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Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society

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Social networks are static illustrations of dynamic societies, within which social interactions are constantly changing. Fundamental sources of variation include ranging behaviour and temporal demographic changes. Spatiotemporal dynamics can favour or limit opportunities for individuals to interact, and then a network may not essentially represent social processes. We examined whether a social network can embed such nonsocial effects in its topology, whereby emerging modules depict spatially or temporally segregated individuals. To this end, we applied a combination of spatial, temporal and demographic analyses to a long-term study of the association patterns of Guiana dolphins, *Sotalia guianensis*. We found that association patterns are organized into a modular social network. Space use was unlikely to reflect these modules, since dolphins' ranging behaviour clearly overlapped. However, a temporal demographic turnover, caused by the exit/entrance of individuals (most likely emigration/immigration), defined three modules of associations occurring at different times. Although this factor could mask real social processes, we identified the temporal scale that allowed us to account for these demographic effects. By looking within this turnover period (32 months), we assessed fission–fusion dynamics of the poorly known social organization of Guiana dolphins. We highlight that spatiotemporal dynamics can strongly influence the structure of social networks. Our findings show that hypothetical social units can emerge due to the temporal opportunities for individuals to interact. Therefore, a thorough search for a satisfactory spatiotemporal scale that removes such nonsocial noise is critical when analysing a social system.

Animal societies are the complex results of the dynamism evoked by a group-living strategy. These societies are composed of a tangle of relationships that vary in number and strength among individuals. There is increasing evidence showing that decoding the structure of such a social network is an effective approach for unravelling the underlying processes organizing an animal society (e.g. Lusseau 2003; Croft et al. 2008; Foster et al. 2012; Mourier et al. 2012; Daura-Jorge et al. 2012).

The general structure of a social network is fundamentally based on the number and strength of dyadic social relationships (Fig. 1a). Animals that form brief groups (or large aggregations) may be engaged in numerous and ephemeral associations (e.g. Clapham 1996). Because virtually all of the individuals could interact, mainly for short duration, a random social network would arise. In contrast, long-lasting associations can lead to a disconnected network composed of strongly connected components representing isolated social units. These stable groups are usually observed in matrilineal societies (e.g. Whitehead 2003). Between these two extremes are the fluid groups, of intermediate size and duration that occur at different levels in space and time. These groups are characteristic of populations with fission–fusion dynamics (Aureli et al. 2008). Such a heterogeneous pattern of social interactions can lead to a modular network structure composed of weakly interlinked groups of individuals, which are strongly internally connected. These modules may correspond to different functional social units (e.g. Lusseau et al. 2006; Guimarães et al. 2007), a large-scale level of complexity within the networked system (Newman 2011).

Different social processes can drive the emergence of these social modules in natural populations. For instance, animals can be brought together by several common biological factors, such as sex, age (Lusseau & Newman 2004; Mourier et al. 2012), kinship (e.g. Frère et al. 2010; Wiszniewski et al. 2010), foraging specializations

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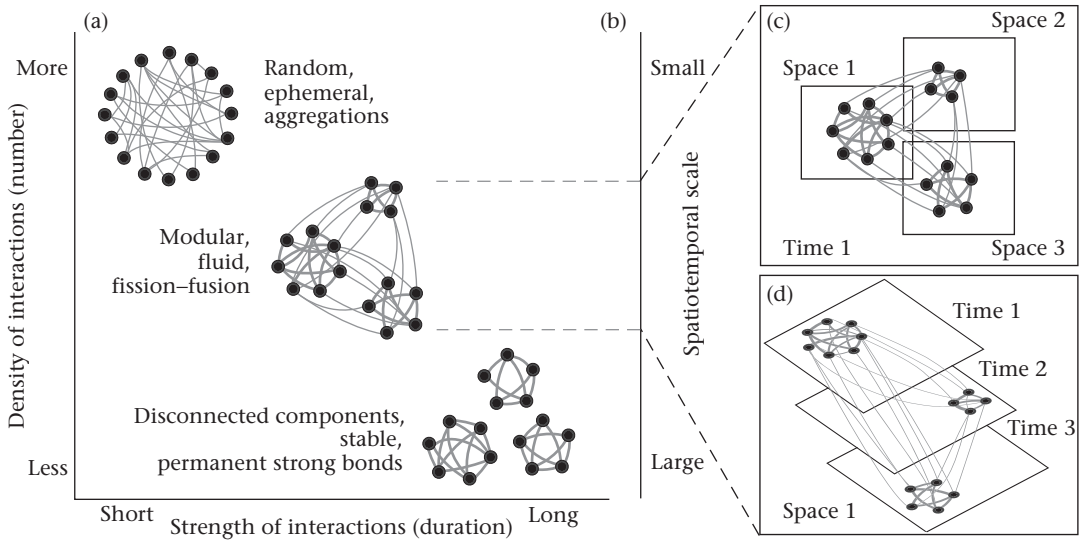

Figure 1. (a) A conceptual framework for social network topologies, based on the density and strength of interactions. Nodes depicting individuals are connected by weighted edges that represent the intensity of a dyadic association. Stability of associations (categorized as ephemeral, fluid or stable) related to grouping patterns (aggregations, fission–fusion and permanent associations) may define the structure of animal social networks, classified here into random, modular and disconnected components. (b) However, social networks may include social interactions realized in different spatiotemporal contexts. By taking into account a third spatiotemporal axis, the same topologies could arise depending on the scale considered. A random network would arise in short-term studies or in studies with a very small spatial resolution because all individuals could interact on such a small scale. In the other extreme, very long studies or those encompassing a very large area would result in disconnected networks, because population units (those that are separated by a complete temporal population turnover or that permanently use distinct areas) would be artificially joined in the same analysis. Dashed line indicates the more common intermediate scale, within which spatiotemporal dynamics can still be an important source of bias. Hypothetical modules of cohesive interactions could arise in a social network according to two scenarios: (c) when individuals of the same population display spatial segregation (i.e. use different areas during the same time), or (d) when individuals inhabit the same area but at different times (because of changes in population composition).

