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CARACTERÍSTICAS INDIVIDUAIS INFLUENCIAM A ESTRUTURA SOCIAL DOS BOTOS-DA-TAINHA QUE COOPERAM COM PESCADORES ARTESANAIS

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"Características individuais influenciam a estrutura social dos botos-da-tainha que cooperam com pescadores artesanais"

Por

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RESUMO

Parte de uma população de botos-da-tainha (*Tursiops truncatus*) desenvolveu uma tática de forrageio especializada em cooperação com pescadores artesanais em Laguna, sul do Brasil. Aparentemente, a estrutura social desta população está acoplada a esta tática de forrageio, formando um módulo social de botos que realizam esta tática com maior frequência, e outros dois módulos distintos com botos que realizam esta tática com menor frequência. No entanto, outras características individuais além da tática de forrageio podem atuar definindo as associações, mas seus efeitos ainda não foram devidamente quantificados. Nesta dissertação, revisitou-se a estrutura social da população de botos-da-tainha que reside no complexo lagunar de Santo-Antônio-Imaruí-Mirim, em Laguna, para testar duas hipóteses. A primeira é que as associações são definidas por homofilia pela tática de forrageio. Portanto, espera-se que indivíduos que cooperam com os pescadores se associem preferencialmente com outros indivíduos que frequentemente utilizam esta tática. A segunda é que existam verdadeiras preferências sociais na população, considerando que indivíduos dentro do mesmo módulo social se associam preferencialmente, independentes de fatores estruturantes associais. Foram coletadas informações sobre características individuais, como idade, sexo, grau de parentesco, área de vida, e frequência relativa de interação com os pescadores artesanais. Considerando que os indivíduos podem apresentar diferentes padrões de associação de acordo com o contexto comportamental, os dados foram divididos em quatro contextos comportamentais (todos os comportamentos, ausência de forrageio, forrageando em cooperação e sem cooperação com pescadores artesanais). Para cada contexto comportamental, a proporção de tempo que os indivíduos estão associados foi calculada utilizando o índice de associação de pesos médios (HWI). Primeiro, para identificar e quantificar as variáveis que influenciam a estrutura social da população, foi utilizado um procedimento de múltipla regressão quadrática (MRQAP). Utilizando subconjuntos de dados, testou-se o efeito do grau de parentesco (n = 12 indivíduos) e do sexo (n = 30) e não foram encontradas relações significativas com as associações. Para o conjunto de dados contendo idade, área de vida e frequência de interação com os pescadores (n = 34), foi encontrado que a sobreposição da área de vida e a tática de forrageio influenciam as associações entre indivíduos, explicando até 50% da variação observada no HWI. Porém, a área de vida reflete a frequência relativa de interação com os pescadores. Segundo, utilizou-se uma nova abordagem para testar a existência de verdadeiras preferências sociais, criando índices de afiliação generalizada (GAI) que removem os efeitos de forças estruturais. Simulações de Monte Carlo foram utilizadas para testar se o desvio padrão (SD) de HWI e GAI, bem como a modularidade das redes de associações e afiliações, diferiam do esperado ao acaso. Verdadeiras preferências sociais foram encontradas em todos os contextos, exceto para o forrageio em cooperação com pescadores. Para os contextos de ausência de forrageio e forrageando sem cooperação com pescadores artesanais, observou-se que a estrutura modular da rede de associações (HWI) é parcialmente mantida na rede de afiliações (GAI). Os resultados mostram que a homofilia pela tática de forrageio é o principal fator estruturando a sociedade de botos-da-tainha de Laguna, e que as preferências sociais se mantêm mesmo sem o efeito das forças estruturais. Estes resultados mostram que existe uma tendência de os indivíduos se associarem por causa da tática de forrageio em cooperação com os pescadores, mas não enquanto realizam a tática.

Palavras-chave: Ecologia comportamental, Estrutura social, fissão-fusão, preferências sociais, redes sociais, *Tursiops truncatus*

ABSTRACT

In southern Brazil, a subset of a bottlenose dolphin (*Tursiops truncatus*) population forages in cooperation with artisanal fishermen. The social structure of this bottlenose dolphin population is coupled to this specialized foraging tactic, in which social modules are defined by individuals that often or rarely forage in cooperation with fishermen. However, other individual traits might also underlie this social structure, but their effects, if any, are yet to be quantified. In this dissertation, the social structure of this population is revisited to test the following two hypotheses. First, associations are driven by homophily around the foraging tactic, in which individuals that frequently forage in cooperation with artisanal fishermen preferentially associate with one another. Second, true preferred associations exist among members of same social module. Six individual characteristics were measured *in situ*: age, sex, genetic relatedness, home range overlap, and frequency of participation in the cooperative foraging tactic with artisanal fishermen. To control for the propensity of individuals to interact socially in different behavioral states, social patterns were analyzed in four behavioral contexts: all behavior, non-foraging, cooperative foraging and non-cooperative foraging. For each behavioral context, associations among pairs of individuals were quantified as the proportion of time they were seen in groups, using the Half-Weight Index (HWI). First, a Multiple Regression Quadratic Assignment Procedure (MRQAP) was used to identify and quantify the influence of individual traits on the social structure. Subsets of the original data were used to test the effect of genetic relatedness (n = 12) and sex (n = 30), but no significantly relationship were found between these variables and the HWI. To the dataset containing age, home range overlap and frequency of participation in cooperative foraging tactic (n = 34), it was found that home range is the strongest structural factor, explaining up to 50% of the observed variations in the HWI, but we emphasize that home range is highly correlated with the cooperative foraging tactic. Second, a novel approach was used to test for the existence of true social preferences, creating generalized affiliation indices (GAI) to remove the effects of the significant structural factors previously identified. Monte Carlo simulations were used to test whether the standard deviation (SD) of HWI and GAI, as well as the modularity of the social networks they define, were different from the null expectancy. True social preferences were observed in all behavioral contexts, except for the cooperative context. In the non-foraging and non-cooperative foraging contexts, part of the modular social structure of the association network (HWI) was maintained in the affiliation network (GAI). Our results show that homophily based on cooperative foraging tactic is the major factor structuring this bottlenose dolphin society, and that true social preferences exist, even after accounting for the effects of non-social processes. These results show that dolphins associate because they use the same foraging tactic, and not to perform this tactic.

Keywords: Behavioral ecology, social structure, fission-fusion, social preferences, social networks, *Tursiops truncatus*

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INTRODUÇÃO GERAL

Compreender as relações entre padrões e processos é um dos maiores desafios em ecologia (HAIRSTON; SMITH; SLOBODKIN, 1960; PAINE, 1980; RICKLEFS, 1987; LEVIN, 1992; VELLEND, 2010). Sistemas biológicos são complexos e geralmente estruturados por processos intrínsecos e extrínsecos de forma não exclusiva (AMARAL; OTTINO, 2004). Uma população de animais é um exemplo desse tipo de sistema. Os indivíduos de uma população interagem com seus coespecíficos e com o ambiente e tendem a se organizar em grupos na busca por recursos para sobreviver e reproduzir (WILSON, 1975). Pressões ecológicas podem influenciar a organização social de uma população, agregando ou dispersando indivíduos em função dos custos e benefícios da vida em grupo (ALEXANDER, 1974; KRAUSE; RUXTON, 2002). Os indivíduos também podem possuir uma tendência a se associarem aos seus semelhantes por atributos individuais (e.g. MANN et al., 2012; CARTER et al., 2013a; MORTON et al., 2015). Porém, ainda é um desafio identificar as similaridades individuais, ecológicas e comportamentais, quantificar suas contribuições e distinguir os efeitos destes componentes de outros fatores externos (WHITEHEAD; JAMES, 2015; STRICKLAND et al., 2017).

Ferramentas analíticas de estudo de sociedades animais

As interações entre pares de indivíduos são os elementos básicos de suas relações sociais, as quais definem a estrutura social da população (HINDE, 1976). Logo, para explicar os padrões sociais é preciso investigar as interações entre pares de indivíduos. Nesse contexto, a teoria de redes é uma forma eficiente de representar interações entre elementos de um sistema. Extensivamente utilizada nas ciências sociais (ver SCOTT, 2017), a teoria de redes também se tornou importante para investigar padrões ecológicos (PROULX; PROMISLOW; PHILLIPS, 2005), incluindo padrões emergentes em ecologia comportamental (CROFT; JAMES; KRAUSE, 2008). Análises de redes podem revelar diversos aspectos relacionados aos padrões de interação entre os indivíduos, como a transmissão de patógenos, fluxo gênico, transmissão de informação e permitir a inferência indireta das consequências do comportamento social na aptidão dos indivíduos (CROFT; JAMES; KRAUSE, 2008; WHITEHEAD, 2008; KRAUSE; LUSSEAU; JAMES, 2009).

Uma das bases da análise de redes sociais de animais é descrever as relações sociais em uma população utilizando índices de associação (CAIRNS; SCHWAGER, 1986; WHITEHEAD, 2008). Esta é uma forma prática para estimar a proporção de tempo que pares de indivíduos são observados juntos. Um dos mais utilizados é o índice de pesos médios, ou *Half-Weight Index* (HWI), indicado para casos em que nem todos os indivíduos de um grupo são registrados ou identificados. O HWI tem sido utilizado, por exemplo, em trabalhos com golfinhos (KOVACS; PERRTREE; COX, 2017), aves (ROSE; CROFT, 2017), cangurus (BEST et al., 2013) e primatas (LAMON et al., 2017). Dependendo do conjunto de dados, outros índices de associação podem representar melhor a relação entre os pares de indivíduos (ver HOPPITT; FARINE, 2018). Recentemente, novos métodos têm gerado métricas mais acuradas, rastreando os indivíduos e seu deslocamento no ambiente (e.g. KRAUSE et al., 2013; STRANDBURG-PESHKIN et al., 2017), automatizando o reconhecimento de indivíduos marcados e não marcados (e.g. PÉREZ-ESCUDERO et al., 2014), a quantificação das associações (e.g. HIRSCH et al., 2013) e a composição dos grupos (e.g. FARINE et al., 2015). Estas inovações metodológicas não só aumentam a resolução dos dados como otimizam a reprodutibilidade (IHLE et al., 2017).

