UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Alexandre Marcel da Silva Machado

O efeito do ambiente e das diferenças individuais em um mutualismo entre botos e pescadores

Florianópolis
2024

Alexandre Marcel da Silva Machado

O efeito do ambiente e das diferenças individuais em um mutualismo entre botos e pescadores

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina como requisito parcial para a obtenção do título de Doutor em Ecologia.

Orientador: Prof. Fábio G. Daura-Jorge, Dr.
Coorientador: Prof. Mauricio Cantor, Dr.

Florianópolis
2024

Machado, Alexandre Marcel da Silva
O efeito do ambiente e das diferenças individuais em um mutualismo entre botos e pescadores / Alexandre Marcel da Silva Machado ; orientador, Fábio Gonçalves Daura-Jorge, coorientador, Mauricio Cantor, 2024.
136 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, Florianópolis, 2024.

Inclui referências.

1. Ecologia. 2. ecologia comportamental. 3. comportamento animal. 4. mutualismo. I. Daura-Jorge, Fábio Gonçalves. II. Cantor, Mauricio. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

Alexandre Marcel da Silva Machado

O efeito do ambiente e das diferenças individuais em um mutualismo entre botos e pescadores

O presente trabalho em nível de Doutorado foi avaliado e aprovado, em 23 de janeiro de 2024, pela banca examinadora composta pelos seguintes membros:

Prof. Raul Costa-Pereira, Dr.
Universidade Estadual de Campinas

Prof. Dominic Cram, Dr.
Edinburgh Napier University

Profa. Natalia Hanazaki, Dra.
Universidade Federal de Santa Catarina

Certificamos que esta é a versão original e final do trabalho de conclusão que foi julgado adequado para obtenção do título de Doutor em Ecologia.

ICP-Edu
Documento assinado digitalmente
Eduardo Luis Hettwer Giehl
Data: 11/04/2024 21:30:40-0300
CPF: ***.442.380-**
Verifique as assinaturas em https://v.ufsc.br

Coordenação do Programa de Pós-Graduação

ICP-Edu
Documento assinado digitalmente
Fabio Goncalves Daura Jorge
Data: 11/04/2024 20:10:58-0300
CPF: ***.254.799-**
Verifique as assinaturas em https://v.ufsc.br

Prof. Fábio G. Daura-Jorge, Dr.
Orientador

Florianópolis, 2024.

Aos indivíduos,
àqueles que inspiram e àqueles que cuidam.

AGRADECIMENTOS

Os últimos anos foram repletos de novos desafios, pessoais e profissionais. Sinto-me privilegiado por chegar até aqui tendo pessoas extraordinárias ao meu lado, que me apoiaram com tanto cuidado, que me inspiraram e trouxeram leveza, e que criaram as oportunidades para que eu pudesse aprender e desenvolver meu trabalho. Expressar minha gratidão em algumas poucas palavras parece até injusto, considerando a tamanha influência que tiveram em minha vida. Mas deixo aqui meus sinceros agradecimentos...

Ao meu orientador, Fábio Daura-Jorge, que por 10 anos me ensinou tanto sobre o trabalho e sobre a vida, que me fez uma pessoa melhor e me inspirou a ir além do que eu imaginava ser um caminho possível. Serei eternamente grato por todas as oportunidades que recebi e por toda a sua dedicação. Obrigado, meu amigo, por nunca perder o otimismo e não me deixar esquecer do essencial.

Ao meu coorientador, Mauricio Cantor, agradeço a sua dedicação inspiradora, por todo o esforço e cuidado dedicado à minha formação. Sou muito grato por essa longa parceria, por me proporcionares novos caminhos e criar oportunidades para que eu continue caminhando para frente, por compartilhar da empolgação a cada passo, e pelo cuidado nos momentos difíceis. Muito obrigado, meu amigo, pela oportunidade de acompanhar sua jornada e por me permitir fazer parte disso.

To my third supervisor, Damien Farine. Thank you for giving me the opportunity to spend a year in your lab with such a fantastic group of people, for sharing your inspiring thoughts about science and life, and for all the insightful ideas, which have provided me a fresh perspective on my work;

À Analice Pereira, minha esposa e melhor amiga. Obrigado por embarcar comigo nessa jornada há quase 12 anos e me permitir navegar ao seu lado entre tempestades e calmarias. Obrigado por todo o cuidado incondicional, por sempre me motivar e me ensinar a viver com mais leveza. Você é essencial. Te amo!

À minha família. Em especial, aos meus pais, Denize e Marcos Machado, e aos meus padrinhos, Álvaro e Esmeralda Silveira, pelo apoio absoluto e suporte que me permitiu percorrer esses longos anos na academia;

Aos amigos, Bianca Romeu, Carolina Bezamat, Eduardo Giehl, João do Valle-Pereira e Rafael Suhs. Obrigado por compartilhar risadas e frustrações, por me permitir aprender com vocês e por fazerem parte da minha jornada, nas muitas horas de carro, de barco, no campo ou em frente ao computador, nas discussões estatísticas e filosóficas. Obrigado por estarem

presente, por todas as conversas inspiradoras, mas também pelas despretensiosas—especialmente quando acompanhadas de um bom café e uma fatia de bolo;

Ao professor Paulo Simões-Lopes, por me instigar a curiosidade desde a graduação e estar sempre disposto a ensinar;

Ao Professor Pedro Castilho, pelo suporte nas atividades de campo em Laguna, pela longa parceria e pela empolgação contagiante em cada nova ideia;

Aos alunos do LAMAq (UFSC) e do LabZoo (UDESC), pela ajuda em campo, em especial à Fernanda Peverari, pela ajuda com a fotoidentificação;

Aos pescadores de Laguna, pela colaboração e paciência nas campanhas de campo;

To the colleagues from the Farine Lab and the Max Planck Institute of Animal Behavior, for such a collaborative and supportive environment;

To the staff of the Universität Konstanz and the staff of the Max Planck Institute of Animal Behavior. Special thanks to Jennifer Golbol and Elke Henkenhaf, for all their help with the visa, registration paperwork and my staying at the guesthouse;

À CAPES, pela bolsa concedida para o doutoramento no Brasil e para a período de estágio doutoral no exterior;

To the DAAD and the PROBRAL program, for the financial support;

Ao CNPq e FAPESC, por financiar o PELD-SELA e viabilizar parte desse trabalho;

To the Animal Behavior Society, for the financial support with a Developing Nations Award;

To the editors and reviewers of Mammalian Biology and Journal of Animal Ecology, for their time and consideration in reviewing my manuscripts;

To the editors of Marine Mammal Science, Journal of Functional Ecology, Mammalian Biology, Biotemas and Latin American Journal of Aquatic Mammals, for the opportunities to learn and contribute with peer-review;

Ao Dr. Luis Macedo-Soares e aos professores Sergio Floeter, Natalia Hanazaki, Kleber Del-Claro, Nivaldo Peroni, Renato Freitas e Eduardo Secchi, que acompanharam e avaliaram o desenvolvimento do meu trabalho desde o projeto, qualificação e SAPECO;

Aos membros da banca, pelo seu tempo e disposição em contribuir com essa etapa da minha formação. Muito obrigado!

À minha *alma mater*, a Universidade Federal de Santa Catarina. Com o fechamento deste documento e a defesa pública de doutorado, encerro um longo ciclo de aprendizado e desenvolvimento pessoal em uma Universidade pública. Assim, agradeço a todos os técnicos, professores e terceirizados que mantém a Universidade e que me proporcionaram trilhar esse caminho de 2010 até aqui.

Muito obrigado a todos por fazerem parte dessa longa e incrível jornada. Àqueles não citados ou desconhecidos, mas que em algum momento me ajudaram, peço desculpas. Mas espero que aceite meu singelo agradecimento: Muito obrigado!

RESUMO

Apesar dos esforços para reconhecer o papel do indivíduo e das diferenças individuais na Ecologia, ainda há uma lacuna sobre o efeito do indivíduo na manutenção de uma cooperação. Parte das evidências empíricas focam na variação individual na frequência de cooperação ou no papel individual na divisão de tarefas em táticas de forrageio cooperativo. No entanto, se os indivíduos diferem na qualidade de seus comportamentos e na resposta às condições ambientais e sociais que afetam a dinâmica de uma cooperação, então as diferenças individuais devem ter implicações para os benefícios obtidos pelos parceiros. Esta tese busca compreender como variações nas condições ambientais e como as diferenças individuais podem afetar mutualismos. Em três capítulos, teve-se como modelo biológico a pesca cooperativa entre botos-da-tainha (*Tursiops truncatus gephyreus*) e pescadores artesanais em Laguna, sul do Brasil, um dos poucos casos ativos de cooperação entre humanos e animais não-humanos. No primeiro capítulo, avalia-se a contribuição relativa das condições ambientais e da abundância de presas na dinâmica da cooperação boto-pescador. Utilizando análises de caminho confirmatórias, testa-se as relações entre as condições ambientais locais, a abundância de presas e o comportamento dos botos e pescadores, e como essas relações afetam o resultado da cooperação. Sugere-se que a cooperação permita a manutenção dos benefícios da pesca cooperativa mesmo com a natureza efêmera das presas. No segundo capítulo, testa-se a hipótese de que as diferenças individuais podem determinar os produtos de interações mutualísticas. Em 306 horas de observações diretas em três anos de amostragem, 37 botos foram observados em 1.426 interações com os pescadores. Utilizando modelos lineares generalizados de efeitos mistos, mostra-se que 44,6% da variação nas capturas pelos pescadores é explicada apenas pela identidade do boto. Três botos acumularam mais de 60% das capturas totais, e apenas dois desses indivíduos fornecem consistentemente mais de 50% de chance de sucesso aos pescadores. Essa contribuição desproporcional não é mediada pela competição por interferência entre os botos, o que pode sugerir que outros mecanismos determinam a variação individual observada, como o processo de aprendizado social da pesca cooperativa com humanos. Portanto, a manutenção dos benefícios parece depender fundamentalmente de alguns poucos indivíduos-chave da população de botos. No terceiro capítulo, descreve-se os desafios metodológicos da coleta e processamento de dados comportamentais utilizando múltiplas plataformas simultâneas de registro de multimidia. Como produto, apresenta-se uma biblioteca de código aberto para a linguagem R para relacionar, por exemplo, dados e metadados de fotografia, vídeo e acústica. Em conclusão, esta tese contribui para a compressão dos mecanismos que regulam a dinâmica de interações mutualísticas, avaliando a importância relativa da abundância de recursos e da ação dos parceiros de outra espécie para a manutenção dos benefícios, bem como revelando a contribuição desproporcional de poucos indivíduos para a manutenção de uma rara cooperação entre animais humanos e não-humanos.

Palavras-chave: Ecologia comportamental; Mutualismo; Comportamento animal.

ABSTRACT

Despite the efforts to unravel the role of individual heterogeneity in Ecology, there is still a gap in our knowledge about the role that individuals and their differences play in cooperation. The existing empirical evidence either focuses on how individuals differ in their frequency of cooperative behaviors or assesses whether individuals play consistent roles in cooperative foraging tactics. However, if individuals differ in the quality of their behaviors and in their response to the changes in the physical and social environment that affect the dynamics of a cooperation, then individual heterogeneity should have implications for the outcomes of cooperative interactions and the benefits accrued by the partners. This thesis aims to understand how changes in environmental conditions and how individual heterogeneity can affect mutualisms. Consisting of three chapters, this thesis uses a human-dolphin mutualism as a model, in which wild bottlenose dolphins (*Tursiops truncatus gephyreus*) and artisanal net-casting fishers cooperate to capture mullet schools in Laguna, southern Brazil—one of the few active cases of cooperation between human and non-human animals in the wild. In the first chapter, the relative contributions of environmental conditions and prey abundance to the dynamics of the dolphin-fisher mutualism are assessed. Confirmatory path analyses were used to test the links between changes in local environmental conditions, prey abundance, the behavior of dolphins and fishers, and how the benefits accrued by fishers are affected by these changes and the outcomes of cooperative interactions. The results suggest the environment plays a minor role in the dynamics of the dolphin-fisher mutualism, and that by cooperating with dolphins, fishers can accrue their benefits even with the unpredictability in prey abundance. In the second chapter, the hypothesis that individual heterogeneity can determine the products of mutualistic interactions was tested. In 306 hours of direct observations over three years of sampling, 37 dolphins were observed in 1,426 interactions with fishers. Using a subset of 745 cooperative events in which 32 cooperative dolphins were identified and the outcomes of their interactions with fishers were quantified, generalized linear mixed-effects models were fit to quantify differences among dolphins in their contributions to the mutualism. It is shown that 44.6% of the variation in fishers' catches is explained by the dolphin identity alone. Three dolphins accumulated more than 60% of the total catch. These individual differences provide disproportionate contributions to the mutualism and were mediated by interference between dolphins, suggesting that other mechanisms, such as social learning of the cooperative foraging tactic, may underlie individual heterogeneity. Therefore, the maintenance of the benefits accrued by fishers in the mutualism seems to depend fundamentally on a few key individuals from the dolphin population. The third chapter discusses methodological challenges of collecting and processing behavioral data using multiple simultaneous platforms of multimedia recording. The outcome is an open-source library for the R programming language to link, for example, behavioral data from photography, video and acoustic recordings. In conclusion, this thesis contributes to the understanding of the mechanisms that regulate the dynamics of mutualistic interactions; by assessing the relative importance of resource abundance, individual differences, and the role of intraspecific interference, it reveals the disproportionate contribution of a few individuals to the maintenance of a rare cooperation between human and non-human animals.

Keywords: Behavioral ecology; Mutualism; Animal behavior.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1 APRESENTAÇÃO

Os capítulos que compõem este documento utilizam princípios da ecologia animal e comportamental para sustentar a tese de que as diferenças individuais desempenham um papel determinante no funcionamento de sistemas mutualísticos. Os dois capítulos iniciais buscam investigar como variações no ambiente e na disponibilidade de presas podem afetar a dinâmica de mutualismos (*capítulo 1*) e quantificar os efeitos das diferenças individuais nos benefícios recebidos pelos parceiros de outra espécie, além de testar a hipótese da competição por interferência entre coespecíficos como um mecanismo subjacente às diferenças individuais (*capítulo 2*). O terceiro e último capítulo é ferramental, e ilustra os desafios metodológicos relacionados à coleta e processamento de dados multimídia procedentes de múltiplas plataformas amostrando simultaneamente. Apresenta-se um *software* de código aberto como contribuição para o estudo do comportamento de animais de vida livre em nível individual (*capítulo 3*). Nos três capítulos, o modelo biológico utilizado é um dos poucos raros casos ativos de cooperação entre animais humanos e não-humanos (*human-wildlife cooperation*, *sensu* Cram et al., 2022): a pesca cooperativa entre botos-da-tainha (*Tursiops truncatus gephyreus*) e pescadores artesanais em Laguna, sul do Brasil.

Os três capítulos desta tese de doutorado foram redigidos em língua inglesa, conforme as exigências das revistas acadêmicas às quais foram ou serão submetidos, conforme indicado na página inicial de cada capítulo. Na próxima seção, o leitor encontrará uma “introdução geral” em português que oferece a fundamentação teórica que sustenta essa tese. Após os capítulos em inglês, o leitor encontrará, também em português, a “conclusão geral”, que sintetiza os achados e principais contribuições desta tese de doutorado.

2 INTRODUÇÃO GERAL

2.1 FUNDAMENTAÇÃO

O papel do indivíduo e das diferenças individuais no comportamento animal foram, por muito tempo, amplamente negligenciados nas teorias ecológicas. Muito dessa simplificação, em parte intencional, foi útil e necessária para compreender a diversidade e complexidade dos sistemas biológicos, em vários níveis de organização ecológica. Como resultado, inúmeras teses que gravitam sobre os fatores determinantes e consequências de padrões e processos relacionados com a ecologia e história de vida de uma determinada espécie, omitem as distintas pressões de seleção que operam sobre a diversidade de fenótipo dos indivíduos de tal espécie. Somente nas últimas duas décadas, a interação entre subdisciplinas da Ecologia se intensificaram, o que possibilitou a identificação de variações individuais no comportamento animal (e.g., Réale et al., 2007; Sih; Bell; Johnson, 2004; Sih; Sinn; Patricelli, 2019), e a compreensão dos mecanismos pelos quais essas variações podem escalar e se manifestar em outros níveis de organização (Wolf; Weissing, 2012) desde populações (Coulson et al., 2006; Coulson, 2020) até comunidades (Araújo; Bolnick; Layman, 2011; Bolnick et al., 2011) e ecossistemas (Brehm et al., 2019; Fuster; Traveset, 2020; Keith et al., 2023). No entanto, ainda há muito a ser revelado sobre as causas e eventuais consequências das diferenças individuais nos padrões comportamentais de uma espécie, e sobre os potenciais efeitos dessas diferenças na emergência e persistência de interações ecológicas, especialmente as positivas.

2.2 O INDIVÍDUO NA ECOLOGIA

Indivíduos nascem, crescem, interagem com outros indivíduos, se reproduzem e morrem. Essa sequência de eventos segue padrões e processos que caracterizam a sua história de vida. Compreender esses padrões e processos é um ponto focal de interesse da Ecologia, pois eles influenciam desde a dinâmica de populações, até a estrutura de comunidades e o fluxo de energia em ecossistemas (Odum; Barret, 1971). No entanto, muitos desses padrões e processos tem origem nas, e são moldados por, decisões individuais motivadas por uma série de fatores complexos e variados. O conjunto de decisões tomadas por um indivíduo, bem como suas interações com outros indivíduos, geram contextos comportamentais complexos (Krebs; Davies, 1981), oferecendo uma variedade de soluções possíveis para os desafios ecológicos e, como resultado, gerando variações entre os indivíduos.

Nesse contexto, em busca de um compromisso entre a complexidade da realidade e o reducionismo necessário para uma abordagem mecanicista, as teorias ecológicas clássicas optaram por omitir o fato de que os indivíduos são diferentes entre si. Por exemplo, modelos clássicos de dinâmica populacional, predador-presa e a teoria de nicho, por muito tempo, assumiam uma equivalência irreal entre os indivíduos de uma mesma população, ou até mesmo de uma mesma espécie. Porém, os indivíduos podem diferir em atributos que são estabelecidos desde o início de suas vidas, ou em atributos dinâmicos, que podem variar ao longo da vida inteira (Dall et al., 2012; Vindenes; Langangen, 2015). Portanto, ao desconsiderar essas diferenças individuais, a Ecologia deixa uma avenida a ser percorrida, com questões fundamentais em aberto (ver Sutherland et al., 2013) sobre os mecanismos subjacentes à variação individual e suas consequências na dinâmica de sistemas e interações ecológicas em diversos níveis de organização.

A variação individual é onipresente e desempenha um papel fundamental no mecanismo que impulsiona a evolução de características adaptativas (Darwin, 1859). A variação entre indivíduos pode ter consequências para a sobrevivência e reprodução dos mesmos (Wilson, 1998), determinando a frequência de seus atributos sujeitos à seleção e sua aptidão (Mayr, 1982). Essa variação pode ser observada em diferenças genéticas (Hughes et al., 2008) e em características fenotípicas associadas à sobrevivência e reprodução (Moyes et al., 2009), mas também na forma como os indivíduos exploram e selecionam seus recursos (Bolnick et al., 2003) e na consistência de seus comportamentos (Bell; Hankison; Laskowski, 2009). Nas últimas duas décadas, essas especializações individuais e as variações consistentes no comportamento, também conhecidas como *personalidade animal*, ganharam relevância na ecologia comportamental.

Especializações individuais estão presentes em uma diversidade de *taxa* (Araújo; Bolnick; Layman, 2011; Sheppard et al., 2021). Um indivíduo especialista desenvolve comportamentos de forrageio consistentes e consome apenas parte dos recursos explorados por todos os indivíduos da população, independentemente das condições ambientais, do dimorfismo sexual ou da ontogenia (Bolnick et al., 2003). Essas especializações podem emergir, não exclusivamente, por mecanismos ecológicos e comportamentais. Um mecanismo simples para explicar a especialização é a distribuição e previsibilidade dos recursos. Por exemplo, animais territorialistas podem se especializar nos recursos mais abundantes e previsíveis em seus habitats (e.g., Mattson; Reinhart, 1995). Especializações também podem emergir como resposta à competição, promovendo a partição de recursos entre coespecíficos como uma solução para evitar conflitos (Sheppard et al., 2018). Indivíduos dominantes, com maior capacidade competitiva, podem monopolizar o acesso aos recursos e forçar, intencionalmente ou não, os subordinados à especialização (e.g., Marshall et al., 2012). Os indivíduos também podem se especializar via aprendizado social de táticas de forrageio (Tinker; Mangel; Estes, 2009), especialmente durante os períodos de cuidado parental (Estes et al., 2003; Rossman et al., 2015), reforçando comportamentos e dietas de seus modelos. Tanto o aprendizado social quanto individual podem reforçar o desenvolvimento de habilidades necessárias para capturar e manipular presas, levando à especialização num processo longo de ganho de experiência e aperfeiçoamento de táticas de forrageio (Partridge, 1976; Whitfield, 1990; Patterson; Krzyszczyk; Mann, 2016).

