

The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen



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Diverse and localized foraging behaviours have been reported in isolated populations of many animal species around the world. In Laguna, southern Brazil, a subset of resident bottlenose dolphins (*Tursiops truncatus*) uses a foraging tactic involving cooperative interactions with local, beach-casting fishermen. We used individual photo-identification data to assess whether cooperative and non-cooperative dolphins were socially segregated. The social structure of the population was found to be a fission–fusion system with few non-random associations, typical for this species. However, association values were greater among cooperative dolphins than among non-cooperative dolphins or between dolphins from different foraging classes. Furthermore, the dolphin social network was divided into three modules, clustering individuals that shared or lacked the cooperative foraging tactic. Space-use patterns were not sufficient to explain this partitioning, indicating a behavioural factor. The segregation of dolphins using different foraging tactics could result from foraging behaviour driving social structure, while the closer association between dolphins engaged in the cooperation could facilitate the transmission and learning of this behavioural trait from conspecifics. This unique case of a dolphin–human interaction represents a valuable opportunity to explore hypotheses on the role of social learning in wild cetaceans.

Keywords: *Tursiops truncatus*; cooperative behaviour; artisanal fishermen; foraging tactics; social learning

1. INTRODUCTION

Several examples of unique, localized foraging behaviour have been described in isolated animal populations or in subgroups within populations. This behavioural diversity in advanced animal societies has sparked intense debate over the role of social processes in the development of foraging skills, and whether intra-population variations of foraging tactics may also drive the structure of these societies [1]. The genus *Tursiops* has remarkable ecological

plasticity in addition to complex cognitive abilities, resulting in differences in social behaviour and foraging tactics, even within populations [2]. Such social variability is apparent in Laguna, southern Brazil, where some individuals of the small (less than 55 individuals), resident bottlenose dolphin population interact cooperatively with artisanal fishermen, mainly during the mullet (*Mugil* spp.) fishing season [3]. Reports of dolphin–fishermen interactions in other populations mostly appear to be commensal [4], with dolphins feeding on fishery discards. In two cases, this appears to be unlikely: between Irrawaddy dolphins (*Orcaella brevirostris*) and fishermen in Myanmar [5]; and in Laguna, where previous studies have reported the human–dolphin interaction as mutualistic, with increased foraging success for both species [3].

Through highly synchronized behaviour with humans, cooperative dolphins in Laguna drive mullet schools towards a line of fishermen and ‘signal’, via stereotyped head slaps or tail slaps, when and where fishermen should throw their nets [3]. One or more dolphins may be observed engaging in these cooperative fishing bouts, but any cooperation or coordination between these dolphins are as yet unclear. The precise origin of this complex cooperation is unknown, but in general, dolphins can develop localized foraging tactics through a number of learned and innate processes, including individual and social learning [2,6]. The exact role of social learning plays in the development of behaviour is still controversial, since ecological and genetic factors may also be determinant [1]. Because a considerable number of dolphins (45%) in Laguna interact with fishermen, by exploring social structure, we are able to investigate the mechanisms behind this cooperative tactic and to examine whether social processes may play a part in the development of this behaviour or *vice versa*. To address this, we tested whether the individuals interacting with fishermen were clustered as a social unit in the population or whether this foraging tactic was independent of the dolphins’ association behaviour. First, we examined dolphin social structure by comparing the association values between and within cooperative and non-cooperative classes. Finally, we assessed whether the clustering observed in the social network of this population could be explained by foraging tactics.