É possível investigar associações preferenciais ou evitadas entre indivíduos utilizando índices de associação (WHITEHEAD, 1999). Também é possível investigar padrões em larga escala, avaliando a modularidade de uma rede (NEWMAN; GIRVAN, 2004; NEWMAN, 2006). Nesse caso, os indivíduos de uma população podem ter uma tendência a se organizar em subgrupos mais coesos, dividindo a população em módulos sociais (e.g. LUSSEAU; NEWMAN, 2004). Considerando que outras forças internas e externas poderiam gerar os padrões observados, é preciso conduzir análises com cautela (PINTER-WOLLMAN et al., 2014). Métricas mais refinadas, como o Índice de Filiação Generalizada (*Generalized Affiliation Indices, GAI)*, removem o efeito de variáveis que poderiam definir as associações entre os indivíduos (WHITEHEAD; JAMES, 2015). As filiações representadas nos GAI seriam definidas por forças puramente sociais. Dessa forma, é possível identificar as verdadeiras associações preferenciais, distinguindo aquelas resultantes da influência de outros fatores, como a proximidade espacial e o uso do espaço (CANTOR et al., 2012).

Existem desafios logísticos, metodológicos e analíticos tanto para investigar a vida social de animais, sejam baleias em ambiente pelágico (e.g. WHITEHEAD; CHRISTAL; TYACK, 2000) ou formigas em ambiente experimental controlado (e.g. MERSCH; CRESPI; KELLER, 2013). Em qualquer dos casos, são necessárias abordagens analíticas adequadas para testar hipóteses relacionadas à organização social, do nível do indivíduo até estruturas mais complexas. Porém, os problemas podem começar na coleta de dados. A forma mais comum de identificar associações entre pares de indivíduos é assumir que os indivíduos em um mesmo grupo e no mesmo estado comportamental, estão associados (WHITEHEAD; DUFAULT, 1999). Primeiro, pode ser difícil identificar verdadeiras associações. Os indivíduos podem estar juntos, mas estarem associados por um fator espacial e não social. Segundo, a estrutura dos dados em pares e a autocorrelação podem inviabilizar testes de hipóteses utilizando ferramentas estatísticas convencionais (ver CROFT et al., 2011), como modelos lineares, pois violam a independência dos resíduos (ZUUR et al., 2009).

Na última década, diversos autores esclareceram muitas das vantagens e limitações da análise de redes sociais em animais (e.g. WEY et al., 2008; JAMES; CROFT; KRAUSE, 2009; SIH; HANSER; MCHUGH, 2009; PINTER-WOLLMAN et al., 2014; FARINE; WHITEHEAD, 2015; CROFT ; DARDEN; WEY, 2016; FARINE, 2018; HOPPITT; FARINE, 2018). Neste esforço, um conjunto de ferramentas e abordagens analíticas foi desenvolvido para endereçar soluções de teste de hipóteses relacionadas aos padrões sociais (WHITEHEAD, 2009; FARINE, 2013, 2014; STRICKLAND et al., 2017; WHITEHEAD; JAMES, 2015). Por conta da falta de independência dos dados, construir modelos nulos passou a ser uma das abordagens analítica mais importante em análises de redes (BEJDER; FLETCHER; BRAGER, 1998; WHITEHEAD 1999; WHITEHEAD et al. 2005; CROFT et al. 2011; FARINE, 2017). Permutar os dados originais para criar uma distribuição teórica permite testar a significância dos resultados observados comparando-os à expectativa nula. Por exemplo, é possível permutar indivíduos entre grupos, restringindo o número de observações por indivíduos e o número de indivíduos em um grupo para testar se existem associações preferenciais ou evitadas (BEJDER; FLETCHER; BRAGER, 1998). A significância estatística é então calculada pela proporção de vezes que os valores observados são maiores ou menores que os valores da distribuição teórica.

Outro interesse particular é testar se a matriz de associação está relacionada às características dos indivíduos ou outros fatores externos. Para isso, é possível testar correlações entre matrizes utilizando o teste de Mantel (MANTEL, 1967), ou o teste de Mantel parcial (SMOUSE; LONG; SOKAL, 1986; MANLY, 2006). Por exemplo, utilizando um teste de Mantel é possível testar se indivíduos com maior sobreposição da área de uso, ou se pertencem a uma mesma classe (e.g. sexo, idade), se associam preferencialmente (e.g. DAURA-JORGE et al., 2012). Com o Mantel parcial é possível controlar para uma terceira variável, como o parentesco (e.g. FRÈRE et al., 2010). Considerando a estrutura dos dados em análises de redes, controlar para o efeito de mais de uma variável é importante para testar múltiplas hipóteses (SNIJDERS, 2011). O procedimento de múltipla regressão quadrática (MRQAP) é uma extensão do teste de Mantel, também baseado em regressão, que permite modelar a variável dependente (matriz de associação) contra uma série de variáveis preditoras (DEKKER; KRACKHARDT; SNIJDERS, 2007). Permutando os resíduos, MRQAP consegue-se ajustar um modelo controlando para os efeitos da colinearidade e autocorrelação na estrutura dos dados (DEKKER; KRACKHARDT; SNIJDERS, 2007). Assim, é possível quantificar o efeito dos múltiplos fatores que definem as associações em sociedades animais (e.g. MANN et al., 2012; HIRSCH et al., 2013; ESTEBAN et al., 2016; KOHN, 2017;). Mas quais fatores devem ser considerados como importantes preditores de associações em sociedades animais?

Correspondência comportamental como estruturador de sociedades animais

Em espécies gregárias, as associações e interações entre indivíduos variam ao longo do tempo. Primatas (VAN SCHAIK, 1999), elefantes (WITTEMYER; DOUGLAS-HAMILTON; GETZ, 2005), girafas (CARTER et al., 2013b) e golfinhos (CONNOR et al., 2000a), vivem em sociedades com associações em constante mudança, em uma dinâmica do tipo fissão-fusão, com variações frequentes no tamanho, composição e coesão dos grupos sociais (AURELI et al., 2008). Mesmo que fluidas, estas associações podem ser motivadas por fatores sociais, influenciando as decisões do indivíduo para se associar ou não aos seus coespecíficos (e.g. BUSIA; SCHAFFNER; AURELI, 2017).

Sabe-se que a composição fenotípica de um grupo social pode influenciar a aptidão individual. Em alguns contextos, indivíduos com fenótipos e comportamentos similares aumentam sua aptidão ao se associar com seus semelhantes (FARINE; MONTIGLIO; SPIEGEL, 2015). Para sociedades humanas, a tendência dos indivíduos se associarem preferencialmente aos seus semelhantes define o princípio da homofilia (MCPHERSON; SMITH-LOVIN; COOK, 2001). A homofilia também pode definir associações em sociedades não-humanas, agregando os indivíduos com base nas características individuais (e.g. LUSSEAU; NEWMAN, 2004). Nesse caso, as características e o comportamento do indivíduo podem ter implicações em outras escalas ecológicas (GORDON, 2011). Em nível da população, variações fisiológicas e comportamentais interindividuais podem refletir no nicho da população e na estrutura social (KRAUSE; CROFT; JAMES, 2007; BOLNICK; KIRKPATRICK, 2012). Até mesmo a personalidade do indivíduo pode definir as associações com seus coespecíficos (MASSEN; KOSKI, 2014). Em primatas, por exemplo, associações estáveis em longo prazo podem ser descritas como “amizades” (ver revisão SEYFARTH; CHENEY, 2012), fazendo um paralelo às preferências sociais sem relação de parentesco em sociedades humanas (MASSEN; KOSKI, 2014).

Porém, em alguns casos seria esperado que associações mais estáveis ocorressem entre indivíduos aparentados. A seleção por parentesco seria uma das formas de compensar os custos da vida em grupo, garantindo o sucesso reprodutivo e o aumento da aptidão dos indivíduos que compartilham a mesma herança genética e cooperam uns com os outros (HAMILTON, 1964; SMITH, 2014). Dessa forma, o parentesco determina as associações entre os indivíduos de uma população, mesmo que de forma não exclusiva (e.g. ARCHIE; MOSS; ALBERTS, 2006; WISZNIEWSKI; LUSSEAU; MÖLLER, 2010; BEST et al., 2014). Mas o parentesco pode não ter influência nas associações (e.g. HIRSCH et al., 2013). Nesse caso, manter relações sociais estáveis sem relação de parentesco pode ter consequências positivas para o indivíduo, aumentando a longevidade, o sucesso reprodutivo e a tolerância aos coespecíficos (e.g. SILK et al., 2010).

O estudo das relações sociais em primatas (ver SMUTS et al., 2008), considerando o alto grau de encefalização (DUNBAR, 1998) e, sofisticação social e comportamental (e.g. TENNIE; JENSEN; CALL, 2016), foi primordial para revelar as implicações da vida social. Ao longo de suas histórias evolutivas, baleias e golfinhos também desenvolveram elevada capacidade cognitiva e estratégias comportamentais sofisticadas em resposta à vida social (ver MARINO et al. 2007; FOX; MUTHUKRISHNA; SHULTZ, 2017). Sociedades de cetáceos são diversificadas. De forma geral, misticetos são geralmente solitários ou mantém associações efêmeras, exceto entre mães e filhotes; os relacionamentos sociais de odontocetos, por sua vez, variam de bastante instáveis a estáveis (MANN; KARNISKI, 2017). Orcas (*Orcinus orca*) e cachalotes (*Physeter macrocephalus*) são exemplos de odontocetos que vivem em sociedades quase-matrilineares, em que as fêmeas tendem a permanecer nas mesmas unidades sociais que suas mães, enquanto golfinhos-nariz-de-garrafa (*Tursiops truncatus*) vivem em sociedades com alta dinâmica de fissão-fusão, com associações em constante mudança (CONNOR et al., 1998).