(e.g. Daura-Jorge et al. 2012), habitat utilization (e.g. Wiszniewski et al. 2009), or local ecological conditions (e.g. Foster et al. 2012). However, social matrices include more than social affinities or ecological factors (e.g. Wolf et al. 2007). Social networks are static depictions of dynamic societies; but we know that social interactions constantly vary in time and/or space (Aureli et al. 2008). Therefore, occasionally a modular structure may be inappropriate because it can be influenced by such nonsocial mechanisms.

Indeed, the fundamental sources of variation in social interactions that can separate or unite individuals in the same context include space use patterns and temporal demographic changes. Differences in ranging behaviour influence social interaction across space (Clutton-Brock 1989), because physically close individuals are more prone to interact (e.g. Kossinets & Watts 2006). Additionally, demographic processes in open social systems mean that the exit and entrance of individuals in the population, both by random birth–death or movement processes, can define the occurrence of an interaction over time (e.g. Lehmann & Boesch 2004). In fact, time dependence of social interactions (Hinde 1976; Whitehead 1995) can be caused by substantial changes in population composition, which would forestall interactions among temporally segregated individuals (Whitehead 1999; de Silva et al. 2011). If a social network could embed such spatiotemporal dynamics in its structure, then social modules could emerge from the opportunities to interact, depicting individuals with similar habitat preferences or that composed the population during the same time. Therefore, additional approaches that isolate the real influence of social processes are required, unmasking or accounting for these indirect effects. Ultimately, one major challenge when describing a social network is to define a feasible spatiotemporal scale within which the social patterns can be adequately described (Fig. 1b).

Here, we carried out a long-term study on the social interactions of Guiana dolphins, *Sotalia guianensis* (P.J. van Bénedèn, 1864), to better understand the poorly known social organization of such an endemic species from the western Atlantic Ocean. Our studied population, however, brings on the challenge of dealing with those mechanisms that could mask the interpretation of real social processes. Fortunately, this is a propitious system to explore the influence of spatiotemporal dynamics in the social network structure because the studied area encompasses a large and highly heterogeneous habitat (Rossi-Santos et al. 2006), and the study duration (8 years) facilitated observation of demographic changes (Cantor et al. 2012). First, we examined whether the fluid social pattern related to a fission–fusion dynamics suggested for this species (Santos & Rosso 2008) could be organized into the predicted modular network presented in Fig. 1a. Then, we analysed whether a modular network structure emerged (1) when individuals, during the same period of time, displayed marked spatial segregation, giving rise to spatial modules (Fig. 1c), or (2) when individuals used the same area but at different periods, giving rise to temporal modules (Fig. 1d). By putting the spatiotemporal dynamics in a social context, we present additional insights on the determinants of nonhuman social networks. We further suggest a preliminary analytical approach that takes into account the influence of ranging behaviour and population changes on the open social systems.

METHODS

Sampling Protocol

Data collection was carried out consistently from April 2002 to March 2010 in the coastal zone of the Abrolhos Bank, an extension of the continental shelf in the eastern Brazilian coast (17°30′S, 39°30′W; see Fig. 3). The study area covered the Caravelas River estuary and its adjacencies, spanning more than 700 km^2 and encompassing a mosaic of open waters protected by coral reef barriers, mangrove forests with channels, sandy beaches and banks of shallow waters (Rossi-Santos et al. 2007). During boat surveys designed to cover the study area homogeneously (see Cantor et al.

2012), we recorded the geographical coordinates (using a global positioning system, GPS) and the size of all sighted groups of dolphins. A group was defined as all individuals within a 50 m radius of each other (cf. Lusseau et al. 2003). We attempted to photograph the dorsal fin of all dolphins in the group, taking as many photographs as possible of both sides and without individual preferences (see Rossi-Santos et al. 2007). To minimize potential disturbances of the presence of the boat, we approached groups of dolphins at distances of 20 m or more, at low speed, on a gradually converging course, and took photographs within 30 min.

We sighted a total of 393 groups of Guiana dolphins after covering more than 13 660 nautical miles (ca. 26 000 km) during 401 sampling days, an effort evenly distributed throughout the years (sampling days were, on average, 1 week apart; Table 1). Dolphins were identified using natural markings on the dorsal fin through standard photo-identification protocols. To avoid misidentifications, calves and individuals without distinctive marks were not included in the analysis (Hammond et al. 1990). Further details on the photo-identification procedure, annual discovery curves, spatial resolution of the study, survey tracks and geographical position of the observed groups can be found in Cantor et al. (2012).

Social Interactions

All of the dolphins identified in the same group during a sampling interval were considered to be associated (Whitehead & Dufault 1999). We used the half-weight index (HWI: Cairns & Schwäger 1987) to quantify the dyadic associations (i.e. the proportion of time that a pair of individuals was observed in the same group, in relation to the amount of time that they were observed in different groups). The index is defined as follows: $HWI = x/(x + yab + ((ya + yb)/2))$, where, x is the number of sampling intervals (days) that dolphins a and b were observed in the same group; yab is the number of sampling intervals with a and b identified but not in the same group; ya is the number of sampling intervals with only dolphin a identified, and yb is the number of sampling intervals with only dolphin b. We considered 1 day as an independent sampling interval (see Whitehead 2008a). Multiple observations of an individual within a sampling interval were rare (we commonly sighted a single group per day; mean $\pm$ SD $= 1.26 \pm 0.33$; Cantor et al. 2012); in such cases we considered only the first group sighted to calculate the HWI.

From the 143 catalogued individuals, we restricted analyses to 49 distinctive individuals that were captured in high-quality photographs and resighted at least three times. Data truncation is commonly used to avoid spurious associations (Whitehead 2008a). Many studies use more restrictive observation thresholds to intentionally remove any transient individual and focus on the social organization of the core of residents (e.g. Wolf et al. 2007; de Silva et al. 2011; de Silva & Wittemyer 2012). Based on the population dynamics of our studied system (see Rossi-Santos et al. 2007; Cantor et al. 2012), we specifically considered transient individuals to explore the dynamics of an open social system and its influence on the interpretation of the social patterns (see Fig. 1). We further tested the consistency of our results under different observation thresholds (see Supplementary Data S2), and accounted for possible sampling biases using a null model approach (see Gotelli & Graves 1996) and bootstrap resampling techniques (see below).