Variações individuais no comportamento podem ser consistentes—e possivelmente correlacionados—ao longo do tempo, independentemente das condições ambientais e do estado do indivíduo (Sih; Bell; Johnson, 2004; Dall; Houston; McNamara, 2004; Réale et al., 2007). Essas variações individuais podem ser medidas em várias dimensões fundamentais do comportamento animal, como ousadia, exploração, atividade, agressividade e sociabilidade (Réale et al., 2007). Mesmo indivíduos geneticamente idênticos, vivendo nas mesmas condições, podem desenvolver diferenças consistentes no comportamento (Laskowski et al., 2022b). Essa consistente variação individual pode ter múltiplas causas não exclusivas (Bergmüller; Taborsky, 2010; Laskowski et al., 2022a), e pode ter consequências para a propensão ao comportamento cooperativo (Carter; English; Clutton-Brock, 2014), o comportamento de forrageio (Toscano et al., 2016), o aprendizado social (Carter et al., 2014), bem como na dinâmica de grupo (Jolles; King; Killen, 2019) e da comunidade (Bolnick et al., 2011), além da aptidão do indivíduo (Moiron; Laskowski; Niemelä, 2020). Alguns indivíduos ainda podem gerar contribuições desproporcionais para o grupo e para o sistema (Sih; Watters, 2005). Essas contribuições podem vir dos papéis fundamentais que o indivíduo desempenha no grupo ou de uma consistência no comportamento de alguns indivíduos-chave (Modlmeier et al., 2014). Por exemplo, em mamíferos sociais, alguns indivíduos bem conectados socialmente podem ser fundamentais para manter o elo e a coesão entre unidades sociais dentro da mesma população (e.g., *Tursiops* spp.; Lusseau; Newman, 2004). Indivíduos mais velhos podem possuir o conhecimento necessário para reconhecer ameaças e garantir o sucesso reprodutivo do grupo (e.g., *Loxodonta africana*; McComb et al., 2001), ou garantir acesso a recursos alimentares em momentos de escassez (e.g., *Orcinus orca*; Brent et al., 2015). Em peixes, a presença de alguns indivíduos mais arrojados e mais exploradores no cardume pode levar a descoberta de novos recursos alimentares em menos tempo (e.g., *Poecilia reticulata*; Dyer et al., 2009). Em insetos eusociais, além da divisão de trabalho e da diferenciação em castas (Wilson, 1979), alguns poucos indivíduos podem ter contribuições desproporcionais para a colônia em relação à sua abundância. Em pequenas colônias de formiga (*Temnothorax albipennis*), um único indivíduo pode ser responsável por mais da metade do transporte das larvas na emigração para um novo ninho (Dornhaus et al., 2008). Em mamíferos, divisões de tarefas podem ser mais raras. Mas alguns exemplos de forrageio social em cães selvagens (*Lycaon pictus*; Estes; Goddard, 1967), leões (*Panthera leo*; Stander, 1992) e golfinhos (*Tursiops truncatus*; Gazda et al., 2005), por exemplo, sugerem que indivíduos podem se especializar em algumas tarefas e desempenham o mesmo papel em repetidas ocasiões.

2.3 INTERAÇÕES MUTUALÍSTICAS E O PAPEL DO INDIVÍDUO

Interações de natureza mutualística são diversas e alguma confusão ainda pode existir ao tentar defini-las (West; Griffin; Gardner, 2007). Pode-se buscar algum consenso em interações entre indivíduos que resultam no aumento mútuo de aptidão usando o termo ‘cooperação’ para interações que ocorrem entre indivíduos de uma mesma espécie (Nowak, 2006), com alguma relação de parentesco ou não (Clutton-Brock, 2009), e ‘mutualismo’ para interações entre indivíduos de espécies diferentes (Bronstein, 1994). No entanto, apesar do foco nos benefícios mútuos para ambas as partes envolvidas, cooperação e mutualismos frequentemente são investigados por perspectivas independentes, com pouca menção de um ao outro. Por exemplo, parte do interesse em mutualismos está em compreender e descrever essas interações a partir das espécies envolvidas e do alinhamento de suas histórias de vida, enquanto esforços teóricos e empíricos para compreender o comportamento cooperativo focam no indivíduo e suas decisões. Mesmo assim, alguns paralelos podem existir nas motivações para o comportamento cooperativo, sendo ele intraespecífico ou interespecífico (Barker et al., 2017). No entanto, o efeito das diferenças individuais e o papel do indivíduo ainda é pouco compreendido em ambos os casos (Barker et al., 2017; Bergmüller; Schürch; Hamilton, 2010).

2.3.1 Forrageio cooperativo

Para sobreviver e reproduzir com sucesso, os indivíduos precisam resolver desafios fundamentais: encontrar, capturar e consumir recursos alimentares para satisfazer suas demandas energéticas (Stephens; Krebs, 1986). Predadores precisam acessar informações sobre o ambiente e suas presas (Krebs; Kacelnik; Taylor, 1978) para otimizar suas decisões sobre quando, onde e por quanto tempo forragear (Pyke, 1984). Assim, alguns predadores conseguem ajustar seu comportamento à distribuição e atividade de suas presas. Por exemplo, aves predatórias conseguem acompanhar mudanças nas atividades de suas presas ao longo do dia e ajustam sua atividade de forrageio aos momentos em que as presas são mais ativas (Lang; Mann; Farine, 2019). Quando as condições ambientais não representam mudanças na disponibilidade das presas, o forrageio social pode ser uma solução. Dessa forma, a tomada de decisão no forrageio passa a influenciar e ser influenciada por outros indivíduos (Giraldeau; Caraco, 2000). O forrageio social é relativamente difundido em vários *taxa*, e as interações entre indivíduos podem variar quanto à estabilidade do grupo, formas de comunicação, especialização individual e compartilhamento de recursos (Lang; Farine, 2017). Alguns predadores podem adquirir informações sobre disponibilidade e distribuição de presas a partir de seus coespecíficos (Kohles; O’Mara; Dechmann, 2022). Essas informações podem ser obtidas de forma inadvertida, como morcegos (*Noctilio albiventris*) que descobrem novos recursos a partir dos sons de ecolocalização de seus coespecíficos durante o forrageio (Dechmann et al., 2009), ou ativamente, como as andorinhas do penhasco (*Hirundo pyrrhonota*) que recrutam ativamente seus coespecíficos para aumentar as chances de acompanhar os movimentos dos insetos e explorar o recurso por mais tempo (Brown; Brown; Shaffer, 1991). No entanto, pode ser desafiador determinar se os indivíduos de fato se beneficiam do forrageio social ou se os indivíduos estão simplesmente mais propensos a formar grupos onde e quando as presas são mais abundantes.

Diferenciar um contexto de forrageio social de uma simples agregação requer uma compreensão abrangente de como as condições ambientais predizem a disponibilidade de presas, como a disponibilidade de presas afeta a capacidade dos predadores de capturar presas, e se o forrageio em grupos aumenta o sucesso dos predadores. Alguns predadores podem simplesmente estar agregados em função de uma presa comum e previsível. Por exemplo, os ursos-pardo forrageando por salmões podem se agregar em áreas de desova de salmão (Deacy et al., 2016), mas não necessariamente os coespecíficos geram algum benefício para o sucesso de forrageio. Nesse caso, na verdade, um aumento na densidade de ursos nas áreas de desova de salmão pode levar a um aumento na competição intraespecífica. Então, os ursos dominantes forçam os ursos subordinados a aumentar sua vigilância e usar áreas menores para evitar conflitos (Gende; Quinn, 2004). Essa diferenciação nos benefícios do forrageio social pode ser mais evidente para predadores que forrageiam em grupos (Hansen et al., 2023), especialmente para aqueles que caçam de forma cooperativa.

Predadores podem sincronizar seus comportamentos em táticas de forrageio cooperativas para aumentar suas chances de encontrar e capturar presas. Por exemplo, orcas (*Orcinus orca*) podem coordenar seus movimentos para provocar ondas e derrubar presas em cima de blocos de gelo flutuantes (Pitman; Durban, 2012). Indivíduos também podem se especializar em funções específicas no grupo e desempenhá-las em repetidas ocasiões. Por exemplo, leoas africanas (*Panthera leo*) consistentemente atuam em posições distintas no grupo durante a caça, com alguns indivíduos perseguindo as presas enquanto outros esperam a presa fugir em resposta aos outros indivíduos do grupo (Stander, 1992). Casos de forrageio cooperativo também ocorrem entre indivíduos de espécies diferentes (e.g., peixes e polvos Sampaio et al., 2021). Por exemplo, garoupas (*Plectropomus pessuliferus*) caçam na coluna d'água e recrutam moreias (*Gymnothorax javanicus*) para perseguir e extrair as presas de fendas das rochas onde as garoupas não conseguem entrar (Bshary et al., 2006). Em um experimento, as garoupas foram capazes de acessar a qualidade do parceiro de outra espécie em interações consecutivas e recrutar os mais competentes (Vail; Manica; Bshary, 2014). Uma parcela fascinante desses casos envolve humanos e animais não-humanos de vida livre coordenando seus comportamentos para obter benefícios mútuos (Cram et al., 2022).

2.3.2 Forrageio cooperativo entre humanos e animais não-humanos

Humanos e animais não-humanos podem exibir formas facultativas de forrageio cooperativo (Cram et al., 2022). Entre os poucos casos ainda ativos, na África subsaariana, caçadores de mel cooperam com apontadores de mel (*Indicator indicator*) para localizar colmeias de abelha em árvores (Spottiswoode; Begg; Begg, 2016). Nesse caso, quando os apontadores de mel se aproximam, os humanos emitem sons estereotipados para atrair os apontadores de mel, que utilizam chamados específicos para guiar os humanos às colmeias. Quando encontram uma colmeia, os caçadores de mel derrubaram a árvore para acessar a colmeia e extrair o mel, e deixam a cera das abelhas para os apontadores de mel. O comportamento cooperativo dos apontadores de mel é aparentemente inato. Mas o sucesso da cooperação depende da comunicação entre as duas espécies, que são influenciadas umas pelas outras em um processo de aprendizado e reforço das tradições culturais de ambas as espécies em diferentes regiões da África (Spottiswoode; Wood, 2023).

Interações entre humanos e golfinhos também são bem documentadas, com casos ativos no sul do Brasil (Simões-Lopes; Fabián; Menegheti, 1998) e em Myanmar (Smith et al., 2009). Em ambos os casos, os golfinhos (*Tursiops truncatus gephyreus* no Brasil e *Orcaella brevirostris* em Myanmar) dão início a interação, conduzindo os cardumes de peixes até os pescadores. Os golfinhos então exibem comportamentos que os pescadores interpretam como o momento de lançar suas redes—ver detalhes e referências em "A sincronia entre botos e pescadores". Outros casos de cooperação dessa natureza já foram extintos ou não foram mais registrados (Van der Wal et al., 2022), como a cooperação entre povos indígenas e lobos (*Canis lupus*) na América do Norte (Pierotti; Fogg, 2017) e a cooperação entre baleeiros e orcas para caçar outros mamíferos marinhos na Rússia e Austrália (Reeves et al., 2023). Ambos esses casos foram extintos após a chegada de colonos, que eliminaram lobos e povos indígenas. Na Austrália, duas orcas cooperativas foram mortas nesse processo, e outras deixaram a área após o declínio na população de presas. Os poucos casos ainda ativos de cooperações entre animais humanos e não-humanos também estão expostos a múltiplas ameaças, que podem levar a degradação do habitat e ao declínio da população de predadores e presas. Ainda, a perda de conhecimentos e práticas importantes para a manutenção dos comportamentos cooperativos pode afetar a sincronia entre predadores e reduzir suas motivações para cooperar. Em última instância, essas ameaças podem colocar em risco culturas de ambas as espécies envolvidas nessas interações (Van der Wal et al., 2022).

2.4 FERRAMENTAS COMPUTACIONAIS PARA A ECOLOGIA DO INDIVÍDUO

A Ecologia já foi criticada por seu foco exclusivamente na história natural e pelo uso de abordagens unicamente descritivas, que a distanciava de outras disciplinas consideradas "ciências duras" (Peters; Peters, 1991; Lawton, 1999; Linquist et al., 2013). No entanto, parte dessas críticas foi amenizada com um movimento em direção à incorporação da matemática, estatística e da computação. Assim, a Ecologia rapidamente tornou-se uma ciência numérica (Legendre, 1983; Lebreton et al., 1992; Kokko, 2007). Nesse processo, a variação individual passou a ter um papel de destaque em modelos baseados em indivíduos. Esses modelos possibilitaram a exploração dos paradigmas da variação individual nas teorias ecológicas (Huston; DeAngelis; Post, 1988), inclusive parametrização com dados empíricos para testar hipóteses que seriam logisticamente desafiadoras (e.g., Stillman; Caldow; Alexander, 2000; Cantor et al., 2015). Além disso, os ecólogos também desempenharam um papel fundamental no desenvolvimento e adaptação de ferramentas estatísticas para investigar a variação individual com dados empíricos (e.g., Stoffel; Nakagawa; Schielzeth, 2017). Especificamente, modelos de efeitos mistos estão intimamente associados aos conceitos da variação individual (Sánchez-Tójar; Moiron; Niemelä, 2022), e têm sido utilizados para estimar componentes da variância e testar hipóteses sobre a variação entre indivíduos, dentro dos indivíduos, e suas respostas às condições ambientais e outros efeitos de interesse (Dingemanse et al., 2010; Dingemanse; Dochtermann, 2013; Cleasby; Nakagawa; Schielzeth, 2015; Hertel et al., 2020; O'Dea; Noble; Nakagawa, 2021). No entanto, a coleta de dados empíricos em nível individual para compreender as causas e consequências da variação individual, seja por modelos baseados em indivíduos ou testes de hipóteses com modelos estatísticos, requer soluções para identificar e rastrear a identidade dos indivíduos e seus atributos em estudos longitudinais (Sheldon; Kruuk; Alberts, 2022).

Dados multimidia estão entre as soluções para identificar indivíduos e registrar seus comportamentos. Em ambientes controlados ou em cativeiro, a coleta e o processamento desses dados podem ser altamente eficientes, combinando múltiplas plataformas de amostragem para fornecer informações sobre a identidade, comportamento e interações entre indivíduos em tempo real (Alarcón-Nieto et al., 2018; Dell et al., 2014; Graving et al., 2019). Já em ambientes naturais, dados coletados *in situ* podem ser processados por meio de ferramentas computacionais para identificar indivíduos de diversos táxons (e.g., aves, Ferreira et al., 2020; primatas, Guo et al., 2020; delfinídeos, Thompson et al., 2022) e classificar seus comportamentos com base em vídeos e áudios *a posteriori* (e.g., Friard; Gamba, 2016). A utilização e combinação dessas ferramentas utilizando múltiplas plataformas é especialmente útil para investigar o comportamento de baleias e golfinhos, que podem percorrer grandes áreas e passar longos períodos debaixo d'água. Ainda, aumentam a gama de técnicas não invasivas que permitem, além da identificação individual, a descrição de padrões comportamentais em nível individual e estimativa de medidas morfométricas. Isso inclui técnicas tradicionais de fotoidentificação, que podem ser utilizadas para identificar os indivíduos de forma não invasiva a partir de marcas naturais (Urian et al., 2015; Würsig; Würsig, 1977), imagens aéreas, que podem ser usadas para registrar comportamentos por uma nova perspectiva (e.g., Torres et al., 2018; Hartman; Van der Harst; Vilela, 2020) e acessar o estado de saúde dos indivíduos (e.g., Horton et al., 2019; Soledade Lemos et al., 2020), e dados acústicos, que podem sugerir atividades de forrageio e formas de interações entre coespecíficos (e.g., Pirotta et al., 2014; e.g., Hamilton et al., 2022; Moore et al., 2020). Ao combinar essas múltiplas plataformas de amostragem, ampliam-se as perspectivas para descrever o comportamento desses animais (e.g., Cantor; Farine; Daura-Jorge, 2023). Porém, para investigar variações no comportamento em nível individual, é necessário coletar um volume de dados muito grande e diverso, o que pode rapidamente inviabilizar o processamento manual. Ou seja, sob risco de inviabilizar o estudo, é imperativo buscar soluções otimizadas e automatizadas que permitam uma triagem e alinhamento eficientes dos dados procedentes destas múltiplas plataformas (ver Machado; Cantor, 2022).

2.5 A INTERAÇÃO BOTO-PESCADOR COMO MODELO DE ESTUDO

Para testar as hipóteses de que variações no ambiente e variações individuais entre coespecíficos podem afetar a dinâmica e os resultados de interações mutualísticas, este estudo utiliza como modelo biológico um caso de forrageio cooperativo entre botos-da-tainha (*Tursiops truncatus gephyreus*) e pescadores artesanais no sul do Brasil (Pryor; Lindbergh; Milano, 1990; Simões-Lopes; Fabián; Menegheti, 1998). A interação boto-pescador é um dos raros casos ainda ativos de cooperação entre humanos e animais não-humanos (*human-wildlife cooperation*; ver Cram et al., 2022) e constitui um modelo ideal para testar as hipóteses abordadas nesta tese. Nesse cenário de forrageio cooperativo entre botos e pescadores artesanais, os benefícios obtidos por ambos os predadores dependem de uma fina sincronia em seus comportamentos (Cantor; Farine; Daura-Jorge, 2023). Além disso, esse sistema está sujeito à variação ambiental, que pode afetar a disponibilidade da principal presa, a tainha migratória (*Mugil liza*) (Lemos et al., 2016; Machado et al., 2021), e a plasticidade comportamental dos indivíduos envolvidos. Indivíduos de ambas as espécies predadoras podem apresentar diferenças em alguma dimensão do uso dessa tática de forrageio cooperativa (botos: Cantor; Simões-Lopes; Daura-Jorge, 2018; pescadores: Valle-Pereira et al., 2022). Essas diferenças individuais podem ter consequências tanto para as interações intraespecíficas, levando ambos os predadores a competir—por exploração ou interferência—ou a cooperar entre si (e.g., Simões-Lopes, 1998; Santos-Silva et al., 2022), quanto na interação interespecífica, entre botos e pescadores.

2.5.1 A sincronia entre botos e pescadores

Os indivíduos de uma pequena população costeira de botos-da-tainha, residente há várias gerações em Laguna, Santa Catarina, desenvolveram uma tática especializada de forrageio em cooperação com pescadores artesanais (Simões-Lopes; Fabián; Menegheti, 1998). Nesta interação, botos e pescadores sincronizam seus comportamentos para superar os desafios enfrentados na captura de presas móveis e efêmeras. Às margens do canal, os pescadores encontram dificuldades para localizar cardumes de peixes nas águas turvas do sistema estuarino. Por outro lado, os botos têm um sistema de ecolocalização altamente eficiente, o que lhes permite localizar e perseguir suas presas mesmo nas águas turvas (Wisniewska et al., 2014; Noren et al., 2017). Neste contexto, botos e pescadores aparentemente cooperam para capturar cardumes, especialmente de tainhas (*Mugil liza*), principal presa alvo dessa interação (Simões-Lopes; Fabián; Menegheti, 1998).

Durante os meses do outono e inverno, as tainhas migram do sul do Brasil e da Argentina para desovar nas águas ao norte, período em que seus cardumes podem adentrar nos sistemas estuarinos (Sadowski; Almeida Dias, 1986). Embora representem uma grande quantidade de biomassa acessível a botos e pescadores, capturar tainhas que se movem rapidamente em grandes grupos pode ser desafiador para ambos os predadores, favorecendo ou exigindo especializações comportamentais e, neste caso específico, certa coordenação de comportamentos entre os indivíduos envolvidos. Os botos que desenvolveram essa tática especializada de forrageio em cooperação com pescadores então conduzem os cardumes para as margens do sistema estuarino. Lá, os pescadores aguardam por comportamentos estereotipados dos botos, como uma exposição rápida do dorso, uma batida de cabeça ou de cauda, que são interpretados como ‘sinais’ para o momento ideal para lançar suas redes (Simões-Lopes; Fabián; Menegheti, 1998).

Evidências recentes sugerem que tanto botos quanto os pescadores obtêm benefícios mútuos quando coordenam seus comportamentos e forrageiam em sincronia (ver Cantor; Farine; Daura-Jorge, 2023). Quando coordenam suas atividades de forrageamento com os botos, e lançam suas tarrafas em resposta aos comportamentos estereotipados dos mesmos, os pescadores aumentam suas chances de sucesso em 17 vezes e conseguem capturar até quatro vezes mais tainhas do que em lances não coordenados (Cantor; Farine; Daura-Jorge, 2023). Quanto aos botos, quantificar os custos e benefícios diretos da interação com os pescadores ainda é um desafio, especialmente por métodos não invasivos (*cf.,* Jensen et al., 2023). No entanto, fortes indícios são observados nos comportamentos acústicos dos botos após o lançamento das tarrafas, que formam um bolsão enquanto afundam com o peso do chumbo nas extremidades da rede e aprisionam as tainhas no seu interior. Quando ambos, botos e pescadores, atuam em sincronia, os botos permanecem submersos por mais tempo e emitem *terminal buzzes*, sons de ecolocalização associados à perseguição ativa de presas (ver Ridgway et al., 2015). Essa emissão de *terminal buzzes* é mais frequente quando há sincronia entre botos e pescadores do que em eventos de forrageio assíncrono ou independente. Isso sugere que os botos intensificam seus esforços de forrageio para capturar tainhas aprisionadas ou desorientadas pelas redes, indicando uma correspondência entre os benefícios obtidos pelos pescadores e a aquisição de benefícios pelos botos quando ambos os predadores coordenam seus comportamentos (Cantor; Farine; Daura-Jorge, 2023).

2.5.2 Os botos do gênero *Tursiops*

Conhecidos comumente como golfinhos-nariz-de-garrafa (ou boto-da-tainha, no Sul do Brasil), os botos do gênero *Tursiops* spp. representam provavelmente o grupo de pequenos cetáceos mais conhecidos e estudado do mundo. Podem ser encontrados em águas temperadas e tropicais de todo o mundo e são especialmente conhecidos por sua notável plasticidade comportamental (Wells; Scott, 2009). Ao longo das décadas, indivíduos desse gênero são estudados em oceanários (McBride; Hebb, 1948), permitindo investigações aprofundadas em diversos aspectos, como suas relações sociais e de dominância entre coespecíficos (e.g., Samuels; Gifford, 1997; e.g., Pérez-Manrique et al., 2022), suas habilidades de comunicação e cooperação para resolução de problemas (e.g., Jaakkola et al., 2018), bem como suas reações às interações com humanos (e.g., Davies; Garcia-Pelegrin, 2023). Em populações de vida livre, esses animais podem viver por mais de 50 anos e atingir 3,8 metros de comprimento (Wells; Scott, 1999). As fêmeas normalmente reproduzem entre os cinco e treze anos de idade, embora esse intervalo possa variar entre populações (Mann et al., 2000). Após uma gestação de 12 meses, as fêmeas dão à luz a apenas um filhote, que geralmente permanece sob seus cuidados durante os primeiros três ou quatro anos de vida (Smolker et al., 1992), período que pode ser prolongado até os oito anos (Mann et al., 2000). Durante esses anos de cuidado parental, as interações entre a mãe e o filhote desempenham um papel determinante para o desenvolvimento social do filhote (Tsai; Mann, 2013) e criam oportunidades para o aprendizado (e.g., transmissão vertical de táticas de forrageio; Krützen et al., 2005). Após o desmame, os filhotes tendem a reduzir suas interações com a mãe (Mann et al., 2000), embora nem sempre se afastem completamente (Greenfield et al., 2022), frequentemente compartilhando as mesmas áreas de vida e desenvolvendo especializações comportamentais semelhantes (Rossman et al., 2015)

As relações sociais dentro das populações de *Tursiops* spp. são dinâmicas. Em populações de botos costeiros, é comum observar uma estrutura social caracterizada pela dinâmica de fissão-fusão, com associações de curta duração que mudam constantemente (Connor et al., 2000). Apesar dessas associações fluidas, preferências sociais e relações de longo prazo podem existir. Nesses casos, essas associações podem ser contexto-específicas, variando com o comportamento (e.g., Gero et al., 2005; Gazda et al., 2015; Machado et al., 2019) ou com a disponibilidade de presas (e.g., Fisher; Cheney, 2023), mas também determinadas pela sobreposição no uso do espaço (e.g., Baker et al., 2018), pelas relações de parentesco (e.g., Frère et al., 2010; Wiszniewski; Lusseau; Möller, 2010) ou pelo sexo (e.g., Ermak; Brightwell; Gibson, 2017; Galezo; Krzyszczyk; Mann, 2018). Em algumas situações, foram observadas sociedades multiníveis, com subunidades hierarquicamente aninhadas. Por exemplo, os machos de *Tursiops aduncus* da população de Shark Bay, na Austrália, que formam alianças de longa duração, geralmente trios de machos sem relação de parentesco (Gerber et al., 2020). Essa sociedade é então estruturada em uma hierarquia de alianças que podem cooperar entre si (Moore et al., 2020) e em diferentes níveis, para competir pelo acesso às fêmeas (Connor; Krützen, 2015; Gerber et al., 2021).

