Behavioral Ecology and Sociobiology (2022) 76: 42
https://doi.org/10.1007/s00265-022-03152-2

ORIGINAL ARTICLE

Social foraging can benefit artisanal fishers who interact with wild dolphins

Bruna Santos-Silva[1] · Natalia Hanazaki[1] · Fábio G. Daura-Jorge[1] · Mauricio Cantor[1,2,3]

Received: 22 December 2021 / Revised: 22 February 2022 / Accepted: 24 February 2022 / Published online: 7 March 2022

Abstract

Social foraging decisions depend on individual payoffs. However, it is unclear how individual variation in phenotypic and behavioural traits can influence these payoffs, thereby the decisions to forage socially or individually. Here, we studied how individual traits influence foraging tactics of net-casting fishers who interact with wild dolphins. While net-casting is primarily an individual activity, in the traditional fishery with dolphins, fishers can choose between fishing in cooperative groups or solitarily. Our semi-structured interviews with fishers show their social network is mapped onto these foraging tactics. By quantifying the fishers' catch, we found that fishers in cooperative groups catch more fish per capita than solitary fishers. By quantifying foraging and social traits of fishers, we found that the choice between foraging tactics—and whom to cooperate with—relates to differences in peer reputation and to similarities in number of friends, propensity to fish with relatives, and frequency of interaction with dolphins. These findings indicate different payoffs between foraging tactics and that by choosing the cooperative partner fishers likely access other benefits such as social prestige and embeddedness. These findings reveal the importance of not only material but also non-material benefits of social foraging tactics, which can have implications for the dynamics of this rare fishery. Faced with the current fluctuation in fishing resource availability, the payoffs of both tactics may change, affecting the fishers' social and foraging decisions, potentially threatening the persistence of this century-old fishery involving humans and wildlife.

Significance statement

Social foraging theory proposes that decisions to forage in groups are primarily driven by cost–benefit trade-offs that individuals experience, but it remains unclear whether, and how much, individual foragers' characteristics influence these trade-offs and consequently the choice to forage in social groups. We study the artisanal net-casting fishers who choose between cooperating with each other or fishing alone when engaging in a rare interaction with wild dolphins. Our findings suggest that cooperative fishers capture more fish than solitary fishers, and that by choosing cooperative partners based on similarities and differences in key social (peer reputation, kinship, friendships) and foraging (fishing frequency) traits; these fishers also experience higher social prestige and more social embeddedness. These results suggest that material gains from foraging—but also non-material benefits accrued from socializing with like-minded individuals—can influence the dynamics of human social foraging.

Keywords Artisanal fishers · Cooperation · Cooperative foraging · Human forager · Social foraging · Social network

Introduction

Social foraging is a prominent strategy in both human and non-human animals. Ecological theory proposes that the decision to partake in social foraging is primarily driven by the trade-offs in the costs and benefits experienced by individual foragers (e.g. Giraldeau and Caraco 2000; Beauchamp 2014). The primary benefit of foraging in groups is increased access to resources, thus higher energy intake (e.g.

Communicated by M. Raymond.

Natalia Hanazaki and Mauricio Cantor share senior authorship.

✉ Mauricio Cantor
mauricio.cantor@oregonstate.edu

Extended author information available on the last page of the article

Creel 1997; Alvard and Nolin 2015), but such benefits can dissipate in large groups where the per capita share becomes prohibitively small (MacArthur and Pianka 1966; Clark and Mangel 1986). Among human foragers, such as hunter-gatherers and artisanal fishers, the social decisions during foraging are also driven by increased material returns—cooperating with peers can increase prey capture success and resulting monetary gains (e.g. Hawkes et al. 1991; Begossi and Richerson 1992; Carpenter and Seki 2011; Turner et al. 2014; Alvard and Nolin 2015). However, while human foragers may be fundamentally driven by the aspiration for maximizing such material benefits, their social environment can also shape their foraging decisions.

Human social relationships are multifaceted and supply a range of non-material benefits (e.g. Christakis 2019). For instance, the bonds we weave in our social networks can provide us both physical and mental well-being (Fowler and Christakis 2008; Holt-Lunstad et al. 2010; Rosenquist et al. 2011), while the extent to which we are connected in our social network (social embeddedness) can provide us social capital in terms of sense of identity, shared values, and access to information (e.g. Hruschka 2010; Apicella et al. 2012). Some of these non-material benefits are valuable in and of themselves, while others can feedback onto material gains (e.g. Turner et al. 2014; Barnes et al. 2016). One example among foragers is how repeated social interactions can establish trust and ensure reciprocity, which is not only important for belongingness, but can promote sharing of current resources and increase chances of future material gains (Hill 2002; Apicella et al. 2012), even in times of scarcity (Begossi 1992; Hawkes 1992). Another example relies on how the social environment influences information acquisition (e.g. Galef and Giraldeau 2001): relative to solitary foragers, well-connected social foragers have greater access to local ecological knowledge about food resources (e.g. Begossi 1992) as well as effective foraging techniques (e.g. Reyes-García et al. 2016). Therefore, in human social foraging, there is more at stake than material gains; more than deciding whether to forage cooperatively, another important decision is choosing with which other individuals to build cooperative relationships.

Similarity is a major driver of social relationships—they tend to form among individuals who share similar traits (McPherson et al. 2001). There are many biological, ecological, and behavioural traits whose similarity can influence individuals to interact socially and cooperate; for instance, kinship (Hamilton, 1964), age (e.g. Carter et al. 2013), foraging tactics (e.g. Machado et al. 2019a), resource needs (Conley and Udry 2010; Alexander et al. 2018), and cooperativeness (e.g. Apicella et al. 2012). Differences in individual traits can also beget social attraction, for example, when low-rank individuals aspire to build relationships of trust and reciprocity with high-status individuals (Lyle and Smith 2014; von Rueden 2020). However, the extent to which individual traits influence social preferences among foragers; thereby, the material and non-material resources they may accrue remain understudied. In southern Brazil, a cultural fishing practice involving artisanal net-casting fishers and wild bottlenose dolphins (*Tursiops truncatus gephyreus*; Simões-Lopes et al. 1998) provides a good opportunity to investigate how trait similarity influence social foraging decisions and their material and non-material outcomes. This is because net-casting is fundamentally an individual foraging practice aimed to catch fish, but in the traditional net-casting fishing with dolphins, fishers can team up in groups to share the labour and the returns (Peterson et al. 2008), and such returns include more than fish but a range of social and non-material gains (Machado et al. 2019b).

This century-old fishing tradition is held by net-casting fishers who learned to interpret the dolphins' foraging behaviour near the coast in a way that increases their fishing success (Pryor et al. 1990; Simões-Lopes et al. 1998). Fishers stand in line at the edge of a deep canal and wait for the dolphins' behavioural cues that indicate when and where to cast their nets (Simões-Lopes et al. 1998). Since the interaction area is restricted, fishers self-organize their activities with an informal rule system defining specific spots in the water that are suitable for casting nets, as well as the access to these spots (Peterson et al. 2008). The fishing spots are allocated on a first-come-first-served basis, but when fishers catch at least two fish with the assistance of the dolphins, they must leave their spot for the next fisher waiting at the beach. Many fishers prefer to fish alone; they wait for their turn to go net-casting with dolphins and keep the whole catch and its gross value, if any, for themselves. By contrast, some fishers choose to cooperate with others, by sharing their fishing spots and their turns to get in the water, helping selling each other's fish at the beach, and/or sharing their collective catch or resultant cash (Peterson et al. 2008). While such foraging decisions can be primarily influenced by the net material returns, individuals can have other motivations for and experience different social implications when deciding between fishing alone or in groups. The traditional fishery with dolphins renders many other non-material benefits—including leisure, sense of place, cultural belongingness (Machado et al. 2019b)—and joining a cooperative group can lead to social benefits unavailable when fishing alone—including forming close one-on-one friendships and enjoying being more socially connected in the fishing community. Individual net-casting fishers vary widely in the required knowledge about the fishing conditions and dolphins' behaviour, in fishing experience, and in their perceptions about non-material benefits of fishing with dolphins (Machado et al. 2019b; da Rosa et al. 2020). It remains unknown if, and how much, fishers' similarity in such social and foraging traits play a role in their decision to fish alone or to form cooperative groups with specific partners, as well as the extent to which these two tactics differ in their material and non-material payoffs.