Mesmo em associações com dinâmica de fissão-fusão, associações estáveis podem existir (e.g. LUSSEAU et al., 2003). As associações podem ser mais fluidas ou estáveis, dependendo do estado comportamental (GERO et al., 2005; GAZDA et al., 2015; MORENO; ACEVEDO-GUTIÉRREZ, 2016), aumentando ou limitando as oportunidades para que os indivíduos se associem, principalmente em resposta à disponibilidade de presas, parceiros e outras pressões ecológicas (GOWANS; WÜRSIG; KARCZMARSKI, 2007). Nesse contexto, surgem oportunidades para o desenvolvimento de táticas especializadas de forrageio (e.g. LOPEZ; LOPEZ, 1985; LOUISE CHILVERS; CORKERON, 2001; GAZDA et al., 2005; SARGEANT et al., 2005; PITMAN; DURBAN, 2012;) e sinais de comunicação distintos (YURK et al., 2002). Quando o comportamento está associado à estrutura social da população (e.g. DAURA-JORGE et al., 2012; MANN et al., 2012), estes casos se tornam particularmente interessantes para compreender a reciprocidade entre os padrões sociais e um processo de aprendizado social (ver CANTOR; WHITEHEAD, 2013). Os indivíduos de uma população podem desenvolver seus repertórios comportamentais observando e copiando seus coespecíficos que compartilham um mesmo grupo com frequência e tal transmissão de comportamentos pode moldar a estrutura de uma sociedade (e.g. CANTOR et al., 2015).

O aprendizado social é um mecanismo importante operando na estrutura de sociedades animais (LALAND; JANIK, 2006), inclusive em sociedades de baleias e golfinhos (WHITEHEAD; RENDELL, 2014). Mais evidências para estes processos vêm de uma população de golfinhos (*Tursiops* sp.), em que alguns indivíduos utilizam esponjas como ferramentas para forragear (KRÜTZEN et al., 2005; MANN et al., 2008). Esta não é a única tática de forrageio utilizada em Shark Bay, mas neste caso os filhotes aprendem com as mães a utilizar as esponjas no rostro para forragear no substrato rochoso (SARGEANT; MANN, 2009; KOPPS; SHERWIN, 2012). Após considerar outros possíveis fatores que poderiam definir associações preferenciais (i.e. parentesco, área de vida, sexo), concluiu-se que a homofilia pela tática de forrageio é o principal fator estruturando a sociedade dos golfinhos de Shark Bay (MANN et al., 2012). Em Laguna, Estado de Santa Catarina, existe um caso paralelo aos golfinhos de Shark Bay, na Austrália.

Padrões sociais de botos-da-tainha em Laguna

A população de golfinhos-nariz-de-garrafa (*Tursiops truncatus*) de Laguna, conhecidos localmente como botos-da-tainha, possui aproximadamente 50 indivíduos residentes e parece se manter constante (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998; SIMÕES-LOPES; FABIAN, 1999; DAURA-JORGE; INGRAM; SIMÕES-LOPES, 2013). Alguns indivíduos desta população desenvolveram por gerações uma tática de forrageio em cooperação com pescadores artesanais (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998). Nesta tática, os botos conduzem e agrupam os cardumes de presas até a linha de pescadores, e realizam movimentos estereotipados, que são interpretados como o momento que as tarrafas devem ser lançadas. Os pescadores aguardam pelo "sinal" às margens do canal ou em pequenas embarcações (PETERSON; HANAZAKI; SIMÕES-LOPES, 2008). Esta interação permite a captura de peixes maiores e em maior quantidade para os pescadores e, possivelmente, confere uma vantagem equivalente aos botos (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998).

Embora aparentemente vantajosa para pescadores e botos, nem todos os botos da população utilizam esta tática de forrageio. Esta heterogeneidade se reflete na estrutura social da população, que é estruturada em dois módulos sociais de botos que raramente ou nunca interagem com pescadores e um módulo social de botos que frequentemente o fazem (DAURA-JORGE et al., 2012). Os indivíduos de um módulo se associam preferencialmente com outros indivíduos do mesmo módulo. A principal hipótese para a emergência de uma estrutura social acoplada à tática de forrageio em cooperação com pescadores artesanais remete à transmissão de informação via aprendizado social, primeiramente de mães para filhotes (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998; SIMÕES-LOPES; DAURA-JORGE; CANTOR, 2016). Porém, outras características individuais poderiam gerar os padrões observados e não foram testadas até o momento.

Os padrões sociais e as forças que governam as associações em populações de botos-da-tainha (*Tursiops truncatus*) têm sido explorados globalmente. Contribuições especiais vêm de populações da Flórida, nos Estados Unidos (WELLS; SCOTT; IRVINE, 1987; WELLS, 2014), Doubtful Sound, na Nova Zelândia (LUSSEAU et al., 2003; LUSSEAU; NEWMAN, 2004), e Shark Bay, na Austrália (SMOLKER et al., 1992; MANN et al., 2012; CONNOR et al., 2017). Além da homofilia pela tática de forrageio (ANSMANN et al., 2012; MANN et al., 2012), as associações em botos-da-tainha podem ser determinadas pelo sexo (CONNOR et al., 2000b; RANDIC et al., 2012; CONNOR; KRÜTZEN, 2015), idade (LUSSEAU; NEWMAN, 2004; BAKER et al., 2017), parentesco (FRÈRE et al., 2010; WISZNIEWSKI; LUSSEAU; MÖLLER, 2010) e uso do espaço (WISZNIEWSKI; ALLEN; MÖLLER, 2009; BAKER et al., 2017).

Objetivos e hipóteses

O objetivo maior desta dissertação é reavaliar a estrutura social da população de botos-da-tainha residente em Laguna (DAURA-JORGE et al., 2012), Estado de Santa Catarina, para identificar e quantificar a influência de variáveis individuais nesta estrutura. Primeiro, testa-se a hipótese de que a homofilia pela tática de forrageio em cooperação com os pescadores seja o principal fator determinando as associações individuais e a estrutura desta população. Dessa forma, espera-se que as outras características individuais, como área de vida, idade, sexo e grau de parentesco, tenham pouco, ou nenhum efeito estruturador no padrão de associações entre indivíduos (Figura 1). Na sequência, testa-se a hipótese de que existam associações preferenciais e que estas sejam verdadeiramente motivadas por processos sociais. Aqui, a expectativa é a existência de pares de indivíduos que são vistos juntos mais frequentemente que o esperado ao acaso, mesmo após a remoção do efeito daquelas características que possam promover a agregação de indivíduos.

Ao testar essas hipóteses, espera-se oferecer uma leitura mais realista dos mecanismos subjacentes que contribuem para a definição das relações sociais nesta população. Isto permitirá uma discussão mais profunda sobre mecanismos coparticipantes desta estruturação social, como por exemplo, o aprendizado social, que pode definir as relações sociais ou mesmo ser facilitado por elas. Neste debate, surgem novas hipóteses sobre as implicações da coparticipação destes múltiplos processos na emergência de um comportamento especializado, além de resolver um pensamento circular: Os indivíduos se associam porque compartilham um mesmo comportamento, ou se associam para realizar este mesmo comportamento? O estudo de caso aqui apresentado contribui para o debate na literatura sobre mecanismos promotores de estruturação social, o papel do aprendizado social e a emergência de comportamentos especializados (RENDELL; WHITEHEAD, 2001; LALAND; JANIK, 2006; CANTOR; WHITEHEAD, 2013; WHITEHEAD, 2017).

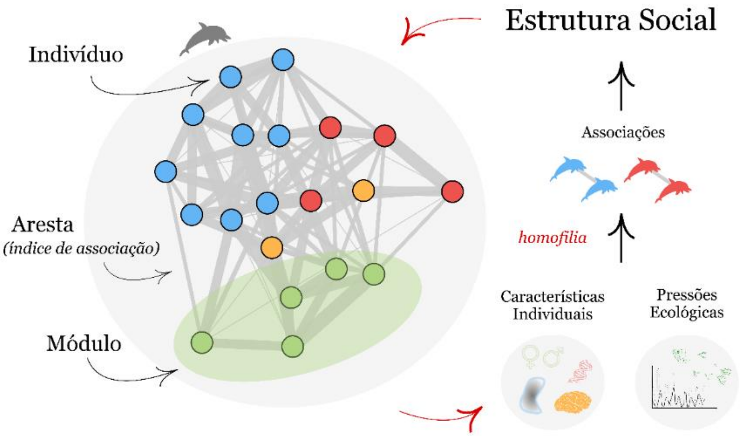

Figura 1: A estrutura social de uma população pode ser definida por pressões ecológicas e pela homofilia por características individuais, entre outros fatores. A homofilia pode promover as associações entre pares de indivíduos, que refletem a estrutura social da população. Ao mesmo tempo, existe uma reciprocidade entre a estrutura social e as características individuais. Na rede social, os indivíduos são representados por nós, e as arestas que os conectam representam alguma medida de associação social entre indivíduos. Aqui, as arestas representam o índice de associação e sua espessura é proporcional ao tempo que os pares de indivíduos foram observados juntos. Heterogeneidade da distribuição de associações entre pares de indivíduos pode resultar em uma estrutura modular. Nesse caso, subconjuntos de indivíduos que passam mais tempo associados entre si são representados por módulos, os quais são mais conectados entre si que com os outros módulos. Aqui, a cor de cada nó representa o módulo a qual o indivíduo pertence.