We estimated the coefficient of variation (CV) of the observed HWI, which describes the heterogeneity of relationships, using maximum likelihood (Whitehead 2008b). We used Pearson correlations to evaluate the accuracy of the observed association matrix relative to the estimated association matrix (for details see Whitehead 2008b) using the SOCPROG 2.4 program (Whitehead 2009).

Table 1
Summary of the sampling effort of the long-term association study of Guiana dolphins, *S. guianensis*, in the Caravelas River estuary, Brazil

Year	Sampling effort		Total observation (h)	Sampling periods (days)	Observed groups	Group size (mean±SD)
	(nautical miles)	(h)				
2002	2340.6	327.0	60.7	53	72	4.2±2.1
2003	2784.4	465.3	58.3	83	78	5.2±31
2004	2214.1	280.7	27.5	60	53	4.0±1.8
2005	1529.4	258.8	44.9	47	40	5.6±4.1
2006	668.6	122.1	22.1	23	22	4.2±1.2
2007	1035.7	217.6	16.7	32	37	5.4±2.8
2008	1518.3	297.8	21.7	48	46	4.5±2.5
2009	1333.4	266.0	16.1	43	32	4.6±2.2
2010	380.0	66.9	4.8	12	13	5.4±1.9

Spatial Patterns of Dyadic Associations

To explore the influence of ranging behaviour on social interactions, we analysed the relationship between dyadic associations and dyadic spatial overlap. An individual's range was estimated using the fixed kernel-density method (Worton 1989). To avoid spatial autocorrelation and exclude the potential influence caused by the presence of our research boat, we used only the first record per sampling day for the group in which each individual was sighted. The ad hoc method was used to estimate the bandwidth value (i.e. the resolution of the smoothing parameter; Worton 1989). The individual range was defined using a 95% contour line (kernel 95%), while the core area was defined using a 50% contour line (kernel 50%). Although we did not obtain sufficient samples to estimate the home range for some individuals, we used the home range framework to estimate individuals' ranges and then used these polygons to generate a proxy of spatial overlap between pairs of individuals. We estimated spatial overlap using the utilization distribution overlap index (UDOI), a generalization of Hulbert's niche overlap concept (Fieberg & Kochanny 2005). A correlation analysis was performed between the association matrix (HWI) and the matrices of individual ranges and core areas of overlap (Mantel correlation, 1000 permutations). In addition, we performed the same correlation analysis between HWI and a probabilistic measure of space sharing (PHR_{ij}), the probability of individual j occurring within the range of individual i (Fieberg & Kochanny 2005). Analyses were performed in the R environment (R Development Core Team 2011) using the adehabitatHR package (Calenge 2006).

Temporal Patterns of Dyadic Associations

We assessed the temporal stability of associations using lagged association rate analysis (LAR; Whitehead 1995). The population LAR g corresponds to the average probability of previously associated pairs being found together again after a given time lag d. Seven candidate theoretical models were fitted to the distribution of $g(d)$ against the time lags to describe how relationships changed over time and to quantify the time lags when associations were less likely to occur (Whitehead 1995). The exponential decay models were based on a combination of three components of societies under fission–fusion dynamics: constant companionships (i.e. individuals associate permanently); casual acquaintances (i.e. individuals associate longer than time lag d but disassociate and might reassociate); and rapid disassociation (i.e. pairs disassociate during time lag d)

(Whitehead 1995). The most parsimonious model was selected using the quasi-Akaike Information Criterion (QAICc), considering the overdispersion of the data (Burnham & Anderson 2002). To determine the occurrence of nonrandom associations, we compared LARs to null association rates (NAR), during which all individuals could be randomly associated (restricting the original number of associates and individual observation frequencies; Whitehead 1995). Standard errors for the LAR and NAR estimates were obtained using a jackknife procedure (Whitehead 1995). These analyses were performed for all individuals (including those resighted less than three times) to avoid a positive bias (Whitehead 2008a) using the SOCPROG 2.4 program (Whitehead 2009).

Demographic Effects

To assess the effect of demographic processes on association patterns, we used lagged identification rates (LIR; Whitehead 2001) to infer information about individual additions to or deletions from the population. This analysis estimated the probability of resighting an individual in the study area (R) after time lag d in comparison to a randomly chosen individual. LIR is constant when the population is closed but declines briefly when individuals are leaving the population. To identify factors responsible for declining LIR, we fitted seven models to the observed LIR using a combination of demographic parameters: population size (N), mean residence time (a), mean time outside the study area (b), emigration (λ), immigration (μ) and mortality rates (δ) (see Whitehead 2001). The parameters of the model were estimated by maximizing the summed loglikelihoods (Whitehead 2001). The QAICc was used to select the most parsimonious model (Burnham & Anderson 2002). The LIR confidence intervals (CI) were obtained using bootstrap replicates (see Whitehead 2008a). All LIR analyses were run in the SOCPROG 2.4 program (Whitehead 2009).

To examine the relation, if any, between association probabilities and absence of individuals in the study area (due to mortality and/or emigration), we used a linear regression between the LAR and LIR for the same time lags under a geometric progression. Based on the LAR and LIR best-fitting models, we defined the time lag in which the association and identification rates had low probabilities of continued existence. To take into account the effect of the presence/absence of individuals on the decay of association probabilities, we analysed the temporal scale of the turnover of individuals between different periods. We divided the total study length (96 months) into integer periods of months (6, 8, 12, 16, 32 and 48 months) and used a Whittaker's index dissimilarity matrix to quantify differences between periods based on the presence of individuals in the population. The significance of the observed dissimilarity in each period was checked by comparing the empirical values to the 95% CI of null distributions generated using a null model (NM1; see Supplementary Table S1). At each of the 1000 iterations, individuals were randomized into these integer periods of months, but constrained by the number of times they were sighted during the entire study.