Here, we study the foraging behaviour and social interactions of net-casting artisanal fishers when interacting with wild dolphins to evaluate how similarity in individual traits can influence social foraging. We hypothesize that, while the decision to form cooperative foraging groups can be influenced by the benefits individuals receive, the decision of whom to cooperate with can be influenced by the traits of the individuals. We first map the social and cooperative interactions among fishers to identify who engages in social foraging or who forages solitarily. Then, we quantify and compare the material benefits (in terms of fish caught)—and qualitatively discuss potential non-material benefits (in terms of social environment)—accrued by fishers who form cooperative foraging groups or forage alone. Based on the principle that trait similarity begets social relationships (McPherson et al. 2001), we finally evaluate whether the choices for one or another foraging tactic, and for specific cooperative partners, are related to similarity in key individual foraging and social traits. We hypothesize that cooperative ties can be related to similarity in foraging traits (fishing experience, frequency, economic dependence) that would primarily influence the material benefits (e.g. fish and cash) and to similarity in social traits (e.g. peer reputation, number of close friends among local fishers, propensity to fish with relatives) that could also influence access to non-material benefits (e.g. local social prestige and broad social embeddedness in the community). We conclude by discussing the role of the foraging tactics in the persistence of this rare fishery involving humans and wildlife.

Material and methods

Study system

The study system is the segment of the artisanal fishing community from the complex lagoon system adjacent to Laguna, southern Brazil (28°20′S, 48°50′W) that engages in the traditional net-casting fishery with wild dolphins. The dolphin-fisher interactions occur in 5 to 8 different sites across the lagoon system, but the main site is the *Tesoura* beach: an easily accessible beach where several fishers from Laguna and adjacent cities interact with the dolphins (Supplementary Fig. S1). Dolphin-fisher interactions happen year-round but are intensified during reproductive migration season (Late April to early July) of the Lebranche mullet (*Mugil liza*); off season other targets include White mullets (*M. curema*), Argentine menhaden (*Brevoortia pectinata*), and a range of local species (Simões-Lopes et al. 1998). Net-casting fishers stand in line, about 3 m apart from each other, on the shallow waters at the edge of the canal waiting for dolphin behavioural cues (e.g. a sudden deep dive) they interpret as the ideal time and place to cast nets (Simões-Lopes et al. 1998). With each nest cast, a fisher can catch anything from zero to a few hundred mullets of about 40 cm in length and 1 kg in weight (Simões-Lopes et al. 1998). The time spent waiting for this right moment varies from a few minutes to many hours, during which fishers close by can exchange information about the fish and the dolphins. There are specific suitable spots in the water for net-casting, and fishers take turns to occupy them (Peterson et al. 2008). Fishers decide whether they fish alone or form cooperative groups with other fishers to share the spots, turns, and/or the fish and resulting cash. As these cooperative ties are formed over the years, fishers do not always start and end their fishing activities together, but rather, they join each other along their daily routine (Peterson et al. 2008).

Data sampling

We interviewed 49 artisanal fishers at the *Tesoura* beach during 26 consecutive days between May and July 2019. The number of interviewees is a representative sample of resident fishers in this area (see Peterson et al. 2008; Machado et al. 2019b; da Rosa et al. 2020, for studies with similar sample sizes). The potential interviewees were identified through participant observation (Schensul et al. 1999), following net-casting fishers at the main cooperative fishing site (Supplementary Fig. S1) and conducting direct observations to identify those who interact with dolphins. The interviews were conducted at the beach when the fishers were waiting for their turn to go into the water to interact with dolphins. After agreeing and signing a free informed consent to participate in this research (ethical approval CEPSH 06457419.6.0000.0121), participants were interviewed individually. Only one approached fisher has declined the invitation to participate in this research.

The interviews were based on a semi-structured questionnaire (Bernard 2006) with questions defined after five pilot interviews carried out earlier in 2019 at the same location. The questionnaire (Supplementary Methods S2) contained questions on the fishers' social-economic aspects (e.g. age, place of birth and residence, number of children, main profession), fishing behaviour (e.g. years of fishing experience, frequency of, and economic dependence on, fishing with dolphins), and social connection with the other artisanal fishers in the area. For the latter, we asked who else they knew among the local fishers and then whether any of them were their close relatives (i.e. genetically-related through a common descent, such as parents or sons, siblings, first cousins), close friends, or acquaintances, which other fishers they perceive as the most skilful and successful, and with whom other fishers, if any, they cooperate when fishing with dolphins. Whenever the interviewee named a fisher with whom they cooperate, we further asked open questions on why they cooperate, how the cooperation works, and what benefits they gain from cooperating; and whether they prefer to cooperate with relatives or the most skilful, successful individuals.

During all the 26 sampling days, from 08:30 to 17:00 h, we used an all-occurrence sampling protocol (Altmann 1974) to record the foraging behaviour of all fishers in the interaction site. For each foraging event—defined as when one or more fishers cast their nets in the presence of dolphins' foraging near the coast (Simões-Lopes et al. 1998)—we quantified the number of nets cast and counted the resultant number of mullets caught, if any, for each individual fisher. For each successful cast, we measured the total length (from the tip of the mouth to the tip of the caudal fin) of up to 10 randomly chosen mullets. We focused on the foraging of the 49 interviewed fishers but also recorded the fishing success of all other fishers in the water during a fishing event with dolphins. Therefore, it was not possible to record data blind because our study involved interviewing and observing focal individuals in the field.

Data analyses

Fishers' social network and foraging tactics

We used network analysis to investigate the structure of the social and fishing interactions among the artisanal fishers who interact with dolphins. We built a social network of fishers based on their answers to the question on which other fishers they regularly cooperate with, which is representative of their history of repeated cooperative foraging interactions over time. The network was defined by a binary adjacency matrix $\mathbf{A}$, where the element $a_{ij}=1$ when fisher i declared to cooperate with j or fisher j declared to cooperate with i, and $a_{ij}=0$ when neither i or j declared cooperation. In the network depiction, nodes representing fishers were connected by undirected binary edges representing declarations of cooperation (the cooperative ties); individuals who did not cooperate were then disconnected from the giant component of the network. Although disconnected, these fishers are still part of the same social environment, and thus, we considered their nodes as part of the social network. The fishers who reported no cooperative interactions were then deemed as "solitary" fishers, whereas all fishers who reported cooperating with at least one other fisher were deemed "cooperative" fishers.

We then tested the existence of distinct groups of cooperative fishers by calculating the modularity, Q (Newman and Girvan 2004) of the giant component of the fishers' social network. A modular structure would contain cohesive subsets of individuals (modules) who are more connected with each other than with the rest of the network, thereby representing cooperative groups. We used a probabilistic null model for one-mode networks (Cantor et al. 2017) to test the significance of the observed modularity. We created an ensemble of 2,000 squared and symmetric adjacency matrices representing theoretical networks, in which the probability of a cell being filled was proportional to the total sum of the columns and rows of the empirical adjacency matrix—in other words, the probability of a cooperative tie connecting two fishers was proportional to the observed number of ties of each of those fishers. This way, the algorithm creates theoretical networks of the same size (number of nodes representing fishers), connectance (proportion of realized links representing cooperative ties), and heterogeneity in the degree (number of ties per fisher) distribution (see Cantor et al. 2017). We then calculated modularity for all theoretical networks to build a benchmark distribution; the observed modularity was considered statistically significant when outside of the 95% confidence interval of the benchmark distribution. The significant modularity partition indicated the distinct modules in the network that defined the fishers' membership to different cooperative groups.