Sociedades de *Tursiops* spp. também podem ser estruturadas com base na homofilia de comportamento. Um exemplo clássico vem também da população de Shark Bay, onde botos aprendem com suas mães a utilizar esponjas como ferramentas para forragear em meio ao substrato rochoso (Krützen et al., 2005; Wild et al., 2019). Indivíduos que adotam essa tática de forrageio especializada tendem a associar-se preferencialmente com outros que também aprenderam e empregam a mesma tática (Mann et al., 2012). Esse processo demonstra uma interligação entre a transmissão cultural da tática de forrageio e a estrutura social da população, criando um ‘ciclo de retroalimentação’ (ver Cantor; Whitehead, 2013), que pode levar ao estabelecimento de tradições—ou seja, táticas de forrageio individual ou social transmitidas culturalmente ou aprendidas individualmente e aprimoradas ao longo da vida (Sargeant; Mann, 2009).

As populações costeiras de *Tursiops* spp. ao redor do mundo desenvolveram um amplo repertório de especializações comportamentais para forragear presas móveis em ambientes com características físicas diversas. Por exemplo, indivíduos em populações que habitam águas rasas aprenderam a usar o substrato lodoso em táticas de forrageio individuais (Lewis; Schroeder, 2003) e sociais (Gazda et al., 2005), bem como a utilizar ferramentas para capturar presas no substrato (Mann et al., 2008; Allen; Bejder; Krützen, 2011). Além disso, aprenderam a interagir com atividades humanas, seja de forma antagonista (Ansmann et al., 2012; Methion; Díaz López, 2019) ou mutualística (Busnel, 1973; Cantor; Farine; Daura-Jorge, 2023). Todavia, testar a hipótese de transmissão cultural ainda representa um desafio para a maioria dessas especializações, incluindo a tática de forrageio cooperativa com pescadores (Simões-Lopes; Daura-Jorge; Cantor, 2016). Até o momento, apenas os casos de uso de esponjas (Wild et al., 2019) e conchas (Wild et al., 2020) como ferramentas tiveram suas vias de transmissão apropriadamente demonstradas. Isso ocorre porque esse processo requer a quantificação da importância relativa do aprendizado social em comparação com a contribuição de predisposições genéticas e outros componentes ecológicos e ambientais associados ao desenvolvimento dessas especializações individuais.

Os botos comumente forrageiam por presas móveis, dispersas e imprevisíveis no tempo e no espaço. Especializações individuais podem emergir a partir de processos sociais, como o aprendizado, mas também de maneiras mais simplificadas, como uma resposta à competição (Sheppard et al., 2021). Embora as oportunidades de monopolização de recursos sejam geralmente raras ao forragear majoritariamente por presas móveis e imprevisíveis, relações de dominância entre botos foram observadas em outros contextos, tanto em cativeiro quanto em animais de vida livre, particularmente em estratégias de acasalamento (Connor; Krützen, 2015). Em animais de vida livre e em contexto de forrageio, um caso particular foi descrito para outra espécie da superfamília dos Odontocetos. Botos do rio Amazonas *Inia geoffrensis* são alimentados por turistas em uma pequena plataforma flutuante, criando uma situação espacialmente limitada e potencialmente monopolizável. Nesse caso, os botos dominantes demonstram comportamentos agonísticos em relação aos botos subordinados, com o objetivo de impedir que eles recebam provisões dos turistas e monopolizem o acesso aos recursos (Alves et al., 2013). De forma semelhante, foram observadas interações agonísticas entre coespecíficos durante o forrageio dos botos-da-tainha que cooperam com pescadores artesanais em Laguna. Nesse caso, a exibição de comportamentos agonísticos e a baixa associação entre coespecíficos poderiam sugerir uma hierarquia de dominância que promove o acesso prioritário à área de interação (Simões-Lopes, 1998). No entanto, ainda persiste o desafio de quantificar interações agonísticas direcionadas entre botos para testar e avaliar o efeito da dominância, se algum, na interação entre botos e pescadores (ver capítulo 2).

2.5.2.1 A população de botos-da-tainha de Laguna

Há uma tendência à formação de ecótipos costeiros e oceânicos de *Tursiops* spp. no mundo todo (Louis et al., 2021, 2023). Os indivíduos que habitam ambientes pelágicos e costeiros enfrentam desafios específicos relacionados aos seus habitats, o que pode levar a diferenciações ecológicas entre esses ecótipos (e.g., Louis et al., 2014). No Atlântico Sul Ocidental, os ecótipos costeiros e oceânicos podem ser distinguidos por meio de características morfológicas e genéticas (Costa et al., 2016; Simões-Lopes et al., 2019). Com base nessas diferenças, o comitê de taxonomia da Sociedade Americana de Mamíferos Marinhos reconhece o ecótipo costeiro como a subespécie *Tursiops truncatus gephyreus*. A estimativa atual sugere a existência de apenas 360 indivíduos somando as pequenas populações encontradas no Brasil, Argentina e Uruguai. O reduzido tamanho das unidades populacionais, a baixa conectividade e diversidade genética entre unidades (Fruet et al., 2014) somam-se à crescente sobreposição e interação com atividades humanas, resultando na classificação do estado de conservação dessa subespécie como vulnerável (Vermeulen et al., 2019).

Uma das maiores unidades populacionais de *Tursiops truncatus gephyreus* encontra-se em Laguna, Santa Catarina. Essa população residente, embora pequena, aparenta estar estável, contando com cerca de 60 indivíduos (Bezamat et al., 2019; Daura-Jorge; Ingram; Simões-Lopes, 2013). Alguns indivíduos dessa população desenvolveram a tática especializada de forrageio em cooperação com pescadores artesanais, que aparentemente influencia a reprodução e a sobrevivência (Bezamat et al., 2019, 2020). A variação no uso dessa tática de forrageio especializada também se reflete no repertório acústico (Romeu et al., 2017), no uso do espaço (Cantor; Simões-Lopes; Daura-Jorge, 2018) e na estrutura social (Daura-Jorge et al., 2012; Machado et al., 2019). No entanto, pressões antropogênicas, como a captura acidental em redes de pesca, poluentes, colisões com embarcações e o ruído gerado pelo tráfego de embarcações, colocam em risco o futuro dessa população e a manutenção de sua cultura. Por exemplo, uma análise de viabilidade populacional sugere que os níveis atuais de mortalidade não natural são insustentáveis. Apenas em um cenário sem mortes não naturais é que a população não entraria em declínio ou, até mesmo, extinção nos próximos cem anos (Bezamat et al., 2021).

2.5.3 O papel das tainhas nas interações entre seus predadores

As tainhas podem ser encontradas em águas tropicais e subtropicais ao redor do mundo. Esses peixes passam parte de suas vidas crescendo e se alimentando em lagoas e sistemas estuarinos até atingirem a maturidade sexual, quando migram para o mar para reproduzir (Herbst; Hanazaki, 2014). A migração das tainhas entre ambientes estuarinos e marinho-costeiros promove a transferência de biomassa e nutrientes entre diferentes sistemas. Por exemplo, as tainhas da espécie *Mugil liza* podem ser encontradas do mar do caribe até a Argentina (Menezes et al., 2015). Anualmente, nos meses do outono e inverno, as tainhas deixam as águas do Uruguai, Argentina e sul do Brasil e migram para o norte, onde desovam nas águas do sul e sudeste do Brasil (Sadowski; Almeida Dias, 1986; Vieira, 1991; Mai et al., 2019) período popularmente conhecido como "safra–da–tainha". O movimento dos cardumes é induzido pela temperatura da água, acompanhando as águas entre 19 e 21ºC, e pela prevalência dos ventos de quadrante sul (Vieira, 1991; Herbst; Hanazaki, 2014). Após a desova, as larvas e juvenis são carregados de volta para o sul pelas correntes marítimas (Lemos et al., 2014). Variações nas condições ambientais podem afetar a dinâmica e a rota dessa migração, podendo induzir a parada dos cardumes em áreas costeiras e o movimento para dentro de estuários (Vieira; Garcia; Grimm, 2008; Mai et al., 2014; Herbst; Hanazaki, 2014). Durante esse processo, grandes e densos cardumes de tainha ficam temporariamente disponíveis para pescadores e outros predadores em ambientes marinhos e estuarinos (ver '*resource waves*' em Armstrong et al., 2016), até serem consumidos ou continuarem sua rota migratória.

Indivíduos do boto-da-tainha (*Tursiops* spp.) em populações por todo o mundo desenvolveram táticas de forrageio especializadas para capturar tainhas. Na Flórida, os botos desenvolveram táticas de forrageio solitário e social para capturar tainhas em águas rasas. Em uma tática de forrageio solitário conhecida como "*mud-plume feeding*" (Lewis; Schroeder, 2003), os indivíduos batem a nadadeira caudal no fundo lodoso para levantar uma pluma de sedimento, desorientando as presas até que estas avancem rapidamente, momento em que são capturadas no meio da pluma. Já na tática de forrageio social conhecida como "*mud ring* *feeding*" (Engleby; Powell, 2019; Torres; Read, 2009), os indivíduos do grupo desempenham papéis distintos (Gazda et al., 2005; Hamilton et al., 2022). Um indivíduo bate a nadadeira caudal para criar um anel de sedimento, conduzindo o cardume em direção a uma barreira formada por outros indivíduos do grupo. As tainhas, encurraladas, saltam à superfície em tentativa de fuga, acabando por serem capturadas pelos botos. Na Austrália, alguns botos da população de Shark Bay adotam uma estratégia em que forrageiam em águas rasas e arrebanham as presas até a praia, encalhando intencionalmente para capturá-las na areia—entre elas a tainha (Sargeant et al., 2005). No sul do Brasil, alguns indivíduos desenvolveram uma tática de forrageio em cooperação com pescadores artesanais (Pryor; Lindbergh; Milano, 1990; Simões-Lopes; Fabián; Menegheti, 1998). Os botos conduzem os cardumes de tainha em direção às margens do estuário, onde pescadores artesanais de tarrafa, que aguardam por comportamentos estereotipados dos botos como um indicativo do momento ideal de lançar as tarrafas, aproveitam essa sincronia entre os dois predadores (ver descrição em *"A sincronia entre botos e pescadores"*). Em um ambiente de águas turvas, a sincronia entre os dois predadores aumenta as chances de sucesso para ambos os predadores (Cantor; Farine; Daura-Jorge, 2023).

A tainha (*Mugil liza*) também é uma das principais presas da pesca no sul do Brasil. Os cardumes de tainhas em migração são historicamente pescados por pescadores artesanais e povos tradicionais (Fossile et al., 2019; Sandoval Gallardo et al., 2021), e desde a década de 1980, a pesca desses peixes também se tornou relevante para a frota industrial. A pesca artesanal dispões de táticas diversas, incluindo o cerco e o uso de redes de emalhe com pequenas embarcações, o arrasto de praia e o uso de tarrafas. Com exceção da pesca artesanal com tarrafas, todas as outras modalidades são regulamentadas e têm suas atividades restritas aos períodos estabelecidos em lei. Enquanto a frota industrial consegue se deslocar e se adaptar às mudanças nas condições climáticas que favorecem a migração dos cardumes de tainhas (e.g., temperatura da água entre 19 e 21°C; Lemos et al., 2016), os pescadores artesanais que utilizam tarrafas e técnicas de cerco de praia precisam aguardar a chegada dos cardumes à costa. Por estarem mais suscetíveis aos movimentos dos grandes cardumes de tainha, esses pescadores artesanais desenvolveram por gerações táticas de pesca em grupo. Essas táticas, como a pesca de arrasto de praia, envolvem a divisão de papeis especializados entre os pescadores, comunicação precisa durante a atividade e a partilha dos recursos obtidos (Devos *et al*., 2019).

Pescadores de tarrafa também encontraram soluções para lidar com as incertezas de um recurso tão efêmero, estabelecendo uma interação colaborativa com parceiros de uma outra espécie de predador. Com tradições transmitidas ao longo de gerações, pescadores artesanais de Tramandaí (Rio Grande do Sul) e Laguna (Santa Catarina) desenvolveram uma tática de pesca em cooperação com botos-da-tainha (Simões-Lopes; Fabián; Menegheti, 1998; Santos; Lemos; Vieira, 2018)—descrita em "*A sincronia entre botos e pescadores*". Essa interação boto-pescador acontece de forma muito localizada e ritualizada, obrigando os pescadores a competir não só pelas tainhas, mas também por espaço para poder interagir com os botos. Como a disponibilidade das tainhas tem alto grau de imprevisibilidade e a competição por espaço se intensifica durante a "safra–da–tainha", alguns pescadores estabeleceram regras informais para autorregular esse sistema (Peterson; Hanazaki; Simões-Lopes, 2008). Em Laguna, por exemplo, os pescadores organizaram um sistema de vagas, em que o pescador que ocupa uma vaga tem a prioridade para lançar as tarrafas em resposta aos comportamentos dos botos. Essas vagas são determinadas pelos próprios pescadores e ocupadas por ordem de chegada. No entanto, como há mais pescadores do que vagas disponíveis, é preciso esperar na fila. Quando um pescador que está ocupando uma vaga executa dois lances de tarrafa bem-sucedidos, ele deve ceder a vaga para o próximo da fila. Alternativamente, os pescadores podem optar por se posicionar entre as vagas e lançar a tarrafa após o lance do pescador que ocupa a vaga e que detém a preferência. Ainda, como os pescadores podem diferir em habilidades de pesca que influenciam o sucesso dos mesmos na interação boto-pescador (Valle-Pereira et al., 2022), eles também podem optar por formar grupos cooperativos, para dividir tarefas, compartilhar vagas e os peixes capturados (Santos-Silva et al., 2022).

2.6 OBJETIVOS

2.6.1 Objetivo geral

O objetivo central desta Tese é compreender os efeitos das variações ambientais e das diferenças individuais no comportamento de forrageio social. Especificamente, esta Tese se concentra na hipótese de que indivíduos do boto-da-tainha (*Tursiops truncatus gephyreus*) diferem na frequência e qualidade de sua participação no forrageio cooperativo com pescadores artesanais em Laguna, sul do Brasil. Para testar essa hipótese, esta Tese investiga e discute os possíveis mecanismos subjacentes às diferenças individuais, além de quantificar se tais diferenças influenciam desproporcionalmente no sucesso de captura dos pescadores artesanais com os quais os botos cooperam.

2.6.2 Objetivos específicos

Capítulo 1:

1. Testar o efeito das condições ambientais e da disponibilidade de presa na dinâmica do forrageio social entre os botos-da-tainha e os pescadores artesanais;

Capítulo 2:

2. Quantificar as diferenças individuais entre os botos no contexto do forrageio social com pescadores, bem como seus efeitos no sucesso de captura de tainhas pelos pescadores artesanais;
3. Identificar os mecanismos subjacentes às diferenças individuais dos botos-da-tainha envolvidos nessa tática de forrageio social com pescadores artesanais;

Capítulo 3

4. Desenvolver ferramentas computacionais para a integração de técnicas de identificação individual e dados multimídia, com o objetivo de investigar o comportamento de animais de vida livre.

3 CAPÍTULO 1: SOCIAL FORAGING BETWEEN HUMANS AND DOLPHINS DRIVES HIGHER PREY CAPTURE DESPITE UNPREDICTABILITY IN FISH ABUNDANCE

Alexandre M. S. Machado[1,2]*
Fábio G. Daura-Jorge[1]†
Damien R. Farine[2–4]†
Penny Tarling[5],
Sergio Escalera[5,6]
Albert Clapés[5,6]
Mauricio Cantor[1,7–9]†*

1 Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil
2 Department of Collective Behaviour, Max Planck Institute of Animal Behaviour, Radolfzell, Germany
3 Department of Evolutionary Biology and Environmental Science, Universität Zürich, Zürich, Switzerland
4 Division of Ecology and Evolution, Research School of Biology, Australian National University, Australia
5 Facultat de Mathemàtiques i Informàtica, Universitat de Barcelona, Barcelona, Spain
6 Computer Vision Center, Universitàt Autónoma de Barcelona, Spain
7 Department of Fisheries and Wildlife, Marine Mammal Institute, Oregon State University, Newport, USA
8 Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behaviour, Konstanz, Germany.
9 Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná, Brazil

† co-senior authorship
* Corresponding authors:
alexandre.marcel@posgrad.ufsc.br
mauricio.cantor@oregonstate.edu

Capítulo submetido à Journal of Animal Ecology como research article.

Manuscrito em revisão para resubmissão.

3.1 ABSTRACT

1. Foraging theory proposes that individuals should modify their foraging behaviour in response to environmental conditions and prey availability. One proposed way to overcome the challenge of finding and capturing unpredictable prey is social foraging. However, the role of environmental conditions shaping prey availability, and whether social foraging can help organisms overcome greater prey unpredictability, is rarely tested empirically.
2. Here, we examine the role of environmental conditions in shaping the outcomes of social foraging in which two apex predators—wild dolphins (*Tursiops truncatus gephyreus*) and human net-casting fishers—synchronize their behaviour to forage on patchy and ephemeral schools of migratory mullet (*Mugil liza*). Specifically, we test whether mullet abundance and the number of mullet caught by fishers is influenced by local environmental conditions, or whether social foraging can buffer fishers (and subsequently dolphins) from fluctuations in mullet availability.
3. We use confirmatory path analysis to investigate the multiple potential links among local environmental conditions, the abundance of fast-moving mullet schools, the number of dolphins and fishers, and whether they foraged synchronously or asynchronously. Our aim is to determine which of these links, if any, influences the outcome of foraging events in terms of prey capture by fishers.
4. Our results confirm two pathways that can lead to higher prey captures. First, fishers caught more prey when mullet were more abundant, but environmental conditions did not predict mullet abundance within the reach of net-casting fishers nor the foraging synchrony among dolphins and fishers. A second, stronger and independent pathway that significantly more dolphins were present during flood tides and their presence resulted in significantly more fishers, more synchronous interactions between the two, and more mullet caught by fishers.
5. Our moment-by-moment analyses demonstrate that the co-occurrence and synchrony in social foraging interactions between predators is more important for prey captures than the local prey abundance, and that both of these factors are largely independent of local environmental conditions. Our results imply that social animals, through collective foraging, can largely decouple their foraging success from the underlying environmental conditions, which can be beneficial to overcoming prey unpredictability and ephemerality.

Key words: foraging specialization, habitat condition, predator-prey, prey availability, social foraging, *Tursiops truncatus*

3.2 INTRODUCTION

Animals live in ever-changing environments, and their foraging success depends on matching their foraging effort with the activity of their prey (McNamara et al., 2011; Miller-Rushing et al., 2010). For example, predatory birds can track the variation in prey activity over the course of the day, foraging more when their prey are more active (Lang et al., 2019). The temporal availability of ephemeral prey and/or the spatial location of patchily distributed prey can usually be anticipated by current environmental conditions (Embling et al., 2012). Baleen whales, for example, forage in areas where environmental conditions predict the presence of krill patches (Barlow et al., 2020). However, for some species, prey availability and environmental conditions can be disconnected, and the lack of environmental cues can make foraging more challenging for predators that hunt highly mobile prey (Navarro et al., 2016). One proposed solution to address this challenge is social foraging, whereby predators' decisions to search for food can both influence and be influenced by other individuals (Giraldeau & Caraco, 2000). For example, predators can use social cues to gain information about the distribution or availability of their prey (Kohles et al., 2022), either inadvertently (e.g., bats can eavesdrop their conspecifics to discover new food patches; Dechmann et al., 2009) or actively (e.g., social songbirds call for conspecifics to forage on the same food patch; Brown et al., 1991). For predators that hunt in groups, social foraging can then stimulate even greater collective benefits when multiple individuals cooperate to hunt their common prey (Krebs & Inman, 1992).

Social foraging is relatively widespread across various taxa (Lang & Farine, 2017). However, determining whether individuals benefit from foraging in groups or if individuals are simply more inclined to form groups when prey are more abundant is often challenging. This is because addressing this question requires a comprehensive understanding of how environmental conditions predict prey availability, how prey availability affects the predators' ability to catch prey, and whether predators catch more prey when hunting together. For example, there are many predator species in which individuals aggregate in specific environments to catch a common and predictable prey (e.g. brown bears *Ursus arctos* fishing for migrating Pacific salmon; Deacy et al., 2016), but it remains unclear whether they gain any benefits by hunting together. By contrast, predators that operate in packs (e.g. killer whales *Orcinus orca* hunting marine mammals; Baird & Dill, 1996), or in larger packs (e.g. African wild dogs *Lycaon pictus* hunting large prey; Fanshawe & Fitzgibbon, 1993), can be more likely to catch more or larger prey, although this relationship could also be driven if packs are more likely to form when prey are more abundant. Finally, social associations among predators can change under different prey abundance regimes (e.g., African lion *Panthera leo* prides fission or fusion according to prey availability; Mbizah et al., 2020), but it is unclear how this affects the foraging performance of individuals. It remains a challenge to simultaneously track and relate environmental conditions, prey abundance, and predator behaviour, making the causal drivers underlying the benefits that predators gain by foraging socially largely unknown.

