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Homophily around specialized foraging underlies dolphin social preferences

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Individuals often associate socially with those who behave the same way. This principle, homophily, could structure populations into distinct social groups. We tested this hypothesis in a bottlenose dolphin population that appeared to be clustered around a specialized foraging tactic involving cooperation with net-casting fishermen, but in which other potential drivers of such social structure have never been assessed. We measured and controlled for the contribution of sex, age, genetic relatedness, home range and foraging tactics on social associations to test for homophily effects. Dolphins tended to group with others having similar home ranges and frequency of using the specialized foraging tactic, but not other traits. Such social preferences were particularly clear when dolphins were not foraging, showing that homophily extends beyond simply participating in a specific tactic. Combined, these findings highlight the need to account for multiple drivers of group formation across behavioural contexts to determine true social affiliations. We suggest that homophily around behavioural specialization can be a major driver of social patterns, with implications for other social processes. If homophily based on specialized tactics underlies animal social structures more widely, then it may be important in modulating opportunities for social learning, and therefore influence patterns of cultural transmission.

1. Introduction

Social animals seeking to maximize foraging benefits face crucial decisions—whom to group with and for how long? Members of foraging groups pay the cost of intragroup competition [1]. One possible solution is to specialize in foraging tactics that reduce resource-use overlap [2,3]. Simultaneously, there are benefits of being social—information sharing, predation avoidance, to name but two. To maintain group cohesion and facilitate group decisions it may be benefitial to behave as the other group members do [4]. Individuals, therefore, may be prone to group with those that behave in the same way, as posited by the homophily principle [5]. When social interactions occur at higher rates among similar than dissimilar individuals, homophily arranges social ties into cohesive, distinct social groups [6], as recently illustrated by modular animal social networks constructed around repertoires of foraging specializations (e.g. [7,8]).

However, multiple processes modulate the opportunities for animals to interact socially, which complicates determining whether individuals are indeed inclined to group with those who behave similarly. While extrinsic factors can aggregate or disperse individuals in time and space—e.g. habitat complexity [9], predation risk [10], demographic changes [11]—individuals can be passively or actively assorted by biological traits, such as age, sex and kin [12,13]. Disentangling the effects of these drivers from the contribution of homophily in clustering individuals remains challenging, but important because by controlling for such effects preferred associations can be discriminated from passive assortment or chance [14]. Here, we evaluated the multiple drivers of the associations of Lahilles' bottlenose dolphins (*Tursiops truncatus gephyreus*) that specialize in foraging with artisanal fishermen [15] to evaluate the extent to which homophily around behavioural specializations can shape social structures over and above other factors that influence grouping formation.

In southern Brazil, bottlenose dolphins herd fish schools towards a line of net-casting fishermen ashore, who cast their nets in response to the dolphins' stereotyped foraging cues [16]. Not all dolphins of this small population use this tactic with the same frequency [17], and their social organization reflects such variation: dolphins that frequently forage with fishermen are more often seen together than with dolphins that forage independently [15]. However, it remains unclear whether this clustering depicts a spatial assortment in different foraging areas or assortment around the above-mentioned biological traits. If homophily underlies this social structure, then active choice of companions (i.e. social affiliations [14]) should occur among dolphins that consistently use the same foraging tactic.

We tested the hypothesis that homophily around a specialized behaviour—here dolphins foraging with the assistance of artisanal fishermen—underlies social preferences and can structure animal populations. First, we quantified the influence of multiple structural factors on dyadic associations, namely the frequency of use of the specialized foraging tactic, home range overlap, and assortment by genetic relatedness, sex and age classes. Next, we removed the effects of the confounding variables from the associations to test for active social preferences that could create modules in the dolphin social network. By accounting for different behavioural contexts that include or not the specialized foraging, we found that social patterns at the population-level result from active individual choices rather than from passive assortment.

2. Material and methods

Our study area comprised the 200 km² lagoon system in Laguna (28°20′ S, 48°50′ W), southern Brazil (electronic supplementary material, figure S1), where approximately 60 bottlenose dolphins reside [18]. We carried out boat surveys during 2007–2009 following a pre-defined route covering the area evenly [19]. Upon encountering a group of dolphins—i.e. all individuals in close proximity to each other (within approx. 50 m radius) engaged in the same behavioural state [20]—we attempted to photograph all individuals and recorded the time, location, group size and behavioural state. Following photo-identification protocols [21], we then identified individuals based on natural long-lasting marks on the dorsal fin, excluding unmarked individuals such as calves [15,20]. We collected skin samples ($n = 13$ using a remote biopsy system; $n = 3$ from stranded photo-identified individuals) to determine sex and pairwise relatedness through molecular analyses and microsatellite genotyping (electronic supplementary material, S1).