Benefits of foraging tactics

We first qualitatively evaluated if cooperative and solitary fishers perceive material and non-material benefits in forming cooperative groups when net-casting with dolphins. Second, we built linear models to investigate whether cooperative and solitary fishers experience different per capita material benefits. We built a generalized linear model (GLM) to evaluate the total mullet caught by each individual fisher as a function of their foraging tactic (cooperative or solitary). We considered a negative binomial structure to deal with overdispersion of the count data, and a log link function. The unit of analysis was each interviewed fisher, combining all mullet they caught throughout the study period. We also built a generalized linear mixed model (GLMM) to evaluate the number of mullets caught in each net cast by each individual fisher as a function of their foraging tactic (cooperative or solitary) and social module size (i.e. number of individuals in each cooperative group; the group size of solitary fishers was 1). We used a nested random effect structure to control for individual differences among fishers and social module composition, as individual fishers from the same cooperative group (i.e. social module) can be more similar to one another, relative to the measured individual traits. In addition, since the sampling unit was the individual casting event, the model predicted the influence of the foraging tactic on the effectiveness of the cast, apart from the variation of fishing effort between fishers in groups or alone. For each model, we created a corresponding null model with only the intercept as a benchmark and used the

Akaike's information criterion corrected for small samples (AICc) and AIC weight to compare corresponding null and candidate models (Burnham and Anderson 2002). The models were validated by a protocol for linear models (Bolker et al. 2009) and using simulated residuals (Hartig 2019). All analyses were performed in R 3.6.2 (R Development Core Team 2019) using R packages "glmmTMB" (Magnusson et al. 2017), "MuMIn" (Bartoń 2018), and "DHARMa" (Hartig 2019).

Influence of individual traits on fishers' foraging tactics

Finally, we investigated whether similarity in individual fisher traits could explain their choices between solitary and social foraging tactics, expressed by their choices for whom, if anyone, to cooperate with. For all fishers in the network—either cooperative or solitary—we considered seven traits (five continuous, two categorical) related to their foraging behaviour and social environment. The individual traits related to foraging were as follows: fishing frequency (number of months per year dedicated to net-casting with dolphins); general fishing experience (fishers' age, in years, as a proxy for accumulated fishing practice; e.g. Silvano et al. 2006); expertise in interacting with dolphins (years of practice net-casting with dolphins, as a proxy for their ability to understand the dolphins' behaviour and react properly); and economic dependency on fishing (whether individuals were full-time or part-time fishers). We expected these foraging traits to primarily influence the material benefits (e.g. fish and resulting cash) of the foraging tactics. The traits related to social environment were: peer reputation (how many times each fisher was cited by their peers as being the most skilled or successful in fishing with dolphins), friendship connectedness (how many times each fisher was cited by their peers as being their close friends), and a binary proxy of genetic kinship (whether each fisher reported to be a close relative or genetically unrelated to the other local fishers). We expected these social traits to primarily influence the fishers' decisions about whom to cooperate with, which could imply in additional non-material benefits (e.g. social prestige and social embeddedness among local fishers). We explored potential differences of each trait between the two foraging tactics using non-parametric (Wilcoxon rank sum with continuity correction and Pearson's chi-squared) tests.

To estimate the influence of individual trait similarity on the probability of fishers to forage cooperatively with specific partners or alone, while controlling for the effects of all the other traits, we built a multi-membership generalized linear mixed model (GLMM) using a Markov chain Monte Carlo (MCMC) sampler under a Bayesian statistical framework (Hadfield 2010). We used MCMC GLMMs because they can deal with the inherently non-independent and relational nature of the social network data and can also control for node dependence by including individual fishers' identities as multilevel random effects (Hart et al. 2021). After checking for correlation among all traits (Supplementary Fig. S3), we built a model in which the response variable was the presence and absence of cooperative ties among dyads of fishers, as defined by the matrix **A**, and so considered a binomial error distribution (family set as categorical, with a logit link function). As independent variables, in the fixed part of the model, we used the similarity among dyads of fishers in each of the seven individual traits. We first computed the Euclidean distance between dyads of fishers for each trait; to make traits more comparable, we rescaled the Euclidean distances to range between 0 and 1, and subtract 1 from all rescaled distances to therefore consider the similarity among pairs of individuals (i.e. each trait ranged from 0 to 1, where pairs of fishers were most different, or most similar within the sample, respectively, regarding a given trait). To account for the non-independence of the data, the members of the dyads were included as correlated random effects (G-structure). We heuristically set the Markov chain length to 300,000, used a burn-in of 100,000, and sampled the chain every 2000 iterations. We specified a set of 6 different uninformative and expanded priors for the variance of both R- and G-structures and used the prior distribution that improved the model diagnosis. We fitted the global model with the seven independent variables in the fixed part of the model and considered a fixed effect as significant when the credible intervals of the posterior distribution (95% High Posterior Density, HPD) do not overlap with zero (Hadfield 2010).

Results

Fishers' individual traits, social network, and foraging tactics

Fishing with dolphins is traditionally a male job, and all 49 interviewed net-casting fishers were men. Their ages varied between 24 and 72 years old (median = 44, Q1 = 37, Q3 = 53), and their expertise in fishing with dolphins ranged from less than a year to 61 years of practice (median = 24, Q1 = 14, Q3 = 37). Out of the 49 interviewees, 13 were full-time fishers who regularly interact with dolphins throughout the year, and 36 were part-time fishers who were retirees or had other jobs (e.g. bricklayer, security guard, salesman). Nearly all fishers reported that there are better fishing spots in the water (47 out of 49 interviewees) and fishers who are locally known as more skilful and more successful than the rest (46 out of 49). There were 24 fishers who reported regularly cooperating with other net-casting fishers when fishing with dolphins, while the remaining 25 fishers reported they only fish solitarily (Fig. 1A). The connected component of the fishers' social network was divided into four modules, as shown by the modularity being significantly higher than the null expectancy ($Q = 0.37$; 95% CI = 0.16–0.36; Supplementary Fig. S2), thereby revealing four groups of regular cooperative foragers.

The individual foraging traits of fishers were not very distinct between the two foraging tactics (Fig. 1). There was a small, non-significant tendency for cooperative fishers to interact with dolphins more frequently throughout the year (Fig. 1B; $W = 263$, $p = 0.427$), and to depend economically on the fishery with dolphins (Fig. 1C; $X^2 = 2.90$, $df = 1$, $p = 0.088$). Age is often assumed as a proxy of experience among artisanal fishers (e.g. Silvano et al. 2006), but we found only a moderate correlation between the fishers' age and their expertise in fishing with dolphins ($r = 0.309$, $df = 1174$, $p < 0.0001$; Supplementary Fig. S3). Both age (Fig. 1D; $W = 188$, $p = 0.026$) and expertise (Fig. 1D; $W = 353.5$, $p = 0.289$) were variable between the tactics, with age tending to be slightly higher among solitary fishers. Among all individual traits, two social traits were the most distinctive between the cooperative and solitary fishers: the number of close friends (Fig. 1F; $W = 468$, $p = 0.0002$) and the peer reputation (Fig. 1G; $W = 471$, $p < 0.0001$). Cooperative fishers tended to have more close friends and higher reputation among the local fishers than the solitary fishers (both variables were correlated, $r = 0.708$, $df = 1174$, $p < 0.0001$; Supplementary Fig. S3). There was a slight tendency for cooperative fishers to fish with close relatives (Fig. 1H; $X^2 = 6.44$, $df = 1$, $p = 0.011$).