2. MATERIAL AND METHODS

(a) Sampling protocol

We conducted boat surveys in good weather (September 2007 to September 2009) using a pre-defined route in the lagoon system adjacent to Laguna (28°20′ S–48°50′ W). Effort was evenly distributed throughout the site and throughout annual seasons (electronic supplementary material, S1). During encounters with dolphins, we collected photo-identification data and recorded location, time, behaviour and school size. Data collection ceased when any individual joined or left the focal group, and we only analysed data collected from groups observed for more than 15 min without changes in composition. A school was defined as all individuals within a 50 m radius of each other engaged in similar behaviour. Individual identification was based on standard photo-identification protocols. To avoid bias, calves were excluded from our analyses, and we only considered groups where all animals were identified and not engaged in cooperative behaviour during sampling. Dolphins were classified as either cooperative or non-cooperative as follows: dolphins observed driving prey schools towards fishermen and performing stereotyped behaviours, such as a head slap or a tail slap [3] were classified as cooperative dolphins; and dolphins that were never observed driving prey schools and/or performing stereotyped behaviours near fishermen were classified as non-cooperative dolphins.

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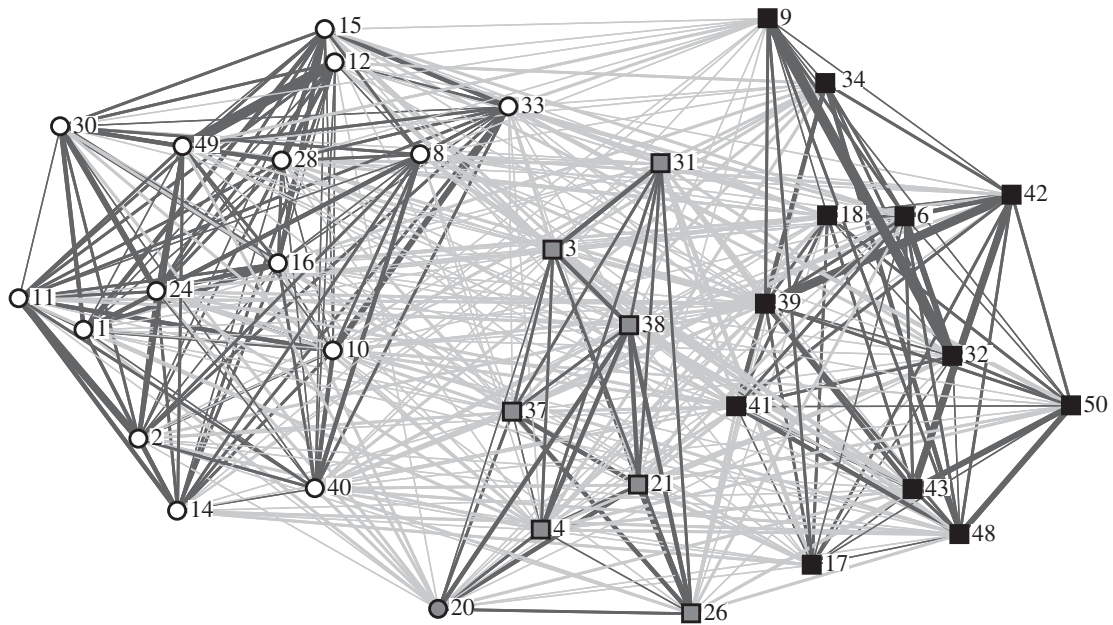


Figure 1. Social network of dolphins from Laguna with three modules defined by the foraging tactic of cooperation with artisanal fishermen. Module 1 (white nodes) comprises cooperative dolphins (circles), module 2 (grey nodes) almost entirely comprises non-cooperative dolphins (squares) (except for dolphin ‘20’) and module 3 (black nodes) comprises only non-cooperative dolphins (squares).

(b) Association measures and individual relationships

To quantify associations between dyads, we used the half-weight index (HWI) [7]. To minimize the effects of sample size and rarely encountered individuals, the data were restricted to animals sighted in less than 5 per cent of sampling days. To test the null hypothesis that observed associations occurred at random (i.e. individuals have no preferred and/or avoided partners), we conducted a Monte Carlo simulation (also applied within each foraging class), permuting individuals among groups (20 000 iterations, 1000 flips each time), retaining the original group size and sighting frequency [8]. To minimize demographic effects, each survey day was a sample unit [7]. We used a Mantel test (1000 permutations) to compare association indices among cooperative and non-cooperative dolphins, to test the null hypothesis that association indices between and within foraging classes have the same mean [7]. To examine the effect of ranging behaviour on association patterns, we correlated the dyadic association and home range overlap matrices using the Mantel test (1000 permutations; details in electronic supplementary material, S2). Analyses were performed using SOCPROG v. 2.4 [9].