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HOMOPHILY BASED ON SPECIALIZED FORAGING TACTIC DRIVES SOCIAL PREFERENCES AMONG DOLPHINS

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ABSTRACT

The social structure of a population is the synthesis of relationships among conspecifics that emerges from the interaction among multiple, non-exclusive social and asocial mechanisms. The combined effect of such mechanisms is particularly challenging to disentangle in animal species that live under fission-fusion dynamics, given that the nature of their social relationships results from ever-changing interactions and ephemeral grouping patterns. In Laguna, southern Brazil, the social structure of a population of bottlenose dolphins (*Tursiops truncatus*) is characterized by fission-fusion dynamics but also seems coupled to a specialized foraging tactic in cooperation with artisanal fishermen. However, the contribution of other factors that may underlie this structure remains unknown. Here, we quantify the contribution of a specialized foraging tactic, home range overlap, sex, age and genetic relatedness in modulating the social relationships in different foraging and non-foraging contexts. We found that dolphins tend to spend more time with those whose home ranges overlap and use the cooperative foraging tactic at similar frequencies, regardless of their sex, age, and degree of genetic relatedness. We found that the cooperative foraging tactic underlies social preferences that scale up and form distinct social communities at the population level, after removing the effects of such factors and accounting for differences in behavioral contexts. Further, we found pairwise social preferences, but only outside the cooperative foraging context, suggesting that dolphins tend to associate because of the cooperative foraging tactic, and not only when performing it. This suggests that dolphins consistently seen together are more likely to be actively seeking one another (a true social preference) rather than being passively assorted due to the use of the same specialized foraging tactic. However, our affiliation metrics indicate that when they perform this foraging tactic, individual dolphins likely only aggregate around the resource patch (the cooperative fishing site). Our findings on homophily based on a socially learned behavior driving social preferences among individual dolphins and shaping the population social structure into social communities emphasize the need to account for behavioral contexts and individual traits to disentangle the drivers of social organization of animals that live under fission-fusion dynamics.

Keywords: social structure, fission-fusion, social behavior, social network, *Tursiops truncatus*

INTRODUCTION

Interactions between pairs of conspecifics are the building blocks of social relationships and their societies (Hinde 1976) and can reflect the trade-offs of living in groups (Krause and Ruxton 2002). A social structure is an emergent property of multiple and non-exclusive structural mechanisms (Croft et al. 2008; Whitehead 2008) — quantifying the contribution of each of them in non-human societies is a timely challenge (Whitehead and James 2015).

Special attention has been given to tackle this challenge when investigating the elements that might affect animal societies with fluid social dynamics (e.g. Farine 2015; Farine and Whitehead 2015; Farine et al. 2015; Strickland et al. 2017). These include both social and asocial structural factors. At the population level, the co-occurrence in space and time, habitat structure, and predation risk can aggregate or disperse individuals, and their opportunities to interact socially (e.g. Kelley et al. 2011; Cantor et al. 2012; Leu et al. 2016). Associations among individuals can also be context-dependent (Goldenberg et al. 2014; Moreno and Acevedo-Gutiérrez 2016), and so can change according to the behavioral state (e.g. Gero et al. 2005; Gazda et al. 2015). At the individual level, a common mechanism is homophily. Individuals rather associate with conspecifics who share similar biological, ecological or behavioral traits (McPherson et al. 2001; Newman 2002); for instance, individuals can prefer or tend to associate with conspecifics of the same age (e.g. Carter et al. 2013a), sex (e.g. Foerster et al. 2015; Gaudin et al. 2015), kinship (e.g. Frère et al. 2010) or foraging tactics (e.g. Mann et al. 2012).

While such mechanisms have illuminated some of the drivers of animal societies, there is still much to be learned. Novel analytical tools have been helping to distinguish truly preferred or avoided dyadic associations from passive assortment of individuals (e.g. Whitehead and James 2015) or the byproduct of asocial processes (e.g. Cantor et al. 2012; Strickland et al. 2017). In doing so, we can investigate more complex social mechanisms structuring animal societies (Laland and Janik 2006; Cantor and Whitehead 2013). For instance, whales and dolphins exhibit behavioral variation hypothesized to be transmitted by social learning processes (Whitehead and Rendell 2014). Cetaceans can learn a specific behavior when associating with a co-specific (e.g. Mann et al. 2012; Cantor et al. 2015). In this case, they tend to share the same behavior and then spend more time together. If they spend more time together because they prefer to be with whom behaves in the same way, these associations are driven by behavioral homophily. The individuals grouped by homophily may also learn novel behavior specializations from each other (e.g. Cantor and Whitehead 2013). Thus, homophily is a mechanism driving the social preferences among individuals, while social learning might be an underling mechanism and/or a product of the social patterns. The combination of these processes may facilitate the emergence of specialized behaviors (Whitehead 2017).

Evidence for such combination of mechanisms has been recently found in cetaceans. For instance, sperm whales (*Physeter macrocephalus*) may learn vocal repertoires from the individuals they socially interact with, which lead their society into sympatric clans with distinct repertoires (Cantor et al. 2015). In Shark Bay, Australia, some bottlenose dolphins learn how to use marine sponges as tools to ferret prey from the seafloor (Krützen et al. 2005). After accounting for the contribution of multiple mechanisms in defining the social relationships of sponger and non-sponger dolphins, it became clear that the tendency to socially interact with individuals who use the same foraging tactic plays a major part in driving the social structure of this population (Mann et al. 2012).

We found a potential parallel case to that of Shark Bay in Laguna, southern Brazil. Individuals from a small and resident bottlenose dolphin population interact with artisanal fishermen in a cooperative foraging tactic (Pryor et al. 1990; Simões-Lopes 1991). Dolphins herd mullet schools towards fishermen, who cast the nets in response to dolphins' stereotyped behavioral cues (Simões-Lopes et al. 1998). However, not all dolphins use the cooperative foraging tactic as frequently as some others do. The social structure of this dolphin population seems coupled to this specialized foraging tactic, with one social module of highly cooperative dolphins and two social modules of less cooperative dolphins (Daura-Jorge et al. 2012). Apparently, individuals associate preferentially with individuals within their social modules. In line with theoretical expectations on the interplay between social structure and socially learned behavior (Cantor and Whitehead 2013), the main hypothesized driver of this structure is the transmission of the foraging tactic via social learning (Simões-Lopes et al. 2016). However, none of the structural factors that potentially may influence dolphin associations, including foraging behavior, was explored to date.

Here, we test two hypotheses. First, we posit that the bottlenose dolphin society of Laguna is structured by homophily, in which individuals with similar traits associate more often. Thus, we expect that individuals who consistently interact with fishermen tend to form groups more often than with those who rarely do so. We test for homophily based on the cooperative foraging tactic while controlling for behavioral contexts and multiple factors that could also assort individuals (home range overlap and passive assortment by age, sex, and genetic relatedness) and quantify how much these traits contribute to shaping the dolphins' large-scale social structure into social modules. Second, we hypothesize that preferred associations observed within social modules (see Daura-Jorge et al. 2012) are true active social preferences. We expect to find individuals consistently seen together within each social module even after controlling for different social contexts and after removing the effects of those structural variables that mask the motivations for individuals to form groups.

METHODS

Data sampling

Sampling protocol

Our study area comprises the Santo-Antônio-Imaruí-Mirim lagoon system, an area of approximately 300 km^2, in Laguna (28°20' S – 48°50' W), southern Brazil. This lagoon system is connected to the Atlantic Ocean and fed by the Tubarão River in southern portion. Approximately 50 resident bottlenose dolphins (*Tursiops truncatus*) inhabit this lagoon system (Daura-Jorge et al. 2013). We carried out boat surveys between 2007 and 2009, and between 2013 and 2017, following a pre-defined route that evenly covers the entire study area (Daura-Jorge et al. 2013). Upon encountering a group of dolphins, we collected photo-identification data and recorded time, location, group size, and whether the dolphins were interacting or not with fishermen (see Daura-Jorge et al. 2012).

We defined a group of dolphins as the total number of individuals encountered within a 50 m radius of each other and engaged in similar behavior (see Lusseau et al. 2003). We photographed all dolphins in the group following the protocol for small cetaceans (Würsig and Jefferson

1990) to identify individuals based on long-lasting natural marks (nicks and marks on the leading and trailing edges; Wilson et al. 1999) and using only high-quality pictures (in terms of angle, focus, exposure; Williams et al. 1993). Calves were not included in our analyses. We assumed that all members of a group were associated (the "gambit of the group"; Whitehead and Dufault 1999). Whenever possible, we collected skin samples from photo-identified individuals for genetic analyses (see below) using a remote biopsy system adapted for small cetaceans, which consisted of modified darts (with custom-built stainless-steel tube tip) fired from a 120-lb crossbow. Opportunistically, we also collected skin samples from stranded carcasses (n=12 photo-identified individuals).

Behavioral contexts

We assigned behavioral states into four behaviorally specific contexts based on the distinctive foraging types of this population and assigned each sighted group to one of them. The first context was the 'cooperative foraging', which describes an unusual foraging tactic nearly exclusive to this population (Simões-Lopes et al. 1998), characterized by individuals consistently herding schools of mullets towards a line of fishermen and performing stereotyped behaviors that are recognized by fishermen as cues to cast their nets (head slap, tail slap, back presentation, partial emersion; see Simões-Lopes et al. 1998). This tactic is easily distinguished from the usual foraging of bottlenose dolphins, which we called here 'non-cooperative'. The non-cooperative foraging context was then characterized by individuals alone or in groups performing frequent asynchronous dives in various directions (e.g. Irvine et al. 1980; Shane et al. 1986), in absence of artisanal fishermen. We emphasize that foraging here is 'cooperative' or 'non-cooperative' in relation to fishermen, not necessarily among dolphins. The third, the 'non-foraging' context, was then characterized by all cases of individuals traveling, socializing, resting and other unknown behavior (e.g. Wursig 1978; Smolker et al. 1992). Finally, the 'all behavior' context included all cases.