Social Network Topology

Social interactions were described using an undirected weighted network (Boccaletti et al. 2006). Nodes representing individuals were connected by edges, the thicknesses of which were proportional to the weight of association (HWI). To explore the network topology, we used two global properties. (1) We used a clustering coefficient to quantify the degree to which nodes tended to cluster together, representing the chance that an individual's associates were associated with each other. We relied on the averaged weight of the edges of a triplet to define the weighted clustering coefficient ($C_{w,am}$; see Opsahl & Panzarasa 2009). (2) We used modularity (M) to quantify the tendency of nodes to cluster into cohesive subgraphs. A modular social network is composed of weakly interlinked social units of individuals that internally are strongly connected to each other. We calculated modularity using a module identification algorithm (Guimerá & Amaral 2005a, b) combined with a stochastic optimization technique, the simulated annealing (SA) method (Guimerá et al. 2004). This procedure was used to identify the network partition that yielded the greatest degree of modularity, maximizing the difference between the observed density of the edges within modules and the density expected by chance. The SA method is one of the most effective methods available (for a comparison see Danon et al. 2005; Olesen et al. 2007), and we further verified the consistency of the results (Supplementary Data S1). We also evaluated network structure consistency due to the removal of sporadically observed individuals, by calculating the clustering coefficient and modularity under different observation thresholds (Supplementary Data S2). In addition, we further explored how our sampling effort could affect the network properties using the bootstrap method to calculate precision (SD).

We tested the empirical network properties (and HWI, see below) with a null distribution obtained from 20 000 random networks of the same size generated by a second null model (NM2; Supplementary Table S1). NM2 reallocated the individuals into groups (i.e. the 1s in the raw group $\times$ individual matrix), constrained by group size (marginal totals of rows) and individual sighting frequency (marginal totals of columns). The resulting cells had different probabilities of being filled according to features of the original dataset (see similar models proposed in: Bascompte et al. 2003; Vázquez et al. 2009). Empirical values were significant if they differed from typical values of the benchmark distribution (i.e. if they fell outside the 95% CI, based on a two-tailed test).

To test whether spatiotemporal mechanisms affected the network topology, we analysed their relationship with the emergence of modules. If differences in space use are important, we expected that individuals composing a certain module would present a higher spatial overlap (individual range and core areas) than that expected by chance, while individuals from different modules would present lower spatial overlaps. To test the temporal effect, we classified individuals according to the period in which they were sighted (32-month periods; see Results) and compared the proportion of dolphins from the different sighting periods in each module. If modules are defined by a temporal segregation, then individuals from the same periods should be more concentrated into the same modules than expected by chance. The significance of both results was checked using a third null model (NM3; Supplementary Table S1). We compared the mean observed values (individual range and core area overlap; proportion of individuals per period) within and between modules to the 95% CI of null distributions of individuals randomly assigned to modules (1000 iterations), while constraining module size (e.g. Daura-Jorge et al. 2012). With the same approach, we further tested the temporal effect by comparing the HWI (Supplementary Data S3) and two local network properties (shortest path length and centrality; Supplementary Data S4) between the different classes of sighting periods. We expected individuals in the same class to occupy the same social position in the network (central or peripheral), to show stronger relationships (higher association indices amongst themselves) and to be

closer in the network (lower average shortest path length) than individuals of different classes.

Association Patterns

Animal association patterns are usually evaluated using Monte Carlo simulations (Bejder et al. 1998), employing a pairwise swapping algorithm that permutes individuals into groups. Because this approach may be biased (Krause et al. 2009), as an alternative, we tested the hypothesis of a random social pattern for this Guiana dolphin population using the null model NM2. Note that our randomization constrained the same features of the original data as would a conventional algorithm (see Bejder et al. 1998).

To rule out demographic effects, we first defined the maximum scale over which associations could be analysed, using the LAR and individual turnover analyses to separate individuals into periods (32 months, see Results). Then, each of the three 32-month periods (i.e. 62, 43 and 49 sampled days, respectively) was split into shorter periods during which demographic effects were less likely to occur (see Whitehead 1999). It is reasonable to assume for this species that the population is closed within periods of 2 months. During each of the 20 000 null model iterations, a 2-month period was randomly selected and the randomization procedure was carried out only within that period (Whitehead 1999).

The existence of long-term preferred companionships (across 2-month periods) in the population would be indicated by a high CV for all observed HWIs. Short-term preferred companionships (within a 2-month period) would be indicated by a low observed HWI mean and a low proportion of nonzero HWIs (Whitehead 1999, 2008a). The P value was defined by the proportion of random matrices whose statistics were higher than the observed values (significant difference indicated by $P > 0.95$; see Whitehead 1999, 2008a). To quantify the number of preferred and avoided associations, the test was extended to dyadic HWI values (cf. Bejder et al. 1998). Association estimates at or below the 2.5 percentile in the null distribution were considered as avoidance, and those at or above the 97.5 percentile were considered as preference.

RESULTS

The Guiana dolphin population was organized as a well differentiated society (HWI CV: $S \pm \mathrm{SE} = 0.87 \pm 0.03$; $S > 0.5$; see Whitehead 2008b) and the estimated association matrix was a moderate but feasible representation of the true pattern ($r \pm \mathrm{SE} = 0.51 \pm 0.03$; $0.4 \leq r > 0.8$; see Whitehead 2008b).

Social Network Topology

The social network of Guiana dolphins was formed by a single component of 49 individuals (nodes), connected by 438 weighted edges (mean HWI $\pm$ SD $= 0.167 \pm 0.114$). The average clustering coefficient was higher than expected ($C_{\mathrm{w,am}} \pm \mathrm{SD} = 0.665 \pm 0.020$; 95% CI $= 0.586$–0.659), indicating a high tendency of individuals to cluster together. The social network was more modular than its random counterparts ($M_{\mathrm{obs}} \pm \mathrm{SD} = 0.209 \pm 0.041$; $M_{\mathrm{random}} \pm \mathrm{SD} = 0.119 \pm 0.005$; 95% CI $= 0.110$–0.129). The partitioning was consistent (Supplementary Data S1) and divided the network into three modules containing M1 $= 21$, M2 $= 6$ and M3 $= 22$ individuals (Fig. 2a). The network topology was maintained in a more restrictive observation threshold (Supplementary Data S2, Fig. S2). The precise estimates (low SD) of the observed network metrics suggested that the sampling effort was sufficient to provide a reliable description of the network structure.