Here, we study a rare but highly accessible system that allows us to simultaneously track two species of apex predators foraging together to catch a patchy and ephemeral prey. In southern Brazil, the century-old traditional fishery involving wild bottlenose dolphins (*Tursiops truncatus gephyreus*) and artisanal net-casting fishers targeting migratory mullet (*Mugil liza*) (Simões-Lopes et al., 1998) is one of the last known cases of human-wildlife cooperation, whereby human and wild non-human animals synchronise their behaviour to achieve mutually beneficial outcomes (*sensu* Cram et al., 2022). The challenge faced by dolphins in this system is to catch individual prey in large, fast-moving, and highly coordinated mullet schools (e.g., Major, 1978; Simões-Lopes et al., 1998). By contrast, fishers are highly adept at catching a large proportion of the schools using their cast nets, but mullet schools move beyond the reach of net-casting fishers and become elusive in highly murky estuarine water, making them a highly unpredictable prey in space and time (e.g., Ortega et al., 2020). Recent evidence suggests that these two predators' species solve their respective challenges by responding to each other's behaviour—foraging synchronously. First, dolphins herd mullet schools towards coastal shallow waters (Cantor et al. 2023), where artisanal net-casting fishers await specific cues from the dolphins that indicate the location of mullet schools, enabling the fishers to cast their nets at the appropriate time and place (Simões-Lopes et al., 1998). Then, dolphins react by remaining underwater and emitting characteristic echolocation terminal buzzes while foraging on the mullet schools disrupted by, and trapped in, the nets (Cantor et al. 2023). When dolphins and fishers forage in synchrony, dolphins are almost three times more likely to actively hunt underwater and fishers are 17 times more likely to catch any mullet compared to when they forage independently or asynchronously, highlighting the mutualistic nature of this interspecific social foraging interaction (Cantor et al., 2023). While by foraging socially and in synchrony each predator can overcome their relative foraging challenges, it remains unclear whether dolphins and fishers simply co-occur when environmental conditions make mullet predictably abundant, and how much of this co-occurrence drives the outcomes of their foraging effort.

Here, therefore, we disentangle the contributions of environmental conditions, prey and predator co-occurrence to those of social foraging in the dolphin-fisher system by combining three distinct data streams. First, we sampled the *in situ* environmental (water, wind and tide) conditions known to be related to mullet migration (Herbst & Hanazaki, 2014; Lemos et al., 2014). Second, we quantified the moment-by-moment abundance of fast-moving mullet schools within the murky waters using a novel deep learning model applied to adaptive resolution imaging sonar data (Tarling et al., 2022). Third, we conducted fine-scale observational tracking of fisher and dolphin abundance, behaviour and the outcome of their social foraging interactions. We used these data to perform a confirmatory path analysis to address three key questions. First, is mullet abundance within the reach of net-casting fishers predicted by changes in fine-scale environmental conditions? We hypothesize that water temperature, wind and tide conditions, which drive mullet migration over regional scales, can influence the movements of mullet schools in and out of the estuarine system, therefore impacting the local mullet availability at the interaction site, where dolphins and fishers forage together. Second, are dolphins and fishers more numerous in moments of high mullet abundance or under specific environmental conditions? We hypothesize that the abundance of foraging dolphins at the interaction site mirrors the periods when mullet schools are more abundant, and that the abundance of fishers in the water, who rely on dolphins as a cue for mullet availability, mirrors the periods of high dolphin abundance. Finally, does the co-occurrence of both predator species result in higher probabilities of successful social foraging? We hypothesize that incidence of synchronous foraging between dolphins and net-casting fishers correlates with their local abundances and consequently leads to an increased likelihood mullet caught by fishers.

3.3 MATERIAL AND METHODS

We simultaneously collected environmental and behavioural data, both above and underwater, to investigate the temporal variation in dolphin-fisher foraging interactions in Laguna, southern Brazil (Fig. 1). We focused our sampling effort on the primary site where these social foraging interactions between dolphins and fishers takes place: a small beach (ca. 100 meters in length) in the inlet canal that connects the estuarine system to the Atlantic Ocean (Cantor et al., 2018). From 09:00 to 17:00, for 15 days (June 22nd to July 1st, and July 4th to July 7th, 2018), we deployed a high-resolution sonar imaging system—the Adaptive Resolution

Imaging Sonar (ARIS3000; Sound Metrics Corp, WA, USA)—while recording environmental variables and using all-occurrence sampling (Altmann, 1974) to continuously record the number of mullet, dolphins and fishers, as well as their behaviour and interactions.

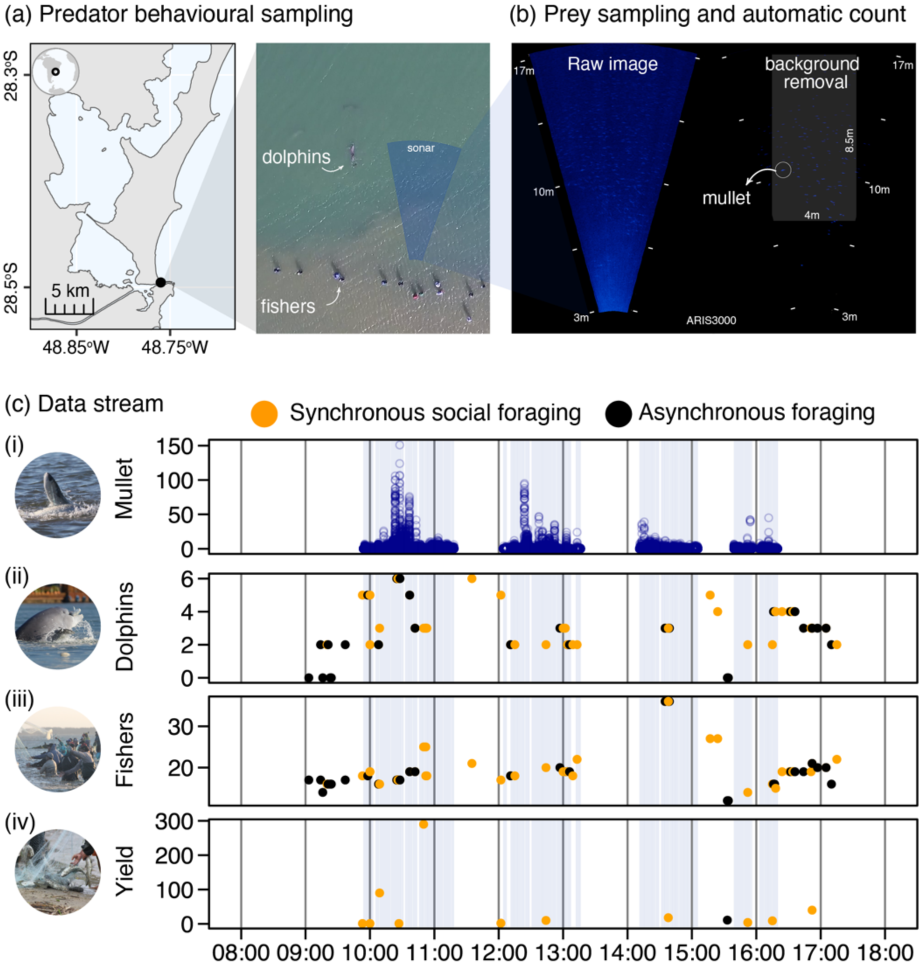

Figure 3.1: **Overview of the study system, sampling methods, and an excerpt of the simultaneously collected and aligned data streams.** (a) Sampling of predator and prey co-occurrence and behaviour in the lagoon system of Laguna, southern Brazil. The aerial image shows the predators from above—bottlenose dolphins (centre) and artisanal net-casting fishers (bottom, in line along the edge of the canal)—and the blue area highlights the underwater image generated by the ARIS3000 sonar sampling, exemplified by (b) the same sonar frame presented on the left as the raw image, and on the right as a processed image with enhanced contrast and removed background. The highlighted rectangular area marks the area cropped to standardize all input samples in the deep learning model with density-based regression used to quantify the mullet abundance. (c) For a sampling day, all environmental and observational data were simultaneously collected with the sonar sampling (shaded blue areas): (i) mullet school detections are represented by blue dots in the frame-by-frame sonar sampling; the number of (ii) dolphins, (iii) fishers, and (iv) mullet caught in synchronous (orange) and asynchronous (black) social foraging events between dolphins and fishers.

3.3.1 Monitoring environmental conditions

We assessed changes in local environmental conditions to investigate whether it could predict changes in mullet abundance, which could drive temporal variation in the abundance of dolphins and fishers engaged in their social foraging interactions and in their joint foraging success. Both empirical data and traditional ecological knowledge suggest that the mullet reproductive migration is triggered by a decrease in sea surface temperature and the prevalence of southern winds (Herbst & Hanazaki, 2014; Lemos et al., 2016). As mullets migrate northwards, a shift from southern to northern winds, along with an increase in water temperature, can bring mullet schools closer to the coast. Tidal currents can also play a role in how mullet schools move through the coast, especially when synchronized with the timing of mullet arrival, as tidal currents can facilitate the movement of schools in and out of estuarine areas (Herbst & Hanazaki, 2014; Lemos et al., 2016). Based on this knowledge, we continuously recorded the water temperature at the interaction site using the sensor from ARIS3000 (see below). At the beginning of each sampling hour, we measured wind speed and wind direction *in situ* using an anemometer (Instrutherm AD-250) and classified wind direction as southern and northern wind quadrants. To assess changes in the tide levels, we obtained data from a weather station located inside the lagoon system (28º 29.1'S, 48º 46.9'W) with a digital Thalimedes positioned at 1 meter from the bottom (Epagri, 2020). We used hourly tide heights measurements to classify tidal currents during each sampling hour as *ebb* or *flood* and to estimate tide velocity as the difference in tide height (in centimetres) from hour to hour.

3.3.2 Quantifying fine-scale mullet abundance

The high turbidity and low visibility (0.25 to 1.0m) of the murky waters of the canal pose a major challenge for accurately estimating prey availability. To overcome this challenge, we used an ARIS3000 sonar imaging system that can detect and measure fish under zero visibility conditions (Cook et al., 2019; Lankowicz et al., 2020; Tarling et al., 2022). The ARIS3000 uses 128 beams to emit sound pulses of very high frequencies (up to 3MHz) converting the returning echoes into digital images. Operating at a sampling rate of around three frames per second, the sonar camera generates a birds-eye view of a 30-degree wedge ranging from 2 to 20m from the sonar (Fig. 1b; Tarling et al., 2022). We mounted the sonar camera on a platform at the edge of the canal slope, where the fishers typically stand, at around 1m depth and in the middle of the 100m wide interaction site (Fig. 1a). We manually adjusted the sonar camera position and angle below the water surface to detect mullets from 2 to up to 20 meters from the edge of the slope into the canal. To avoid any disturbance to the dolphins' behaviour, we operated the sonar at very high frequencies of 1.8 to 3MHz, which were 10 to 60 times above the dolphins' audible range (upper-frequency limit of functional hearing: 50 to 169 kHz Finneran et al., 2008; Houser et al., 2008).

To process the sonar images, we first used the native ARIS Scope software to increase contrast and apply a background subtraction filter that removes any background noise (i.e. any static part of the footage) thereby leaving only mullet in motion (Tarling et al., 2022). We can safely assume that the fast-moving, densely packed schools visible in the sonar images are indeed mullets because they are the dominant schooling fish species in the area from May to July (Simões-Lopes et al., 1998). Given the varying range of the sonar beam across samples, we cropped all analysed sonar images to a range of 8 to 17 meters to avoid any noise from the sea bottom near the edge of the canal (too close to the sonar) and to minimize any bias in mullet abundance due to the maximum sampling area (too far from the sonar). We then exported these video samples and cropped their frames to a standard sampling area of 4 by 8.5m (Fig. 1b).

We employed our novel deep learning model (Tarling et al., 2022) to accurately count mullet in the sonar images. This deep learning model was specifically developed to process and accurately count dense, fast-moving mullet schools from the low-resolution sonar images (Tarling et al., 2022) by using a density-based regression approach derived from methods commonly used to count people in crowds (Liu et al., 2018; Oh et al., 2020). To address the lack of labelled biological population data, the model was simultaneously trained on a self-supervised task to learn the relative abundance of fish in pairs of overlapping image crops from a set of unlabelled images. To ensure the model was well-adapted to varied and imbalanced datasets of images captured in the wild, which often contain noise (e.g. nets and dolphins) and occlusions, we also incorporated uncertainty regularisation (Tarling et al., 2022).

To assess prey patchiness, we tested if the mullet school sizes in the frame-by-frame data followed a power law distribution; likewise, to assess prey ephemerality, we tested if the time-integrated mullet abundance was distributed according to a power law (Supplementary Material, Fig. S1—S5). To estimate school sizes, we considered the total mullet counts frame-by-frame of the sonar imaging. We then summarized these data in a time-integrated mullet abundance by dividing the total number of mullet detections by the number of frames sampled per sampling hour.

3.3.3 Quantifying predator abundance, behaviour and social foraging

We used behavioural all-occurrence sampling techniques (Altmann, 1974) to record fisher foraging (net casts), dolphin cues, and their relative abundance over time (both dolphins and fishers regularly arrived at, and departed from, the interaction site). We defined a foraging event as the moment when fishers cast their nets; in the context of the dolphin-fisher system, these events can be categorized as either 'synchronous' or 'asynchronous' foraging. Synchronous events characterize the cooperative foraging between humans and dolphins (Cantor et al., 2023) and are defined as when fishers cast their nets following a dolphin cue (i.e. a stereotyped behaviour such as a sudden dive arching their back; see Simões-Lopes et al., 1998) that discloses the presence and location of the fish schools and typically increases their joint foraging success (Cantor et al., 2023). Asynchronous foraging events are defined as when fishers cast their nets in the absence of dolphins, in the absence of a dolphin cue, or not in synchrony (i.e., too late and too far) with a dolphin cue; all of which typically do not increase their joint foraging success (Cantor et al., 2023). At each foraging event, whether synchronous or asynchronous, we counted the number of individual dolphins at the interaction site (within 50m from the sandbank to the middle of the canal; Fig. 1a), the number of fishers in the water, and the number of fishers that cast their nets in response to behavioural cues from dolphins. As our long-term photo-identification survey data revealed that not all individuals from this small and resident population of bottlenose dolphins forage with artisanal fishers (Daura-Jorge et al., 2013; Bezamat et al., 2019; Cantor et al., 2023), we also photo-identified all individual dolphins in the field and disregard dolphins passing by. Thus, we limited our counts to dolphins that remained present and foraging prior to and after the net-casting events. To assess the outcome of each foraging event, we thoroughly inspected all the nets cast when fishers returned to the beach, and counted the number of mullet caught, if any.

3.3.4 Statistical analyses

We used path analysis with local estimation (Lefcheck, 2016) to investigate the temporal variation in the rates and outcomes of social foraging between dolphins and fishers. Path analysis allow us to simultaneously test multiple causal hypotheses within a single network, where one variable can act both as response variable on one path and as a predictor on another path (Shipley, 2000). Here, we used a single path model based on the fitting of five individual linear mixed models to test the following five hypotheses derived from our three key questions: (i) changes in local environmental conditions affect mullet abundance at the interaction site; (ii) high numbers of dolphins at the interaction site coincide with moments of high mullet abundance, or specific environmental conditions that mirror mullet abundance; (iii) high number of fishers in the interaction site coincides with moments of high dolphin abundance, or specific environmental conditions; (iv) synchronous social foraging events between dolphins and fishers are more frequent when both predators are more abundant at the interaction site; and (v) both synchronous social foraging events and mullet abundance play a role in defining the outcome (in terms of mullet caught) of the dolphins' and fishers' joint foraging effort.

To perform this analysis, we first selected the observational data (i.e., counts of dolphins, fishers, foraging events and mullet caught) that intersected with the sampling time of the sonar data (Fig. 1c). Second, we filtered off sonar frames with noise (detected objects other than mullet schools, such as nets) and summarised all variables to the respective sampling hour. To quantify mullet abundance for each sampling hour, we summed the number of detections from our deep learning models and divided this total by the number of frames within that hour to account for differences in sampling time. Similarly, to quantify the abundance of dolphins and fishers for each sampling hour, we calculated the mean number of individual dolphins and fishers identified at the interaction site within each hour. Third, we transformed some variables to meet the model assumptions and avoid convergence issues when fitting them with a Poisson distribution. Tidal currents and wind direction were transformed into numerical predictors by assigning values of -0.5 to ebb currents and southern winds, and 0.5 to flood currents and northern winds. All response variables were transformed using the natural logarithm of one plus the input vector. Before fitting the path model, we conducted an exploratory data analysis (Zuur et al., 2010) and removed from the analysis one sampling hour considered to be an outlier in mullet abundance (i.e., an unusually high detection that could represent a processing error).

We fit the path model using linear mixed effect regression models. For each component model, we included a random intercept for the sampling day to account for day-to-day variation in large-scale factors influencing the mullet migration, and an autoregressive correlation structure (AR1) to account for the correlation among sampling hours. We used the Fisher's C statistic to assess the overall goodness-of-fit of the single path model and test whether our hypothesized pathways aligned with the relationships indicated by the data. We opted to omit links that were not hypothesized *a priori*. To check the assumptions of normality and heteroscedasticity, we visually inspected the residuals of each linear mixed-models (Supplementary Material, Fig. S6–S10). We fit linear mixed-models and the path model using the `nlme` (Pinheiro et al., 2021) and the `piecewiseSEM` (Lefcheck, 2016) R-packages, respectively. To assess each model fit, we used the theoretical marginal and conditional R^2_{GLMM} (Nakagawa et al., 2017).

3.4 RESULTS

We collected data on local environmental conditions, prey abundance, and fisher and dolphin abundance, dolphin cues and net casts, and the number of mullet caught by fishers over 87 hours, spanning 15 days. From these data, we processed a total of 560,127 unique frames from the sonar videos, of which 511,861 were free of noise, and 109,455 contained mullet detections (median = 3 mullet, mean ± SD = 9.15 ± 22.29, range = 1–697). We found that both the mullet school sizes and the time-integrated mullet abundance both followed a power law distribution (Supplementary Material, Figs. S4–S5), suggesting that the prey was patchily distributed (only a few frames with large schools) and ephemeral (the time gap between detections of mullet schools is unpredictable).

Aligning the sonar and the observational datasets resulted in 652 foraging events with precise numbers of fishers and dolphins involved. We observed 312 synchronous social foraging events (when fishers cast nets in response to the dolphins' foraging cue), and 340 asynchronous foraging events (243 when fishers did not follow the dolphin's cue and 97 in the absence of dolphins). In foraging events without dolphins, the number of active fishers in the water ranged from 1 to 31 (median = 7, mean ± SD = 9.87 ± 7.91). There were only four events in which dolphins were foraging at the interaction site and there were no fishers in the water. Across all foraging events with dolphins present at the interaction site, the number of active fishers in the water ranged from 1 to 38 (median = 21, mean ± SD = 20.95 ± 7.55). Across all foraging events, a total of 2,060 mullets were caught by the fishers, 87% (1,797) out of which were caught as a result of synchronous social foraging events.

The path model showed a good fit to the data (C = 41.382, df = 32, P = 0.124), and provided evidence for several causal relationships in the dolphin-fisher system (Fig. 2). There was no clear effect of changes in local conditions of water temperature, wind or tide predicting mullet abundance at the fine spatiotemporal scale of the dolphin-fisher interaction, either within a day (Marginal R^2_{GLMM} = 0.08) or across days (Conditional R^2_{GLMM} = 0.08). By contrast, the flood phase of tidal currents had a direct and positive effect on the abundance of dolphins (Table

1 path vii). However, the number of dolphins present was not significantly related to changes in mullet abundance.

The number of fishers in the water was not significantly influenced by local environmental conditions. However, there were more fishers in the water when more dolphins were present at the interaction site (Table 1 path x). The presence of more dolphins (Table 1 path xvi) and more fishers (Table 1 path xvii) together created more opportunities for synchronous social foraging events. Despite the direct and positive effect of mullet abundance on the amount of mullet caught by fishers (Table 1 path xix), the model suggested a direct effect of synchronous foraging events on the number of mullet caught (Table 1 path xviii); this effect was 2.96 times higher than the effect of mullet abundance. The coefficients of statistically clear paths are highlighted in Figure 2 and all path coefficients are reported in Table 1. Further details about the component model and model validation are reported in the Supplementary Material (Tables S1–S5, Figs. S6–S10).