Perceived and accrued benefits of foraging tactics

When fishers were asked about their perceptions about benefits of cooperating with other fishers, the majority of the answers indicated that cooperating is advantageous (30 out of 42 mentions). The most frequently mentioned advantage was receiving assistance in selling the fish while keeping their fishing spot (15 out of 42 answers), followed by sharing the fish or resultant cash (5 and 8 out of 42 answers,

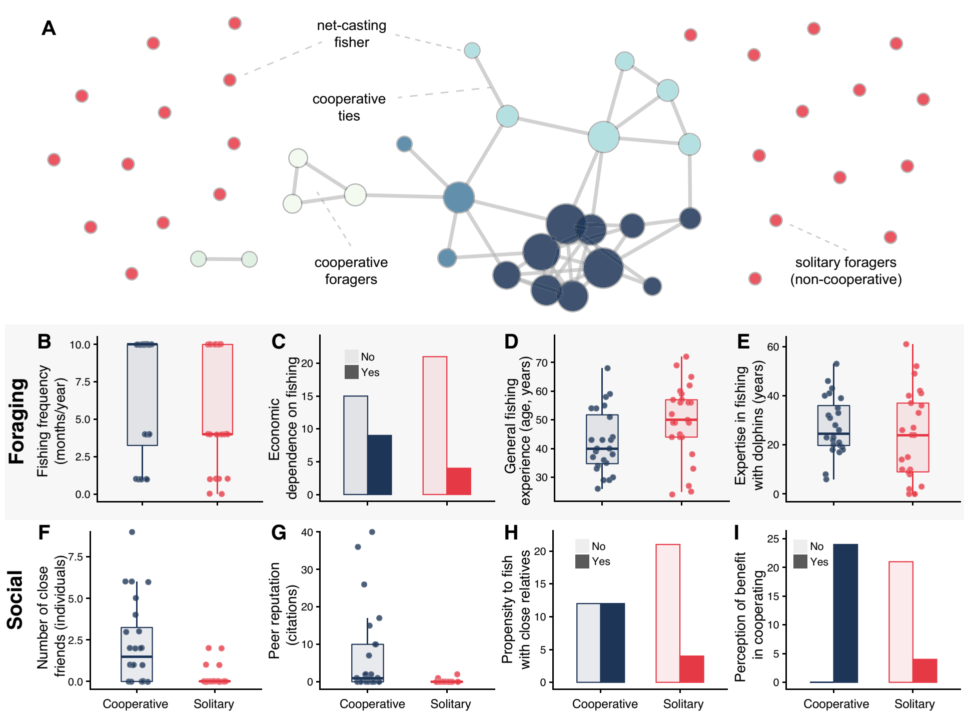

Fig. 1 Foraging tactics among the artisanal net-casting fishers who participate in the traditional fishery with wild dolphins in southern Brazil. **A** Fishers' social network of artisanal fishers indicating their two tactics when net-casting with dolphins: cooperative and solitary foraging. The network contains 49 individual fishers (nodes) who are linked by their self-declared cooperative ties. There were 24 fishers who declared forming cooperative groups with other fishers; 22 out of which are part of the giant component of the network containing 4 modules (blue-shaded nodes defining the cooperative groups), and two individuals cooperate with each other. The remaining 25 fishers (disconnected red nodes) do not cooperate with anyone and only fish solitarily. The size of nodes is proportional to their number of cooperative ties. **B–E** Distribution of individual traits related to foraging behaviour and to **B–H** social environment between fishers who engage in each tactic, cooperative (blue) and solitary (red) foraging. **I** Number of individual fishers from each foraging tactic who perceive any material or non-material benefit in cooperating with other fishers. In the boxplots **B**, **D–G**, boxes show the median and interquartile range, whiskers show the range, and each circle ($n = 49$) is an interviewed fisher; the barplots **C**, **H–I** indicate the number of interviewed fishers in each category

respectively), and working in partnership (2 answers). Among the 24 fishers who form cooperative groups, 21 answered that they prefer to cooperate with skilled and successful fishers—those who were scored high by their peers in the reputation ranking. These benefits of cooperating were reported by all 24 cooperative fishers, and by only 4 out of the 25 solitary fishers (Fig. 1I; $X^2 = 35.28$, $df = 1$, $p < 0.0001$). These four solitary fishers reported the same benefits of sharing the fishing spot, the catch, and selling the fish, but as most of the other solitary fishers, they perceive that any benefits in cooperating would be dampened by the uncertainty in the others' catch.

The two foraging tactics (Fig. 2A–D) differed in terms of material gains, as the cooperative fishers tended to outperform the solitary fishers in catching fish both in a total number of mullets caught and in mullets caught per net cast (Fig. 2E–G). Overall, during 26 sampling days in the 2019 mullet season, net-casting fishers caught a total of 1186 mullets with 42.9 cm ± 7.00 SD ($n = 771$) in average total length. The foraging success of all fishers was 0.26 mullet per net cast ($n = 14{,}542$ nets; mean = 4.53 ± 9.43 SD, range = 0–85 mullet per net) and 0.44 mullet per foraging event ($n = 2687$ events including or not interaction with dolphins). The total catch was, on average, higher for the cooperative (mean number of mullets caught = 4.83 ± 8.90 SD; mullets per successful net cast = 5.04) than for the solitary fishers (mullets = 1.41 ± 2.19 SD; mullets per successful cast = 2.23). The negative binomial GLM of the total mullet caught by each interviewed fisher as a function of their foraging tactic showed that the effect of solitary tactic was significantly negative and large ($\beta = -2.28$, SE = 0.60, $p < 0.001$), therefore indicating that cooperative fishers tend to be more successful than solitary fishers (Fig. 2F). This model had considerable explanatory power (Nagelkerke $R^2 = 0.32$), more support (AICc weight = 0.986) than the null model (AICc = 8.45, AICc weight = 0.014), and met all the premises (uniformity: $D = 0.125$, $p = 0.394$; lack of overdispersion: ratio observed/simulated = 0.706, $p = 0.614$; no outliers: exact binomial test, $p = 1.00$). The GLMM relating the mullet caught by each net cast by each fisher, but this time considering the size of the social module they belong to, indicated a significantly positive and large effect of the cooperative tactic ($\beta = 1.77$, SE = 0.43, $p < 0.0001$; intercept corresponding to the solitary tactic was at − 0.423,

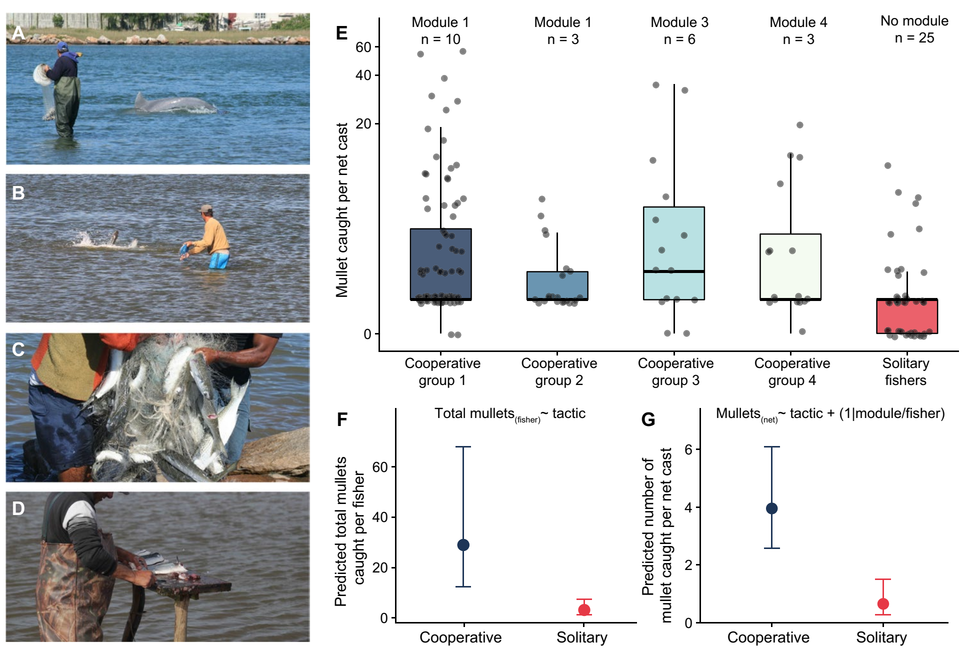

Fig. 2 Observed and predicted success of artisanal net-casting fishers using two foraging tactics. **A** Net-casting with dolphins can be a **B** solitary or **C** a cooperative foraging endeavour, whose main benefits include increased resources and **D** partnerships that are beneficial for sharing the fish, and the fishing and selling activities. **E** Observed number of mullet caught (log scale) in each net-casting event by individual fishers who engage in one or another foraging tactics: forming cooperative groups (blue shades) or fishing solitarily (red). Blue shades indicated catches by fishers of each of the four cooperative groups (n = number of fishers), defined by the modules in their social network (Fig. 1A). The boxes show the median and interquartile range, whiskers show the range, and each circle is an individual net-casting event. **F** Total mullets caught by fishers using each foraging tactic, as predicted by the negative binomial generalized linear model relating all mullets caught per fisher throughout the study as a function of their tactic (cooperative vs. solitary). **G** Mullets per net cast of individual fishers using each tactic, as predicted by the generalized linear mixed model relating the number of mullets caught in each net-casting event by each fisher as a function of their tactic, controlling for module size (number of individuals in each cooperative group). Whiskers in **F** and, **G** represent 95% confidence intervals. Photographs by F.G. Daura-Jorge (**A**, **C**) and E. Ehrhardt (**B**, **D**)