Spatial Patterns and Network Topology

Spatial distribution did not influence dolphins' probability of associating. Individuals that used more similar areas (i.e. pairs with a higher spatial use overlap) did not tend to show higher association indices. There was no correlation between HWIij and PHRij 95% (Mantel test: $r = 0.009$, $N_{\mathrm{assoc.}} = 666$, $P = 0.460$) and a significant but weak correlation between HWIij and individual range (Mantel test: UDOI 95%: $r = 0.311$, $N_{\mathrm{assoc.}} = 666$, $P = 0.001$) or core area overlap (UDOI 50%: $r = 0.283$, $N_{\mathrm{assoc.}} = 666$, $P = 0.001$).

Dolphins from different modules were spatially overlapped (Figs 2b, 3). Neither individual ranges nor core areas of overlap within modules were as high as expected, except for a slightly higher mean individual range overlap in module 1 (mean $= 0.97$, 95% CI $= 0.64$–0.96; Fig. 2b). Likewise, individual ranges and core areas of overlap of dolphins from different modules did not differ from those expected by chance, apart from a slightly smaller mean individual range overlap between modules 2 and 3 (mean $= 0.49$, 95% CI $= 0.57$–0.93; Fig. 2b).

Temporal Patterns and Network Topology

LAR decreased throughout the study, indicating the time dependence of association probabilities and a significant dissociation over the study. The most parsimonious LAR model (based on the QAICc) suggested that most associations were brief, because rapid dissociations and casual acquaintances were common features (Supplementary Table S2). These associations were nonrandom because the association rate remained higher than that of the null association model over the entire study period (Fig. 4a).

Time also influenced the probability of resighting individuals in the study area. LIR showed the same pattern of decline during the study as that of LAR (Fig. 4b). Three LIR exponential decay models were supported by the QAICc ($\Delta\mathrm{QAICc} \leq 2$). The first two models consisted of parameters that indicated the occurrence of emigration or mortality. The third model suggested the occurrence of reimmigration, in which temporary emigrants returned to the population (Supplementary Table S3).

LAR and LIR were highly and positively correlated both for the observed values ($R^2 = 0.924$, $t = 9.85$, $P < 0.0001$) and for the values predicted by the best-fitting models ($R^2 = 0.999$, $t = 237.01$, $P < 0.0001$). This strong relationship suggested interplay between probabilities of association and presence in the study area. From the best-fitted LAR model, the probability of associations was estimated to decline by half after approximately 975 days, while the best LIR model predicted the same decrease after approximately the same amount of time (964 days) (Fig. 4a, b). This time lag was exactly the same period during which individual turnover was higher than that expected by chance (975 days $\approx$ 32 months). Significant changes in the population composition were only detected when the entire study was divided into three periods of 32 months (Fig. 4c).

The scale of such a high population turnover was reflected in the network modular topology. Modules were composed of individuals that were in the population during the same time (i.e. that were observed during one or more 32-month periods; Fig. 2a, c). Thus, hereafter individuals were categorized according to three sighting periods: Beginning (individuals sighted exclusively during the first 32-month period, plus individuals sighted during both the first and second periods), End (individuals sighted only during the third period, plus individuals sighted during both the second and third periods), or All (individuals sighted during all three 32-month

