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Spatial consequences for dolphins specialized in foraging with fishermen

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According to theory, individuals forage in ways that maximize net energy intake. Distinct foraging strategies may emerge within a population in response to heterogeneous resources, competition and learning, among other drivers. We assessed individual variation in, and ecological consequences of, an unusual, specialized foraging tactic between animals and humans. In southern Brazil, bottlenose dolphins, *Tursiops truncatus*, herd fish schools towards artisanal fishermen, who cast nets in response to behavioural cues from the dolphins. This apparent cooperative tactic likely involves costs as well as benefits for both interacting parties, but such trade-offs remain poorly understood, especially for dolphins. We show that individual dolphins vary markedly in the frequency with which they interact with fishermen, and that this foraging variation is linked to ranging behaviour. Not all individual dolphins interact with fishermen; those that routinely do so concentrate around the limited interaction sites and have smaller home ranges than independent foragers. This suggests that foraging with fishermen increases foraging success and reduces search costs (i.e. foraging range). Competition for interaction sites may offset such benefits, since some individuals often forage at the high-quality sites while others forage at low-quality sites. Taken together, our findings suggest that two alternative tactics emerge in the population from trade-offs involving food access, foraging area, learning techniques and competition: dolphins either forage by themselves over larger areas on unpredictable resource patches (passing fish schools), or learn to interact with fishermen to access and compete for more predictable resource patches (interaction sites). By revealing some of the ecological drivers of this remarkable human–animal interaction, our study contributes two broader insights. First, specialized foraging can have ranging consequences for individuals and so structure the population spatially; second, interspecific cooperation may be founded upon intraspecific competition.

Individuals are different. Variation between individuals is fundamental in evolutionary theory as it is upon such differences that natural selection operates. However, traditional ecological theory implicitly assumed that individuals of the same species are ecologically equivalent, overlooking individual variation as noise (see Bolnick et al., 2011; Wolf & Weissing, 2012). The last decade has seen a surge in studies addressing intra- and interpopulation variation (e.g. Réale et al., 2010; Sih, Bell, & Johnson, 2004), explicitly recognizing that individual animals differ genetically and phenotypically, and so behave in different ways.

Different foraging tactics lead to heterogeneous resource use within populations (e.g. Bolnick et al., 2003; Estes, Riedman, Staedler, Tinker, & Lyon, 2003) and may emerge from individual differences in age, sex, competitive ability and/or personality types related to resource exploitation (e.g. Bolnick et al., 2011; Sih et al., 2004). Such variation may increase fecundity and reduce mortality risk and competition within and between species (e.g. Araújo, Bolnick, & Layman, 2011; Biro & Stamps, 2008), ultimately affecting demographic parameters (Violle et al., 2012) and ecological networks (e.g. Dupont, Trøjelsgaard, & Olesen, 2011). Given such broad implications, understanding the causes and implications of behavioural variation among conspecifics is important in ecology and evolution (Bolnick et al., 2011).

The cognitive abilities of cetaceans, along with the unpredictability of the three-dimensional marine environment, make them excellent subjects to study individual behavioural variation (see Whitehead & Rendell, 2014, and references therein). The behavioural repertoires of bottlenose dolphins (*Tursiops* spp.), for example, vary markedly both within and between populations,

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especially due to diverse foraging strategies. For instance, a remarkable array of foraging specializations exists among sets of individuals within the population of Shark Bay, Western Australia, including the use of large shells to entrap fish (Allen, Bejder, & Krützen, 2011) and use of marine sponges as a tool to dislodge prey from the seafloor (e.g. Mann, Stanton, Patterson, Bienenstock, & Singh, 2012). Another remarkable foraging specialization occurs in southern Brazil, where some dolphins forage with the assistance of artisanal fishermen (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Peterson, Hanazaki, & Simões-Lopes, 2008; Simões-Lopes, Fabián, & Menegheti, 1998). This so-called 'cooperative fishing' is a distinctive foraging tactic involving coordinated behaviour, perhaps also mutually understood signalling, between two top predators in two different environments (Simões-Lopes et al., 1998; Zappes, Andriolo, Simões-Lopes, & Di Beneditto, 2011).

On the aquatic side, small groups of adult dolphins chase fish schools towards shallow waters where fishermen stand in line or on moored canoes. On the terrestrial side, fishermen cast their nets in response to the dolphins' stereotyped behavioural cues (Peterson et al., 2008; Simões-Lopes et al., 1998). This interspecific interaction is highly localized and occurs between artisanal fishermen and the small and highly resident population of bottlenose dolphins of Laguna nearly every day (Daura-Jorge et al., 2012; Simões-Lopes, Daura-Jorge, & Cantor, 2016; Simões-Lopes et al., 1998). However, not all local net-casting fishermen know how to fish with dolphins (Peterson et al., 2008); similarly, not all dolphins interact with fishermen (Daura-Jorge et al., 2012). This partial participation suggests that this interspecific foraging tactic is individually specialized (see Bolnick et al., 2003; Patrick & Weimerskirch, 2014) and as such, the decision to participate or not may reflect a cost–benefit balance for both individual fishermen and individual dolphins.