SE = 0.4203, $p = 0.314$). This further showed that cooperative fishers tended to be the most successful, regardless of fishing effort (Fig. 2G). The second model also had enough explanatory power when considering the fixed effect (marginal $R^2 = 0.269$) and even more when considering the random effects (conditional $R^2 = 0.483$) indicating the importance of individual variation. This model had more support (AICc weight = 0.961) than the null model (AICc = 6.39, AICc weight = 0.039), and it meets most premises (lack of overdispersion: ratio observed/simulated = 1.217, $p = 0.412$; no outliers: exact binomial test, $p = 0.3509$) except uniformity ($D = 0.167$, $p < 0.001$).

Influence of individual traits on foraging tactics

The multi-membership model (cooperative ties ~ frequency + experience + expertise + dependency + reputation + friendship + kinship + mm(fisher_i + fisher_j)) suggested a significant effect of the similarity in one foraging trait and in three social traits on the choice for cooperative partners (Table 1). Similarity in the number of months per year dedicated to net-casting with dolphins (frequency), in the propensity to fish with relatives (kinship), and in the connectedness with other close fisher friends (friendship), all had a positive influence on the chance of individuals to form a cooperative foraging tie. By contrast, the peer reputation as a skilled and successful fisher (reputation) had a negative effect on the incidence of cooperative ties (Supplementary Figs. S4, S5). Each of the modules in the fishers' social network representing cooperative foraging groups varied in these traits, but overall members of such groups tended to fish frequently during the year, fish with close relatives, have more close friends among the local fishers, and have both high and low reputation. By contrast, the solitary fishers were more variable in the fishing frequency and had few local close friends and low reputation (Supplementary Fig. S6). Similarity around the other foraging behaviour traits—general fishing experience, expertise in, and economical dependency on, interacting with dolphins—did not significantly influence the choice between solitary and social foraging tactics, expressed by their partner choices (Table 1).

Discussion

In mapping the social interactions among net-casting fishers during a rare fishery with wild dolphins in southern Brazil, we found that fishers who engage in cooperative groups experience different foraging and social returns than those who fish solitarily. We also found that key individual traits—differences in peer reputation and similarities in fishing frequency, number of close friends, and tendency to fish with close relatives—influence the fishers' propensity for social foraging. While the decision to cooperate or not within this traditional fishery is primarily influenced by the fish caught, the fishers' characteristics can play a role in the decision of whom to cooperate with, if anyone. These findings reinforce that human social foraging decisions are primarily influenced by material gains from foraging but suggest that such decisions can also be influenced by non-material benefits accrued from socializing with similar individuals.

Benefits of different foraging tactics

We documented different foraging benefits, both perceived and accrued, among the artisanal fishers who form cooperative groups or not when net-casting with wild dolphins. When investigating the fishers' perceptions about the benefits of social foraging, we found that all cooperative fishers identify several benefits in fishing in groups. As with other human foragers (e.g. Hill 2002), the artisanal fishers commonly report opportunities for sharing the labour and their returns—here, sharing fishing spots, larger catches, assistance in selling the catch—which can be interpreted as a form of energy optimization. Theory suggests that foraging in cooperative groups can increase prey capture (e.g. Giraldeau and Caraco 2000) but also imply in less energy expenditure (Dyble et al. 2016); in our case, when one fisher is in the water interacting with dolphins, the others can optimize the group's time by selling their catch or resting before their turn to go fish. In line with the evidence that hunters and fishers tend to share resources with others who have previously helped and with those with whom they trust (e.g. Gurven et al. 2000; Apicella et al. 2012; Bliege and Power 2015), another benefit of forming cooperative groups perceived by the artisanal fishers is the possibility of sharing the immediate catch and/or its resultant cash, and to reciprocate in further fishing events. Reciprocity can be beneficial in the unstable environment of fisheries (Begossi 1992) when the delays to reciprocate are likely to be short enough to translate into material benefits (Hawkes 1992; Begossi 2014). By fishing together, fishers can rely on their partners' success, which on average increases the per capita profit compared to when they fish alone (e.g. Alvard and Nolin 2015). On the other hand, most net-casting fishers who fish solitarily do not perceive any benefits in cooperating; they mostly reported that the main cost of cooperation is the risk of having to share their catch with inexperienced, usually unsuccessful fishers, thereby reducing their potential per capita gain.

Resource sharing implies that the decision about forming a cooperative foraging group also depends on the number of individuals in that group (e.g. Clark and Mangel 1986; Krause and Ruxton 2002). Being a member of large cooperative groups may increase the collective effort, but it may also reduce the individual payoffs, especially when the resources

Table 1 The influence of individual traits on the cooperative ties of artisanal net-casting fishers who interact with wild dolphins. The engagement of fishers in social foraging (i.e. binary cooperative ties in the social network) could be influenced by four individual traits related to foraging behaviour and the access to material benefits (e.g. fish and resulting cash), and to three individual traits related to their social environment and potential access to non-material benefits (e.g. social prestige and connectedness). Each trait is briefly described, along with their measure, type, context, and potential resulting benefit. A Markov Chain Monte Carlo generalized linear mixed model (MCMC GLMM) with categorical error distribution and log link function aims to explain the incidence of cooperative ties among fishers (response variable) as a function of the trait similarity among dyads of artisanal fishers (independent variables), considering the individual fishers' identities (multilevel random effects). Statistical significance is given by the credible intervals (95% high posterior density, HPD) of the posterior distribution (Posterior mean) not overlapping with zero (Supplementary Figs S4, S5), here indicated by asterisks (MCMC $p < 0.05$)

Individual traits of fishers		Trait context (and potential benefit)	MCMC GLMM						
Trait description	Measure (variable type)		Model part	Variable describing trait similarity among dyads	Posterior mean	Low HPD	High HPD	Effective sample size	MCMC p
Engagement in social foraging	Self-reported cooperative ties with other fishers in the social network (binary)	Social foraging	Response variable	Cooperative ties	-	-	-	-	-
-	-	Fisher identity	Multilevel random effects	mm (fisher_i + fisher_j)	4.912	1.922	8.755	72.10	-
-	-	-	Intercept	-	−12.300	−16.859	−8.902	100.0	< 0.01*
Frequency of fishing with dolphins	Number of months per year dedicated to net-casting with dolphins (continuous)	Foraging behaviour (material)	Independent variable	Frequency	2.627	1.376	4.012	175.20	< 0.01*
General fishing experience	Age in years (continuous)	Foraging behaviour (material)	Independent variable	Experience	0.773	−1.596	4.396	100.0	0.580
Expertise in interacting with dolphins	Years of practice net-casting with dolphins (continuous)	Foraging behaviour (material)	Independent variable	Expertise	1.110	−2.182	4.418	100.0	0.520
Economic dependence on fishing with dolphins	Whether and individual is full-time or part-time fisher (categorical)	Foraging behaviour (material, non-material)	Independent variable	Dependency	0.477	−0.297	1.434	100.0	0.340
Peer reputation as skilled and successful fisher	How many times each fisher was cited by other local fishers as being the most skilled or successful in fishing with dolphins (continuous)	Social environment (non-material)	Independent variable	Reputation	−3.782	−7.451	−1.267	100.0	< 0.01*
Friendship connectedness	How many times each fisher was cited by other local fishers as being their close friends (continuous)	Social environment (non-material)	Independent variable	Friendship	6.480	4.187	9.995	100.0	< 0.01*