(c) Social units and network structure

A weighted social network was defined by the association index matrix showing individuals (nodes) connected by their HWI (links). We evaluated network structure using: weighted clustering coefficients [10] (a measure of network connectivity) between and within dolphins of the two foraging classes; and modularity matrix technique controlling for gregariousness of individuals [7], which quantifies the tendency of nodes to cluster into cohesive sub-graphs and identifies the most parsimonious network division (an additional algorithm, hierarchical cluster analysis, was also explored in electronic supplementary material, S3, to support the partition found by the modularity technique). To test for seasonal bias, the modularity was also applied using data collected during (April to June) and outside the mullet season (results in electronic supplementary material, S4). To test whether the emerging modular structure was related to cooperative foraging, we investigated the proportion of cooperative and non-cooperative dolphins in each module. The significance of this proportion, as well as the weighted clustering coefficient values, was evaluated by checking if the observed values were outside the 95% confidence intervals of a random distribution (1000 iterations) generated by null models programmed in R [11]. One null model randomized the individuals among modules, but maintained the individual observation frequency, while another null model randomly assigned foraging class to individuals.

3. RESULTS

We observed 501 schools during 95 sampling days. Identifications of 35 individuals were analysed,

comprising 16 cooperative and 19 non-cooperative dolphins. The mean levels of association (real = 0.051, random = 0.050, $p > 0.999$) and the CV of association indices (real = 1.145, random = 0.769; $p > 0.999$) were significantly higher than expected, indicating the occurrence of few non-random and long-term preferred (41 pairs, 57% formed by cooperative dolphins, dyadic $p > 0.975$) and avoided (1 pair, dyadic $p < 0.025$) companions within the population. Association indices were significantly higher between individuals within same foraging class (HWI: mean = 0.077 ± 0.017 s.d.) than between classes (HWI: mean = 0.027 ± 0.012 s.d.; Mantel test; $p < 0.001$). Considering only cooperative dolphins, the mean association was also higher than expected (HWI: mean = 0.083, random = 0.081, $p > 0.975$), while this was not observed between non-cooperatives (HWI: mean = 0.072, random = 0.072, $p < 0.975$). A significant but weak positive correlation was observed between the social and the spatial matrices (Mantel test; $r = 0.318$; $p < 0.001$; electronic supplementary material, S2).

The social network was densely connected (realized/potential links = 0.71) by 424 weighted edges (HWI: mean = 0.051 ± 0.058 s.d., range = 0.01–0.46; figure 1). The clustering coefficient was higher than expected for cooperative dolphins and lower than expected for non-cooperative dolphins (figure 2a). The ‘difference between classes’ values were also higher than expected, suggesting that clustering coefficient was significantly higher for cooperative dolphins ($p = 0.007$; figure 2a). The network was divided into three modules when modularity was maximized at 0.272 (figure 1). Although this modularity value is slightly below the hypothetically good division provided by a 0.3 cut-off [7], it reinforces the relationship between the association patterns and the cooperative foraging tactic (electronic supplementary material, S3). Module 1 exclusively comprised dolphins that cooperated with fishermen.