To account for behaviour-specific associations (e.g. [22]), we assigned dolphin groups to the following behavioural contexts. The 'cooperative foraging' context defined the specialized foraging tactic whereby dolphins herd fish schools towards a line of artisanal fishermen ashore who cast nets in response to the dolphin stereotyped behavioural cues [16]. The 'non-cooperative foraging' context represented typical dolphin foraging characterized by frequent, asynchronous dives in various directions [23], away from fishermen. The 'non-foraging' context included three other distinctive behavioural states: travelling, socializing and resting [24], away from fishermen. Finally, 'all behaviour' combined all these contexts.

We considered group members to be associated [25], and calculated the simple-ratio index (SRI) to quantify the proportion of time each pair of individuals spent associated [25] in each behavioural context. To avoid spurious associations with juveniles and eventual transient individuals, we restricted our dataset (41 individuals and 503 groups) to adults resighted more than 25 times (34 individuals and 497 groups).

We quantified five structural factors that could affect social patterns: the proportion of use of 'cooperative' and 'non-cooperative' foraging tactics (*fp*), home range overlap (HRO), genetic relatedness, and sex and age classes (full methods in electronic supplementary material, S2). To quantify the contribution of such factors in driving associations, we used the multiple regression quadratic assignment procedure (MRQAP) and double-semi-partialling methods [26]. The dependent variables were each of the four context-dependent SRI matrices, and the independent variables were matrices representing pairwise similarity of each of the five structural factors. We performed three independent MRQAPs, dropping non-significant structural factors that constrained sample size. The first MRQAP included 12 individuals for which all factors were known; the second included 30 individuals for which all but the genetic relatedness factor were known; the third included all 34 individuals (electronic supplementary material, S3, tables S1–S3). We evaluated the empirical coefficients using a randomized distribution of regression coefficients (20 000 iterations), and the influence of structural variables on associations using the adjusted R^2.

We used generalized affiliation indices (GAI) to remove the effect of the significant structural factors from the associations, and so represent active association preferences among individuals (i.e. social affiliations [14]). To develop a GAI for each behavioural context, we fitted a binomial generalized linear model with the corresponding SRI matrix as the dependent variable, and the significant structural factors identified by the MRQAP as independent variables [14]: SRI$_{(\text{all behaviour})} \sim$ FP + HRO; SRI$_{(\text{cooperative foraging})} \sim$ HRO; SRI$_{(\text{non-cooperative foraging})} \sim$ FP + HRO; SRI$_{(\text{non-foraging})} \sim$ FP + HRO, where SRI$_x$ = context-dependent SRI matrix, FP = Euclidean distance of *fp* (electronic supplementary material, table S3). GAI are the deviance residuals of such models, which represent the assortment of individuals not explained by the significant factors in each context [14].

