Caraco 2000; Beauchamp 2014). Similarly, during group movement, coordination will occur when benefits, such as decreased energy expenditure (Weimerskirch *et al.* 2001; Portugal *et al.* 2014) or pooled navigational ability (Berdahl *et al.* 2018), outweigh the costs incurred by consensus decision-making (Conradt & Roper 2005). On an individual level, animals within a group may not experience equal outcomes from social behaviours, leading to individual differences in level of gregariousness (Krause *et al.* 2015) and therefore individuals may continuously evaluate the cost–benefit trade-off of sociality, leading to the formation and division of groups overtime (fission–fusion dynamics, Aureli *et al.* 2008). Thus, an individual's decision to participate in social behaviours may vary based on circumstances (Sueur *et al.* 2011).

Individual gregariousness may, therefore, be differently selected for between different contexts leading to social plasticity in which individuals adjust the expression of social behaviours across time or space to maximise the benefits gained and minimise the costs of social associations (Oliveira 2009,

2012; Montiglio *et al.* 2018). Social plasticity may be expected when the cost and benefits of associating differ between contexts, or when different individuals experience different social outcomes in the same context. Throughout temporal cycles, such as daily or seasonal changes, individuals experience a variety of conditions and undertake temporal changes in activity or life history that may influence the costs and benefits received from social associations (Krause & Ruxton, 2005; Ward & Webster, 2016). However, to date, there has been little work empirically evaluating the effects of different contexts on individual variation in social behaviours. In one study of semi-feral ponies (*Equus caballus*), individuals were found to show interannual consistency but seasonal flexibility in their gregariousness (Stanley *et al.* 2018), which was found to be driven by seasonal changes in male harassment related to breeding status. Similarly, the costs and benefits of sociality in any given social context may be influenced by external spatial conditions, such as resource distribution, which can also differentially impact individuals (Webber & Vander Wal 2018). For example, eastern water dragons (*Intellagama lesueurii*) vary their use of social tactics depending on their spatial location within their home range, and these differences were found to be stronger in females (Piza-Roca *et al.* 2018). Thus, individuals may vary their degree of gregariousness between social contexts depending on the context-specific trade-offs.

Alternatively, individual gregariousness may be constrained across different contexts, due to individually consistent expression of behaviours. Consistent individual differences in

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behaviours (termed personality) are seen across a broad range of animal taxa (Sih *et al.* 2004; Réale *et al.* 2007). Previous work has demonstrated that personality can influence an individual's social associations (Krause *et al.* 2010; Ilany & Akçay 2016), which could lead to individuals of a given personality type expressing a specific social phenotype (e.g. Croft *et al.* 2009; Aplin *et al.* 2013; Johnson *et al.* 2017). Additionally, while personality can influence an individual's gregariousness, it has also been shown in a number of studies that an individual's social position within a group may also remain consistent across time and/or contexts (Jacoby *et al.* 2014; Aplin *et al.* 2015; Firth *et al.* 2017; Formica *et al.* 2017; Krause *et al.* 2017; Kulahci *et al.* 2018); however, little work has addressed such consistency in social metrics across various scales (i.e. gregariousness vs. associations). Such consistency in social traits, such as social network position, could potentially drive consistency in other behaviours. Thus, an individual's sociality may carry-over across contexts, and may in itself reflect a social personality (Réale *et al.* 2007; Wilson *et al.* 2012).

To understand how behavioural and spatial contexts driving behavioural plasticity or consistency interact to influence individual variation in sociality it is necessary to address the multidimensional nature of animal social associations that occur across a wide-range of contexts and scales (Finn *et al.* 2019). However, despite our understanding of the complexity of factors influencing animal sociality, few studies have attempted to quantify the context-dependent influences on gregariousness and social associations, and even fewer at the fine temporal scale relevant to decision-making in wild populations. Many analytical approaches to the study of animal social behaviours are generally designed to examine sociality within a single context (such as foraging or aggression) in isolation, or aggregate across contexts, losing any variation that may exists in social metrics across contexts. Recently, research has demonstrated that considering only one social context can underestimate an individuals' gregariousness. For instance, if an individual had only weak social associations in a single context, but was social across a high number of contexts, a higher measure of gregariousness would be observed when considering multiple contexts (De Domenico *et al.* 2015b; Finn *et al.* 2019). Additionally, when considering behaviours that occur with different frequencies, a single context or aggregate approach can be dominated by the most frequent behaviours (but see Silk *et al.* 2006). Only recently have studies begun to consider variation within and between social associations across multiple contexts, yet these approaches have still often analysed networks of different social contexts in separate models (e.g. Madden *et al.* 2011; Gazda *et al.* 2015; Kulahci *et al.* 2018 but see Firth & Sheldon 2016). A recently developed framework for applying multilayer social network analysis to ecological research (Silk *et al.* 2018; Finn *et al.* 2019) allows researchers to implicitly consider the multifaceted nature of social associations to more fully understand the complex role of sociality in group-living animals.