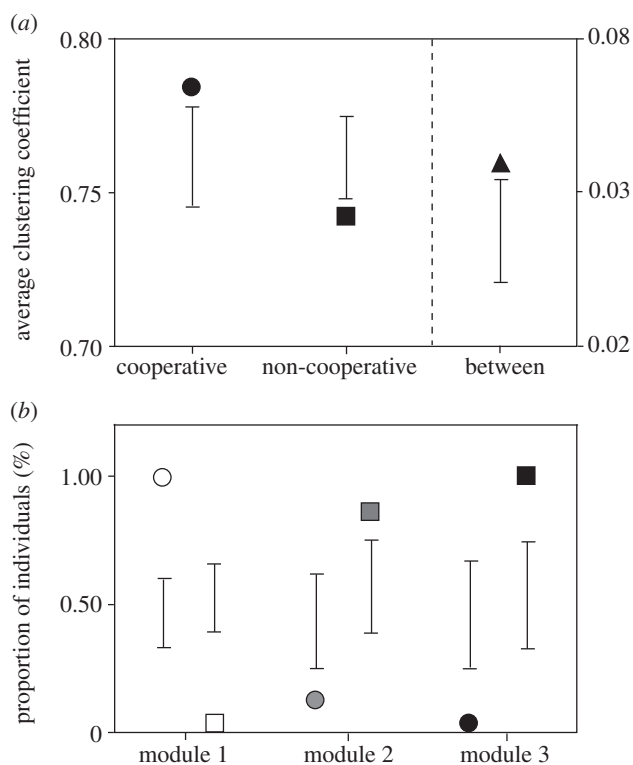


Figure 2. (a) The mean clustering coefficient of bottlenose dolphins classified by the cooperative foraging tactic (the triangle represents the difference between the mean values observed for each foraging class, which was 0.04 and higher than expected by chance); (b) proportion of cooperative dolphins (circles) and non-cooperative dolphins (squares) in each module. Whiskers represent the 95% CI from null models and symbols represent the observed values.

In contrast, module 3 only included non-cooperative dolphins. In module 2, only one of the eight dolphins cooperated with fishermen. These proportions differed significantly from random (figure 2b). Comparing data collected during and outside the mullet season, we found the same relationship between the modular structure and foraging class (see electronic supplementary material, S4). Interestingly, for all cases, dolphin ‘20’ seems to be a ‘social broker’ [12], spending time with individuals from both foraging classes.

4. DISCUSSION

The social structure of dolphins in Laguna combines the fission–fusion dynamics of a dense but weakly connected social network, with a modular topology coupled to the foraging cooperation with artisanal fishermen. Specifically, association values were higher within than between classes of cooperative and non-cooperative dolphins, indicating stronger intra-class relationships. As a result, the social network was divided by foraging class, clustering dolphins according to foraging tactic. Modular structures in other dolphin populations commonly appear to be driven by space-use patterns [13]. In Laguna, however, the ranges of cooperative dolphins were nested within the ranges of non-cooperative dolphins, with only a weak correlation between the social and spatial matrices. Considering our densely connected network and the absence of a significant spatial segregation, the intriguing question emerges: why do

only some dolphins cooperate with fishermen if they all have the ‘opportunity’?

The origin and maintenance of behavioural traits within social units are probably the combined result of ecology, genetics and social learning [1]. In the absence of spatial constraints, an environmental component alone is not enough to confine the spread of the cooperative tactic throughout this population. The results of ongoing molecular genetics work will enable us to consider a genetic factor, or even the role of kinship in the transmission of the cooperative behaviour. This would be consistent with the previous hypothesis of a matrilineal component [3], where the mother–calf relationship may create conditions suitable for information exchange and behavioural learning [1]. Curiously, the module comprising exclusively cooperative dolphins is socially more connected, with stronger relationships, and this property may facilitate the propagation of behaviour through social learning. The human side of this dolphin–fishermen interaction is maintained through inter-generational information transfer, i.e. teaching by elders, and it is likely that a similar process is used to transmit complex behavioural traits between generations of dolphins, as found in other localized behaviours such as ‘sponging’ in Shark Bay, Western Australia [2,6].

The link between association patterns and foraging tactics provides an excellent opportunity to investigate the role of learning between conspecifics in the emergence of specialized behaviours in wild animal populations. Here, it seems that the interplay between social structure and foraging tactic is ultimately promoted by a combination of mechanisms, and currently we cannot completely discard the contribution of kinship and genetic determination (the temptation of the ‘ethnographic method’) [1]. However, the closer association among dolphins that engage in cooperative foraging with humans is likely to facilitate social-learning processes related to the development and maintenance of this cooperation.

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