Home Range Overlap

To estimate individual home ranges — i.e., the area routinely used to meet their daily needs (Burt 1943) —, we used a fixed-method with a 95% probability contour (Worton 1989) in ArcGIS 9.2 (ESRI 2008) with the Hawth Tools extension (Beyer 2004), always discarding land areas. To select the bandwidth value (i.e., the smoothing parameter), we used the least square cross-validation (LSCV; Seaman et al. 1999; Horne and Garton 2006). Home ranges were based on location data from surveys and, to minimize any potential spatial autocorrelation bias, we randomly selected a single record per individual per sampling day. We calculated home range overlap (*HRO*) for each pair of individuals as $HRO_{ij} = (R_{i,j}/R_i) * (R_{i,j}/R_j)$, where R_i and R_j are the total home range size for dolphins i and j, respectively, and $R_{i,j}$ is the overlap between the i's and j's areas (Silva et al. 2008).

Individual traits

To determine the sex and estimate genetic relatedness between pairs of individuals, we collected and analyzed skin samples from 26 biopsied individuals. Additionally, combining field observations on body size and reproductive events from previously field data (Simões-Lopes 1991; Simões-Lopes et al. 1998) with fishermen's knowledge (Rosa et al., unpublished data), we classified individuals into two age classes: “adult” or “senior”, since all calves and juveniles were excluded from our analyses. All individuals classified as “senior” were observed in the field area for more than 30 years.

Genetic Analyses

Microsatellite genotyping and analyses

We conducted three multiplex PCR procedures using the QIAGEN Type It Kit to amplify 15 microsatellite loci. Similar numbers of variable loci have been used to provide information about dolphins' inter-individual kinship (e.g. Frère et al. 2010; Wiszniewski et al. 2010; Ball et al. 2017). To determine if individuals were likely to be related with those who often use the same foraging tactic, we genotyped 15 microsatellite loci. DNA was extracted from 25mg of skin samples using salting-out protocol (Sunnucks and Hales 1996). DNA purity and concentration were determined by spectrophotometry on NanoDropp ND-1000 (ThermoScientific, UK). Ten nanograms of DNA was applied in multiplex PCRs to amplify the microsatellite loci using the Qiagen Type-it Microsatellite PCR kit and following the polymerase chain reaction (PCR) conditions described in Rosel et al. (2017). Genotyping was conducted on an ABI 3130 with the Genescan LIZ-600 size standard (conducted at Centro de Pesquisa sobre o Genoma Humano e Células-Tronco, Universidade de São Paulo), and viewed with GeneMapper v5 (Applied Biosystems). Quality control was applied to all microsatellite genotyping to ensure consistency across PCR amplification and genotyping runs by adding one no-DNA and two positive controls in all PCRs.

We used the software MSTools (Park 2001) to verify duplicates, i.e. individuals that were sampled more than once. We found 10 pairs of duplicates in our data set (including samples with more than one duplicate) according to 15 microsatellite, sex and photo-identification data. Therefore, we removed one sample of each duplicate pair, resulting in a total of nine individuals removed from the subsequent analyses. We also excluded two samples that were considered degraded during laboratorial analysis.

We used the Microchecker v2.2.3 (Van Oosterhout et al. 2004) to check for the presence of genotyping errors due to null alleles, allelic dropout, and incorrect scoring of stutter. We tested each locus for the Hardy-Weinberg equilibrium (HWE; Guo et al. 1992) and linkage disequilibrium using the software GENEPOP v4.2 (Rousset 2008) and 10,000 dememorizations, 1,000 batches, and 10,000 interactions per batch. The sequential Bonferroni technique was applied for the significance correction for multiple tests (Holm 1979).

Finally, we used the COANCESTRY v1.0.1.8 software (Wang 2011) to estimate mean pairwise relatedness values (*r*) for the 26 genotyped individuals using the Queller and Goodnight's index (Queller and Goodnight, 1989). The genetic relatedness between individuals *i* and *j* ranges from r_{ij} = -1 to r_{ij} = 1, and individuals are considered highly related when $r_{ij} > 0.5$ (e.g. parent-offspring), moderate when $0.25 \leq r_{ij} \geq 0.5$ (e.g. half-siblings; grandparents) and considered unlikely related when $r_{ij} < 0.25$ (Queller and Goodnight 1989). All the statistical analyses with the nuclear data were conducted at NMSC SEFSC Marine Mammal Molecular and Genetics Laboratory (MMMGL).

Sex

We determined the sex of individuals with two complementary approaches. The molecular sexing was conducted for those individuals (n = 26) we had skin samples available for the genetic analyses through the use of the polymerase chain reaction (PCR) to amplify fragments of ZFX and SRY genes with primers designed for Tursiops truncatus following the PCR profile described in Righetti (2017). Additionally, we used our long-term field observations to complement our sex classification for those individuals we were unable to determine the sex through molecular analyses. We assumed as females the individuals sighted consistently in close associations with calves, and as males otherwise.

Statistical Analyses

Cooperative foraging tactic

We calculated relative frequencies of participation of each individual dolphin *i* in the cooperative behavior as the proportion between the number of cooperative foraging records and the total number of foraging records ($fp_i = CooperativeRecords/TotalRecords$). To minimize pseudoreplication issues when calculating this relative frequency, whenever an individual was repeatedly observed per sampling group, we randomly selected only one sighting per group and maximum two per day, which was collected at least two hours apart.

Social Associations

To quantify associations among pairs of individuals as the proportion of time they were seen in groups, we used the Half-Weight Index (Whitehead 2008), which ranges from 0 (when individuals were never seen together) to 1 (when always seen together). The HWI is given by $HWI = (\frac{x}{x+0.5(Y_i+Y_j)})$, in which x is the number of groups which individuals i and j were observed together, while Y_i is the number of groups in which only *i* have been observed, and Y_j is the number of groups in which only *j* has been observed. To avoid spurious associations, we excluded calves from analyses and restricted our whole dataset to individuals observed in more than 5% of records (*cf.* Daura-Jorge et al. 2012). We calculated association indices — and all the following statistical analyses — for each of the four behavioral contexts: All behavior (n=497 groups); Cooperative foraging (n=120); Non-cooperative foraging (n=219); and Non-foraging (n=158).

Influence of structural variables on social structure

To identify and quantify the contribution of individual traits in driving social structure, we used a Multiple Regression Quadratic Assignment Procedure (MRQAP) with the "double-semi-partialling" method (Dekker et al. 2007). To investigate possible linear relationships between the association matrix and individual traits, we used the HWI as the dependent variable, and the frequency of participation in cooperative foraging with artisanal fishermen (*fp*), home range overlap (HRO), age, sex, and genetic relatedness as independent variables. In the MRQAP models, the *fp* pairwise relationships was given by a distance matrix **D** where d_{ij} = d(i, j), i.e. the Euclidean length between the *fp* of individual *i* and the *fp* of the individual *j*, which ranged from d(i, j)=0 (equal *fp*s) to d(i, j)=+∞. The home range overlap and genetic relatedness were given by the quantitative matrices **H** and **G** respectively, where h_{ij} = HRO_{ij} and $g_{ij}=r_{ij}$. Finally, age and sex were given by binary matrices **A** and **S,** respectively, where a_{ij}=1 and s_{ij}=1 when individuals *i* and *j* were of the same category (e.g. both female, or both adults) and a_{ij}=0 otherwise (e.g. *i* is female and *j* is male; *i* is adult and *j* is senior).

Since biopsy dolphins in the wild is challenging, we could not obtain sex and genetic relatedness of all individuals, preventing us to perform a single MRQAP. Hence, we analyzed three subsets of the original dataset separately. First, we performed an MRQAP for the 12 individuals, which all traits were known, to test whether genetic relatedness was a significant predictor of associations. Second, we excluded the relatedness variable and performed the MRQAP for 30 individuals to test whether sex was a significant predictor of associations while controlling for *fp*, HRO, and age. Then, we excluded the sex variable and performed another MRQAP for 34 individuals to which information on the remaining individual traits were available (*fp*, HRO and age). All MRQAP procedures were carried out for each of the four behavioral contexts. P-values are shown as the probability, given the relationship between the estimated regression coefficient (β) and the theoretical distribution (r). That is, a regression coefficient is estimated for each permutation to build a theoretical distribution. Then, empirical values are compared to calculate P-values as a proportion of the estimated coefficient regression being smaller or greater than the null expectancy. We expected all empirical regression coefficients, except *fp*, to be greater than the null expectancy. Since *fp* was represented by a distance metric in the MRQAP models, we expected its regression coefficient to be smaller than the ones estimated by chance.

We calculated General Affiliation Indices (GAI; Whitehead and James 2015) to test the existence of affiliations between dyads after removing the effect of structural factors. We fitted a binomial generalized linear model (GLM) with the unfolded matrices of HWI of each of the four behavioral contexts as the dependent variables, and the significant structural factors selected in the MRQAP as independent variables. To calculate the GAIs, we divided the deviance residuals from these GLMs by the HWI denominator (*cf.* Whitehead and James 2015).

Association and affiliation networks

We compared networks defined by the two social metrics, HWI and GAI, in all the four behavioral contexts. In the association networks, nodes representing photo-identified individuals were connected by links whose thicknesses were proportional to their HWI. In the affiliation networks, individuals were linked by GAI given by the best-fitting model. We then evaluated whether these networks were structured into modules, in which individuals are strongly connected into cohesive subgroups that are weakly connected to each other (e.g. Lusseau et al. 2003). To quantify the tendency of individuals to cluster into such subgroups, we calculated modularity using an algorithm that maximized the metric *Q* (see Newman 2006).

Null Models

We used a null model approach to test the significance of the observed modularity and test for social preferences and avoidances. For each of the four behavioral contexts, we generated an ensemble of 1,000 theoretical networks based on data-stream randomizations of the raw observation data via a swapping algorithm (e.g. Manly 1995; Bejder et al. 1998). The algorithm randomizes the original group-by-individual matrix but constrains three important features of the data: the number of groups and individuals (matrix dimension), group size (row totals) and individual frequency of observation (column totals). Then, for each theoretical matrix, we calculated a HWI association matrix, with which we built a GAI using the same predictors as done for the empirical data. For all the resultant theoretical networks, we then calculated modularity to build a theoretical modularity distribution to which we compared the observed modularity values. We considered the observed modularity to be statistically significant when it fell outside the 95% confidence interval of the benchmark distribution.