Coloniality is an extreme case of group living where large aggregations of individuals at breeding or roosting sites provide significant opportunities for social associations across a range of behaviours. Indeed, the high availability of social information in these aggregations has been highlighted as an important mechanism in the formation and maintenance of colonial living (Danchin & Wagner 2007; Evans *et al.* 2016). Thus, colonial species, such as 95% of seabird species (Coulson 2001), present interesting systems in which to examine individual sociality across multiple contexts. During the breeding season, seabirds make numerous trips between the colony and variable foraging areas. Previous studies have shown seabirds can form groups at the colony during outward travel (Daniel *et al.* 2007; Weimerskirch *et al.* 2010; Machovsky-Capuska *et al.* 2013; Jones *et al.* 2018) and during commuting travel between colony and foraging locations (Berlincourt & Arnould 2014; Tremblay *et al.* 2014; Thiebault *et al.* 2014a), which can allow the colony to act as a centre for foraging information, and can lead to individuals engaging in following behaviour (Harel *et al.* 2017). At sea, seabirds are also known to form foraging aggregations (Coulson 2001; Evans *et al.* 2015; Cook *et al.* 2017), and evidence from experimental and modelling approaches have demonstrated that these aggregations can provide social information by attracting individuals to a foraging locations through the observation of other foraging individuals (local enhancement; Buckley 1997; Thiebault *et al.* 2014b; Bairos-Novak *et al.* 2015; Boyd *et al.* 2016). However, it remains unclear to what extent these aggregations indicate active social choices in comparison to patterns emerging due to shared space use associated with a clumped resource. Furthermore, due to the vast number of individuals in many colonies and large spatial scales covered by seabirds, there has been limited direct quantification of the importance of individual variation in the use of social strategies.

In this study, we provide a unique direct quantification of the variation in individual gregariousness and assess consistency of social associations across multiple foraging contexts and scales (overall gregariousness vs. dyadic associations) using a novel multidimensional network approach. We collected data simultaneously from 85% of the actively breeding individuals from a small colony of Australasian gannets (*Morus serrator*; hereafter gannets) and examined four key foraging states: (1) colony co-departures, (2) commuting movements, (3) foraging movements and (4) colony co-returns. Gannets, like many colonial seabirds, frequently associate with both conspecifics and heterospecifics at sea (Vaughn *et al.* 2010), and have been shown to associate during colony departure (Jones *et al.* 2018) and while rafting (Carter *et al.* 2016). Specifically, we aim to quantify the prevalence of aggregations in gannets across four foraging states. We employ null models that account for individual spatial patterns to determine the extent to which these aggregations represent social associations and quantify the interindividual variation in gregariousness. By examining the patterns of association across the entire foraging trip, we are able to test the hypotheses that the colony or foraging sites (or both) are important locations of social foraging associations. We predict that if individuals form social associations during colony departure this provides evidence in support of the idea that social foraging information can be transferred at the colony site. If local enhancement is a key social foraging behaviour, we predict a high level of associations during foraging.

To test the hypothesis that individual sociality is influenced by behavioural contexts and scale we assess the pattern of associations across four foraging states at two levels; overall social tendency (gregariousness) and the persistence of dyadic associations. On an individual level, we assess individual consistency in gregariousness and measure the overlap in specific social associations between each foraging stage. If individuals maintain a high overlap between social associations during colony departures, commuting and foraging states indicating overall consistency in their choice of associates across the foraging stages, this would provide evidence that information may transfer across foraging state (i.e. colony as a location of information transfer), as social associations will need to be maintained across the foraging trip. We further predict that low overlap between foraging and other states would provide evidence that foraging associations form at prey patches, indicating that local enhancement is a prominent social tactic.

Finally, gannets from this colony are known to undertake location-specific foraging strategies, in which some individuals specialise on foraging within a shallow inshore bay area with larger solitary prey, and others forage predominantly in the deeper off shore strait in which they encounter small shoaling prey (Wells *et al.* 2016). This allows us the opportunity to simultaneously test the hypothesis that gregariousness will vary with these different location-specific foraging strategies. We predict that when social associations are related to foraging benefits, gregariousness will vary depending on resource type and distribution, with individuals displaying higher levels of gregariousness when prey is clustered and less predictable.

METHODS

Study system and behavioural classification

The study was conducted at the Pope's Eye colony located in Port Phillip Bay, south-eastern Australia (38°16'42" S, 144°41'48" E), in January 2015, during the chick-rearing period. We recorded location data (2-min resolution) from 85 birds, accounting for 85% of the active breeders in the colony at the time. Analyses were restricted to complete foraging trips during the period of maximum overlap in individuals with concurrent GPS tracking (January 9–22, 2015). During foraging trips, seabirds undertake several distinctive behaviours which can be inferred from location data using hidden Markov models (HMM, as in Dean *et al.* 2013; Grecian *et al.* 2018). We identified three behaviours, which represent (1) fast-directed commuting flights, (2) slower tortuous foraging movements and (3) resting at sea. For additional details of GPS deployment and behavioural classification see the Supplemental Materials.

Social associations

To identify social associations from the GPS data we extracted the temporal and spatial co-occurrences of individuals separately for departing, commuting, foraging and returning (Figure S1). Individuals were defined as associating during colony departure or return, when either co-departing or co-returning to the colony within 3 min of another individual and

with a difference in angle of travel less than 45° (see supplemental materials for further details on threshold selections). We next defined commuting associations by applying a distance, time and heading threshold to periods defined as commuting from the HMM approach. Gannets were considered to be associating during commuting if they were travelling within 1500 m of one another for > 5 min, a distance that is well within the visual range of gannets (Thiebault *et al.* 2014b). Here again, we considered only associations in which the difference in angle of travel was less than 45°. We defined a foraging association using a distance and time threshold only, as angle of travel varies greatly during foraging. Individuals were considered to be associating if they were recorded within 500 m for > 5 min during fixes that were classified as either foraging or rest, as individuals resting on the water may still provide foraging cues, especially as resting often follows or precedes a bout of foraging (Ropert-Coudert *et al.* 2004). Only associations in which one or both individuals were classified as foraging were retained in the social network analysis to ensure rest-rest associations were not included in the foraging network.