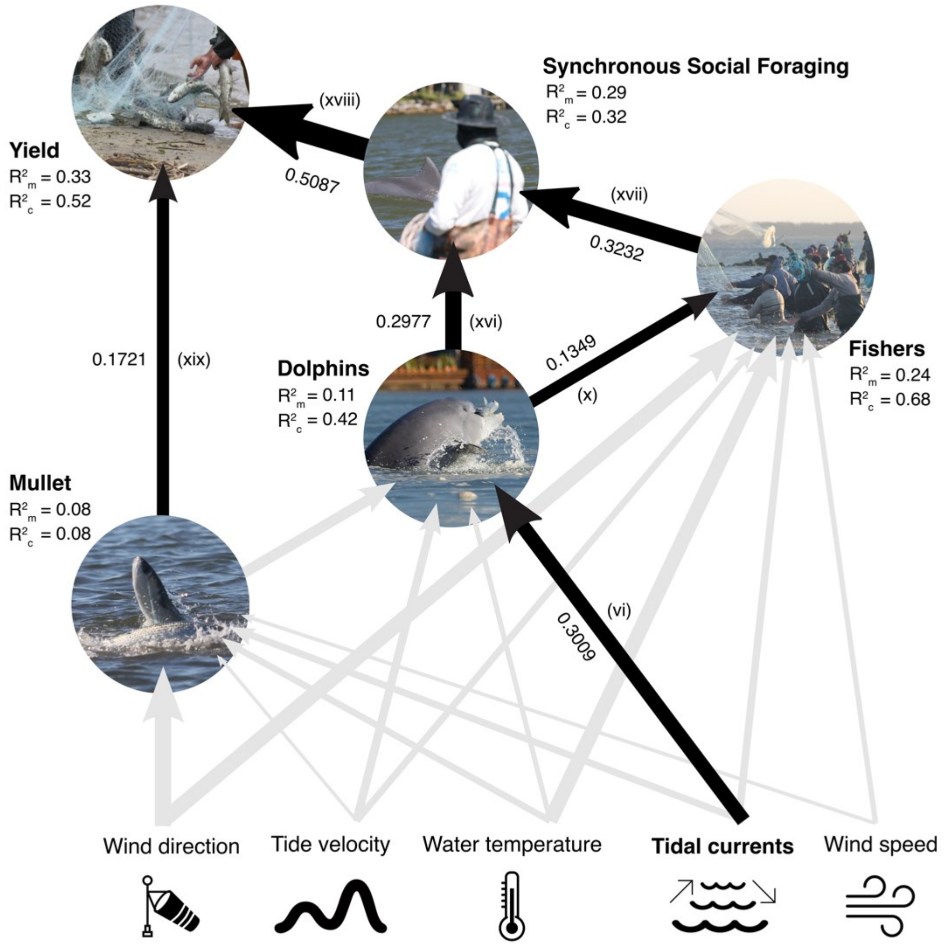

Figure 3.2: **Confirmatory path analysis revealed two non-exclusive pathways that maximize successful foraging outcomes.** The first pathway occurs when dolphins are more abundant (typically during the flood current of the tidal cycle, vi), with this increase leading to a greater number of fishers (x) and, subsequently, a greater number of synchronous foraging events (xvi, xvii) resulting in more mullet caught (xviii). In the second pathway, more mullet are caught when there is greater mullet abundance (xix). Nodes represent the abundance of prey ('mullet') and predators ('dolphins', 'fishers'); whether social foraging events between dolphins and fishers are synchronous ('synchronous social foraging'); and the number of mullet caught by fishers ('yield'). Paths in black represent statistically clear positive coefficients (Roman numerals; Table 1), while paths in grey represent statistically unclear coefficients. Path thickness indicate the relative effect sizes across models representing the standardized path coefficients (given by numbers). See Table 1 for all standardized path coefficients. Marginal and Conditional R^2_{GLMM} are given for each model to represent the proportion of the total variance explained by fixed, and both fixed and random effects, respectively.

3.5 DISCUSSION

Our findings reveal that social foraging among predators—here, human fishers and wild dolphins—can overcome the challenges of foraging on patchy and ephemeral prey, such as schools of migratory mullet. While higher prey abundance—which varies independently of local environmental conditions—corresponds to greater foraging success (number of mullet caught by fishers), this effect is substantially smaller than the effect of synchronous social foraging between fishers and dolphins. That social foraging has a greater impact on prey capture supports previous studies suggesting that this system is mutualistic (Simões-Lopes et al. 1998) and emphasizes the key role of behavioural synchrony between these two apex predators for catching more fish (Cantor et al., 2023).

There are multiple routes through which individuals can adapt their foraging behaviour in response to environmental conditions and prey patchiness. A key prediction of foraging theory—predator behaviour should mirror the spatial and temporal distribution of prey (Stephens & Krebs, 1987)—has been challenging to test in the wild because predator behaviour and prey distribution are both, independently, influenced by multiple factors operating at different spatiotemporal scales. For example, large-scale climatic conditions can shape population-level dynamics in prey species and predict the distribution of predators at large scales (e.g., Barlow et al., 2020; Pirotta et al., 2014); however, the foraging behaviour of predators primarily hinges on how prey behave at much finer spatiotemporal scales, specifically within their local environment (e.g., Torres et al., 2008). In other words, while the environment can predict what prey do at larger scales, this prediction may not be as evident for predators at fine scales since they can only perceive the local environmental conditions (e.g., Cade et al., 2021). These local conditions are much more susceptible to noise and variation in terms of prey distribution and availability compared to what would be possible for predators to perceive if they had access to regional-scale information. Our results illustrate this mismatch. We found that mullet schools—the main prey target by foraging dolphins and fishers—are not predicted by local environmental conditions in the dolphin-fisher system. But why is this the case?

The large-scale dynamics driving mullet abundance on a regional scale appears to make mullet unpredictable for both dolphins and fishers during their local foraging activities. During the austral autumn and winter, regional mullet availability increases along the coasts of northern Argentina and southern Brazil, as changes in sea water temperature and wind conditions triggers their reproductive migration (Sadowski & Almeida Dias, 1986; Vieira & Scalabrin, 1991). Some predators can track these environmental cues at this large, regional scale, enabling them to follow the resource wave. For example, the southern Brazilian industrial fishing fleet follow water temperature conditions at regional scales to pursue migrating mullet schools (e.g., Lemos et al., 2016). The regional processes that drive mullet schools northwards to spawn must synchronize with local wind and current conditions to then bring these schools close to the coast. At this point, they enter estuaries and lagoons, becoming available to coastal resident dolphins (Teixeira et al., 2020) and artisanal fishers (Herbst & Hanazaki, 2014).

Thus, different combinations of regional and local processes contribute to make mullet a resource that is available in time-limited waves. As illustrated by our fine-scale sonar data mullet abundance, in which mullet are primarily detected in large schools at irregular time intervals (Supplementary Material Figs. S1–S5), at the scale at which dolphins and fishers can perceive, is patchy and ephemeral. Thus, mullet abundance would only increase locally if regional environmental processes (e.g., water temperature and wind conditions that influence the latitudinal migration of mullet schools) match with the local conditions (e.g., tidal currents that facilitate the movement of mullet schools in and out of estuaries). This multiscale nature may explain why dolphins do not necessarily forage more at the interaction site when mullets are abundant. However, we did find more variation in the abundance of dolphins and fishers between than within days. Such variation suggests either some degree of response to varying conditions at the regional scales or the ability of some more competitive individuals to maintain their access to this resource while restricting that of their conspecifics.

We further found that fine-scale environmental conditions not only fail to predict mullet abundance at the fine scale, but also do not predict dolphin abundance. This implies that it is not only fishers who struggle to detect mullet in the murky estuarine waters of the interaction site (Simões-Lopes et al. 1998), but also the dolphins themselves. We did find that dolphins are more numerous during the flood phase of tidal currents, likely because the current interacts with the canal bathymetry, creating favourable foraging opportunities for dolphins (Pirotta et al., 2014). In Laguna, the mullet schools entering the inlet typically move along the edges of the canal and seek protection among the rocky jetties (Herbst & Hanazaki 2014); during flood tides, currents can force and dislodge mullets out of these rocky shelters, making them more susceptible to being herded by dolphins toward the line of fishers (Cantor et al., 2023). Thus, when regional conditions favour mullet approaching the coast, they may become more available to dolphins, and thus to fishers, particularly during flood tides (although flood tides during unsuitable regional conditions are unproductive).

The unpredictability of mullet abundance has significant implications for the foraging tactics used by both artisanal fishers and wild dolphins. Net-casting fishers adopt a sit-and-wait tactic at the interaction sites, relying almost entirely on dolphins to facilitate their access to prey, as synchronous social foraging events produce nearly all successful catches. Dolphins likely follow a similar pattern, as they forage intensively in and around the nets when fish are caught by fishers (Cantor et al., 2023). Our findings confirm previous results (Cantor et al., 2023) indicating that synchrony is key to the success of foraging events and extends this by demonstrating that synchronous social foraging is substantially more important than local mullet abundance in driving the success of this human-wildlife cooperation. These findings also support previous hypotheses suggesting that social foraging with dolphins likely increases fishers' catch rates (Simões-Lopes et al., 1998; Santos et al., 2018), despite these previous studies having no data on mullet abundance and, thus, being unable to distinguish benefits of social foraging from the mere co-occurrence of fishers and dolphins during periods of high mullet abundance. Our study therefore extends these previous works and advances the field by showing that social foraging tactics can help social predators to overcome the challenges posed by the unpredictable and ephemeral nature of their prey.

3.6 ACKNOWLEDGEMENTS

We thank all fieldwork volunteers and Pedro Castilho for their essential help during data collection, and the Sound Metrics Corp team for software support. This study is part of the Brazil–Germany PROBRAL Research Program funded jointly by CAPES and DAAD (#88881.198854/2018–01), and of the SELA Long-Term Ecological Research Program (PELD CNPq #445301/2020–1). This study received further support from the Max Planck Society and the Centre for the Advanced Study of Collective Behaviour funded by DFG under Germany's Excellence Strategy (EXC 2117–422037984); AMSM received a CAPES doctoral scholarship (finance code 001) and a CAPES/DAAD PROBRAL exchange scholarship; FGDJ was supported by CAPES (#88887.374128/2019–00), CNPq (#308867/2019–0), and FAPESC (TR2012000295, 2021TR387 and 2021TR000581); DRF was supported by the ERC European Union's Horizon 2020 (#850859) and an SNSF Eccellenza Professorship (#PCEFP3_187058); and MC was supported by a CAPES postdoctoral fellowship (88881.170254/2018–01), the Department for the Ecology of Animal Societies at the Max Planck Institute of Animal Behaviour and at Oregon State University via the Marine Mammal Research Program Fund, the Jungers Faculty Development and Research Fund. This work has been partially supported by the Spanish project PID2019-105093GB-I00 and by ICREA under the ICREA Academia programme.

3.7 CONFLICTS OF INTEREST

We declare no conflicts of interest.

3.8 DATA AVAILABILITY STATEMENT

Data and code to reproduce the analysis are available as a supplementary material for peer review. Data and code to reproduce the statistical analysis will be available to an open, digital repository upon editorial decision.

3.9 AUTHOR CONTRIBUTIONS

AMSM: conceptualization, data curation, formal analyses, investigation, methodology, project administration, software, validation, visualization, writing—original draft, review and editing, and supplementary material, editing and review. FGDJ: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, editing and review. DRF: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, editing and review. PT: data curation, formal analyses, methodology, software, writing—editing. SE: methodology, resources. AC: methodology, resources. MC: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, supervision, writing—original draft, editing, and review. All authors contributed critically to the manuscript and gave final approval for publication.

3.10 REFERENCES

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. https://doi.org/10.1080/14794802.2011.585831

Baird, R. W., & Dill, L. M. (1996). Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology*, *7*(4), 408–416. https://doi.org/10.1093/beheco/7.4.408

Barlow, D., Bernard, K., Escobar-Flores, P., Palacios, D., & Torres, L. G. (2020). Links in the trophic chain: Modeling functional relationships between in situ oceanography, krill, and blue whale distribution under different oceanographic regimes. *Marine Ecology Progress Series*, *642*, 207–225. https://doi.org/10.3354/meps13339

Bezamat, C., Simões-Lopes, P. C., Castilho, P. V., & Daura-Jorge, F. G. (2019). The influence of cooperative foraging with fishermen on the dynamics of a bottlenose dolphin population. *Marine Mammal Science*, *35*(3), 825–842. https://doi.org/10.1111/mms.12565

Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, *42*(4), 551–564. https://doi.org/10.1016/S0003-3472(05)80239-8

Cade, D. E., Fahlbusch, J. A., Oestreich, W. K., Ryan, J., Calambokidis, J., Findlay, K. P., Friedlaender, A. S., Hazen, E. L., Seakamela, S. M., & Goldbogen, J. A. (2021). Social exploitation of extensive, ephemeral, environmentally controlled prey patches by supergroups of rorqual whales. *Animal Behaviour*, *182*, 251–266. https://doi.org/10.1016/j.anbehav.2021.09.013

Cantor, M., Farine, D. R., & Daura-Jorge, F. G. (2023). Foraging synchrony drives resilience in human-dolphin mutualism. *Proceedings of the National Academy of Sciences of the United States of America, 120(6), e2207739120.* https://doi.org/10.1073/pnas.2207739120

Cantor, M., Simões-Lopes, P. C., & Daura-Jorge, F. G. (2018). Spatial consequences for dolphins specialised in foraging with fishermen. *Animal Behaviour*, *139*, 19–27. https://doi.org/10.1016/j.anbehav.2018.03.002

Cook, D., Middlemiss, K., Jaksons, P., Davison, W., & Jerrett, A. (2019). Validation of fish length estimations from a high frequency multi-beam sonar (ARIS) and its utilisation as a field-based measurement technique. *Fisheries Research*, *218*, 59–68. https://doi.org/10.1016/j.fishres.2019.05.004

Daura-Jorge, F. G., Ingram, S. N., & Simões-Lopes, P. C. (2013). Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. *Marine Mammal Science*, *29*(2), 293–311. https://doi.org/10.1111/j.1748-7692.2012.00571.x

Deacy, W., Leacock, W., Armstrong, J. B., & Stanford, J. A. (2016). Kodiak brown bears surf the salmon red wave: Direct evidence from GPS collared individuals. *Ecology*, *97*(5), 1091–1098. https://doi.org/10.1890/15-1060.1

Dechmann, D. K. N., Heucke, S. L., Giuggioli, L., Safi, K., Voigt, C. C., & Wikelski, M. (2009). Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1668), 2721–2728. https://doi.org/10.1098/rspb.2009.0473

Embling, C. B., Illian, J., Armstrong, E., van der Kooij, J., Sharples, J., Camphuysen, K. C. J., & Scott, B. E. (2012). Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: A functional data analysis approach. *Journal of Applied Ecology*, *49*(2), 481–492. https://doi.org/10.1111/j.1365-2664.2012.02114.x

Epagri. (2020). *Banco de dados de variáveis ambientais de Santa Catarina* (Documentos No. 310; Epagri, p. 20).

Fanshawe, J. H., & Fitzgibbon, C. D. (1993). Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, *45*(3), 479–490. https://doi.org/10.1006/anbe.1993.1059

Finneran, J. J., Houser, D. S., Blasko, D., Hicks, C., Hudson, J., & Osborn, M. (2008). Estimating bottlenose dolphin (*Tursiops truncatus*) hearing thresholds from single and multiple simultaneous auditory evoked potentials. *The Journal of the Acoustical Society of America*, *123*(1), 542–551. https://doi.org/10.1121/1.2812595

Herbst, D. F., & Hanazaki, N. (2014). Local ecological knowledge of fishers about the life cycle and temporal patterns in the migration of mullet (*Mugil liza*) in Southern Brazil. *Neotropical Ichthyology*, *12*(4), 879–890. https://doi.org/10.1590/1982-0224-20130156

Houser, D. S., Gomez-Rubio, A., & Finneran, J. J. (2008). Evoked potential audiometry of 13 Pacific bottlenose dolphins (*Tursiops truncatus gilli*). *Marine Mammal Science*, *24*(1), 28–41. https://doi.org/10.1111/j.1748-7692.2007.00148.x

Kohles, J. E., O'Mara, M. T., & Dechmann, D. K. N. (2022). A conceptual framework to predict social information use based on food ephemerality and individual resource requirements. *Biological Reviews*, *97*(6), 2039–2056. https://doi.org/10.1111/brv.12881

Krebs, J. R., & Inman, A. J. (1992). Learning and Foraging: Individuals, Groups, and Populations. *The American Naturalist*, *140*, S63–S84.

Lang, S. D. J., & Farine, D. R. (2017). A multidimensional framework for studying social predation strategies. *Nature Ecology & Evolution*, *1*(9), 1230–1239. https://doi.org/10.1038/s41559-017-0245-0

Lang, S. D. J., Mann, R. P., & Farine, D. R. (2019). Temporal activity patterns of predators and prey across broad geographic scales. *Behavioral Ecology*, *30*(1), 172–180. https://doi.org/10.1093/beheco/ary133

Lankowicz, K. M., Bi, H., Liang, D., & Fan, C. (2020). Sonar imaging surveys fill data gaps in forage fish populations in shallow estuarine tributaries. *Fisheries Research*, *226*, 105520–105520. https://doi.org/10.1016/j.fishres.2020.105520

Lefcheck, J. S. (2016). PiecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Lemos, V. M., Avila Troca, D. F., Castello, J. P., & Paes Vieira, J. (2016). Tracking the southern Brazilian schools of *Mugil liza* during reproductive migration using VMS of purse seiners. *Latin American Journal of Aquatic Research*, *44*(2), 238–246. https://doi.org/10.3856/vol44-issue2-fulltext-5

Lemos, V. M., Varela, A. S., Schwingel, P. R., Muelbert, J. H., & Vieira, J. P. (2014). Migration and reproductive biology of *Mugil liza* (Teleostei: Mugilidae) in south Brazil. *Journal of Fish Biology*, *85*(3), 671–687. https://doi.org/10.1111/jfb.12452

Liu, X., van de Weijer, J., & Bagdanov, A. D. (2018). Leveraging Unlabeled Data for Crowd Counting by Learning to Rank. *2018 IEEE/CVF Conference on Computer Vision and Pattern Recognition*, 7661–7669. https://doi.org/10.1109/CVPR.2018.00799

Major, P. F. (1978). Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Animal Behaviour*, *26*, 760–777. https://doi.org/10.1016/0003-3472(78)90142-2

Mbizah, M. M., Farine, D. R., Valeix, M., Hunt, J. E., Macdonald, D. W., & Loveridge, A. J. (2020). Effect of ecological factors on fine-scale patterns of social structure in African lions. *Journal of Animal Ecology*, *89*(11), 2665–2676. https://doi.org/10.1111/1365-2656.13334

McNamara, J. M., Barta, Z. Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, *14*(12), 1183–1190. https://doi.org/10.1111/j.1461-0248.2011.01686.x

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Nakagawa, S., Schielzeth, H., & Johnson, P. C. D. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J R Soc Interface*, *14*(134). https://doi.org/10.1098/rsif.2017.0213

Navarro, J., Cardador, L., Fernández, Á. M., Bellido, J. M., & Coll, M. (2016). Differences in the relative roles of environment, prey availability and human activity in the spatial distribution of two marine mesopredators living in highly exploited ecosystems. *Journal of Biogeography*, *43*(3), 440–450. https://doi.org/10.1111/jbi.12648

Oh, M., Olsen, P., & Ramamurthy, K. N. (2020). Crowd Counting with Decomposed Uncertainty. *Proceedings of the AAAI Conference on Artificial Intelligence*, *34*(07), Article 07. https://doi.org/10.1609/aaai.v34i07.6852

Ortega, J. C. G., Figueiredo, B. R. S., da Graça, W. J., Agostinho, A. A., & Bini, L. M. (2020). Negative effect of turbidity on prey capture for both visual and non-visual aquatic predators. *Journal of Animal Ecology*, *89*(11), 2427–2439. https://doi.org/10.1111/1365-2656.13329

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2021). *nlme: Linear and Nonlinear Mixed Effects Models* (3.1-153).

Pirotta, E., Thompson, P. M., Miller, P. I., Brookes, K. L., Cheney, B., Barton, T. R., Graham, I. M., & Lusseau, D. (2014). Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. *Functional Ecology*, *28*(1), 206–217. https://doi.org/10.1111/1365-2435.12146

Sadowski, V., & Almeida Dias, E. R. (1986). Migração da tainha (*Mugil cephalus* Linnaeus, 1758, sensu latu) na costa sul do Brasil. *Boletim Do Instituto de Pesca*, *13*(1), 31–50.

Santos, M. L., Lemos, V. M., & Vieira, J. P. (2018). No mullet, no gain: Cooperation between dolphins and cast net fishermen in southern Brazil. *Zoologia*, *35*, 1–13. https://doi.org/10.3897/zoologia.35.e24446

Shipley, B. (2000). A New Inferential Test for Path Models Based on Directed Acyclic Graphs. *Structural Equation Modeling: A Multidisciplinary Journal*, *7*(2), 206–218. https://doi.org/10.1207/S15328007SEM0702_4

Simões-Lopes, P. C., Fabián, M. E., & Menegheti, J. O. (1998). Dolphin interactions with the mullet artisanal fishing on southern Brazil: A qualitative and quantitative approach. *Revista Brasileira de Zoologia*, *15*(3), 709–726. https://doi.org/10.1590/S0101-81751998000300016

Stephens, D. W., & Krebs, J. R. (1987). *Foraging theory* (p. 247). Princeton University Press.

Tarling, P., Cantor, M., Clapés, A., & Escalera, S. (2022). Deep learning with self-supervision and uncertainty regularization to count fish in underwater images. *PLOS ONE*, *17*(5), e0267759–e0267759. https://doi.org/10.1371/journal.pone.0267759

Teixeira, C. R., Botta, S., Daura-Jorge, F. G., Pereira, L. B., Newsome, S. D., & Simões-Lopes, P. C. (2020). Niche overlap and diet composition of three sympatric coastal dolphin species in the southwest Atlantic Ocean. *Marine Mammal Science*, mms.12726-mms.12726. https://doi.org/10.1111/mms.12726

Torres, L. G., Read, A. J. A. J. R., & Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? *Ecological Applications*, *18*(7), 1702–1717. https://doi.org/10.1890/07-1455.1

Vieira, J. P., & Scalabrin, C. (1991). Migração reprodutiva da tainha (*Mugil platanus* Gunther, 1980) no sul do Brasil. *Atlântica*, *13*(1), 131–141.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Table 3.1: Path analysis coefficients. Estimates are given for each path (Figure 1), with standard error (Std.Error), degrees of freedom (DF), p-values and a respective standardized coefficient (Std. Estimate). Standardized coefficients are based on the standard deviation (SD), given that if the predictor goes up by 1 SD, the response goes up by the coefficient value in SD. Therefore, Std. Estimate can be used to compare the strength of direct and indirect effects.