As in other rare cases of foraging interactions between humans and wild animals (Spottiswoode, Begg, & Begg, 2016), the dolphin–fisherman tactic seems to benefit both interacting parties (Simões-Lopes et al., 1998). Fishermen catch larger and more fish when interacting with dolphins than when fishing alone (Simões-Lopes et al., 1998). Dolphins likely reap similar benefits (Simões-Lopes et al., 1998, 2016). However, the energetic trade-offs and ecological consequences of this foraging tactic are much less clear. Assessing payoffs and foraging performance of individual dolphins is far more challenging because these interactions take place in water with limited visibility. Considering that prey distribution and foraging strategy modulate the use of space in many animal taxa (e.g. Schofield et al., 2010; Towner et al., 2016) and that energy expenditure during foraging is directly related to the area covered (Pyke, Pulliam, & Charnov, 1977), if cooperative fishing between fishermen and dolphins is indeed advantageous, then individuals of both species that routinely use this tactic should concentrate their foraging activities around sites where such interactions occur. Artisanal fishermen from Laguna show a high degree of site fidelity, typically using the same fishing sites, close to their homes (Peterson et al., 2008). We hypothesized that individual dolphins that interact with fishermen have home ranges concentrated around cooperative fishing sites and so benefit by not having to travel widely to find food, while dolphins that do not interact with fisherman have to forage over larger areas to meet their energetic requirements.

Our aim was to investigate whether individual foraging variation, here represented by how often dolphins partake in interactions with artisanal fishermen, has broader consequences on behaviour. Our overarching hypothesis was that such a specialized foraging tactic alters how individuals interact with their physical environment. First, we evaluated whether individual dolphins varied in the frequency with which they interacted with fishermen and whether their interaction frequency was related to their home range size. If home range decreases with the relative frequency of cooperative foraging, then this foraging tactic may offer positive ecological outcomes in terms of reducing spatial requirements. Second, we evaluated whether individual dolphins varied in the frequency with which they used interaction sites. Such individual variation would suggest some degree of resource partitioning (prey, space) resulting from intraspecific competition at higher-quality sites. We discuss how the two alternative foraging tactics—interacting with fishermen or foraging independently—emerge from energetic trade-offs, and how social and ecological processes interact and contribute to their maintenance at the population level.

METHODS

Data Sampling

Between 2007 and 2009, we carried out 95 daily surveys using a 5 m boat in the lagoon system adjacent to Laguna, southern Brazil (28°30′S, 48°502′W), to record foraging and ranging behaviour of all individuals of the small and highly resident bottlenose dolphin population (Daura-Jorge, Ingram, & Simões-Lopes, 2013). We looked for groups of dolphins while evenly sampling the study area both spatially (always including the five fishing sites where the dolphin–fisherman interactions occurred) and temporally (carrying out a similar number of field surveys throughout the year) (details on sampling effort in Daura-Jorge et al., 2012). Groups were defined as all individuals in close proximity (within a 50 m radius of each other) and engaged in similar behaviour (as in Daura-Jorge et al., 2012). For every dolphin group encountered, we performed a 20 min photo-identification session and recorded location, time, number of individuals and behaviour. All individuals were identified and catalogued based on long-lasting natural marks on the dorsal fin (as in Daura-Jorge et al., 2012; Daura-Jorge et al., 2013). To properly identify all group members, we took at least four photos from both sides of the dorsal fin of all individuals, without preferences; we interrupted the photo-identification session whenever any individual entered or left the focal group, and we discarded data from individuals with no identifiable marks, including all calves.

We classified foraging behaviour based on previous long-term studies with this population (Simões-Lopes et al., 1998, 2016). 'Noncooperative foraging' was characterized by dolphins diving frequently, asynchronously and in various directions; that is, foraging independently of artisanal net-casting fishermen. 'Cooperative foraging' was characterized by dolphins driving fish schools towards fishermen and performing one of four stereotyped behaviours (back presentation, head slap, partial emersion, tail slap) that fishermen interpret as the cue to the correct time to cast their nests (see Simões-Lopes et al., 1998). Importantly, fishermen never provision dolphins with fish (see their informal ruling system in Peterson et al., 2008). We emphasize that the foraging classes 'noncooperative' and 'cooperative' are used relative to their interactions with the fishermen, not with other dolphins; in both situations, dolphins may or may not cooperate with each other and this was irrelevant to our analyses.

At each cooperative fishing site, we also recorded the number of cooperative foraging events of each photo-identified dolphin. The five cooperative fishing sites included in our study were close to each other (see Results) but differed in four key aspects: area, depth, proximity to the sea and number of fishermen engaged. At one end, cooperative site 'A' was the deepest and was closest to the mouth of the canal, where there were typically 10–50 fishermen. At the other end, site 'E' was the shallowest and was further inside