We used the same approach to test the null hypothesis that individuals associate at random. For each behavioral context, we compared the Standard Deviation (SD) of the observed GAI to benchmark distributions of the SD of the theoretical GAI matrices. We considered preferred and avoided social affiliations to exist between daily sampling periods whenever the SD of observed GAI was higher than the SD of the theoretical GAI matrices (Whitehead 2008; Whitehead and James 2015), meaning that the observed GAI data is more variable than the null expectancy.

RESULTS

The mean relative frequency of participation of individual dolphins in the cooperative foraging with fishermen was *fp* = 0.25 ± 0.17 SD. Their home ranges were small (mean = 28.83 km^2 ± 14.65 SD), often overlapping with one another (mean HRO = 47% ± 17 SD; Figure 1). Out of the 41 photo-identified individuals, we found that 30 individuals were adults and 11 were senior; 21 individuals were females, 16 were males, and the sex of the remaining could not be determined. Eighteen out of the 26 genotyped individuals were photo-identified and matched to individuals catalogued between 2007-2009. Their average pairwise genetic relatedness was $r = -0.06 \pm 0.37$ SD. We gathered all individual traits for 12 dolphins and their relationships are given in the Figure 2.

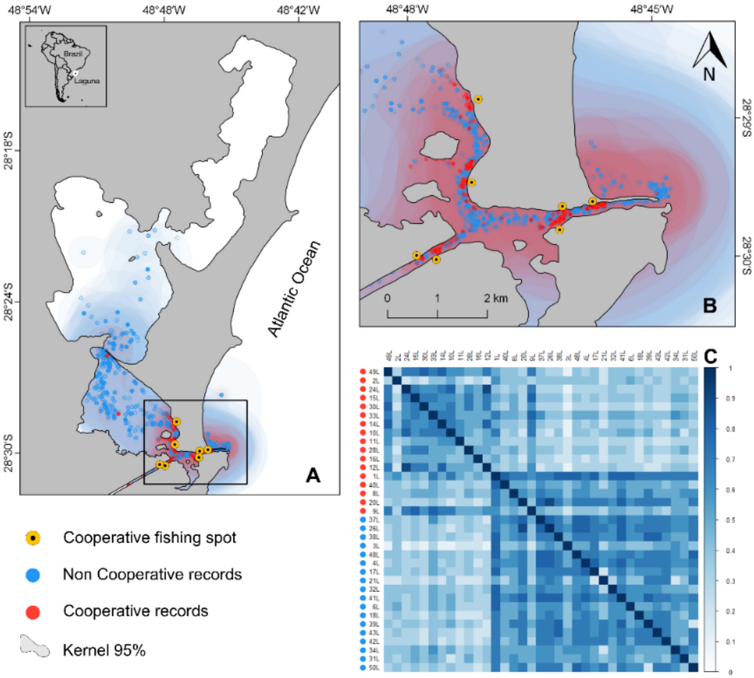
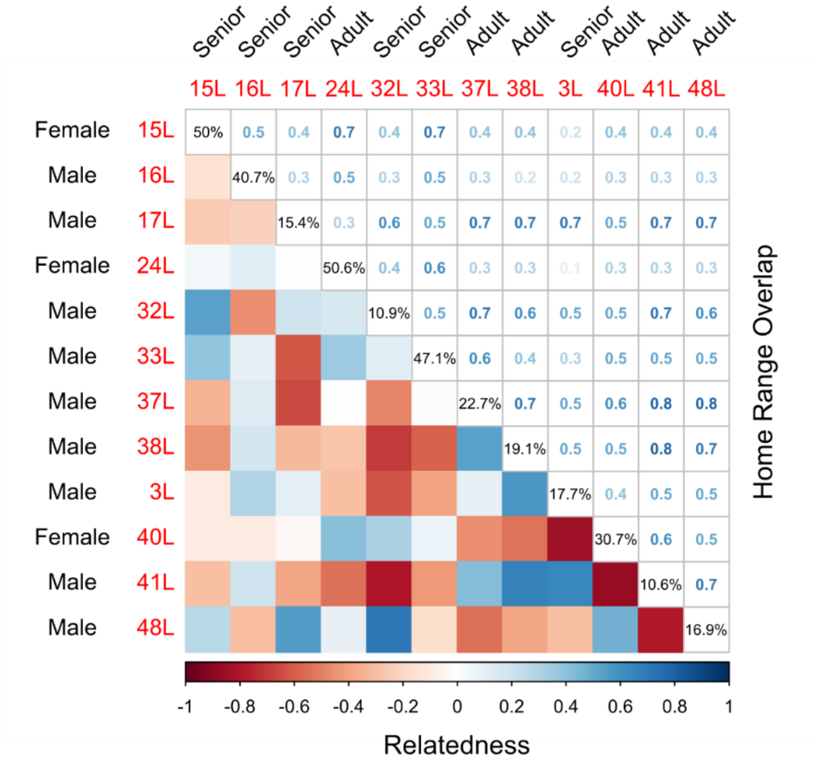


Figure 1: (A) The study area, Santo Antônio-Imaruí-Mirim lagoon system in Laguna, southern Brazil. Yellow circles indicate the fishing sites where dolphins forage with artisanal fishermen. Blue circles indicate sightings of photo-identified individuals during the non-cooperative foraging behavioral context. Red circles indicate individuals recorded during the cooperative foraging context with fishermen. The overlapped shaded areas indicate the 95% kernel estimates of individual home ranges. Following the classification in Daura-Jorge et al. (2012), individuals that frequently interact with fishermen were considered cooperative dolphins (red), and the remaining were considered non-cooperatives (blue). (B) Details of the overlapping of individual home ranges and foraging behavior around the cooperative fishing sites. (C) Home range overlap between pairs of individuals, in which darker shades indicate greater overlap and lighter shades otherwise. Individuals are sorted by relative frequency of participation in cooperative foraging tactic (higher *fp* at the top-left; lower *fp* at the bottom-right).



		Senior	Senior	Senior	Adult	Senior	Senior	Adult	Adult	Senior	Adult	Adult	Adult
		15L	16L	17L	24L	32L	33L	37L	38L	3L	40L	41L	48L
Female	15L	50%	0.5	0.4	0.7	0.4	0.7	0.4	0.4	0.2	0.4	0.4	0.4
Male	16L		40.7%	0.3	0.5	0.3	0.5	0.3	0.2	0.2	0.3	0.3	0.3
Male	17L			15.4%	0.3	0.6	0.5	0.7	0.7	0.7	0.5	0.7	0.7
Female	24L				50.6%	0.4	0.6	0.3	0.3	0.1	0.3	0.3	0.3
Male	32L					10.9%	0.5	0.7	0.6	0.5	0.5	0.7	0.6
Male	33L						47.1%	0.6	0.4	0.3	0.5	0.5	0.5
Male	37L							22.7%	0.7	0.5	0.6	0.8	0.8
Male	38L								19.1%	0.5	0.5	0.8	0.7
Male	3L									17.7%	0.4	0.5	0.5
Female	40L										30.7%	0.6	0.5
Male	41L											10.6%	0.7
Male	48L												16.9%

Figure 2: The subset of 12 individual bottlenose dolphins for which all individual traits were available: age and sex classes, home range overlap, relative frequency of participation with fishermen, and genetic relatedness. Alphanumeric codes indicate individual photo-identification labels, along with genetically-determined sex, and field-based age classes. In the upper triangle, numbers indicate home range overlap between pairs of individuals, where values close to 1 indicate higher overlap. Numbers in the diagonal indicate the relative frequency of participation in the cooperative foraging tactic. In the lower triangle, the color code indicates genetic relatedness between individuals, where values greater than 0.5 indicate highly related pairs (i.e. parent-offspring), and values lower than 0.25 indicate unlikely related pairs.

What drives the population social structure?

Overall, home range overlap (HRO) and relative frequency of participation in cooperative foraging tactic (*fp*) were significant predictors of the associations among dolphins in all behavioral contexts. Across all MRQAP models, 20% to 50% of the variance on the observed associations measured by the HWI were explained by the predictors (see R^2, Table 1).

The first MRQAP using data of individuals with all known traits (n = 12) indicated that genetic relatedness was not a significant predictor of association in any of the behavioral contexts (Table 1). Indeed, there were unlikely-related individuals sharing the same foraging tactic, even when such individuals had higher relative frequencies of participation in the cooperative foraging tactic (Figure 2). The second MRQAP with data for all traits but genetic relatedness (n = 30) showed that sex was not a significant predictor of association in any behavioral context. Finally, the third MRQAP with data for most individuals (n = 34) reinforced that both the relative frequency of participation in the cooperative foraging tactic and home range overlap were significant predictors of association in all behavioral contexts—except for the Cooperative context when only home range overlap defined associations (Table 1).

Given that home ranges could be anywhere from fully discrete (HRO=0) to fully overlapped (HRO=1), the observed regression coefficients for home range overlap that were positive and higher than the null expectancy indicated that the more the individuals' ranges overlap the more they spent time together in groups, regardless of the behavioral context. Since the pairwise relationships of relative frequency of participation in the cooperative foraging was given by Euclidean distances, the regression coefficients are inversely correlated with the association index; that is the smaller the *fp* distance (meaning similar *fp*s) the higher the association indices. The negative regression coefficients indicated that individuals that used the cooperative foraging tactic at similar relative frequencies (high or low) tended to spend more time together in the same groups. Importantly, this was true for all behavioral contexts, except for the cooperative context when individuals were foraging in cooperation with artisanal fishermen. The fact that individuals with similar *fp* spent more time together when doing something else than interacting with fishermen indicated that the effect frequency of participation in the cooperative tactic on social associations was not simply an effect of staying together when foraging.