Path	Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P-value	Std.Estimate	
i	Mullet abundance	Tide velocity	-0.0398	0.0463	67	-0.8590	0.3934	-0.1011	
ii	Mullet abundance	Wind direction	0.5623	0.3043	67	1.8478	0.0690	0.3374	
iii	Mullet abundance	Tidal currents	0.0396	0.2042	67	0.1940	0.8468	0.0256	
iv	Mullet abundance	Wind speed	-0.0102	0.0171	67	-0.5989	0.5513	-0.0906	
v	Mullet abundance	Water temperature	0.0086	0.1061	67	0.0811	0.9356	0.0142	
vi	Dolphins	Tide velocity	0.0197	0.0246	68	0.8003	0.4263	0.0792	
vii	Dolphins	Tidal currents	0.2951	0.1088	68	2.7136	0.0084	0.3009	**
viii	Dolphins	Water temperature	-0.0145	0.0596	68	-0.2433	0.8085	-0.0379	
ix	Dolphins	Mullet abundance	0.0901	0.0609	68	1.4777	0.1441	0.1423	
x	Fishers	Dolphins	0.1893	0.0840	66	2.2530	0.0276	0.1349	*
xi	Fishers	Tide velocity	0.0010	0.0191	66	0.0520	0.9587	0.0028	
xii	Fishers	Wind direction	0.4387	0.2803	66	1.5652	0.1223	0.2964	
xiii	Fishers	Tidal currents	0.0378	0.0967	66	0.3905	0.6974	0.0274	
xiv	Fishers	Wind speed	0.0066	0.0096	66	0.6842	0.4962	0.0657	
xv	Fishers	Water temperature	0.1257	0.0706	66	1.7799	0.0797	0.2343	
xvi	Synchronous social foraging	Dolphins	0.5026	0.1820	70	2.7612	0.0073	0.2977	**
xvii	Synchronous social foraging	Fishers	0.3888	0.1350	70	2.8809	0.0053	0.3232	**
xviii	Yield	Synchronous social foraging	1.0825	0.1824	70	5.9363	0.0000	0.5087	***
xix	Yield	Mullet abundance	0.3912	0.1762	70	2.2196	0.0297	0.1721	*

3.11 SUPPLEMENTARY MATERIAL

3.11.1 Are mullet schools patchily distributed and ephemeral?

After aligning and linking the sonar data with the observational and behavioural data, we ended up with 560,127 frames from the sonar videos. After filtering off frames with predicted noise from the deep learning models, we kept 511,861 frames, of which 109,455 had at least one mullet detected (Figure S1). The distribution of mullet detections for all frames is shown in figure S2, and the distribution by sampling day is shown in Figure S3.

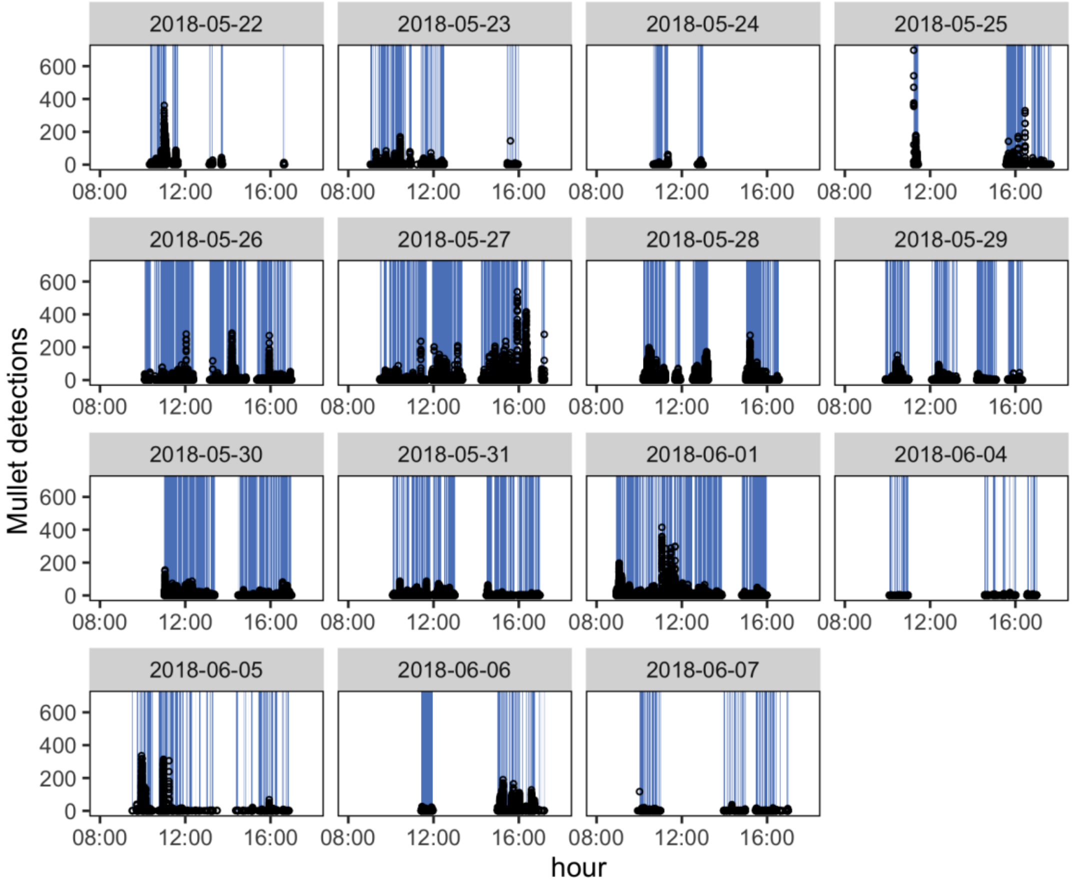

Fig. S 1: Mullet detections by sampling day. Blue shaded areas mark the duration of each sonar video, and each dot is a frame with mullet detection (frames with no mullet and/or with predicted noise were filtered off).

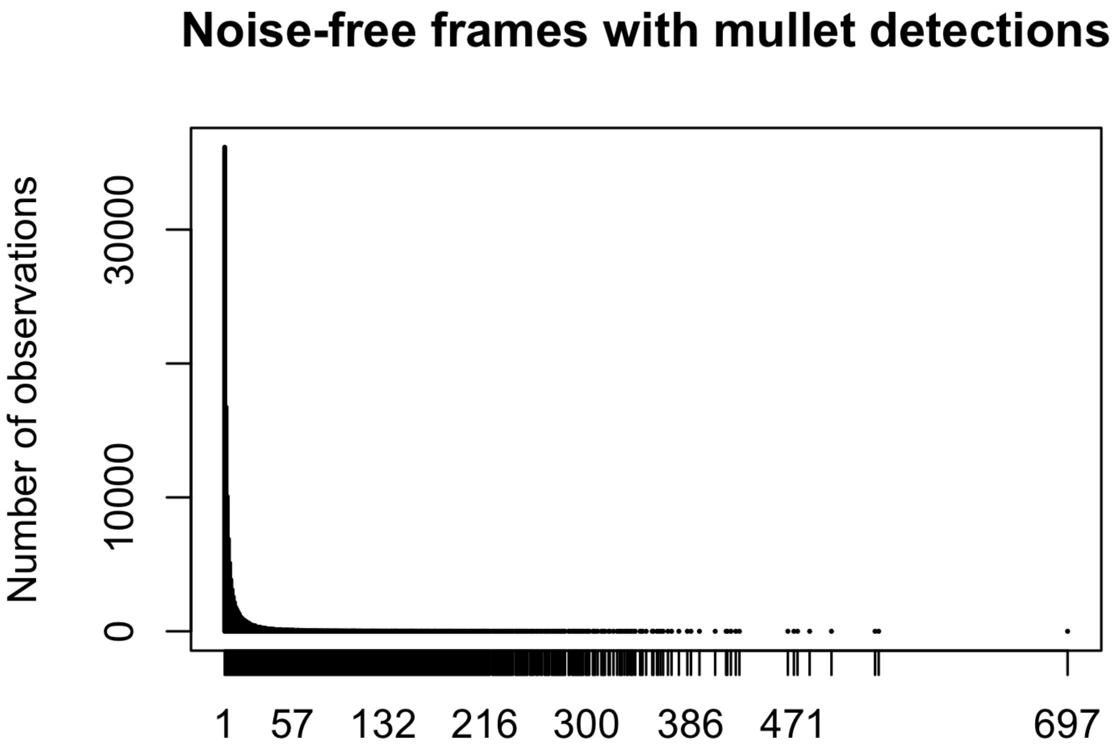

Fig. S 2: Distribution of mullet detections in 109,455 frames.

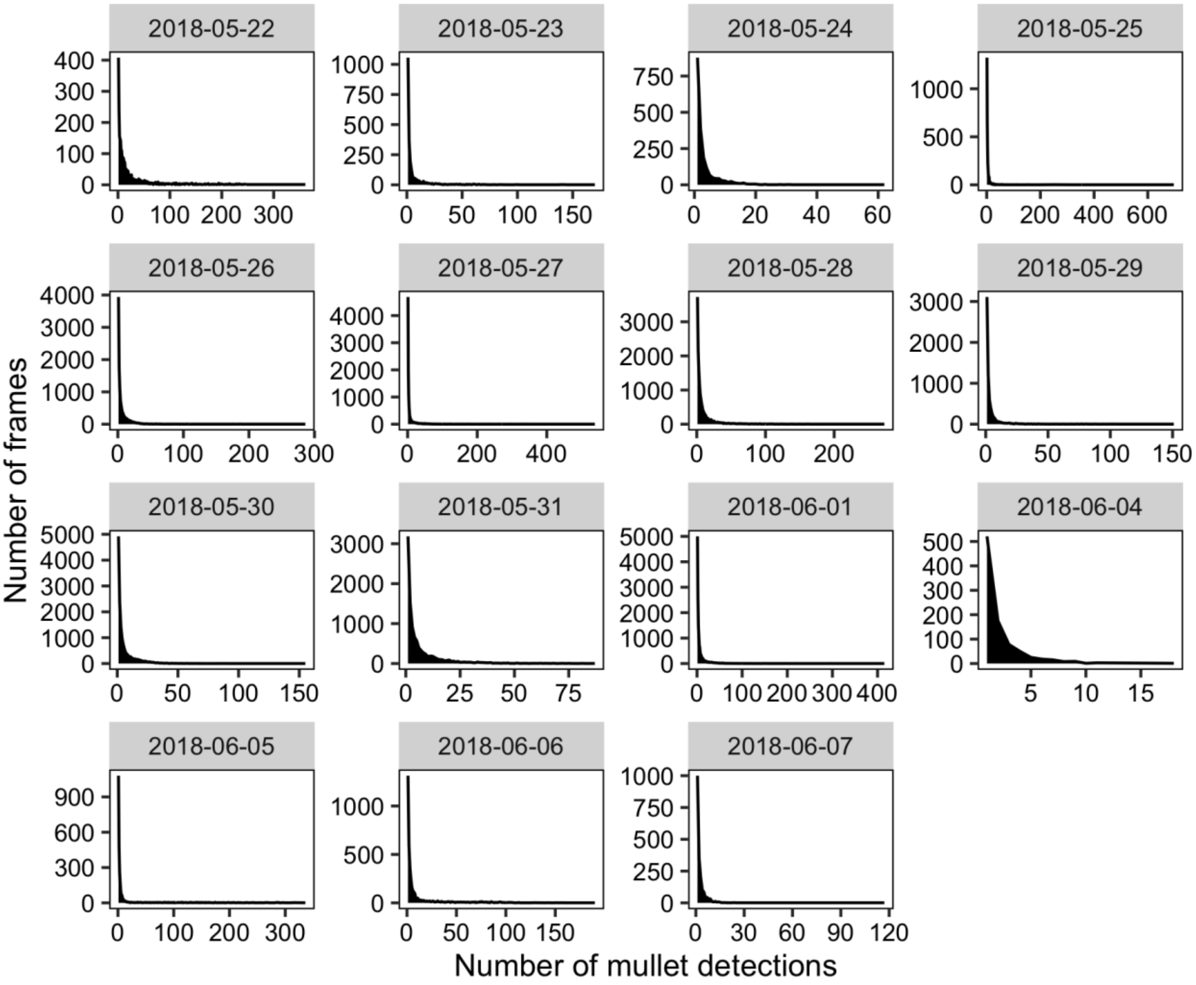

Fig. S 3: Distribution of mullet detections by sampling day. Frames with no mullet detections were filtered off.

3.11.2 Testing the power law hypothesis for mullet detections

We tested if the distribution of mullet school sizes across noise-free frames and the time integrated mullet abundance across sampling hours were both power law distributed. We used the `poweRlaw` R package (Gillespie, 2015) to fit a discrete power-law distribution to the mullet detections frame-by-frame (Figure S4), filtering off frames with no mullet detections. We cannot reject the null hypothesis that the data is generated from a power law distribution (P = 0.853). This result for the frame-by-frame data reinforces the patchiness of mullet schools, as ca. 0.1% of the frames had mullet schools above the lower threshold of the power law distribution (271).

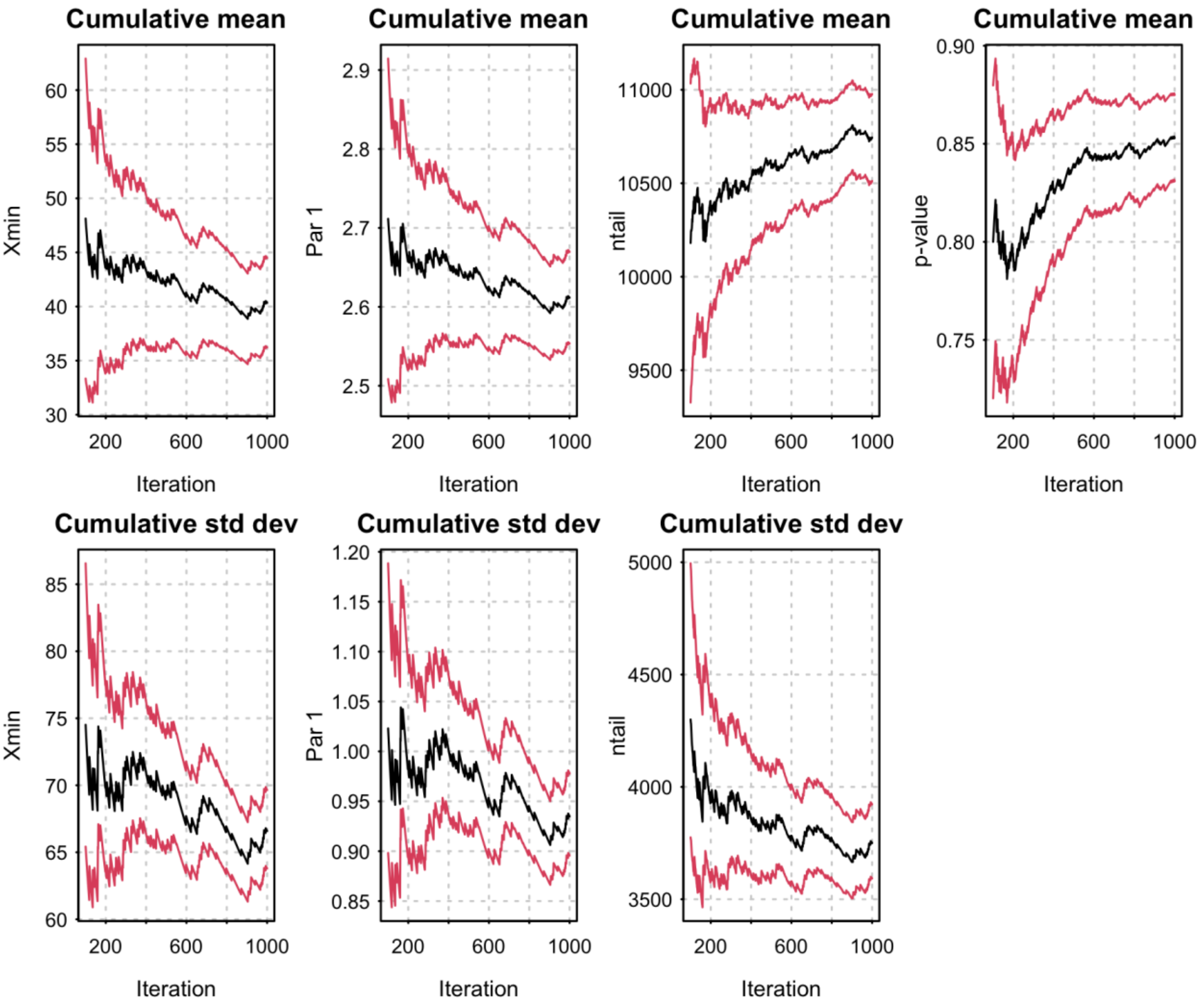

Fig. S 4: Results from 1,000 bootstraps using the frame-by-frame data of mullet detections. The first row shows the mean estimate of the lower threshold (Xmin), the scaling parameter (α), the number of data points greater than or equal to the estimated lower threshold, and the p-value. The second row shows the estimate of standard deviation for each parameter. Using 90% of the bootstraps, black lines give the cumulative mean and standard deviation, and the red lines show the approximate 95% confidence intervals for each parameter.

We also fit a continuous power-law distribution to the time integrated data of mullet abundance across the 87 sampling hours (Figure S5), which takes into account the total number of mullet detected by the number of frames sampled within a sampling hour. We cannot reject the null hypothesis that the data is generated from a power law distribution (P = 0.447). This result for the time integrated data for sampling hours reinforce the ephemeral nature of mullet schools, with only 16% of sampling hours above the lower threshold (4.71).

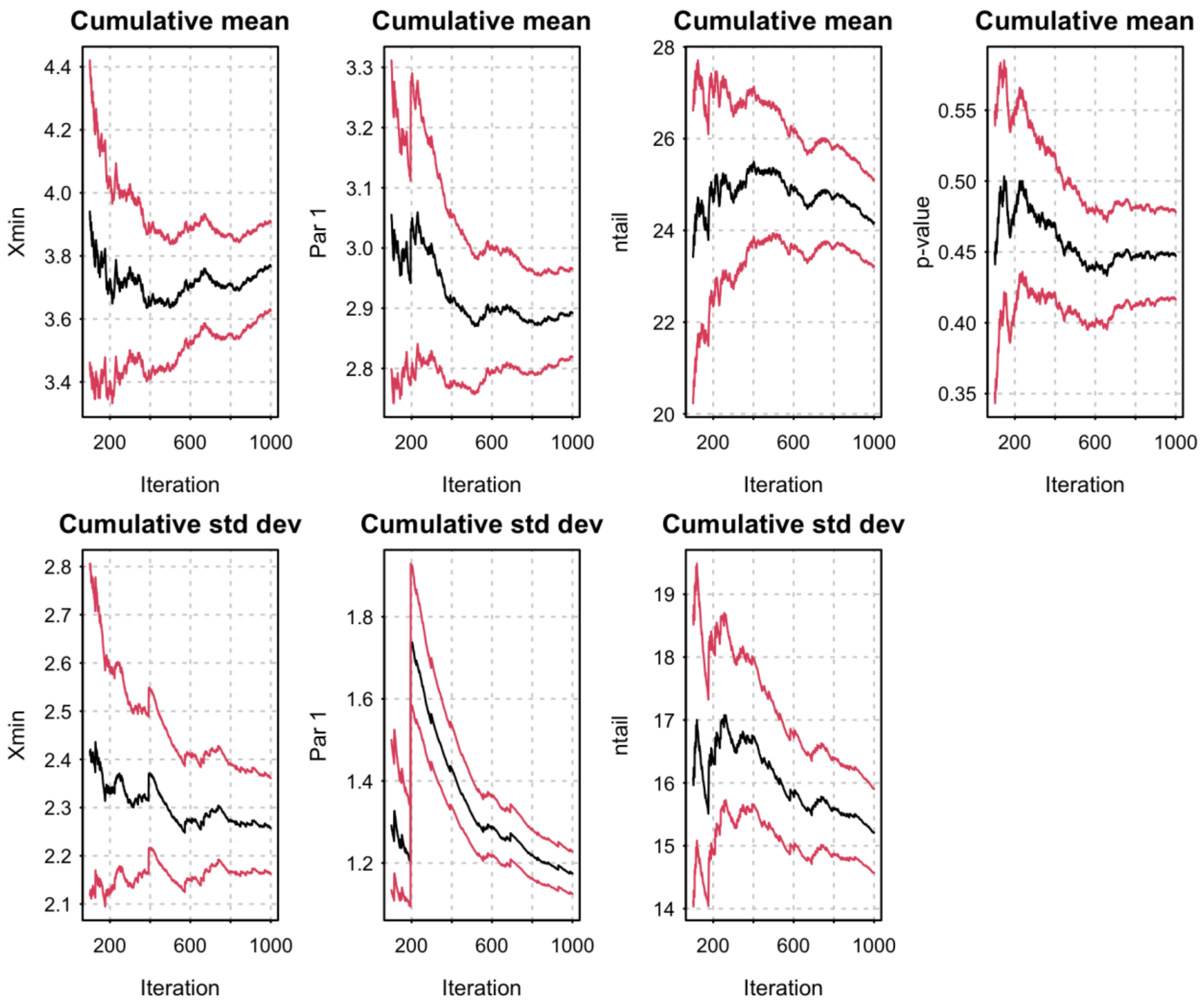

Fig. S 5: Results from 1,000 bootstraps using the time integrated data of mullet detections in 87 sampling hours. The first row shows the mean estimate of the lower threshold (Xmin), the scaling parameter (α), the number of data points greater than or equal to the estimated lower threshold, and the p-value. The second row shows the estimate of standard deviation for each parameter. Using 90% of the bootstraps, black lines give the cumulative mean and standard deviation, and the red lines show the approximate 95% confidence intervals for each parameter.

3.11.3 Component Models

3.11.3.1 Mullet

3.11.3.1.1 Model coefficients

Table S 1: Coefficients from the “Mullet” component model.