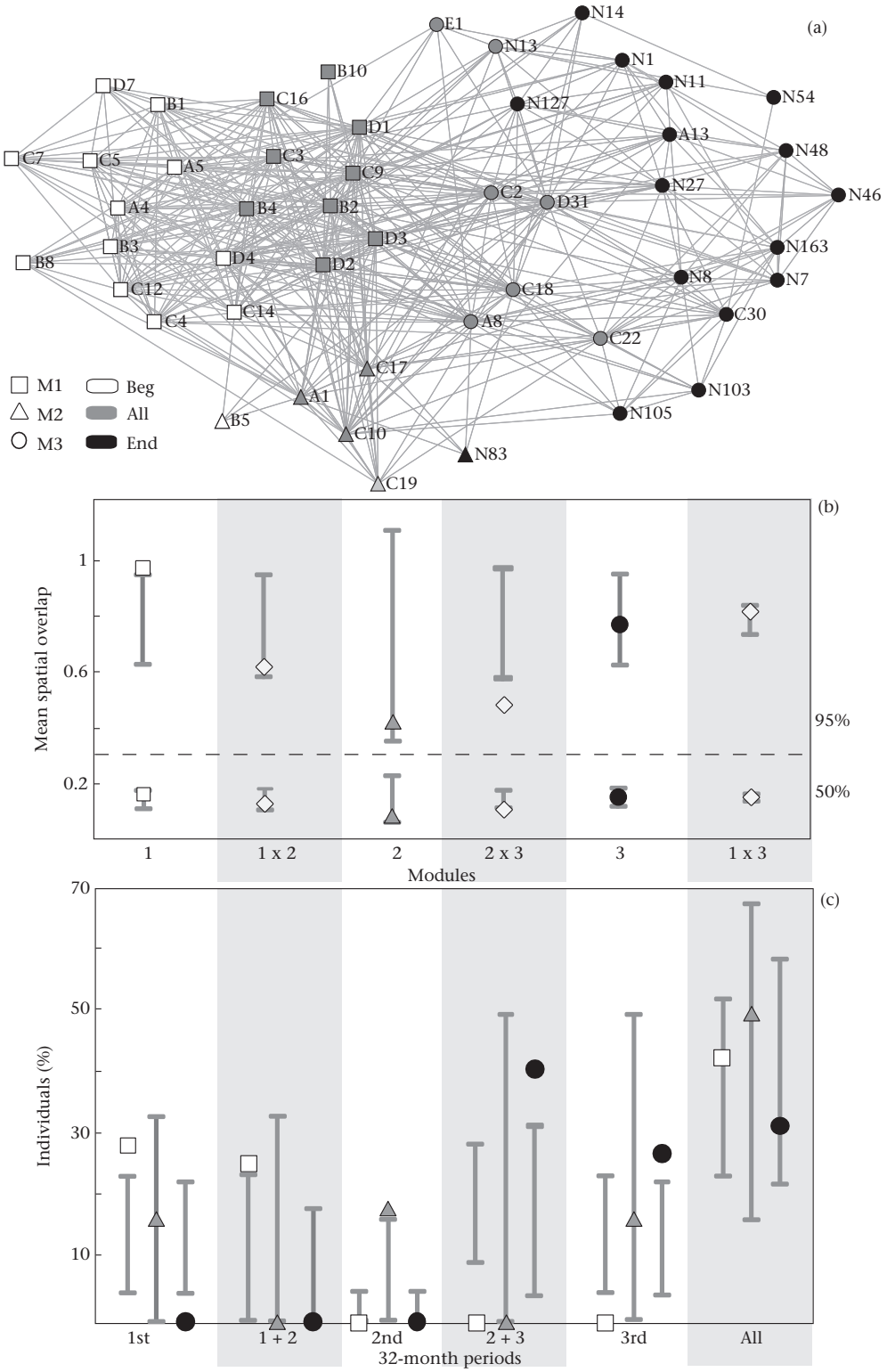

Figure 2. (a) Social network of Guiana dolphins displaying three modules (M1: square; M2: triangle; M3: circle), defined by sighting period. White nodes indicate dolphins sighted at the beginning of the study; black nodes indicate dolphins sighted at the end of the study; grey nodes indicate dolphins sighted throughout the entire study (see text). Node C19 represents the individual sighted exclusively during the second period. (b) Mean spatial overlap of dolphins within (white bands) and between (grey bands) the three modules. Pairs of data points in each band correspond to the kernel-based spatial overlap, where mean core area overlap (50% utilization distribution overlap index, UDOI) is shown below the dashed line and mean individual range overlap (95% UDOI) is shown above the dashed line. (c) Proportion of dolphins from the different 32-month sighting periods (1st, 2nd and 3rd) composing the three modules (the triplet data points in each band). Grey bands refer to dolphins sighted during periods of transition (1 + 2 and 2 + 3) and recorded during the entire study (All). Whiskers in (b) and (c) represent 95% confidence intervals generated using null model NM3.

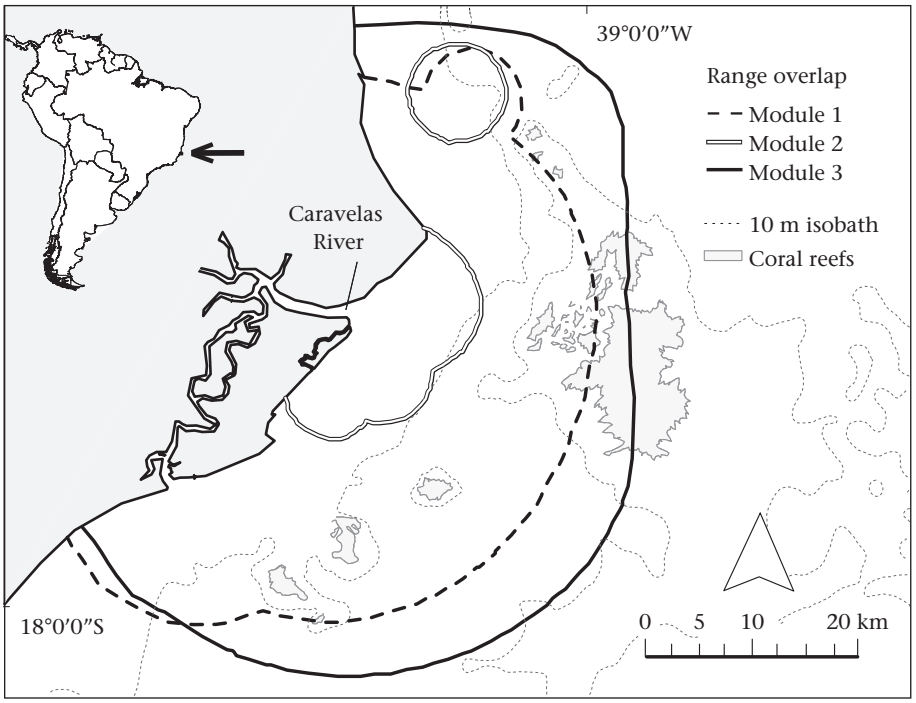

Figure 3. Caravelas River estuary in the Abrolhos Bank, on the eastern coast of Brazil, and the extreme boundary of the merged individual ranges (95% probability kernel contours) of all Guiana dolphins from each module of the social network.

periods). The proportion of dolphins sighted at the beginning of the study was significantly concentrated in module 1. Individuals sighted at the end of the study were mainly found in module 3. Module 2 was composed of individuals from all three periods, in addition to a single individual sighted exclusively during the second period. The dolphins recorded during all three periods were equally distributed across the modules (Fig. 2c).

Association Patterns

Within the temporal scale of a 32-month turnover, in which it was feasible to investigate social patterns controlling for demographic effects, Guiana dolphins showed significant, high association indices. A similar trend was observed among dolphins that composed the same module (Supplementary Data S3, Fig. S3). The dyadic associations were lower and more variable than expected. Among all of the individuals that inhabited the study area during the same 32-month period, the mean levels of association were not significantly different from those expected by chance. This result indicated the nonoccurrence of short-term preferred companionships. The CVs of the association indices were significantly higher within the periods, suggesting the occurrence of long-term companionships. However, only a few dyads were nonrandomly associated, as indicated by a low percentage of avoided and preferred associations (i.e. HWI values were lower, $P < 0.025$, and higher, $P > 0.975$, than expected, respectively; Table 2).

DISCUSSION

Our long-term study on Guiana dolphin social interactions shows that societies with fission–fusion dynamics can be structured in a modular network (Fig. 1a). The network represented a well differentiated society, with few strong and many weak ties, illustrating the fluidity of associations. The tendency of the nodes to cluster indicates that not all of the dolphins interacted directly with each other, and this heterogeneous interaction pattern was structured into modules of denser associations. Different mechanisms drive the modular structure of a social network and detecting them is critical for understanding the forces driving social patterns (e.g. Lusseau et al. 2006; Wolf et al. 2007; Wiszniewski et al. 2009; Daura-Jorge et al. 2012). From our major finding, the modular structure gave rise to a challenging question: how much of this structure could be explained by social processes? Indeed, our results illustrate a spatially merged but temporally split society, revealing that space and time are major factors that must be contextualized when analysing a social system.