Table 1 (continued)

Individual traits of fishers			MCMC GLMM						
Trait description	Measure (variable type)	Trait context (and potential benefit)	Model part	Variable describing trait similarity among dyads	Posterior mean	Low HPD	High HPD	Effective sample size	MCMC p
Propensity to fish with close relatives	Whether other local net-casting fishers are close relatives or unrelated individuals (categorical)	Social environment (material, non-material)	Independent variable	Kinship	0.899	0.185	1.876	100.0	0.040*

are scarce. During our study in 2019, the net-casting fishers of Laguna experienced an atypically unproductive mullet season: there were only a few catches compared to previous mullet seasons at the same beach, which aligns with the current trend of overexploitation of the mullet stock in southern Brazil (Sant'Ana et al 2017; de Abreu-Mota et al. 2018; Machado et al. 2021). We found that cooperative fishers tend to outperform solitary fishers and catch more mullets per capita; however, we also found a high variation in individual catches. It is possible that the perception about the benefits of cooperation reported by the cooperative net-casting fishers was informed by previous, more productive years where the fishing success rate was higher. In a scenario of high fluctuation in fish availability, the payoffs of both foraging tactics may change. If these fluctuations result in a higher probability of failure per net cast, cooperative fishers may still outperform solitary fishers. If the availability starts to drop—meaning there are fewer fish to be caught by both cooperative and solitary fishers—solitary fishers may end up obtaining more fish per capita since they do not share their catch with others, but cooperative fishers can still enjoy some of their social benefits in maintaining cooperative ties and close social relationships with others. However, should the low fish availability persist for years, we hypothesize that cooperativeness among fishers would tend to disappear, with solitary foraging prevailing as the dominant tactic.

Individual traits and foraging choices

While the social network of the artisanal net-casting fishers is clearly structured into sets of individuals who form or not cooperative groups when fishing with dolphins, it is not immediately clear whether individual characteristics or social preferences contribute to such structure around foraging tactics. We speculate that the decision to form cooperative groups or fish solitarily is not only an individual but also a collective decision. That is, while an individual net-casting fisher can choose between cooperating or not with other fishers, some of his individual traits may be considered key requirements for this individual to be accepted by a cooperative group. We found that similarities and disparities in key individual traits related to foraging and social behaviour of net-casting fishers can explain—at least partially—the use of one foraging tactic over another.

Among the foraging traits, there was an assortment among fishers who are more frequently at the interaction site. Since co-occurrence in space and time is a requisite for social and foraging interactions (e.g. Cantor et al. 2012), in theory, the more frequent the fishers are at the fishing site, the more chances for social interaction they have. Among the dolphins, for example, the individuals that are more frequently at the interaction sites foraging with net-casting fishers are those who form stronger and more cohesive social groups in other contexts (Machado et al. 2019a). Repeated interactions form the basis of more elaborated social relationships (Hinde 1976) including cooperation, because repeated interactions create opportunities for reciprocity over time (see Axelrod and Hamilton 1981). Thus, compared to the fishers who only occasionally net-cast in that area, the fishers who are often fishing with dolphins have plenty of opportunities to re-encounter and cooperate with one another. Some of the evidence for this process comes from studies with other primates, where repeated social interactions between the same individuals lead to the development of trust and promote the emergence of reciprocity (Puga-González and Sueur 2017)—a pathway for cooperation (Trivers 1971).

It is possible that fishers who are more frequently fishing with dolphins are also the most skilled, and so the most successful, fishers. Thus, we expected the assortment around frequency of fishing to also represent, indirectly, an assortment around similar foraging success. Human foragers, in general, tend to search for opportunities to interact and share information with others with similar skills (Conley and Udry 2010; Alexander et al. 2018). This idea aligns with the evidence that (i) fishers accumulate over time a specific knowledge about fishing techniques and the suitable ecological conditions for fishing (Johannes et al. 2008), and that (ii) being more experienced can lead to higher fishing success (Branch et al. 2006). However, we did not find evidence for cooperative foraging among fishers to be directly influenced by similarity among individuals in traits related to fishing experience—measured in terms of age, years of net-casting practice, and economic dependence on fishing with dolphins. While in theory, a combination of active social preferences around fishing experience could contribute to the formation of more, or stronger, cooperative ties among artisanal fishers, our data on foraging traits points primarily to the fishing frequency at the same site influencing the formation of cooperative groups.

Regarding the social traits that could influence with whom fishers tend or not to form cooperative groups, we found that cooperative fishers tend to have close relatives and more close friends fishing in the area, as well as higher social reputation. Fishing cooperatively with genetically related others could be interpreted in light of inclusive fitness (Hamilton 1964), or simply through the tendency to develop trust relationships with familiar individuals (e.g. Begossi 2014). The number of close friends among the local fishers is an indication of social embeddedness, i.e. how socially connected a fisher is within the community. We found that fishers with similar number of friends tend to form cooperative ties among themselves, which highlights how social capital could influence the decision on whom to cooperate with and reinforces the idea that humans are more willing to cooperate with trusted partners than with strangers, especially when cooperating is costly (e.g. Markovits et al. 2003; Apicella et al. 2012). Different than friendship that represents social proximity between individuals, peer reputation indicates how skilled and successful in fishing with dolphins individuals are perceived to be. We posit that low-reputation fishers may not be successful in developing cooperative ties or other relationships of trust with other local fishers, which could explain why solitary fishers have few or no close friends, and were rarely perceived as successful fishers in the context of the fishery with dolphins. Some solitary fishers may also be less connected to the social life of the community at large and so experience lower reputation—this may be especially the case of visitors and part-time fishers who do not have many other opportunities to socialize with local fishers. The dissortative effect of reputation on the propensity to form cooperative ties suggests that the more different the reputation rank between fishers, the more likely they are to cooperate with each other. This pattern may reflect high-reputation fishers avoiding cooperating with each other, or low-reputation fishers seeking to join cooperative foraging groups containing high-reputation fishers because associations with such high-status individuals can translate into social privilege and greater access to information and resources (Henrich and Gil-White 2001; von Rueden 2020). Overall, our findings reinforce that the decision to engage in social foraging may be driven by individual payoffs, but they also highlight that the decision of whom to cooperate is, at least partially, influenced by the traits of the individual foragers.

Concluding remarks and implications

The human side of this positive dolphin-fisher interaction is characterized by a social network of artisanal net-casting fishers structured by cooperative and solitary foraging. We found that forming cooperative foraging groups can be beneficial for fishers, and that the formation of such groups is influenced by some of their individual foraging and social traits. We expect that highly productive fishing years can guarantee the material returns of both social and individual foraging tactics, thereby supporting the persistence of both the fishers' cooperative ties and the persistence of the traditional fishery with dolphins as a whole. Should the fish availability tend to decline (Sant'Ana et al 2017; de Abreu-Mota et al. 2018), the cooperative ties among fishers could be replaced by competitive ones in response to resource scarcity, and the non-material benefits of these social relationships are unlikely to outweigh the need for monetary or energetic returns.

A possible outcome of this change is the traditional fishery with dolphins to become restricted to amateur and opportunistic solitary fishers who do not depend economically on fishing (Machado et al. 2019b) but are more interested in other non-material services provided by the interaction with dolphins—recreation, a sense of place, and need to be part of a community (Machado et al. 2019b)—and thereby engage in this fishery moved by its intrinsic cultural values. Should that be the case, fishers who currently rely on fishing with dolphins as a main source of income could be excluded from the tradition. Both changes—in the payoffs of the foraging tactics and in the composition of the fishing community that interacts with dolphins—could have implications for the persistence of this century-old tradition in years to come, highlighting that understanding fisher behaviour is an important component of fisheries management (Fulton et al. 2011; Andrews et al. 2021).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03152-2.