For each foraging individual we determined the proportion of an individual's colony departures, returns, commuting and foraging bouts that were classified as associating. To quantify individual sociality during each foraging state we used social network-based techniques (Krause *et al.* 2015). For colony co-departure and co-return networks, we defined an edge (connection between a pair of individuals) by the number of co-departures and co-returns made by each dyad respectively. For the co-commuting and co-foraging networks, associations generally did not last the length of an entire commute or foraging bout, thus we defined edges by the sum of the duration of associations for each dyad. As we have complete tracking data on all individuals studied, raw association values were used to construct networks (Hoppitt & Farine 2018). To ensure common scale across the networks and to control for differences in frequencies of behaviours, all edge weights were scaled between 0 and 1 (0 being the lowest value and 1 the maximum value or duration of associations respectively).

For each network we calculated the network density (ratio of observed edges to all possible edges) and calculated the degree and weighted degree centrality (hereafter weighted degree) for each individual; network measures were calculated using igraph v. 1.2.4.1 (Csardi & Nepusz 2006). Degree is the total number of associates an individual has and weighted degree (also known as strength) is a measure of the number and strength of an individual's associations and can be seen as a general metric of the gregariousness of an individual (Wey *et al.* 2008). Given the low number of repeated associations over our study period between the same individuals during co-departures, returns and commuting, we did not assess preferential associations between individuals within each foraging state and instead assessed an individual's general level of gregariousness.

To examine how the networks for each state relate to one another, we used a multilayer social network (Silk *et al.* 2018; Finn *et al.* 2019), in which each set of associations represents a separate layer within an overall network structure. In

particular, we used a multirelational multiplex network in which each layer represents the same (or a subset of the same) individuals in a different social context, in this case the four foraging states studied, (Finn *et al.* 2019) and the connections between layers connect individuals to themselves in other layers. Additionally, to assess how social associations are linked across contexts, we constructed an additional final network layer (hereafter called the 'outcome' layer) in which we defined social associations based on a shared outcome of a previous social association (i.e. joint commuting leading to foraging, or joint foraging leading to commuting). For this network layer, an association was defined as any association that either (1) started at a shared origin (either a foraging patch or the colony) and resulted in joint commuting or (2) started in a joint commute and ended at a shared destination. Edge weights were again defined as the number of associations of each dyad scaled between 0 and 1 as above.

Location-specific foraging strategy

Gannets breeding at Pope's Eye colony exhibit distinctive location-specific foraging trips characterised by different environmental features (Wells *et al.* 2016) and previous work in this population has shown that individuals are consistent in their location-based foraging (Angel 2015). We identified three different trip types from the data; (1) trips with > 70% of fixes within Port Phillip Bay (bay trips), (2) trips with > 70% of fixes outside the bay (strait trips) and (3) trips with < 70% of fixes in either the bay or strait (switch trips) (Fig. 1). Individuals were then classified as bay or strait specialists if > 70% of trips were defined as bay or strait trips, respectively, with all other individuals classed as 'switch' individuals (as in Rodríguez-Malagón 2018; Table S1).

Statistical analysis

Null models
To examine if social associations during each foraging state were observed more often than expected by chance, we compared the network density and the observed weighted degree to null models obtained from data-stream permutations of the GPS data for each of the four networks (Farine 2017). Unlike typical data-stream permutations, to maintain an individual's specific movement patterns, we randomised GPS data within individuals by randomly swapping the day each trip occurred on. This method conserved individual differences in spatial movement, while breaking the temporal association of the data (Spiegel *et al.* 2016), allowing us to determine if co-occurrences are driven by active group formation or a by-product of persistent use of the same space. After each permutation, we recalculated the departure, commuting, foraging and returning associations as described above. We then compared the observed network density and mean weighted degree from each network to the distribution of network densities and weighted degrees obtained from 1000 permutations of the data respectively. *P*-values were obtained as the proportion of times the values obtained from the permutated data that were more extreme (larger) than the observed value.

Individual gregariousness across foraging contexts

To determine if individuals expressed flexible or consistent gregariousness across foraging states we used the network-based consistency analysis as described in Wilson *et al.* (2012). This network-specific method is used to account for the non-independent nature of association data. As this method is designed to assess the change in relative position of individuals rather than the absolute value of weighted degree we first determined the ranked weighted degree within each observed network. We then computed the sum of each individual's variance in ranked weighted degree across the observed departure, return, commuting and foraging networks (SV_O). We then compare the observed value SV_O to the sum of variance values obtained from calculating the variance in ranked weighted degree from the null models obtained from 1000 permutations (SV_R). As a low value of SV_O demonstrates that the relative ranking of individuals across networks is consistent, significance was calculated as the proportion of SV_R values from the data permutations that were more extreme (lower) than the observed SV_O.

Variation in social associations across foraging contexts

Next, to assess how individual social associations vary across foraging states and to determine how these different portions of the foraging trip are linked through the outcome network, we assessed the similarity in network structure between the four network layers. We computed the edge overlap between layers in the multiplex social network using the software Mux-Viz (De Domenico *et al.* 2015a), which quantifies the proportion of common links between dyads that are conserved between network layers, as a measure of how social associations are carried over between contexts. This method considers weighted network edges and gives a measure of consistency in dyadic associations across contexts. We also calculated the pairwise correlation between network layers by using Mantel tests to calculate the similarity between the respective association matrices (Smouse *et al.* 1986), as this method has frequently been used to assess the correlation between matrices. However, this method may be strongly impacted by zero values as matrices must be the same size for comparison (thus non-interacting individuals in one layer must be included in all layers for comparison).