Predictor	**Estimate**	**Std.Error**	**DF**	**Crit.Value**	**p-value**	**Std.Estimate**
Tide velocity	-0.0398	0.0463	67	-0.8590	0.3934	-0.1011
Wind direction	0.5623	0.3043	67	1.8478	0.0690	0.3374
Tidal currents	0.0396	0.2042	67	0.1940	0.8468	0.0256
Wind speed	-0.0102	0.0171	67	-0.5989	0.5513	-0.0906
Water temperature	0.0086	0.1061	67	0.0811	0.9356	0.0142

3.11.3.1.2 Validation of model assumptions

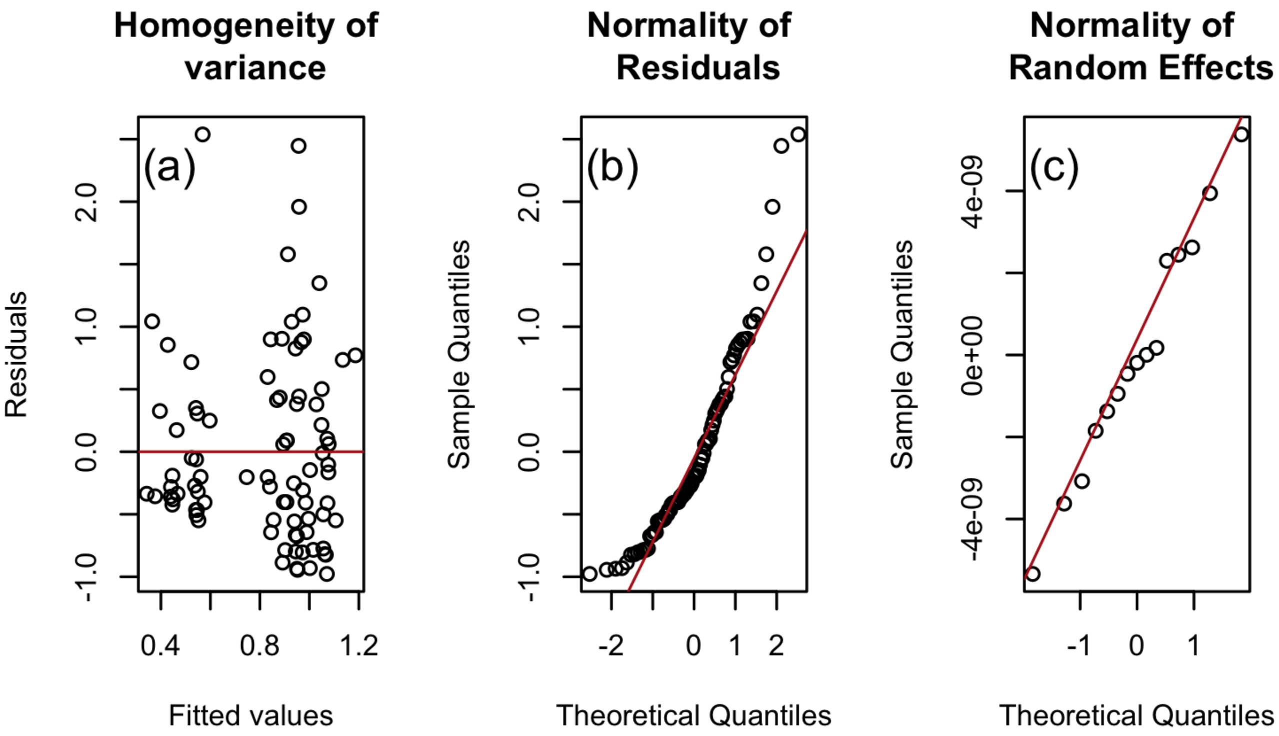

Fig. S 6: Visual inspection of the homogeneity (a) and normality (b) of the residuals, and normality of the random effects (c) for the “Mullet” component model.

3.11.3.2 Dolphins

3.11.3.2.1 Model coefficients

Table S 2: Coefficients from the “dolphins” component model.

Predictor	Estimate	Std.Error	DF	Crit.Value	p-value	Std.Estimate	
Tide velocity	0.0197	0.0246	68	0.8003	0.4263	0.0792	
Tidal currents	0.2951	0.1088	68	2.7136	0.0084	0.3009	**
Water temperature	-0.0145	0.0596	68	-0.2433	0.8085	-0.0379	
Mullet abundance	0.0901	0.0609	68	1.4777	0.1441	0.1423	

3.11.3.2.2 Validation of model assumptions

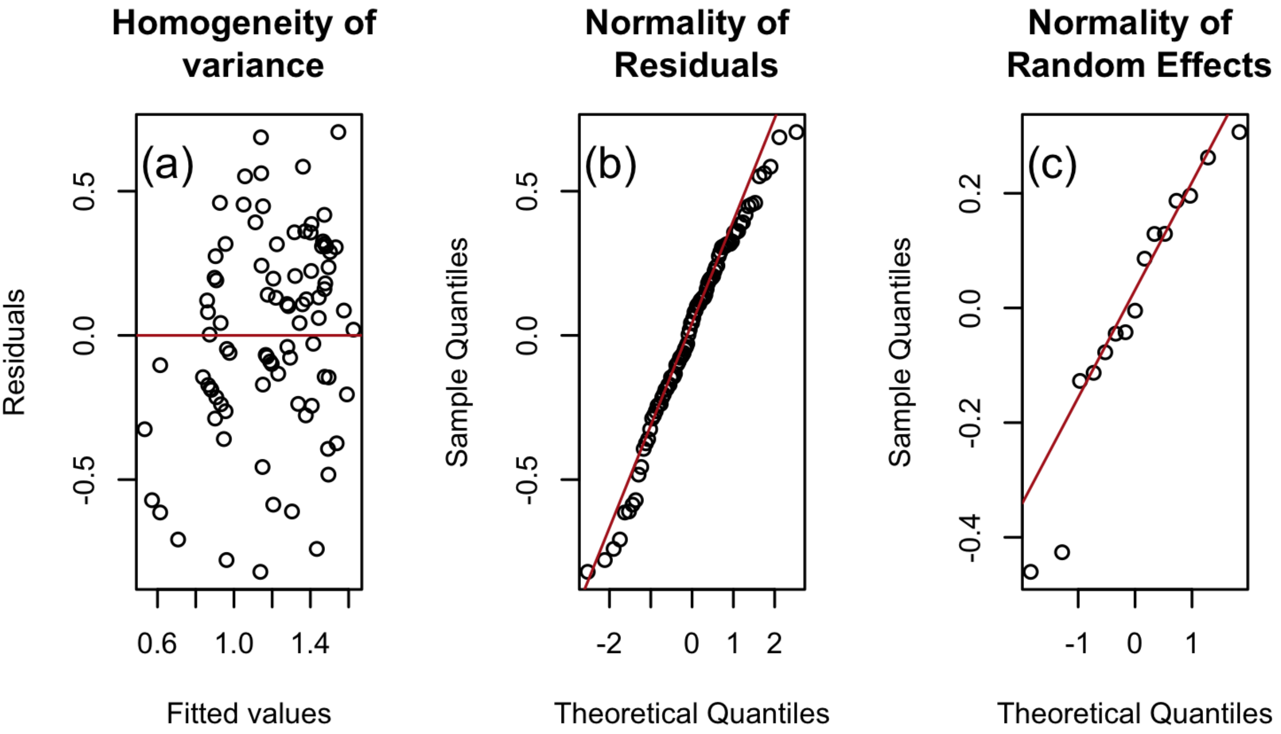

Fig. S 7: Visual inspection of the homogeneity (a) and normality (b) of the residuals, and normality of the random effects (c) for the “dolphins” component model.

3.11.3.3 Fishers

3.11.3.3.1 Model coefficients

Table S 3: Coefficients from the "fishers" component model.

Predictor	Estimate	Std.Error	DF	Crit.Value	p-value	Std.Estimate	
Dolphins	0.1893	0.0840	66	2.2530	0.0276	0.1349	*
Tide velocity	0.0010	0.0191	66	0.0520	0.9587	0.0028	
Wind direction	0.4387	0.2803	66	1.5652	0.1223	0.2964	
Tidal currents	0.0378	0.0967	66	0.3905	0.6974	0.0274	
Wind speed	0.0066	0.0096	66	0.6842	0.4962	0.0657	
Water temperature	0.1257	0.0706	66	1.7799	0.0797	0.2343	

3.11.3.3.2 Validation of model assumptions

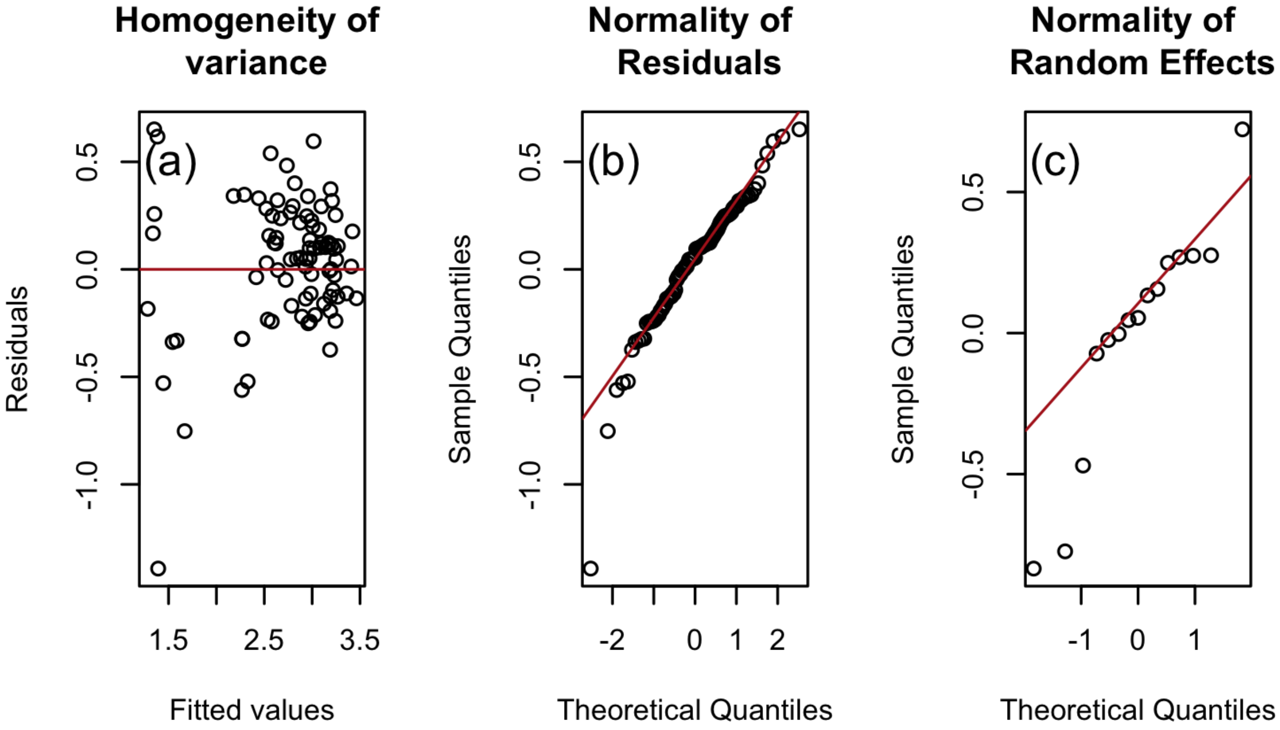

Fig. S 8: Visual inspection of the homogeneity (a) and normality (b) of the residuals, and normality of the random effects (c) for the "fishers" component model.

3.11.3.4 Foraging synchrony

3.11.3.4.1 Model coefficients

Table S 4: Coefficients from the “Foraging synchrony” component model.

Predictor	**Estimate**	**Std.Error**	**DF**	**Crit.Value**	**p-value**	**Std.Estimate**	
Dolphins	0.5026	0.182	70	2.761	0.0073	0.2977	**
Fishers	0.3888	0.135	70	2.881	0.0053	0.3232	**

3.11.3.4.2 Validation of model assumptions

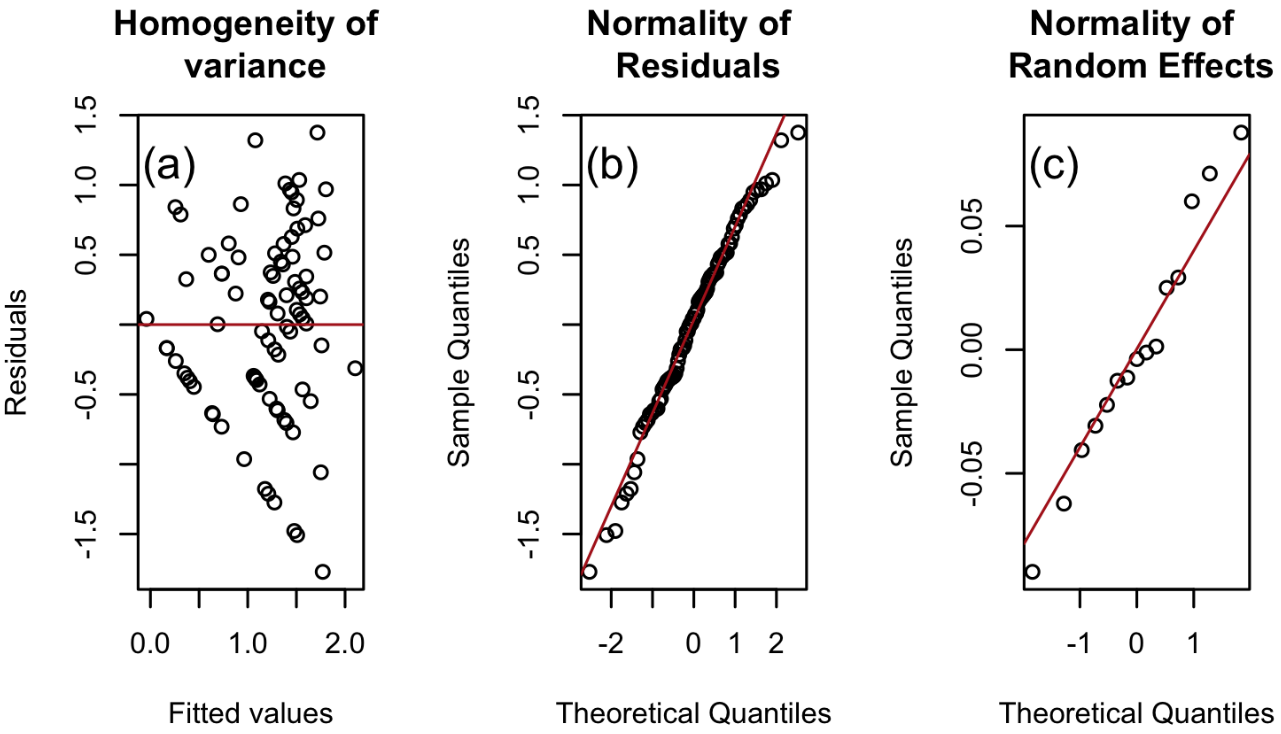

Fig. S 9: Visual inspection of the homogeneity (a) and normality (b) of the residuals, and normality of the random effects (c) for the “Foraging synchrony” component model.

3.11.3.5 Yield

3.11.3.5.1 Model coefficients

Table S 5: Coefficients from the “yield” component model.

Predictor	Estimate	Std.Error	DF	Crit.Value	p-value	Std.Estimate	
Cooperative foraging	1.0825	0.1824	70	5.936	0.0000	0.5087	***
Mullet abundance	0.3912	0.1762	70	2.220	0.0297	0.1721	*

3.11.3.5.2 Validation of model assumptions

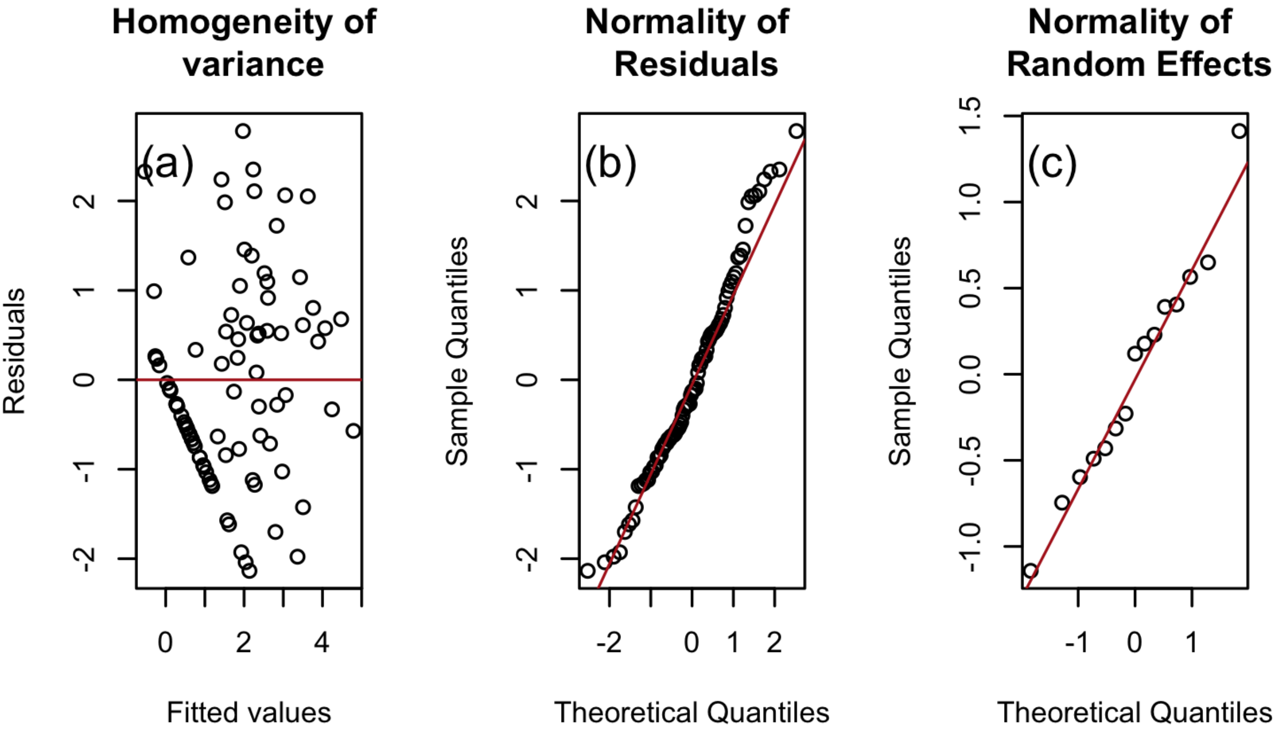

Fig. S 10: Visual inspection of the homogeneity (a) and normality (b) of the residuals, and normality of the random effects (c) for the “yield” component model.

3.11.4 References

Gillespie, C. S. (2015). Fitting heavy tailed distributions: The poweRlaw package. **Journal of Statistical Software**, *64*(2), 1–16. http://www.jstatsoft.org/v64/i02/

4 CAPÍTULO 2: INDIVIDUALS CONTRIBUTE DISPROPORTIONATELY TO HUMAN-DOLPHIN MUTUALISM

Alexandre M.S. Machado[1,2]*
Mauricio Cantor[1,3-5,†]
Damien R. Farine[2,6,7,†]
Carolina Bezamat[1]
Fábio G. Daura-Jorge[1,†]*

1 Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil
2 Department of Collective Behaviour, Max Planck Institute of Animal Behaviour, Radolfzell, Germany
3 Department of Fisheries and Wildlife, Marine Mammal Institute, Oregon State University, Newport, USA
4 Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behaviour, Konstanz, Germany
5 Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná, Brazil
6 Department of Evolutionary Biology and Environmental Science, Universität Zürich, Zürich, Switzerland
7 Division of Ecology and Evolution, Research School of Biology, Australian National University, Australia

† co-senior authorship
* Corresponding author: alexandre.marcel@posgrad.ufsc.br; daura.jorge@ufsc.br

Manuscrito em preparação

4.1 ABSTRACT

Despite growing evidence supporting consistent behavioural differences among individuals, our understanding about the role of such variations in mutualism remains limited. Most empirical studies on the implications of such individual difference focuses on partner-choice or intra-species division of labour, but if individuals consistently differ in performing specific behaviours, then individuals may provide asymmetrical contributions to the mutualistic system. Here, we quantify individual differences in a rare case of human-wildlife cooperation involving wild dolphins and artisanal net-casting fishers in southern Brazil. Dolphins herd mullet schools towards fishers and provide a behavioural cue that fishers interpret as the moment to cast their nets: when both species act in synchrony, their chances of successfully catching mullet increase. However, not all dolphins engage regularly in this social foraging tactic with fishers, potentially resulting in performance differences and asymmetrical contributions to the outcome of this tactic. To investigate these differences, we tracked the social and foraging behaviour of dolphins by combining photo-identification and observational data to quantify the cues produced by each dolphin, to assess how much individual dolphins differs in their engagement on this social foraging tactic, and to investigate how individual differences in the use of this tactic determine the outcomes of this mutualistic system, in terms of mullet caught by fishers. We then explored whether dolphins interfere in the foraging behaviour of conspecifics, and whether such interference competition has any further effects on the outcomes of the dolphin-fisher interaction. Our findings suggest that key individual dolphins disproportionately contribute to the outcomes and benefits accrued by the human partners. Given the minor influence of interference among dolphins, this distinct contribution of each dolphin to the interaction may stem from their different foraging abilities, likely acquired through individual or social learning processes.

Key words: cooperation, mutualism, foraging specialization, social foraging, individual quality

4.2 INTRODUCTION

Despite mounting evidence of consistent individual differences in behaviour (Sih et al., 2019; Laskowski et al., 2022), empirical evidence on the consequences of such individual differences for the dynamics of mutualisms remains scarce. While special attention has been given to understanding how individuals differ in propensity (e.g., English et al., 2010) or in consistency when cooperating with conspecifics, such as specialized individual roles within cooperative hunting groups of dolphins (*Tursiops truncatus*; Gazda et al., 2005) and lions (*Panthera leo*; Stander, 1992), much less is known about individual differences in their ability to contribute to the outcomes of a cooperative interaction (hereafter performance). One example of this is seen in seed dispersal, a mutually beneficial interaction in which the personality of seed-dispersing mice determines patterns of seed selection, dispersal range, and the proportions of seed consumption, thereby shifting the interaction from mutualism to antagonism (Brehm et al., 2019). Individual differences in performance can also determine partner-choice when individuals can actively coordinate their behaviour to achieve mutual benefits. Then, competent individuals are more likely to be recruited by their partners in consecutive interactions, as seen in cooperative hunting between groupers and moray eels (Vail et al., 2014). In a mutualistic interaction between humans and greater honeyguides birds (*Indicator indicator*), honeyguides may not choose their human partners, but they can choose to switch tactics, either guiding humans to beeswax or scavenging for beeswax (Cram et al., 2023). The decision-making to contribute to the mutualism by guiding humans or scavenge is influenced by individual traits associated with the competitive ability of individuals, highlighting an overlooked key mechanism underlying individual differences in the study of mutualisms.

Competition can modulate mutualism outcomes across different systems and conditions (Jones et al., 2012). Within and between species of socially interacting animals, individuals can compete while exploiting common resources (exploitative competition) or actively interfere on each other's foraging behaviour (interference competition). Such interference among conspecifics can result in dominance hierarchies, granting dominant individuals priority access to resources, while subordinates are left with limited or no access (e.g., Nakano, 1995). Even the presence of dominant individuals in the group is sufficient to affect the foraging behaviour of subordinates (Saito, 1996). In cooperative foraging among different species, while individuals may compete for a common resource and potentially shift cooperative interactions to antagonism (Moran et al., 2022), cooperators may also compete for access to high-performance partners. Ultimately, if dominance and individual performance are correlated (e.g., Hartley et al., 2019), competitive interference would then modulate the quality of the partners and thus the outcomes of their cooperative interactions.