Acknowledgements We are deeply grateful to the fishers for their collaboration. We thank all researchers and volunteers who helped with data sampling (J.V.S. Valle-Pereira, A.M.S. Machado, C. Bezamat, B. Romeu, E. Erdhardt, D.R. Farine, P.V. Castilho, N. da Silva, L.F. da Rosa, C.F. Alves), and field logistics (P.V. Castilho); D.R. Farine, J.V.S. Valle-Pereira, and A.M.S. Machado for insightful discussions; and S. Zank, P.C. Simões-Lopes, M.S. Dechoum, D. Herbst, P. Lopes, and two anonymous reviewers for comments on our manuscripts.

Author contribution BS-S: data sampling, data analyses, writing. NH: study design, writing, editing, revising, supervision. FGD-J: data analyses, editing, revising. MC: study conception and design, data analyses, writing, editing, revising, supervision. The manuscript was approved by all authors.

Funding Open Access funding enabled and organized by Projekt DEAL. This study was supported by research grants from the Animal Behaviour Society, the National Geographic Society (Discovery Grant WW210R-17), the Max Planck Society, the Max Planck Digital Library, and it is part of the Brazil-Germany PROBRAL Research Program funded jointly by CAPES and the Deutscher Akademischer Austauschdienst (CAPES-DAAD 23038.002643/2018–01) and the SELA Long-Term Ecological Research Program (PELD CNPq, 445301/2020–1). BS-S. received a MSc scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, CAPES-Brazil (Finance Code 01); NH received a research productivity scholarship from Conselho Nacional de Ciência e Desenvolvimento Científico e Tecnológico, CNPq-Brazil (304515/2019–1); FGD-J received a research productivity scholarship from Conselho Nacional de Ciência e Desenvolvimento Científico e Tecnológico, CNPq-Brazil (308867/2019–0) and was supported by Fundação de Amparo à Pesquisa do Estado de Santa Catarina (FAPESC 2021TR387); MC was supported by CAPES (88881.170254/2018–01) and the Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior.

Data availability We provide all the (anonymized) data in the open-access repository: https://bitbucket.org/maucantor/social_fishers/src/master/socialfishers_data/

Code availability We provide all the (customized) R code to replicate the analyses and Figs in the open-access repository: https://bitbucket.org/maucantor/social_fishers/src/master/

Declarations

Ethics approval This study was approved by the ethics committee at Universidade Federal de Santa Catarina, Brazil (CEPSH 06457419.6.0000.0121). All personal data were anonymized.

Consent to participate All people interviewed signed a free informed consent to participate in this research. Each person was interviewed individually.

Conflict of interest The authors declare no competing interests.

References

Alexander SM, Bodin Ö, Barnes ML (2018) Untangling the drivers of community cohesion in small-scale fisheries. Int J Commons 12:519–547. https://doi.org/10.18352/ijc.843

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267. https://doi.org/10.1163/156853974X00534

Alvard MS, Nolin DA (2015) Rousseau's whale hunt? Coordination among big-game hunters. Curr Anthropol 43:533–559. https://doi.org/10.1086/341653

Andrews EJ, Pittman J, Armitage DR (2021) Fisher behaviour in coastal and marine fisheries. Fish Fish 22:489–502. https://doi.org/10.1111/faf.12529

Apicella CL, Marlowe FW, Fowler JH, Christakis NA (2012) Social networks and cooperation in hunter-gatherers. Nature 481:497–501. https://doi.org/10.1038/nature10736

Axelrod R, Hamilton W (1981) The evolution of cooperation. Science 211:1390–1396

Barnes M, Kalberg K, Pan M, Leung PS (2016) When is brokerage negatively associated with economic benefits? Ethnic diversity, competition, and common-pool resources. Soc Networks 45:55–65. https://doi.org/10.1016/j.socnet.2015.11.004

Bartoń K (2018) MuMIn: Multi-model inference. R package version 1.42.1, https://CRAN.R-project.org/package=MuMIn

Beauchamp G (2014) Social predation: how group living benefits predators and prey. Academic Press, London

Begossi A (1992) Fishing activities and strategies at Búzios Island (Brazil). In: Meyer R, Zhang C, Windsor ML, McCay BJ, Hushak LJ, Muth RM (eds) Proceedings of the World Fisheries Congress, Theme 2, Athens, May 1992. Fisheries resources and utilization, Oxford and IBH Pub. Co, Calcutta, 1996, pp 125–141

Begossi A (2014) Ecological, cultural, and economic approaches to managing artisanal fisheries. Environ Dev Sustain 16:5–34