Variation in gregariousness across spatial contexts

To assess how between individual gregariousness varied across location-specific foraging strategies, we repeated the analysis comparing mean weighted degree to the corresponding null models for each of the three spatial foraging strategies separately (bay, strait and switch). As the bay specialists were a small male-only subgroup of the study population, we repeated the network consistency analysis and edge-overlap analysis for a multilayer network constructed as described above, but excluded the bay-specialist individuals. All statistical analyses were performed in R v.3.5.1 (R Core Team 2016). Additionally, to determine how spatial context is reflected in the social organisation of individuals, we conducted a network
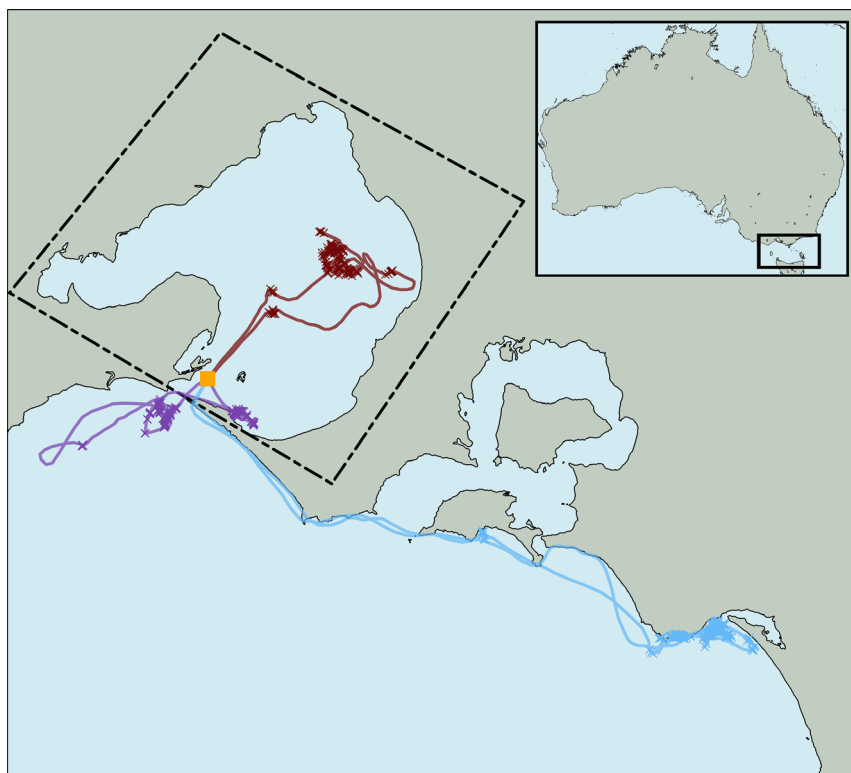
Figure 1 Map of the study area around Pope's Eye gannet colony, located in Port Phillip Bay, Australia. The colony site is represented by the orange square. Example of foraging trips are shown for a bay specialist (red), a strait specialist (blue) and a switch individual (purple) with the area used to define the bay shown by the dashed box. Foraging locations as identified via hidden Markov models are marked on each trip by crosses. Insert shows Australia, with the colony and surrounding foraging area marked with a box.

clustering analysis for community detection (as in Finn *et al.* 2019) using MuxViz (De Domenico *et al.* 2015a; multilayer InfoMap method, see Supplementary Methods for additional details). In this approach, we assess if social clusters detected correspond with the location-specific foraging strategies.

RESULTS

Social associations

In total, we recorded 2877 h of commuting, 4398 h of foraging and 6717 h of resting behaviours. From these data, we detected 173 colony co-departures, 199 colony co-returns, 477 commuting associations and 7738 foraging associations. Associations during commuting were the least frequently observed behaviour, with foraging, colony co-departures and co-returns occurring at higher rates (mean proportion of social bouts per individual; commuting = 0.13, foraging = 0.32, co-departures = 0.28 and co-returns = 0.31). The patterns of associations were found to vary between foraging states (Fig. 2).

For all four states studied, the observed network density was significantly greater than the density obtained from the null models indicating all networks were more connected than expected compared to the null (Table 1). The density of the foraging and commuting networks had the greatest differences to the corresponding null models (Figure S5). Similarly, both mean degree (number of associates) and mean weighted degree (strength of associations) were found to be significantly larger than expected given the null models, and there was high between-individual variation in the number and strength of associations expressed as degree and weighted degree (Table 1, Figures S6 and S7). Again, the number of associates during foraging was found to have the greatest difference from the null model.

Individual gregariousness across foraging contexts

The observed sum of variance calculated from weighted degree was significantly lower than the sum of variances obtained from the null model permutations ($SV_O = 5.64$, SV_R range = 5.19–7.99, $P = 0.012$), indicating that individuals were consistent in their relative sociality across foraging contexts.