To test for social preferences, social division and assortativity around these structural factors, we used null models that permuted individuals among groups (constraining the empirical group sizes, number of groups and individuals, and frequency of observation) to create an ensemble of 20 000 randomized SRI matrices, and 20 000 randomized GAI as done for the empirical data. We tested for social preferences between dyads by comparing the standard deviation (s.d.) of the observed context-dependent SRI and GAI with randomized s.d. distributions, considering preferences when the observed s.d. was higher than the null expectancy [25]. We tested for population-level social division (i.e. strongly connected modules of individuals) by plotting the context-dependent SRI and the non-negative GAI matrices as networks and comparing their empirical
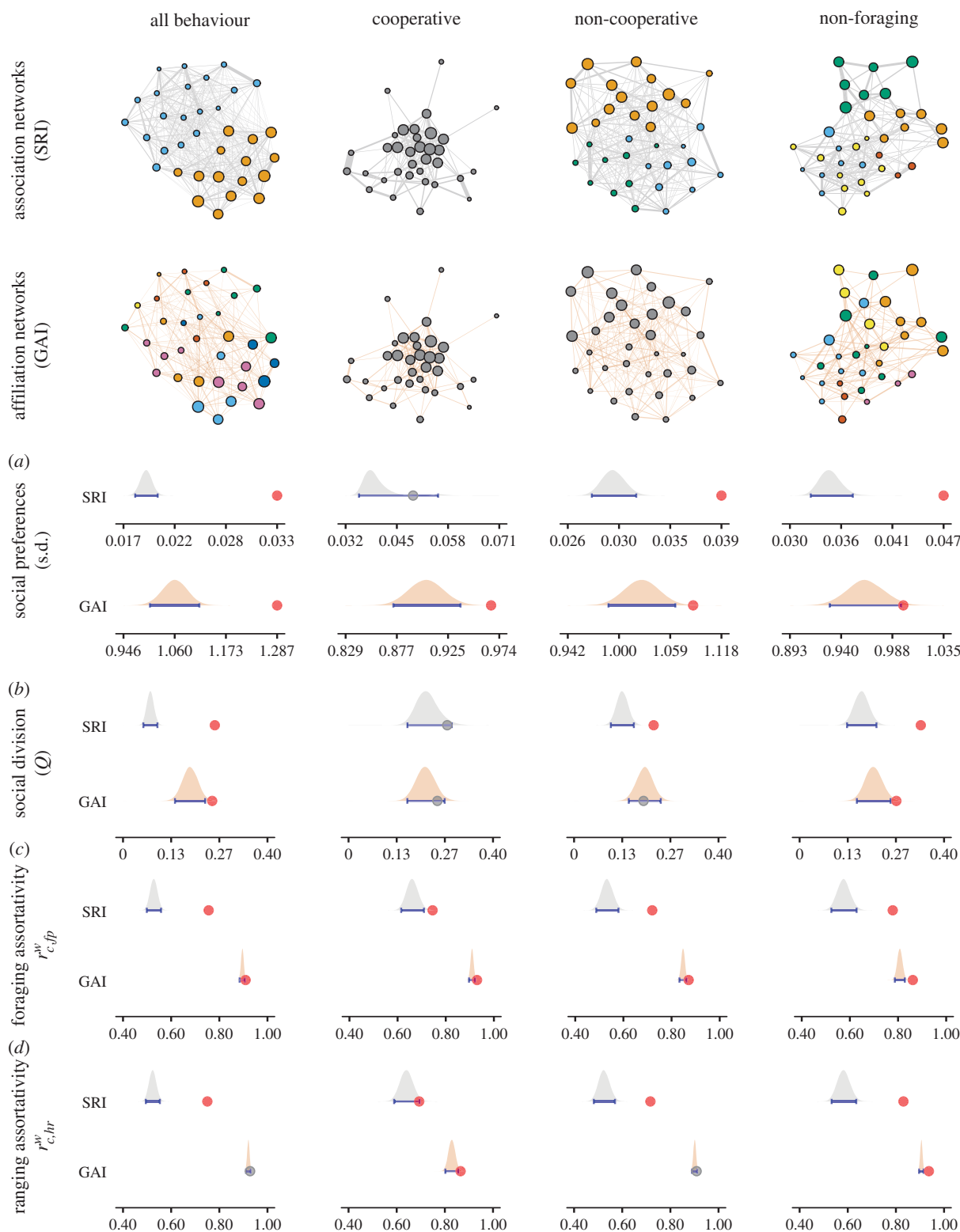
Figure 1. Dolphin social preferences at the individual and population level across behavioural contexts. Nodes representing photo-identified individuals are proportional to the frequency of use of the specialized foraging tactic and colour-coded by social modules; individuals are connected by links whose thicknesses are proportional to SRI in the association networks and to GAI removing confounding factors (electronic supplementary material, tables S1−S3) in the affiliation networks (for better visualization, only positive GAIs were plotted). In the density plots, red dots denote statistically significant observed values; grey dots indicate non-significant values; shaded distributions indicate null expectancy; and blue whiskers indicate 95% confidence intervals. The specialized foraging tactic underlies social patterns as shown by (*a*) significant standard deviations (s.d.) of SRI and GAI indicating social preferences; (*b*) significant modularity (*Q*) indicating social division; and significant assortativity by both (*c*) frequency of foraging with fishermen and (*d*) home range size. Values in the scales are rounded. (Online version in colour.)

modularity (*Q*) [25] with that of the randomized matrices. Finally, we evaluated whether the specialized foraging tactic (i.e. high *fp*, low home range size, *hr* [17]) was coupled to social preferences and social division by testing the network assortativity [27] by *fp* ($r^w_{c,fp}$) and by *hr* ($r^w_{c,hr}$), and evaluating the within-module *fp* and *hr* values. We considered empirical s.d., *Q*, $r^w_{c,fp}$, $r^w_{c,hr}$ values statistically significant when they fell outside the 95% confidence interval of their corresponding benchmark distributions (full methods in the electronic supplementary material, S4−S7).