Begossi A, Richerson PJ (1992) The animal diet of families from Búzios Island (Brazil): an optimal foraging approach. J Hum Ecol 3:433–458
Bernard HR (2006) Research methods in anthropology: qualitative and quantitative approaches. Rowman & Littlefield Publishers, Walnut Creek
Bliege BR, Power EA (2015) Prosocial signaling and cooperation among Martu hunters. Evol Hum Behav 36:389–397. https://doi.org/10.1016/j.evolhumbehav.2015.02.003
Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135. https://doi.org/10.1016/j.tree.2008.10.008
Branch TA, Hilborn R, Haynie AC et al (2006) Fleet dynamics and fishermen behavior: lessons for fisheries managers. Can J Fish Aq Sci 63:1647–1668. https://doi.org/10.1139/F06-072
Burnham KP, Anderson DR (2002) A practical information-theoretic approach. Model selection and multimodel inference. Springer, New York
Cantor M, Wedekin LL, Guimarães PR Jr, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC (2012) Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. Anim Behav 84:641–651. https://doi.org/10.1016/j.anbehav.2012.06.019
Cantor M, Pires MM, Marquitti FMD et al (2017) Nestedness across biological scales. PLoS ONE 12:e0171691. https://doi.org/10.1371/journal.pone.0171691
Carpenter J, Seki E (2011) Do social preferences increase productivity? Field experimental evidence from fishermen in Toyama Bay. Econ Inq 49:612–630. https://doi.org/10.1111/j.1465-7295.2009.00268.x
Carter KD, Brand R, Carter JK, Shorrocks B, Goldizen AW (2013) Social networks, long-term associations and age-related sociability of wild giraffes. Anim Behav 86:901–910. https://doi.org/10.1016/j.anbehav.2013.08.002
Christakis NA (2019) Blueprint: the evolutionary origins of a good society. Little, Brown Spark, New York
Clark W, Mangel M (1986) The evolutionary advantages of group foraging. Theor Popul Biol 75:45–75. https://doi.org/10.1016/0040-5809(86)90024-9
Conley TG, Udry CR (2010) Learning about a new technology: pineapple in Ghana. Am Econ Rev 100:35–69. https://doi.org/10.1257/aer.100.1.35
Creel S (1997) Cooperative hunting and group size: assumptions and currencies. Anim Behav 54:1319–1324. https://doi.org/10.1006/anbe.1997.0481
da Rosa DS, Hanazaki N, Cantor M, Simões-Lopes PC, Daura-Jorge FG (2020) The ability of artisanal fishers to recognize the dolphins they cooperate with. J Ethnobiol Ethnomed 16:30. https://doi.org/10.1186/s13002-020-00383-3
Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simões-Lopes PC (2012) The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biol Lett 8:702–705. https://doi.org/10.1098/rsbl.2012.0174
de Abreu-Mota MA, Medeiros RP, Noernberg MA (2018) Resilience thinking applied to fisheries management: perspectives for the mullet fishery in southern-southeastern Brazil. Reg Environ Change 18:2047–2058
Dyble M, Thompson J, Smith D, Salali GD, Chaudhary N, Page AE, Vinicius L, Mace R, Migliano AB (2016) Networks of food sharing reveal the functional significance of multilevel sociality in two hunter-gatherer groups. Curr Biol 26:2017–2021. https://doi.org/10.1016/j.cub.2016.05.064
Fowler JH, Christakis NA (2008) Dynamic spread of happiness in a large social network: longitudinal analysis over 20 years in the Framingham Heart Study. BMJ 337:a2338–a2338. https://doi.org/10.1136/bmj.a2338
Fulton EA, Smith AD, Smith DC, van Putten IE (2011) Human behaviour: the key source of uncertainty in fisheries management. Fish Fish 12:2–17. https://doi.org/10.1111/j.1467-2979.2010.00371.x
Galef BG Jr, Giraldeau LA (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 61:3–15. https://doi.org/10.1006/anbe.2000.1557
Giraldeau LA, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton
Gurven M, Allen-Arave W, Hill K, Hurtado M (2000) "It's a wonderful life": signaling generosity among the Ache of Paraguay. Evol Hum Behav 21:263–282. https://doi.org/10.1016/S1090-5138(00)00032-5
Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J Stat Softw 33:1–22
Hamilton WD (1964) The genetical evolution of social behaviour, I. J Theor Biol 7:1–16. https://doi.org/10.1016/0022-5193(64)90038-4
Hart JDA, Weiss MN, Brent LJN, Franks DW (2021) Common permutation methods in animal social network analysis do not control for non-independence. bioRxiv. https://doi.org/10.1101/2021.06.04.447124
Hartig F (2019) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1, https://cran.r-project.org/web/packages/DHARMa/index.html
Hawkes K, O'Connell JF, Blurton Jones NG (1991) Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet. Phil Trans R Soc B 334:243–251
Hawkes K (1992) Sharing and collective action. In: Smith EA, Winterhalder B (eds) Evolutionary ecology and human behaviour. Aldine de Gruyter, Hawthorne, NY, pp 269–300
Henrich J, Gil-White F (2001) The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol Hum Behav 22:165–196. https://doi.org/10.1016/S1090-5138(00)00071-4
Hill K (2002) Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate. Hum Nat 13:105–128. https://doi.org/10.1007/s12110-002-1016-3
Hinde RA (1976) Interactions, relationships and social structure. Man 11:1–17. https://doi.org/10.2307/2800384
Holt-Lunstad J, Smith TB, Layton JB (2010) Social relationships and mortality risk: a meta-analytic review. PLoS Med 7:859. https://doi.org/10.1371/journal.pmed.1000316
Hruschka DJ (2010) Friendship: development, ecology and evolution of a relationship. University of California Press, Berkeley
Johannes RE, Freeman MMR, Hamilton RJ (2008) Ignore fishers' knowledge and miss the boat. Fish Fish 1:257–271. https://doi.org/10.1111/j.1467-2979.2000.00019.x
Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, New York
Lyle HF, Smith EA (2014) The reputational and social network benefits of prosociality in an Andean community. P Natl Acad Sci USA111:4820–4825. https://doi.org/10.1073/pnas.1318372111
MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609. https://doi.org/10.1086/282454
Machado AMS, Cantor M, Costa APB, Righetti BPH, Bezamat C, Valle-Pereira JVS, Simões-Lopes PC, Castilho PV, Daura-Jorge FG (2019) Homophily around specialized foraging underlies dolphin social preferences. Biol Lett 15:20180909. https://doi.org/10.1098/rsbl.2018.0909
Machado AMS, Daura-Jorge FG, Herbst DF, Simões-Lopes PC, Ingram SN, de Castilho PV, Peroni N (2019) Artisanal fishers' perceptions of the ecosystem services derived from a

dolphin-human cooperative fishing interaction in southern Brazil. Ocean Coast Manage 173:148–156. https://doi.org/10.1016/j.ocecoaman.2019.03.003

Machado AMS, Giehl EL, Fernandes LP, Ingram SN, Daura-Jorge FG (2021) Alternative data sources can fill the gaps in data-poor fisheries. ICES J Mar Sci 78:1663–1671. https://doi.org/10.1093/icesjms/fsab074

Magnusson A, Skaug HJ, Nielsen A, Berg CW, Kristensen K, Maechler M, van Bentham KJ, Bolker BM, Brooks ME (2017) glmmTMB: Generalized linear mixed models using template model builder. R package v. 0.1.3, https://cran.r-project.org/web/packages/glmmTMB/index.html

Markovits H, Benenson JF, Kramer DL (2003) Children and adolescents' internal models of food-sharing behavior include complex evaluations of contextual factors. Child Dev 74:1697–1708

McPherson M, Smith-Lovin L, Cook JM (2001) Birds of a feather: homophily in social networks. Ann Rev Sociol 27:415–444. https://doi.org/10.1146/annurev.soc.27.1.415

Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. Phys Rev E 69:1–15. https://doi.org/10.1103/PhysRevE.69.026113

Peterson D, Hanazaki N, Simões-Lopes PC (2008) Natural resource appropriation in cooperative artisanal fishing between fishermen and dolphins (*Tursiops truncatus*) in Laguna, Brazil. Ocean Coast Manage 51:469–475. https://doi.org/10.1016/j.ocecoaman.2008.04.003

Pryor K, Lindbergh J, Lindbergh S, Milano R (1990) A dolphin-human fishing cooperative in Brazil. Mar Mamm Sci 6:77–82. https://doi.org/10.1111/j.1748-7692.1990.tb00228.x

Puga-González I, Sueur C (2017) Friendships and social networks in an individual-based model of primate social behaviour. JASS 20:10. https://doi.org/10.18564/jasss.3450

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reyes-García V, Gallois S, Demps K (2016) A multi-stage learning model for cultural transmission: Evidence from three indigenous societies. In: Terashima H, Hewlett B (eds) Social learning and innovation in contemporary hunter-gatherers: Evolutionary and ethnographic perspectives. Springer, Heidelberg, pp 47–60

Rosenquist JN, Fowler JH, Christakis NA (2011) Social network determinants of depression. Mol Psychiat 16:273–281. https://doi.org/10.1038/mp.2010.13

Sant'Ana R, Kinas PG, Miranda LV, Schwingel PR, Castello JP, Vieira JP (2017) Bayesian state-space models with multiple CPUE data: the case of a mullet fishery. Sci Mar 81:361–370. https://doi.org/10.3989/scimar.04461.11A

Schensul SL, Schensul JJ, Lecompte MD (1999) Essential ethnographic methods: observations, interviews and questionnaires. Rowman and Littlefield, Walnut Creek

Silvano RAM, MacCord PFL, Lima RV, Begossi A (2006) When does this fish spawn? Fishermen's local knowledge of migration and reproduction of Brazilian coastal fishes. Environ Biol Fish 76:371–386

Simões-Lopes PC, Fabián ME, Menegheti JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. Revta Bras Zool 15:709–726. https://doi.org/10.1590/S0101817519980003000016

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Turner RA, Polunin NVC, Stead SM (2014) Social networks and fishers' behaviour: exploring the links between information flow and fishing success in the Northumberland lobster fishery. Ecol Soci 19:38. https://doi.org/10.5751/ES-06456-190238

van Putten IE, Kulmala S, Thébaud O, Dowling N, Hamon KG, Hutton T, Pascoe S (2012) Theories and behavioural drivers underlying fleet dynamics models. Fish Fish 13:216–235. https://doi.org/10.1111/j.1467-2979.2011.00430.x

von Rueden C (2020) Making and unmaking egalitarianism in small-scale human societies. Curr Opin Psychol 33:167–171. https://doi.org/10.1016/j.copsyc.2019.07.037

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Bruna Santos-Silva[1] · Natalia Hanazaki[1] · Fábio G. Daura-Jorge[1] · Mauricio Cantor[1,2,3]

1 Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88040-900, Brazil

2 Department of Fisheries, Wildlife and Conservation Sciences, Marine Mammal Institute, Oregon State University, Newport, OR 97365, USA

3 Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Radolfzell, BW 78315, Germany