Variation in social associations across foraging contexts

Of the observed social associations, we recorded 287 'outcome' events resulting from a social association carrying-over from one foraging state to another, providing evidence of direct temporal carry-over of social associations from one foraging state to a subsequent state. Joint foraging, from associations formed at the foraging patch, that led to co-commuting was the most frequent observed outcome (32% of outcomes) followed by co-commutes, where individuals formed an association in flight, that then resulting in co-foraging (29% of
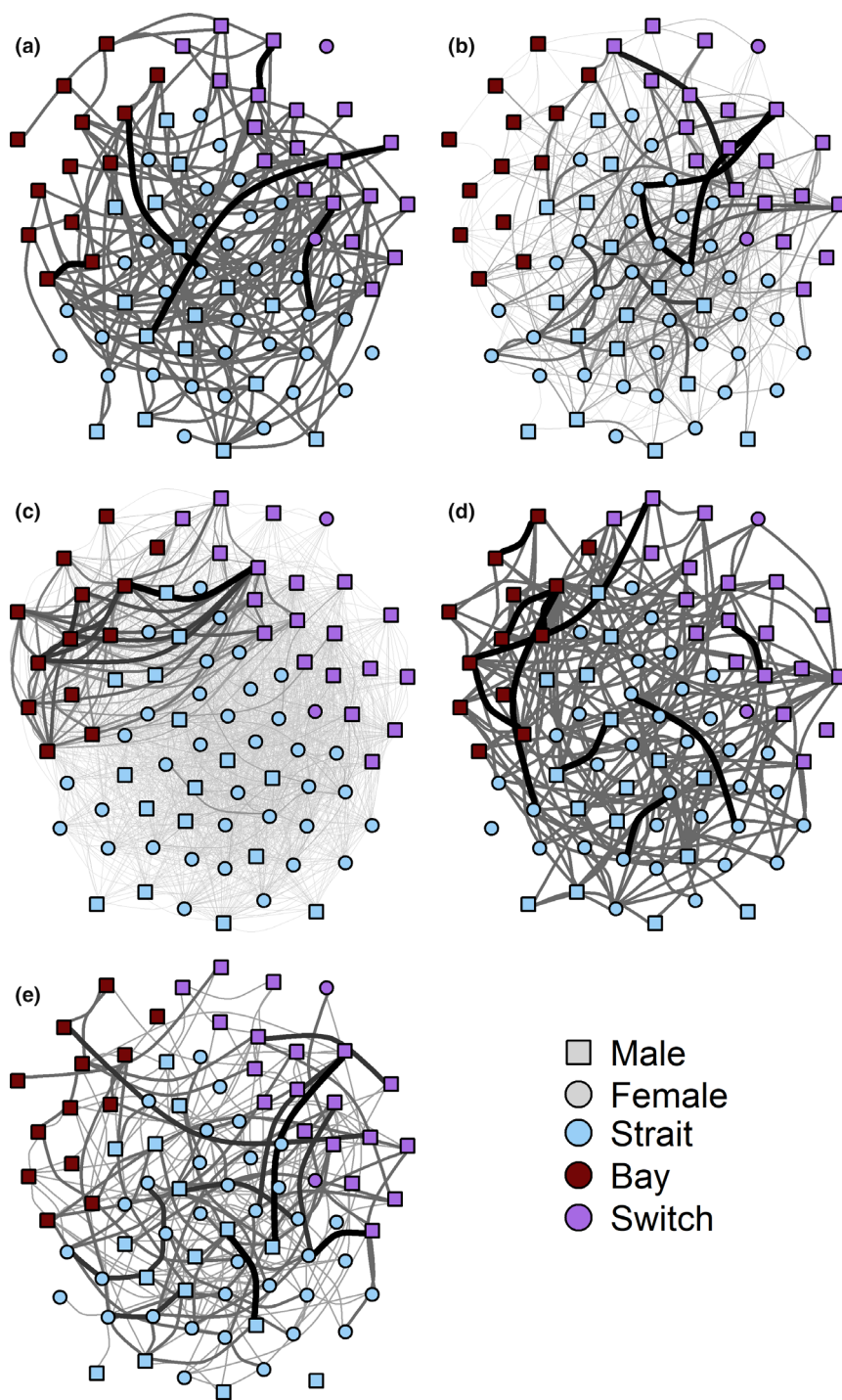
Figure 2 Gannet social networks from associations during (a) colony co-departures, (b) commuting, (c) foraging, (d) colony co-return and (e) 'outcome' network layer in which associations represent the carry-over outcomes of associations (i.e. joint commutes that end in foraging/colony or foraging/colony co-occurrences that end in commuting). Males are represented by squares and females by circles. Bay specialist are shown in red, strait specialist in blue and individuals that did not specialise ('switch' individuals) shown in purple. Edge weights are scaled in thickness from the minimum (lightest line) to maximum (darkest line) association strength recorded in each given layer.

outcomes). Both colony co-departures leading to commuting and co-commuting ending in the colony accounted for 19.5% of outcomes each. In all cases, an instance in which carried over across three states (i.e. forage to commute to forage) was considered as two separate incidents (i.e. one forage leading

to commute and one commute leading to a forage) for analysis purpose.