3. Results

We analysed social associations, foraging and ranging behaviours of the 34 well-sampled adult dolphins (mean resightings = 34.60 ± 5.97 s.d., range = 26–48), corresponding to approximately 56% of the population [18,28]. We observed 497 groups (mean size = 2.37 ± 0.86 s.d.; 74–83% individuals identified [19]): 120 in the cooperative foraging, 219 in the non-cooperative foraging, and 158 in the non-foraging contexts (electronic supplementary material, S8). The most significant predictors of dolphin associations in all behavioural contexts were the foraging tactic with fishermen and home range overlap, explaining 46% of the total variance in SRI (35% in non-cooperative and 31% in non-foraging contexts). In the cooperative context, however, only home range overlap influenced (18%) the associations (full MRQAP results in electronic supplementary material, tables S1–S3).

We rejected the null hypothesis that dolphins associate randomly in all but the cooperative foraging context, as the observed s.d. of SRI was higher than the random s.d. However, when GAI removed the influence of frequency of foraging and home range overlap from SRI, we rejected the null hypothesis of random affiliations in all behavioural contexts (figure 1a). Therefore, preferred social affiliations were always detected, even when dolphins were foraging with fishermen.

At the population level, the modularity (Q) of the association (SRI) networks was higher than expected in all but the cooperative context. However, the modularity of the affiliation networks (GAI) revealed that social modules are not detectable in foraging contexts (figure 1b). Social modules were typically distinguished between those composed of dolphins that often interact with fishermen and have small home ranges, and those of dolphins that rarely interact and forage over large areas (figure 1; electronic supplementary material, table S4). All association and affiliation networks were to some degree assorted by the similarity in frequency of foraging with fishermen (figure 1c). The affiliation networks suggested that individuals can also be spatially assorted during the cooperative and non-foraging contexts (figure 1d).

4. Discussion

We found that homophily around specialized behaviour in wild dolphins underlies their active dyadic social preferences and leads to social differentiation at the population level. By parsing out many of the potential drivers of social associations, we show that the combined influence of small home range and high frequency of foraging with artisanal fishermen is superior to the influence of genetic relatedness, sex and age on social structure; by separating these social patterns into behavioural contexts, we further show that the effect of this specialized foraging tactic is not simply a passive or spatial assortment of dolphins performing the same tactic. These findings support that behavioural specializations can define social affiliations and thus shape animal social structures.

Do dolphins associate because they forage with fishermen or do they forage with fishermen because they associate? More than reinforcing this foraging specialization as a driver of the population-level social structure [15], our findings reveal that dolphins prefer to affiliate with others that forage with fishermen at similar frequencies, but not in order to

perform such a foraging tactic. This is strikingly clear when dolphins are engaged in activities other than foraging—when travelling, socializing or resting, the dolphin social preferences are evident and structure their social networks into distinctive social modules. The social division based on different foraging tactics indicates that active choice of companions extends beyond the context of their foraging interactions with fishermen. Although dolphins still show dyadic social preferences when foraging, they spatially aggregate at specific fishing spots when interacting with fishermen [17], which temporarily dismantles the modular social structure.

The key finding is that dolphins actively seek to be with similar others outside of the specialized foraging context. Such social affiliations among dolphins that forage in the same way may be reinforced by the differences in vocal repertoires of their social modules [29], which could function in mediating the recognition of preferred affiliates. The homophily around the specialized foraging with net-casting fishermen in Laguna closely resembles the Shark Bay population where the dolphins' associations are structured by homophily around the tactic of using marine sponges as foraging tools [7]. Both studies combined strengthen the evidence for socially learned behavioural specializations as important drivers of non-human societies [6,7].

Homophily is widely observed in nature and can influence a range of social processes, from social clustering to the evolution of cooperation [30]. The socially distinctive modules that can result from homophily narrow the pathways for the transmission of genes, diseases, parasites, as well as for the transmission of socially learned information related to behaviour specializations [7]. Given that dolphins often copy and emulate their related and unrelated peers [8], social learning is likely to be involved in the spread and maintenance of the specialized foraging tactic among dolphins in Laguna [31]. When dolphins actively associate with few similar others, learning is facilitated within social modules rather than between modules [32]. Thus, by modulating opportunities for social learning, homophily can reinforce social differentiation and broaden behavioural divergence [6], thereby influencing the evolution of specializations and their transmission patterns. Revealing the causes of social differentiation among animals is crucial for understanding the ecological drivers of behavioural specializations and the extent to which intraspecific competition, individual learning, cultural transmission and genetics are involved [7,33].

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