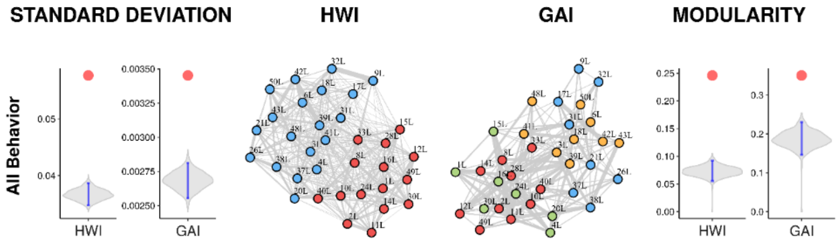
Table 1: MRQAP shows the influence of individual traits of bottlenose dolphins on associations. Matrices of individual traits (predictors) were regressed against the association matrix (HWI) in each behavioral context (All behavior, cooperative foraging, non-cooperative foraging, non-foraging) using three distinct subsets of the data. The number of individuals in each subset is given by *n*. FP is the Euclidean distance of the individuals' relative frequency of participation in the cooperative foraging tactic. HRO is the home range overlap between pairs of individuals, given by an index that ranges from 0 to 1. Age and Sex are binary matrices, in which individuals of the same class are represented by 1, and different classes by 0. Relatedness is the genetic relatedness between pairs of individuals, given by a coefficient that ranges from -1 (completely unrelated) to 1 (completely related). The adjusted R^2 varies from 0 to 100%, indicating how much of the variation on association indices was explained by the predictors. For each of the 2000 permutations, a regression coefficient (β) was estimated to build the null expectancy (r) to which the empirical regression coefficients were compared. Bold font indicates significant predictors in a one-tailed test in which P-values are given by the proportion of times the empirical regression coefficient was smaller or greater than the null expectancy. P-values are complementary, totaling 1. We considered FP significant when $\beta \geq r$ thus $P<0.05$ (*); all the other predictors were significant when $\beta \leq r$, thus $P>0.95$ (**).

Subset	Context (HWI)	Predictors	Regression Coefficient (β)	P (β≥r)	P (β≤r)	R^2 (Adj.)
n = 12	All Behavior	FP	-0.0002	0.713	0.287	59%
		HRO	0.1273	<0.001*	1.000**	
		Age	0.0211	0.073	0.927	
		Sex	-0.0274	0.947	0.053	
		Relatedness	0.0129	0.240	0.760	
	Cooperative	FP	0.0009	0.804	0.196	28%
		HRO	0.1238	0.989**	0.011*	
		Age	-0.0072	0.362	0.638	
		Sex	-0.044	0.047*	0.953**	
		Relatedness	0.0252	0.799	0.201	
	Non-Cooperative	FP	$3.61 * 10^{-1}$	0.496	0.504	37%
		HRO	$9.33 * 10^{-4}$	0.980**	0.020*	
		Age	$2.95 * 10^{-4}$	0.927	0.073	
		Sex	$-2.83 * 10^{-4}$	0.098	0.902	
		Relatedness	$6.94 * 10^{-3}$	0.602	0.398	
	Non-Foraging	**FP**	-0.0011	0.049*	0.951**	46%
		HRO	0.114	0.991**	0.009*	
		Age	0.0228	0.865	0.135	
		Sex	0.0018	0.524	0.476	
		Relatedness	0.005	0.574	0.426	
n=30	All Behavior	**FP**	-0.0002	0.002*	0.998**	50%
		HRO	0.113	1.000**	<0.001*	
		Age	0.0211	0.775	0.225	
		Sex	0.002	0.615	0.385	
	Cooperative	FP	$-5.4 * 10^{-1}$	0.377	0.623	18%
		HRO	$7.71 * 10^{-4}$	0.999**	<0.001*	
		Age	$-1.89 * 10^{-3}$	0.435	0.565	
		Sex	$2.99 * 10^{-3}$	0.614	0.386	
	Non-Cooperative	FP	-0.0002	0.135	0.865	36%
		HRO	0.099	1.000**	<0.001*	
		Age	0.002	0.630	0.370	
		Sex	0.0009	0.540	0.460	
	Non-Foraging	**FP**	-0.0011	<0.001*	1.000**	37%
		HRO	0.1248	1.000**	<0.001*	
		Age	0.014	0.942	0.058	
		Sex	0.007	0.790	0.210	
n=34	All Behavior	**FP**	-0.0006	<0.001*	1.000**	50%
		HRO	0.117	1.000**	<0.001*	
		Age	0.006	0.846	0.154	
	Cooperative	FP	-0.0002	0.173	0.827	20%
		HRO	0.084	1.000**	<0.001*	
		Age	0.002	0.585	0.415	
	Non-Cooperative	**FP**	-0.0004	0.014*	0.986**	38%
		HRO	0.108	1.000**	<0.001*	
		Age	0.005	0.775	0.225	
	Non-Foraging	**FP**	-0.0008	<0.001*	1.000**	33%
		HRO	0.1197	1.000**	<0.001*	
		Age	0.006	0.846	0.154	

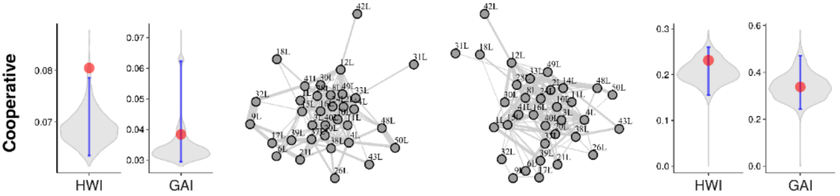
Social affiliation patterns

We rejected the null hypothesis of random association among pairs of individuals. The observed standard deviation (SD) of association indices (HWI) was higher than the null expectancy in all behavioral contexts (Figure 3), indicating the existence of preferred and/or avoided associations between sampling periods. At the population level, we found that dolphins tended to cluster into more cohesive sub-groups: the association networks (HWI) were divided into social modules in all behavioral contexts, except in the cooperative foraging context. That is, the maximized modularity of the association networks was higher than the null expectancy in the All behavior (Q = 0.24, 95% CI = 0.05-0.09), non-foraging (Q = 0.31, 95% CI = 0.12-0.20) and non-cooperative foraging contexts (Q = 0.21, 95% CI = 0.09-0.15).

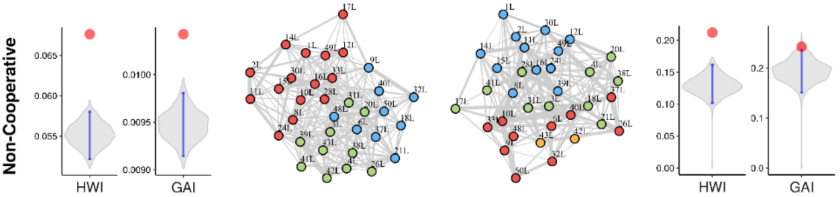
The existence of social preferences among pairs of individuals and the modular social divisions at the population level we found using the rough association indices were also evident when we used the more refined generalized affiliation indices (GAI) in which structural factors that may bring individuals into groups were controlled. We also rejected the null hypothesis of random affiliations in favor of the existence of social preferences and/or avoidances. That is, the empirical standard deviation of GAI was higher than expected by chance in all behavioral contexts (Figure 3)—again, except in the cooperative foraging context (SD = 0.038, CI 95% = 0.029-0.062). Divisions in the large-scale social structure was also evident when using GAI: we observed the same tendency to form clusters in the affiliation networks (GAI), in which the maximized modularity values were higher than the null expectancy in the All Behavior (Q = 0.35, 95% CI = 0.14-0.23), Non-Foraging (Q = 0.37, 95% CI = 0.17-0.29) and Non-Cooperative foraging contexts (Q = 0.24, 95% CI = 0.15-0.23).



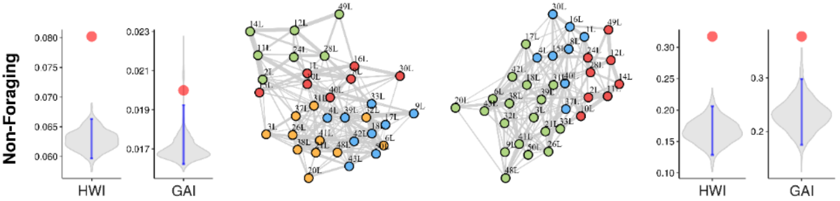
All Behavior GAI = HWI ~ HRO + FP



Cooperative GAI = HWI ~ HRO



Non-Cooperative GAI = HWI ~ HRO + FP



Non-Foraging GAI = HWI ~ HRO + FP

Figure 3: Violin plots at the left show the null distributions of standard deviation of Half Weight Indices (HWI) and Generalized Affiliation Indices (GAI). The blue lines show the 95% confidence interval calculated from 1,000 theoretical matrices. Red dots indicate the observed value of HWI and GAI for each behavioral context. For both HWI and GAI, higher SD than expected by chance indicated the existence of preferred or avoided associations between sampling periods. Social networks of bottlenose dolphins in Laguna using the Half-Weight Index (HWI) and Generalized affiliation indices (GAI) in four behavioral contexts. GAIs removed the effects of structural factors that were shown significant in the MRQAP analysis (Table 1). Nodes representing photo-identified individuals, and color-coded by social modules, are connected by links whose thickness are proportional to HWI and GAI values. In the GAI networks, only positive links are shown. Violin plots at the right show the null distributions of modularity values for the HWI and GAI networks. Blue lines show the 95% confidence interval calculated from 1,000 theoretical networks. Red dots indicate the observed modularity.

DISCUSSION

Our findings suggest that homophily based on a specialized foraging tactic of cooperating with artisanal fishermen underlies the social preferences among individual dolphins, and that such effect scales up and shape the population social structure into social modules. Specifically, we show that dolphins have a tendency to cluster into more cohesive social groups that mirrors the combined effect of adopting a specialized foraging tactic and the reduced home range that it entails. We further demonstrate that such social preferences are robust to the removal of other factors that may bring individuals together, such as passive assortment by sex, age classes, and genetic relatedness.