There was generally low edge overlap between all behaviour layers, with the highest edge overlap being between the foraging and commuting layers and between the foraging and

Table 1 Summary of network metrics for each foraging stage network. Network density, mean degree and mean weighted degree are given

Foraging state	Network density	P-value	Mean degree (range)	P-value	Mean weighted degree (range)	P-value
Co-departure	0.05	0.02	3.95 (0–13)	< 0.001	2.04 (0–7.0)	< 0.001
Commuting	0.11	< 0.001	9.67 (0–23)	< 0.001	1.64 (0–5.2)	< 0.001
Foraging	0.46	< 0.001	39.1 (3–64)	< 0.001	1.89 (0.1–9.1)	< 0.001
Co-return	0.05	0.004	4.45 (0–18)	< 0.001	2.34 (0–10.5)	< 0.001

For mean degree, the number of associates, and mean weighted degree, a general metric of gregariousness, the range of individual values observed are given in parenthesis. All metrics are compared to the distribution of values obtained from 1000 network permutations and P-values are given as the proportion of times the permutated values that were more extreme (higher) than the observed value.

return layers (Fig. 3). This indicates low consistency in dyadic associations between behavioural states and that birds associating with individuals in one context do not associate with the same individuals in another. When comparing the results from the multilayer edge overlap to pairwise correlations between the association matrices using Mantel tests, we found generally similar results (Table S2). However, the Mantel test identified very low correlation between the commuting and foraging matrices, despite the relatively higher edge overlap found between these two layers. This may result from including individuals that only had associations in one layer, but were absent from another layer, as this would drive down the correlations. By contrast in the edge-overlap approach, these occurrences would be considered as edges that were not preserved between the two layers.

Variation in gregariousness across spatial contexts

When considering the spatial foraging strategies separately, gannets that restricted their trips to the bay were found to not have a higher weighted degree during colony co-departures and foraging than expected by chance (Table 2, Fig. 4). This analysis indicates that the spatiotemporal overlap of bay

individuals during colony co-departures and foraging is not greater than is expected in comparison to the spatial null models, meaning bay gannets did not form social groups at a rate higher than expected given their spatial use of the bay. In contrast, for all other foraging states and spatial strategies, we found the overall pattern remained with the mean weighed degree significantly higher than expected given our null models. As individuals within the bay were found not to associate at a higher rate than expected from our null models, we repeated the analysis of individual consistency and overlap in social associations across foraging states excluding bay-only individuals and obtained similar results to our whole network analysis (consistency in sociality for non-bay individuals: $SV_O = 4.56$, SV_R range = 4.19–6.93, $P = 0.002$, edge-overlap analysis: Table S3).

Using InfoMap community detection approaches we found that when considering each layer separately, the foraging network best predicts the location-based strategies of individuals. The foraging network consisted of two communities; one community composed exclusively of bay and switch individuals and the second community composed of strait and switch individuals and two bay foragers (Figure S9). Using multilayer community analysis, we found similar results to the foraging layer alone, with all four layers showing the same general pattern of bay specialist and strait specialist clustered in different communities (Figure S9).

DISCUSSION

We provide a novel quantification of sociality across multiple contexts and scales demonstrating that individuals express consistent gregariousness across behavioural contexts and flexibility in social associations using a recently developed multilayer network analysis. Our results highlight that sociality needs to be measured across contexts and scales (associations vs. overall social tendency) to fully understand how individuals adjust their use of social behaviours. Specifically, we demonstrate that the spatiotemporal overlap between individuals occurs more often than expected by chance, while controlling for the specific spatial movement patterns of individuals. We thus, provide strong evidence that individuals actively associate socially during colony departure, foraging, commuting and colony return, although these relationships are formed opportunistically with available birds allowing individuals to maintain consistent levels of gregariousness in a highly variable social environment. Additionally, when we consider how gregarious tendencies vary across spatial
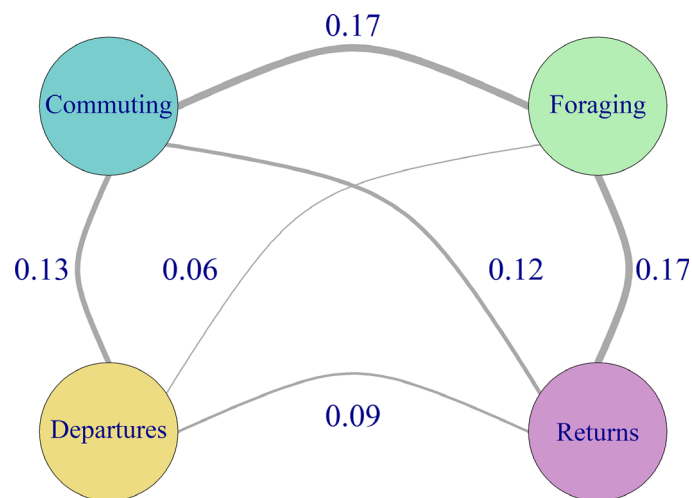

Figure 3 Multilayer edge comparison of foraging state layers depicted as a network with nodes representing each state (departure, commuting, foraging and returns) from the multilayer gannet social network. Edge values represent the proportion of shared edges between pairs of layers, which is a measure of the consistency of dyadic social associations across contexts.