In the Same Place

Nonrandom patterns of space use can produce complex structures in fission–fusion networks (e.g. Ramos-Fernández et al. 2006). For instance, the combination of resource availability and pronounced habitat preferences can separate dolphins into discrete social modules (e.g. Lusseau et al. 2006; Wiszniewski et al. 2009). Habitat preferences would be expected to shape the Guiana dolphin social network in the Caravelas estuary because dolphins in this population inhabit a patchy mosaic of habitats, from inner-river regions to offshore coral reefs, in a heterogeneous manner (Rossi-Santos et al. 2006, 2010). Additionally, individuals have relatively small individual ranges (Rossi-Santos et al. 2007). Although there was a variation in ranging behaviour (Fig. 3; see also Cantor et al. 2012), all of the dolphins greatly overlapped their individual ranges and core areas. Spatial segregation was not clearly detected in a considerable spatial resolution (one of the largest studied areas for the species, spanning more than 700 km^2; see Cantor et al. 2012). In addition, the degree of overlap was not closely related to the dyadic association level or to the dolphins composing the modules.

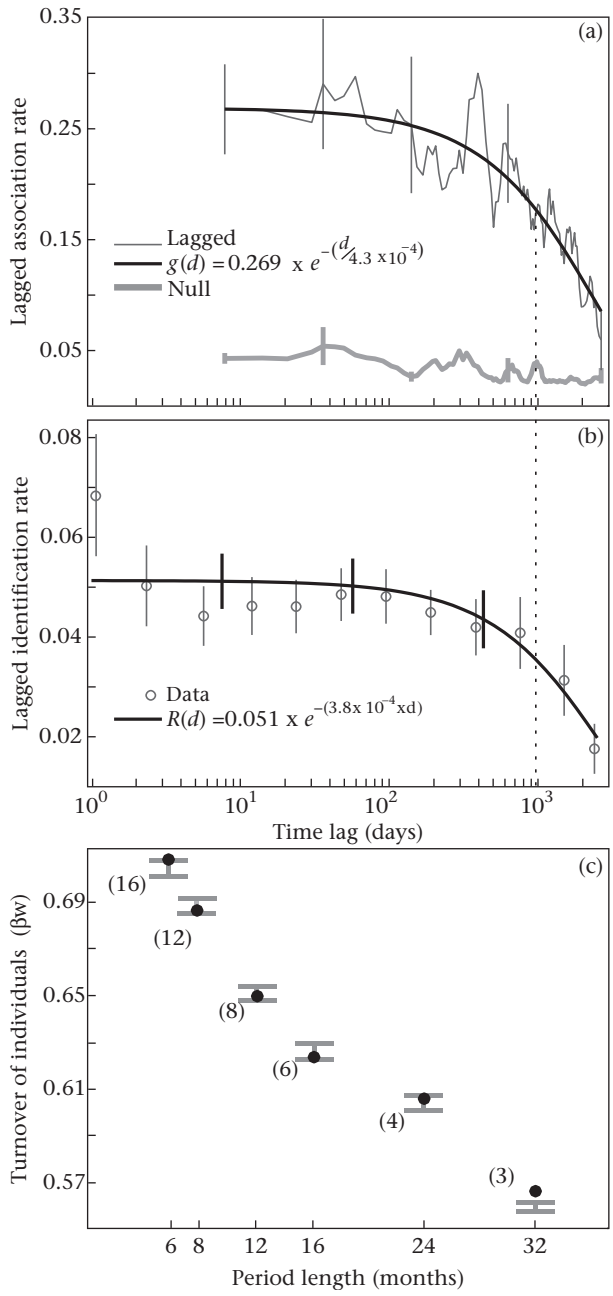

Figure 4. (a) Lagged association rates (LAR) for all individuals, suggesting rapid dissociations and casual acquaintances (see Supplementary Table S2). Null association rates represent cases in which animals associated randomly. (b) Lagged identification rates (LIR) were best described using a model that indicated the occurrence of emigration and mortality (see Supplementary Table S3). Bars represent the SE estimated using a jackknifing procedure. Dashed lines in (a) and (b) indicate the approximate time lag (≈975 days) during which LAR and LIR decayed by half. (c) Differences between individuals composing the population (turnover) as a function of time period. Values in parentheses indicate the number of periods into which the total study length was divided. Whiskers represent 95% confidence intervals generated using null model NM1.

Such a nested ranging behaviour among Guiana dolphins from different modules suggests that space use patterns are not enough to explain the modular topology observed in this study. However, nonsocial factors can still be influencing this dolphin social network (see Whitehead 1999; Parsons et al. 2009; Elliser & Herzing 2011). We showed that the population dynamics has split this society into temporal modules.

At Different Times

Time dependence is an essential feature of sociality that was clear in the Guiana dolphins associations we studied. The probabilities of association between individuals decreased over time, and the population essentially displayed grouping patterns generalized as rapid dissociations (which last for less than 1 day) and casual acquaintances (which last longer than 1 day and then disassociate). Such temporal patterns can have many causes (Whitehead 2008a), such as environmental features, dispersion, physiology (see Whitehead 1995) or geographical traits (Lusseau et al. 2003). The decay of the association probabilities of the Guiana dolphins observed here was mainly due to a demographic effect.

The association probabilities among Guiana dolphins were strongly coupled with their permanence in the study area, suggesting that dissociations were also a result of the absence of some individuals. Because this population is characterized by an apparently stable population size and individual variation in residence patterns (Cantor et al. 2012), the movement of individuals through our studied area and adjacencies is probably the main demographic mechanism for additions and deletions of individuals in the population. In fact, emigration and reimmigration are relevant demographic parameters for this population, which was highlighted by a robust-design mark–recapture model considering temporary emigration from the same dataset (Cantor et al. 2012) and the best LIR models presented here. In addition, since this population shows high survival probabilities (Cantor et al. 2012), we would expect that, if exit of individuals were mainly promoted by death events, then the LIR exponential decays would be less pronounced than those observed. Therefore, movement processes affected the association patterns by preventing some individuals from using the area at the same time. As a consequence, the association probabilities decayed over time, inflating the occurrence of associations of short duration (casual acquaintances).