A myriad of factors drives social relationships of dolphins, many of which are individual traits. For instance, similarity in ranging patterns (e.g. Wiszniewski et al. 2009; Titcomb et al. 2015), age (e.g. Lusseau and Newman 2004), sex (Connor 2007; Morteo et al. 2014; Galezo et al. 2017), kinship (e.g. Krutzen et al. 2003; Parsons et al. 2003; Frère et al. 2010), and behavior (e.g. Louise Chilvers and Corkeron 2001; Mann et al. 2012) can all influence the tendency of individual dolphins to spend time together and repeatedly form groups. Here, our analyses accounted for the influence of all such traits in promoting grouping among individual dolphins. Our results on the combined effect of ranging and foraging behavior promoting dolphin associations strengthen the idea that individual choice for a specialized foraging tactic can be a key social driver in bottlenose dolphin populations with long-lasting behavioral traditions (Ansmann et al. 2012; Daura-Jorge et al. 2012; Mann et al. 2012).

Individuals can have differences in ranging behavior and preferences for certain habitats (e.g. Baker et al. 2017). Those whose home ranges greatly overlap can have more opportunities to interact (Cantor et al. 2012; Carter et al. 2013b; Best et al. 2014) and so social relationships could arise from similar spatial use patterns. The same can happen with foraging behavior. Often individuals have different preferences for what, where and how to eat (e.g. Ford et al. 1998; Bolnick et al. 2003; Estes et al. 2003). Individuals whose dietary preferences or foraging repertoire overlap may also have more opportunities to interact with each other; therefore, those who use the same foraging tactics may end up spending more time together (e.g. Mann et al. 2012). Interestingly, among the Laguna dolphins, the relative frequency of cooperative foraging and home range size are negatively correlated (Daura-Jorge et al. 2012): individuals who routinely engage in the specialized foraging with fishermen have markedly smaller home ranges than those who rarely or never use this specialized foraging tactic (Cantor et al. 2018). This suggest that the ranging behavior is primarily shaped by the cooperative foraging tactic because foraging with artisanal fishermen can be rewarding to the point that individuals do not need to forage further from the interaction sites to meet their energetic requirements (Cantor et al. 2018). Therefore, while home range size indicates individual variation in space use, it reflects individual variation in foraging marked by the cooperation with fishermen. We demonstrate that such synergetic effect of ranging and foraging similarity shapes associations among dolphins. Our finding not only reinforces that foraging specialization influence the society of Laguna dolphins (Daura-Jorge et al. 2012), but it resolves the circular question: do dolphins associate because they interact with fishermen or they interact with fishermen because they associate (Cantor & Whitehead 2013)?

If associations were driven by a foraging tactic, one could expect dolphins to associate to forage that way. Social interactions can be brief among foraging dolphins. Individuals may aggregate around a resource patch and break apart into smaller groups afterwards (e.g. Smolker et al. 1992; Connor 2000). However, bottlenose dolphins can also have behaviorally-specific preferred associations (Gero et al. 2005) that endure in some but not all behavioral contexts (Gazda et al. 2015). We show that dolphins associate because they use the same foraging tactic and not to perform this tactic. By breaking down associations by behavioral contexts, we found that dolphins have preferred companionships and tend to cluster into modules when they are not foraging (i.e. travelling, socializing, mating) and when foraging without the presence of fishermen. But when individuals associate during the cooperative foraging tactic, there is no evident social division at the population level. Such social patterns are also detectable when we estimate social relationships using a more refined metric of affiliation, removing the effects of structural factors that may bring individuals together. There are preferred companionships only outside of the cooperative foraging context.

Given that the social division and dyadic preferences are found only when individuals associate not engaged in cooperative foraging with fishermen, we suggest that homophily based on this foraging tactic—and not during the performance of the foraging tactic—is the driver of social preferences. Individuals who consistently use the cooperative foraging tactic are consistently seen in groups when they are not performing the cooperative tactic, likely representing individuals actively seeking to be with one another rather than passive assortment or chance (Whitehead and James 2015). During the cooperative context, the associations may be spurious or may not be entirely social; the affiliation metric did not reveal any preferences, suggesting that in this context individuals may only aggregate around a high-quality resource patch (Whitehead and Dufault 1999). That is, while two given individuals can be engaged in the cooperative foraging tactic at 50 m from each other, they are simply sharing the foraging site but not necessarily associated with one another. Instead, these dolphins may be even competing for the use of the cooperative foraging site (Simões-Lopes 1998; Cantor et al. 2018).

Unlike other bottlenose dolphin populations, we found no evidence of biological traits such as sex, age or kinship influencing whether individuals group or not. Assortment by sex, such as in in male alliances, has been shown to increase mating opportunities of bottlenose dolphins (Connor et al. 2000). Female-female grouping can also occur by reproductive state (Möller and Harcourt 2008), which can improve calf survival (Frère et al. 2010). Further, one could expect to find genetic relatedness defining associations if kin selection influences the establishment of preferred associations (see also Hamilton 1964). Grouping normally helps individuals to avoid predators (e.g. Mann and Barnett 1999) by actively defending their conspecifics or as a dilution effect (Hamilton 1971; Pitman et al. 2001). However, individuals of this bottlenose dolphin population do not have to travel far for mating opportunities because they are highly resident in a small lagoon system, often overlapping home ranges in ever changing interactions, with no evidence for kin-based homophily. We found no evidence for homophily within age-classes (Baker et al. 2017). More refined data on age will provide a better understanding of differences in age-related specific behaviors and possible interactions with other biological traits (Wells 2014; Patterson et al. 2016). Lastly, there are no records of predators (i.e. sharks) in the bottlenose dolphin population of Laguna.

In summary, if none of these biological traits modulate pairwise associations, and if even after removing structural factors the social division and social preferences are well marked, we suggest that dolphins actively choose whom they interact with. Then, such social preferences scale up to shape the population social structure. In sperm-whales, individuals have long-term social preferences, and distinct vocal repertoires that might help whales to recognize their social units (Cantor et al. 2015; Gero et al. 2015). Likewise, dolphins who constantly use the cooperative foraging tactic whistle differently, suggesting that dolphins could rely on their vocal repertoire to recognize those who are their preferred affiliates (Romeu et al. 2017). And if they do so, dolphins may tend to copy behavior—foraging tactics included—from their peers within their social communities, which would reinforce such a social distinction (see Cantor & Whitehead 2013; Simões-Lopes et al. 2016).

Homophily and social learning can shape both human and non-human societies (McPherson et al. 2001; Fu et al. 2012; Mann et al. 2012; Cantor et al. 2015). The social dynamics of the Laguna bottlenose dolphin population is marked by the interplay between socially learned behaviors and homophily (e.g. Cantor and Whitehead 2013). Such interactions have important implications for individual and whom they preferentially interact with (Hinde 1976), which have implications for the population

(Laland and Janik 2006; Zefferman 2016; Whitehead 2017). We suggest that by combining field experiment with simulations (e.g. Kopps and Sherwin 2012; Cantor et al. 2015; Ilany and Akcay 2015) and long-term monitoring (e.g. Ansmann et al. 2012; Mann et al. 2012) one can continue to shed light on the origins and the evolution of behavioral specializations in wild populations.

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CONSIDERAÇÕES FINAIS E CONCLUSÕES

Neste trabalho, revisitou-se a estrutura social de uma população de botos-da-tainha, aparentemente estruturada por uma tática de forrageio especializada em cooperação com pescadores artesanais. Após controlar as diferenças no estado comportamental e outras características individuais que poderiam definir as associações, observou-se que a homofilia pela tática de forrageio em cooperação com os pescadores artesanais é a força primária que governa as associações entre indivíduos, estruturando assim a população em módulos sociais distintos.

Separando as associações por contextos comportamentais e utilizando métricas refinadas para remover das associações o efeito da tática de forrageio e da sobreposição na área de vida, encontrou-se que as associações preferenciais e a estrutura social modular se mantêm, exceto quando forrageando em cooperação com os pescadores. De forma geral, isso sugere que, dada a oportunidade, os indivíduos escolham ativamente com quem se associar. Em nível da população, as preferências sociais levam a uma estrutura social em módulos. Como as preferências e a estrutura social modular não se mantêm durante o forrageio em cooperação com os pescadores, estes resultados revelam que as associações ocorrem pela tática de forrageio cooperativa e não com a finalidade de utilizar esta tática.

As contribuições desta dissertação podem ser vistas em duas escalas. Em uma escala local, agora pode-se afirmar que a tática de forrageio define as preferências sociais e estrutura esta sociedade de botos-da-tainha em módulos distintos, e outras características individuais não influenciam a estrutura social. Em uma escala ampla, este trabalho contribui para a compreensão da variação intraespecífica dos padrões sociais e das forças que governam as associações em sociedades animais com dinâmicas de fissão-fusão. Ainda, ao demonstrar o papel da tática de forrageio na estrutura social, este trabalho reforça a hipótese do aprendizado social contribuindo para a estruturação de sociedades animais.

Porém, ainda não é possível concluir sobre o efeito do aprendizado. O aprendizado social pode ser um produto das associações, ou a motivação das associações. Este resultado reforçaria a ideia do aprendizado social como mecanismo para a emergência da estrutura social em módulos e para manutenção da estratégia de forrageio cooperativo. Esta população de botos-da-tainha é um excelente estudo de caso para testar a hipótese de que cultura pode estruturar sociedades animais. É provável que a homofilia e o aprendizado estejam atuando em sinergia nos padrões sociais observados e, provavelmente, são elementos importantes para especialização da tática de forrageio com pescadores. Estudos em longo prazo, simulações e abordagens experimentais irão esclarecer as implicações ecológicas e evolutivas destas associações preferenciais por uma tática de forrageio, tanto para o indivíduo quanto para a população.