Table 2 Mean weighted network degree, a general metric of gregariousness, during colony departures, returns, commuting and foraging behaviours, across the three spatial foraging strategies (bay; > 70% of trips within Port Phillip Bay, strait; > 70% of trips outside the bay, and switch; < 70% of trips in either category), compared with weighted degrees obtained from 1000 network permutations

Behaviour	Observed mean weighted degree	Range of mean weighted degree from permutations	P-value
Departure			
All	2.04	0.94–1.66	**< 0.001**
Bay	1.92	0.88–2.50	0.11
Switch	2.23	0.84–2.13	**< 0.001**
Strait	1.98	0.81–1.62	**< 0.001**
Commuting			
All	1.64	0.28–1.39	**< 0.001**
Bay	0.73	0.10–1.20	**0.028**
Switch	1.62	0.22–1.39	**< 0.001**
Strait	1.88	0.29–1.47	**< 0.001**
Foraging			
All	1.89	0.88–1.49	**0.001**
Bay	4.15	3.50–6.12	0.86
Switch	2.11	1.04–1.89	**0.001**
Strait	1.23	0.11–0.24	**0.001**
Return			
All	2.34	1.08–1.72	**< 0.001**
Bay	4.08	1.25–3.63	**< 0.001**
Switch	2.19	0.83–2.00	**< 0.001**
Strait	1.96	0.79–1.74	**< 0.001**

Significant values are shown in bold.

contexts, we find that social decisions during colony departure and foraging are mediated by spatial foraging strategy, with bay-foraging individuals having a non-significant level of gregariousness in comparison to the null models, indicating that individuals match their tendency to be social to the conditions they experience. This is further evident in the community structure underlying the foraging and multilayer networks, in which the community clusters detected strongly match the individual spatial foraging strategies.

We found strong evidence that gannets engage in social behaviours across four foraging contexts studied (colony departure, commuting, foraging and colony return) and that individuals are consistent in their relative weighted degree, a measure of gregariousness or tendency to be social. This finding demonstrates that individuals are consistent in the expression of social behaviours across multiple foraging contexts. Our study adds to the findings of several recent studies highlighting that individuals may express consistency in sociality across contexts (Firth & Sheldon 2016; Formica *et al.* 2017; Krause *et al.* 2017; Kulahci *et al.* 2018), providing further evidence that individuals may express consistent levels of gregariousness that may itself be considered a social personality.

Although we demonstrate that individuals express overall consistency in their level of gregariousness across foraging contexts, our analysis at the level of social associations demonstrates that relationships between gannets were generally not preserved between different foraging contexts. Our finding of low edge overlap (multilayer analysis) and low correlation (Mantel test) between behavioural contexts indicates that gannets form flexible social associations that vary between foraging contexts. Previous studies in seabirds have often inferred that joint departure from the colony represents social information transmission between individuals (e.g.
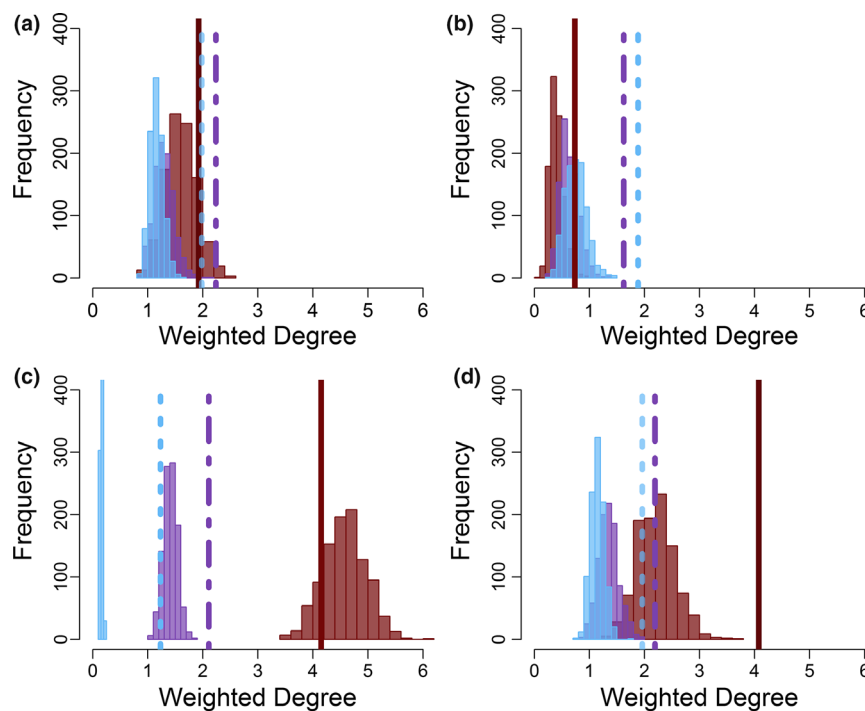

Figure 4 Distribution of mean weighted network degree, a general metric of gregariousness, from 1000 data-steam permutations for (a) colony co-departures network layer, (b) commuting network layer, (c) foraging network layer and (d) colony co-returns network layer. Lines indicate observed mean weighted degree, with strait specialist shown in blue (dotted), bay specialist in red (solid) and switch individuals in purple (dash).

Weimerskirch *et al*. 2010; Racine *et al*. 2012) and recent works have demonstrated that individuals co-departing together can share foraging areas (Cook *et al*. 2017; Sutton *et al*. 2017; Jones *et al*. 2018). Our study demonstrates that although social associations formed across four foraging contexts, there was only small carry-over in specific associations across contexts. However, our network of social outcomes does show that in some cases associations formed in one context do directly carry-over to a subsequent context. This result, paired with the relatively higher edge overlap found between the commuting and foraging layers provides some support for the idea that individuals could benefit from either combined search effort (Beauchamp 2014) or potentially follow conspecifics to food patches (as in Harel *et al*. 2017). However, the use of these behaviours may be highly opportunistic, due to constraints such as individuals waiting for their mate to return prior to being able to depart, which undoubtedly limits the overall frequency observed. Additionally, the fact that relatively few social connections were maintained between states suggests that social associations frequently form independently during each foraging state. Thus, our finding suggests that there may be additional benefits to the coordination of movement beyond immediate foraging gain, such as decreased movement costs from group flight (Weimerskirch *et al*. 2001; Portugal *et al*. 2014), although given the spatial and temporal resolution of our data we were unable to test for such benefits. Given the observation that joint commuting behaviour ending in a co-return to the colony occurred as frequently as co-departure leading to commuting, this could provide some evidence to further support the idea that coordinated movement provides flight benefits, as there is no foraging benefit to coordinating colony returns. Furthermore, our results suggest that perhaps consistency of social associations are not required for information transmission in this case, as individuals may respond to information from any conspecific source rather than attending to specific individuals, particularly as the scale of these associations occurs over a distance range that may not allow for individual recognition. Therefore, our results show that while social behaviour at the colony and during commuting may contribute to social foraging information, these behaviours also present alternate social benefits.