The exit of individuals from a fission–fusion social system can change its dynamics by decreasing stability and increasing group size (e.g. Lehmann & Boesch 2004), which may define distinct social units (e.g. Elliser & Herzing 2011). The Guiana dolphin population underwent a marked population turnover, with a change in the population composition from the beginning to the end of the study. We identified the temporal scale of large changes in the population composition as a 32-month period, during which the association and identification rates had their most pronounced decay. As a result, the individuals sighted within these periods were found to be concentrated in certain modules of the network.

The modular network configuration further suggests a population composed of a core of long-term resident individuals along with other visitors that use larger areas around the highly heterogeneous local habitat (see Cantor et al. 2012). The module division was corroborated by the dolphins' association intensity and their positions in the network, both of which were independently classified according to the period that each dolphin was present in the population (see Supplementary Data S3, S4, Figs S2, S3). Transient individuals (those sighted exclusively at the beginning and end of the study) were more closely and strongly connected among themselves and occupied a peripheral position in the network. In contrast, resident individuals (sighted throughout the entire study) were spread through all of the modules and had a more central position in the social network (Supplementary Data S4), being the core of the population. These results support the proposal of nonsocial factors leading to a modular structure, because the population turnover observed here defines three temporal units in the Guiana dolphin network (Fig. 1d). We suppose that this turnover was mainly promoted by transient individuals that use the

Table 2
Guiana dolphins' observed and expected association index (HWI), calculated using the null model NM2, for all of the individuals sighted during each 32-month period

	First period			Second period			Third period		
Groups	130			141			138		
Individuals	33			36			36		
Preferred	4 (11.5%)			4 (12.9%)			9 (29.0%)		
Avoided	2 (7.7%)			4 (12.9%)			4 (12.9%)		
HWI	**Observed**	**Expected**	***P***	**Observed**	**Expected**	***P***	**Observed**	**Expected**	***P***
Mean	0.094	0.094	0.487	0.066	0.066	0.499	0.067	0.063	0.171
SD	0.110	0.108	0.954*	0.107	0.094	0.998*	0.115	0.097	0.999*
CV	1.170	1.153	0.952*	1.611	1.432	0.998*	1.724	1.532	0.993*
Nonzero	0.580	0.571	0.656	0.433	0.440	0.358	0.394	0.409	0.022

Asterisks indicate significant results (one-tailed test at $\alpha = 0.05$). Preferred/avoided dyads showed higher/lower HWI than that expected by chance (two-tailed test at $\alpha = 0.05$); percentage is based on the expected number of significant dyads (5% of possible pairs). CV: coefficient of variation; nonzero: proportion of nonzero HWI.

study area occasionally (Supplementary Data S2), driving the first level of complexity in social organization.

Static Network Structure, Fluid Social Structure

At a fine temporal scale, when we excluded the demographic turnover effect, a nonrandom fluidity in the social relationships across this Guiana dolphin population was evident. The same fluid grouping pattern observed throughout the entire study was found within the 32-month turnover scale (see Supplementary Fig. S4a–c). Scaling down to the dyads, the association levels were mostly low and variable, but a few nonrandom preferences and avoidances were noticed among many fluid associations.

These outcomes point to fission–fusion dynamics in this Guiana dolphin population: there was high temporal variation in group size and composition, even with moderate spatial cohesion among members (see Aureli et al. 2008). Considering the agreement of our findings with those from another studied population (Santos & Rosso 2008), we suggest that the fission–fusion social organization may be a general pattern for Guiana dolphins. However, there is evidence of a latitudinal difference in the average group size in this species that should be further explored (e.g. Daura-Jorge et al. 2005; Santos & Rosso 2007). Social systems with fission–fusion dynamics usually show pronounced group size variation as a response to several ecological variables (Wrangham 1982), and this variability may affect social interactions and organization (Gowans et al. 2008). Because Guiana dolphins are exposed to different habitat structure and prey abundance throughout their distribution, a varying degree of fission–fusion dynamics may be observed for different populations, with additional factors influencing the emergence of social units.

Conclusions

The Guiana dolphin society observed here combined the fluid associations of a fission–fusion system with a predicted modular structure that was mainly defined by a high population turnover that temporally segregated the individuals. Our findings show that the emergence of different social units in a population can be driven by mechanisms that are simpler than those previously considered, including the temporal opportunities for individuals to interact.

We emphasize the weakness of blindly focusing on a fixed illustration of a dynamic system. Social networks may not always essentially represent social processes. Because social analyses are data-hungry, the common practice involves perusing social matrices piled up by long-term efforts (see Whitehead 2008a). Such databases usually came from studies that were not directly designed to collect social data and may include different adjacent areas and several years (Whitehead 2008a). In such cases, it is possible that nonsocial or indirect effects are underlying the social patterns. This is because an interaction in a social network is usually defined by the co-occurrence of individuals in a group (Whitehead & Dufault 1999; Croft et al. 2008), which creates a contact network; thus individuals observed in different areas or periods of time would be part of different modules.

Particularly, the network may contain demographic effects that generate unwanted bias in social patterns. We need to discern between population changes mainly caused by death/birth and those caused by movement processes. The former scenario contains little or no social information (see Whitehead 1999, 2008a) and can yield social modules that are only sampling artefacts. In this case, some temporally segregated individuals (i.e. that are not in the population at the same time) would be placed in separate artificial units. Population changes mainly caused by emigration/immigration movements can also carry the same biases if not properly accounted for; but it may still be an indirect social mechanism, evidencing habitat selection, social avoidance/preference, and individual heterogeneity in philopatry, ranging behaviour or sociality.

As network formalism becomes popular in behavioural sciences, we need a thorough search for the satisfactory scales that place social processes apart from nonsocial noise. To this end, one should contextualize both the spatial and temporal mechanisms by combining social analyses with other methods (i.e. mark–recapture modelling to elucidate population dynamics; spatial analyses to estimate ranging behaviour; lagged identification and association rates to evaluate time dependence). Isolating the social mechanism that draws a social network ensures a more realistic portrayal of the target population's social system and an adequate interpretation of open, dynamic and complex animal societies.

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Supplementary Material

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