Local enhancement, where individuals are attracted to actively foraging conspecifics (Pöysä 1992), has been modelled as an important social foraging tactic in colonial seabirds (Boyd *et al*. 2016). Here we demonstrate strong evidence for the importance of the use of local enhancement as we find a high frequency of social associations during foraging behaviour, beyond that can be explained by shared space use at foraging patches. In the case of small colonies, modelling work demonstrates that social behaviours will be limited by available opportunities (Grünbaum & Veit 2003; Boyd *et al*. 2016). For instance, while we tracked 85 birds only half this number will be on a foraging trip at any one time, as one partner generally attends the chick at all times during this period. In particular, behaviour at the colony and commuting may be especially limited, for instance as individuals are constrained in their ability to depart the colony by their partner's return and commuting opportunities are transient. Thus, for smaller colonies, local enhancement may be the favoured form

of social information acquisition, over information acquisition at the colony, especially in species such as gannets that have highly visible white plumage (Bretagnolle 1993) and forage using plunge dives (Weimerskirch *et al*. 2010) that can be detected at a large distance given the high visual range of gannets (Thiebault *et al*. 2014b). Furthermore, heterospecific group foraging may also be of relatively higher importance to small colonies, which have limited conspecific social opportunities, which is something that remains to be examined.

When examining how sociality varies with external conditions, we found that for bay specialists there was no evidence of individual gregariousness beyond the level expected by chance, during colony departures and foraging, when controlling for individual spatial patterns within the bay. In fact, when compared with the null models, the observed overlap between bay-foraging individuals trended toward occurring less than expected by chance. This novel finding, adds to only one other study that addresses how social behaviours may vary in response to spatial features of the habitat (Piza-Roca *et al*. 2018), and builds on the idea that integrating our understanding of individual social behaviours and spatial ecology is necessary for understanding a broad range of ecological and evolutionary processes (Webber & Vander Wal 2018). Although these individuals foraging within the bay represent a small proportion of the population, it is interesting to note that gannets from this colony have been shown to target different prey when foraging in these different areas, with large non-schooling fish dominating the prey obtained within the bay and small schooling fish providing the main prey items outside the bay (Wells *et al*. 2016). Such spatially driven differences in prey have also been observed in related northern gannets, with inshore large non-schooling prey being found to provide a more spatially predictable resource (Garthe *et al*. 2007). Our finding of a lack of social associations in bay foragers indicates that there are either high costs and/or low benefits to foraging socially in the bay. This matches with the predictions of social foraging theory that social foraging is most beneficial when foraging resources are less predictable and competition is low, as is the case of schooling fish (Barta & Szép 1992; Giraldeau & Caraco 2000; Beauchamp 2014). Indeed, gannets foraging on aggregated prey have been shown to have higher prey capture rates when attacking within seconds of a previous dive, indicating that when targeting schooling prey, foraging success may be actively enhanced by social foraging (Thiebault *et al*. 2016), while no such benefit will be expected for solitary prey. Furthermore, it has been recently shown that although capture success is lower in solitary foraging gannets, profitability of prey items was higher, highlighting that there are trade-offs between social and solitary foraging (Cansse *et al*. 2020). Thus, our findings highlight the context-dependent use of social strategies depending on the conditions experienced.

In summary, we simultaneously recorded the foraging behaviour of a large majority of a colonial breeding population across multiple foraging contexts, allowing us to examine how context and individual behavioural variation influence individual social behaviours. We then employed a novel multilayer social network approach to assess how social associations vary across contexts. Our findings provide strong evidence

that individuals are consistent in their level of gregariousness but show flexibility in their choice of associates. We also provide evidence of the context-dependent use of social strategies both across social contexts and with different habitat use. These findings suggest that individuals are able to adjust their social associations in response to the available opportunities, while expressing consistency in gregariousness. Finally, we highlight the importance of the use of local enhancement at foraging patches and opportunistic social associations across co-movement behaviours. Future work that is able to directly quantify the energetic or fitness trade-offs during both search and capture portions of foraging provided by social associations under different contexts is necessary to further understand the drivers of sociality in animal groups.

AUTHOR CONTRIBUTIONS

TBJ, SCP, JPYA and JAG conceived the study. TBJ and JCE analysed the data. MARM, MRW and JPYA collected the data. TBJ wrote the manuscript, which was edited by SCP, JAG, JCE and JPYA. All the authors contributed to the revising of the final version of this manuscript.

DATA ACCESSIBILITY STATEMENT

Data archives at Figshare: https://doi.org/10.6084/m9.figshare.11971875.v2

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.