Here, we investigate the consequences of intraspecific individual differences and interference on the outcomes of a dolphin-fisher interaction in southern Brazil. This system is among the few active cases of human-wildlife cooperation (*sensu* Cram et al., 2022) where two apex predator species synchronise their behaviours to forage for a common, patchy and ephemeral prey—migratory mullet schools (*Mugil liza*). Dolphins herd mullet schools towards artisanal net-casting fishers waiting in shallow waters and give a behavioural cue that fishers interpret as the moment to cast their nets (Simões-Lopes et al., 1998). Fishers achieve higher foraging success when responding in time to the dolphin cue compared to when they do not act in synchrony with dolphins (including when dolphins are absent). When fishers respond in time to the dolphin cue, dolphins respond by engaging in more active foraging and emitting more echolocation clicks after the nets hit the water, suggesting that synchronous foraging can also increase dolphins' foraging success (Cantor et al., 2023). The dynamics of this human-dolphin mutualism seems unaffected by variations in environmental conditions, as dolphins and fishers accrue mutual benefits through their collective foraging efforts, even with unpredictability in mullet abundance (Machado et al., *in prep*)[1].

Foraging synchrony is, therefore, the key to successful cooperation between fishers and dolphins. However, this synchrony could be affected by individual differences in performance on both the terrestrial and aquatic sides of this cooperation. Individual fishers differ in fishing performance, likely due to variations in net-casting skills and their understanding of the dolphin's behaviour (Da Rosa et al., 2020; Valle-Pereira et al., 2022). These performance differences influence their reputation among peers and affect the decision-making and partner choice when forming cooperative fishing groups (Santos-Silva et al., 2022). Fishers' perceptions suggest that dolphins also vary in fishing performance, as they distinguish between 'good' vs. 'bad' dolphins, that is, skilled cooperative dolphins that increased the fishers' chances of catching mullet vs. noncooperative dolphins that forage by themselves (Peterson et al., 2008). These perceptions may be partly explained by differences in dolphins' frequency of use of the cooperative foraging tactic and their spatial fidelity to fishing sites (Cantor et al., 2018). Both dolphins and fishers may also face spatial or ecological constrains from the carrying capacity on their side of the cooperative fishing site at a given time. In

---

[1] Capítulo 1: Social foraging between humans and dolphins drives higher prey capture despite unpredictability in fish abundance.

response to intraspecific competition, fishers developed an informal rule system to organize individual access to fishing spots (Peterson et al., 2008). Dolphins, by contrast, should be more susceptible to intraspecific competition to access interaction sites and their human partners (Simões-Lopes, 1998).

The existence of individual differences in both partners and their susceptibility to intraspecific competition makes the human-dolphin mutualism an appropriate system to investigate the role of individual differences in performance and conspecific interference in shaping mutualism outcomes. Here, we use multiplatform sampling to track the foraging behaviour of individually photo-identified dolphins and their contributions to the cooperative foraging with human partners. First, we quantify whether individual dolphins vary in their overall time spent in the dolphin-fisher cooperative tactic, the rate of foraging cues they produce, and whether the fishers' success of the cooperative foraging consistently increases when specific dolphins participate. Second, we tested for the effect of conspecific interference on dolphins' cue rates, number of successful interactions with fishers, and number of fish captured by fishers as a result of interactions with specific dolphins. We show that there are key individuals that disproportionately contribute to the outcomes of the social foraging with fishers. Although the differences in performance may exist among dolphins, there is also significant within-individual variation. Furthermore, our findings suggest that competitive interference may not significantly affect the outcomes of dolphin-fisher cooperative foraging.

4.3 METHODS

4.3.1 Field data collection

We combined continuous behavioural data sampling with classic photo-identification methods to record cooperative fishing events between dolphins and artisanal net-casting fishers and then quantify the contributions of individual dolphins to the outcomes of their cooperative foraging activities in Laguna (28°20'S, 48°50'W), southern Brazil. We continuously recorded all occurrences (Altmann, 1974) of fishers' net-casting, cooperative foraging between dolphins and fishers, and the outcomes of their interactions in terms of mullet caught by fishers over 45 days in 2019 (n = 20), 2022 (n = 14) and 2023 (n = 11). We focused the data collection during the peak of the mullet migratory reproductive season (from May to July when this resource is mostly available; Herbst & Hanazaki, 2014) and in the primary site where the dolphin-fisher interaction takes place (a 100-m beach in the inlet canal).

4.4 QUANTIFYING DOLPHIN-FISHER INTERACTIONS AND THEIR OUTCOMES

Our daily sampling effort ranged from 2 to 8.7 hours (mean = 6.8h ± 1.6 SD), depending on weather conditions. Every day, before the start of the sampling effort, we synced the clocks from all sampling platforms to the best precision possible using a high-resolution GPS clock as reference (©Bad Elf Pro). To assess the contributions of individual dolphins to their human partners, we focused on synchronous social foraging interactions, defined as the cooperative events at which fishers cast their nets in response to a dolphin cue (Cantor et al., 2023), such as a sudden deep dive arching their backs in front of fishers (Simões-Lopes et al., 1998). At the beach, behind the edge of the canal where fishers stand, we recorded the timestamp of every synchronous event and quantified the number of fish caught by each fisher by pursuing their nets, brought to the beach immediately after the event. Furthermore, two photographers conducted photo-identification to quantify foraging dolphins and identify which dolphin gave the cue in each synchronous event, detailed next.

4.4.1 Individual identification

We conducted standard photo-identification protocols to identify every individual dolphin present at the interaction site. Two photographers equipped with Canon DSLR cameras (60D, 7D, 7D Mark II, 6D Mark II or 90D) and telephoto lenses (70–200m, 70–300mm or 100–400mm) standing close to the fishers took pictures simultaneously, but with two distinct goals. One photographer moved along behind the edge of the canal where the fishers stand to monitor changes in dolphin group composition at the interaction site. The second photographer was positioned behind the fishers on a 1.5m platform above water-level, focusing on capturing images of the dolphins giving a cue in synchronous events; this photographer was the most experienced researcher in the long-term, boat-based survey of the dolphin population and thus very familiar with individual dolphin identities. Thus, we relied on this photographer to estimate group sizes and identify the dolphin giving a cue, which were later confirmed using photo-identification data. Both photographers limited their photo-identification efforts to dolphins actively foraging at the interaction site, disregarding dolphins passing by on the other side of the estuary (ca. 150–200m away). To match dolphin identifications with the correct timestamps of social foraging events, the photographer maintained constant communication through hand-held radios with other researchers collecting behavioural data on the beach and annotating photos in the camera using the rating function in Canon DSLR cameras.

We processed metadata from 33,238 photos using ExifTool (https://exiftool.org) and R 4.1.2 (R Core Team, 2021) to obtain precise timestamps for all dolphin sightings (see Machado & Cantor, 2022). We relied on the natural and long-lasting marks on the dolphin dorsal fins for individual identification based on a reference catalogue compiled during our long-term monitoring of the bottlenose dolphin population in Laguna, southern Brazil (e.g., Daura-Jorge et al., 2012; Bezamat et al., 2020). We then excluded 7,281 photos lacking relevant information about dolphins' identities, 3,189 photos of unmarked individuals that could not be matched to the long-term survey's photo-identification catalogue, and 639 photos of 15 calves as they are still under parental care, making data collection dependent on their mothers. From the remaining 22,129 photographs of 48 identified individuals (adults and juveniles), we inferred groups within each sampling day using a data-driven approach (Psorakis et al., 2015). We applied Gaussian mixture models (using `gmmevents` from the `asnipe` R package; Farine, 2013) to the photo-identification data stream to identify 'visiting events' at the interaction site, using the time difference in seconds between 06:00 AM and every photo taken within a sampling day (see Supplementary Material Figure S1). Given the nature of photo-identification data and the variations in inter-breath intervals, which can affect the number of photos taken of each dolphin, we adjusted timestamps to the nearest minute and retained only one photo of each individual per minute. We considered clusters of dolphins arriving, persisting, and leaving the area as proxies for groups of dolphins. To delineate biologically meaningful groups and minimize gaps between groups, we merged groups using a chain-rule approach based on the composition and time window of consecutive groups. Whenever groups consisted of the same individuals and were less than 530 seconds apart, we combined them into a single group. Our premise was that within this interval, individuals had enough time to perform two long dives of up to 265 seconds while foraging (see Irvine et al., 1981), and they might have been missed by photographers.

Based on our long-term survey of this population (e.g., Daura-Jorge et al., 2012; Bezamat et al., 2020), dolphins could be identified in the field even without a photo precisely matching the timestamps of the dolphin cue. After processing all photo-identification data, we reviewed each synchronous event trying to assign the correct dolphin identity to each event. Whenever possible, we used auxiliary data from field notes, photo ratings in the metadata, and opportunistic video footage from unoccupied aerial vehicles and ground-based videos (Machado & Cantor, 2022; Cantor et al., 2023) to manually identify the dolphin responsible for giving the cue. When identities could not be confirmed or precisely assigned to a synchronous event, we coded them as 'not available' to avoid overestimating individual contributions. When synchronous events did not align with any recognized group, we used a customized algorithm to assign the event to the nearest group in which the dolphin was present, applying the same 265-seconds threshold as used for the duration of a long dive (Irvine et al., 1981). This approach allowed us to infer group size and composition for each synchronous event and estimate the duration for which each individual was observed at the interaction site, based on the duration of their presence in the length of groups.

4.4.2 Inferring interference competition

While dominance among dolphins have been observed in both captivity (Samuels & Gifford, 1997) and the wild, particularly in the context of male mating strategies (Connor & Krützen, 2015), dominance in a foraging context is less expected for wild dolphins. This is due to the nature of their foraging, which often involves fast-moving and unpredictable prey, making it challenging to monopolize food resource patches. Thus, it is assumed that scramble competition, in which individuals compete to access resources simultaneously, should have greater relevance for wild dolphins than interference competition. However, even in case of unpredictable prey, foraging can take place in limited spaces that are susceptible to potential monopolization. For example, in provisioning sites, dominant Amazon River dolphins *Inia geoffrensis* have been observed interfering with conspecifics to prevent subordinates from receiving provisions (Alves et al., 2013). In the cooperative fishing site in Laguna, it is plausible that dolphins with superior competitive abilities could potentially monopolize the area. Although direct observations have suggested that dolphins may display agonistic behaviours at the fishing site during interactions with fishers (Simões-Lopes, 1998), precise quantification of these agonistic and competitive interactions between pairs of dolphins is challenging due to the limited visibility of dolphins, who spend most of their time submerged in murky waters. To address this limitation, we employed an automated approach to infer the outcomes of such interactions based on changes in group composition during the foraging with fishers, assuming that such changes reflected displacements initiated by better competitors.

To assess whether individual dolphins can interfere in the foraging behaviour of their conspecifics, we used our continuous photo-identification data at the cooperative fishing site. We calculated the time difference between two consecutive dolphin groups and assessed the membership of these groups. If the time interval between groups were less than 530 seconds apart (enough time for dolphins to take two long dives of up to 265-seconds while foraging;

Irvine et al., 1981), we verified whether any photo-identified dolphin from group i was absent in group $i+1$, and whether new photo-identified dolphins arrived in group $i+1$. We assumed that individuals arriving in group $i+1$ to had displaced those from group i. We then built a matrix of interactions, coding individuals who arrived and displaced others as *winners*, and the displaced individuals as *losers*, while omitting individuals that persisted from group i to group $i+1$. Using this matrix of dyad interactions, we estimated a dominance hierarchy for each year (see Supplementary Material Figure S2–S3) of sampling using a randomized Elo-rating procedure with 1,000 randomizations to account for the temporal sequence of interactions (Sánchez-Tójar et al., 2018). We used data from 242 individual dolphins who interacted with conspecifics at least three times to calculate the Elo-rating. Through 1,000 randomizations, we computed the median Elo-rating for each individual in each sampling year (see `elo_scores` from `aniDom`; Farine & Sánchez-Tójar, 2021), which we then standardized (see `scale_elo` from `EloRating`; Neumann, 2020) to represent ranks ranging from 0 (lowest rank) to 1 (highest rank).

4.4.3 Statistical analyses

We used two sets of models to test our hypothesis concerning the potential impacts of individual differences and interference competition on the outcomes of social foraging the between dolphins and fishers. First, we quantified overall individual differences by summarizing daily individual data to determine whether some dolphins consistently spend more time at the dolphin-fisher interaction site, produce higher cue rates, and contribute more effectively than others to the success of synchronous events. To analyse these aspects, we fit generalized linear mixed-effect models (Bolker et al., 2009) to the daily individual data using a negative binomial error structure with a log link function for both the time spent in the area and the number of cues produced. To model cue rates, we used the total number of cues within a day as the response variable and included the corresponding time spent at the interaction site within the same day as an offset term. Subsequently, we used a rank-based correlation to test if the point estimates of random intercepts were correlated, and a Pearson's correlation to test whether the coefficients for time spent at the interaction were consistent with data from boat surveys that quantified the proportion of time individuals were seen foraging with fishers at any fishing site. To determine whether dolphins consistently provided successful fishing to their human partners, we fit a binomial error structure with a logit link function, combining the number of successful and unsuccessful cooperative foraging events as the response variable. We fit all three models with only the intercept and dolphin identity as random intercepts, allowing for variation among individuals. Then, we calculated repeatability for each model to estimate the proportion of among-individual variation (Dingemanse & Dochtermann, 2013).

Second, we investigated individual differences among dolphins and the relative importance of individual differences and interference competition in the outcomes of the social foraging between dolphins and fishers. For each dolphin within a group, we quantified the number of cues produced during the duration of the group, the number of successful and unsuccessful synchronous events and the contributions to the social foraging between dolphins and fishers in terms of mullet caught by fishers. To test whether interference plays a role in the outcomes of the social foraging with fishers, we assigned each dolphin its respective Elo-rating in a given year, omitting calves and eight individuals for which annual Elo-ratings were unavailable. We also calculated the maximum Elo-rating of conspecifics within each of group, excluding the focal dolphin. When only one dolphin was observed, we attributed a score of 0 to this variable. We then fit another set of three generalized linear mixed-effects including dolphin identity as random intercepts, but now including an interaction between the Elo-rating of the focal dolphin and the maximum Elo-rating of conspecifics in the group as a proxy for the effect of socially mediated interference. We used a negative binomial error structure with a log link function to model the number of cues produced and contributions to the fishers (i.e., number of fish), including an offset term for the time of cues produced, and the number of cues given to the contributions. We used a binomial error structure with a logit link function to model the proportion of successful and unsuccessful events.

We carried out all data processing and statistical analyses in R (4.1.2). To avoid convergence issues, we fit generalized mixed-effects models using the R package `glmmTMB` (Brooks et al., 2017) and calculated repeatability using the performance R package (see function `icc`; Lüdecke et al., 2021). The data and code to reproduce the analyses will be available in an open on-line repository (*github.com/machadoams/boto-ind-var*) and as a supplementary material.

4.5 RESULTS

We recorded a total of 1,425 social foraging events between dolphins and fishers during 306 hours of direct observation of dolphin-fisher interactions. Across all sampling years, we identified 48 dolphins—omitting calves—in 716 groups, as inferred from our photo-identification data. These groups were composed from 1 to 9 individuals (median = 2 ± 1.2 SD). After aligning synchronous foraging events with the group data from photo-identification and filtering out events missing information, we ended up with 745 synchronous foraging events in which we could identify the dolphin giving the cue and quantify the outcomes of each interaction. After omitting 2 unmarked individuals and 2 calves, we observed 32 different dolphins participating in the dolphin-fisher interaction at least once. Our records exhibited a substantial variation in the number of cues produced by individual dolphins, ranging from a minimum of 1 to a maximum of 145 cues produced across three years of sampling (mean = 25.4 ± 35.1 SD). Individual success rate also varied considerably, ranging from 0 to 67% (mean = 25% ± 21%): 8 dolphins did not contribute to any successful synchronous foraging events, whereas the remaining 24 dolphins made distinct contributions to the total catch of 2,538 mullet caught, the result of the social foraging interactions with fishers.

4.5.1 Individual differences among dolphins

We quantified individual differences among dolphins in three key dimensions: the time spent at the interaction site, the rate of cues produced per unit of time, and whether fishers succeed more in catching mullets with some dolphins than others (Fig. 1). We found that some dolphins consistently spend more time at the dolphin-fisher interaction site on a daily basis ($R = 0.306$) but individual differences in cue rates are less repeatable ($R = 0.011$). The predicted individual differences in time spent at the interaction site and cue rates were negatively, but mildly correlated ($\rho = -0.382$; $S = 7540$; $P = 0.032$), suggesting that dolphins spending more time at the interaction site may have lower cue rates (Supplementary Material Figure S4). The coefficients derived from all fit models can be found in Supplementary Material Tables S1–S3. We also found a positive correlation between the coefficients of time spent at the interaction site and the proportion of times individuals were observed interacting with fishers from 2007 to 2022 ($r = 0.563$; $t_{25} = 3.408$; $P = 0.002$; Supplementary Material Figure S5). This finding reinforces varying levels of individual specialization in this social foraging tactic with humans. This correlation is consistent with the relatively low repeatability observed in the proportion of positive outcomes in these interactions ($R = 0.13$), indicating that only a small subset of dolphins consistently provided benefits to fishers compared to their peers (Fig. 1).

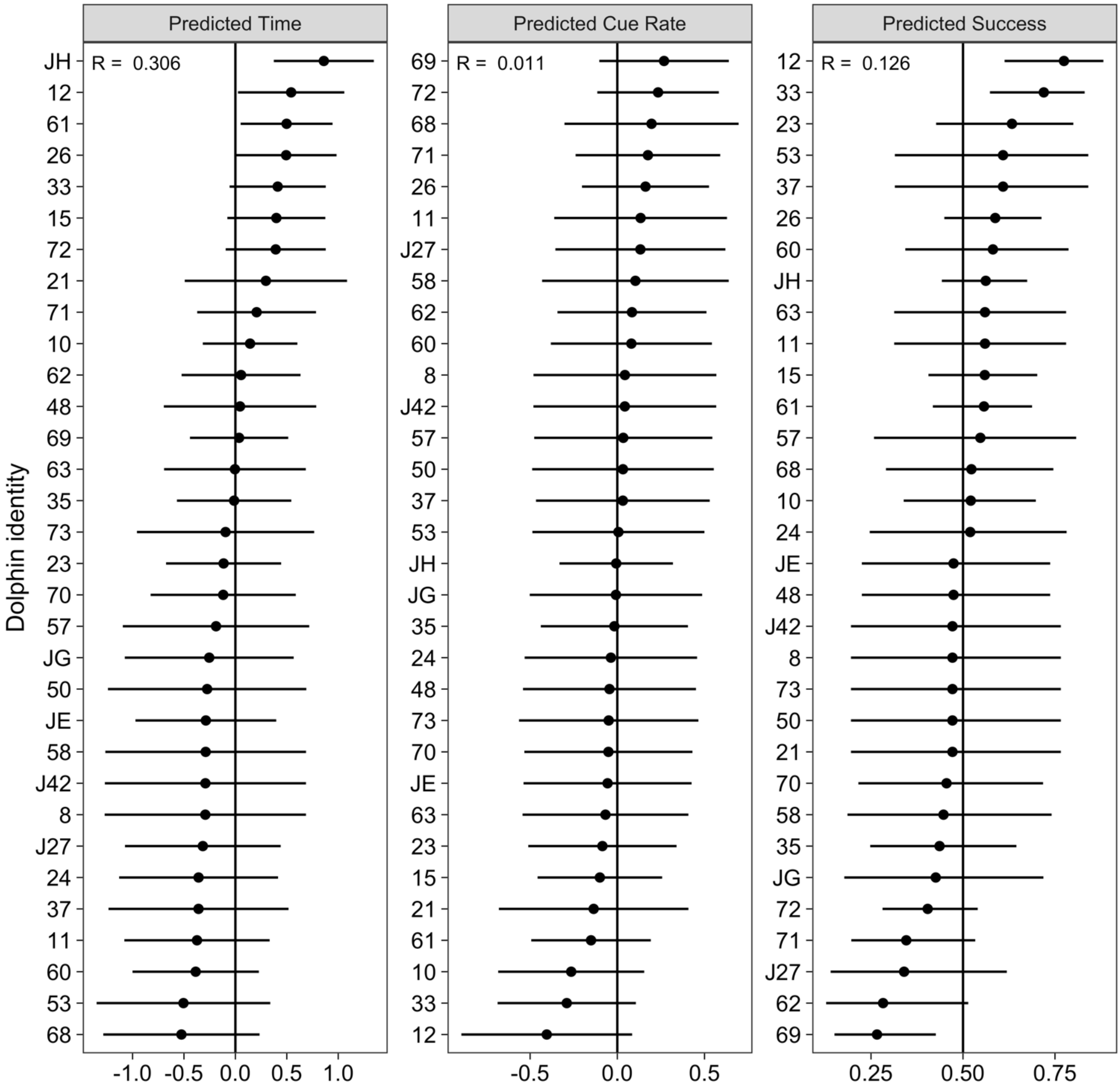

Figure 4.1: Individual differences in the daily time, cue rates and success of dolphins in the dolphin-fisher social foraging. Points show the random intercept estimates, and the lines show the 95% confidence intervals for each individual dolphin. In each model, the global mean is indicated by the black vertical line, and the repeatability coefficient by the R values. The estimates for the predicted success were back transformed from the logit link function and range from 0 to 1.

4.5.2 The relative importance of interference competition and individual differences

To test the effect of socially mediated interference, we summarized our data based on the groups inferred using our photo-identification data (Fig. 2). We found a low level of among-individual difference in cue rates (R = 0.012), likely due to substantial within-individual variation. Although we detected a marginal signal of interference affecting cue rates ($\beta = -1.41$, Std. Error = 0.715, Z = -1.97, P = 0.0491), this influence accounted for less than 1% of the variance in cue rates (Marginal R^2_{GLMM} = 0.172%). The proportion of positive outcomes in the interaction remained consistent with the daily models, showing low repeatability (R = 0.134). However, two dolphins (#12 and #33) consistently exhibited higher success rates than others. We found a statistically significant effect of the individual Elo-rating on the proportion of successful outcomes (β = 1.25, Std. Error = 0.568, Z = 2.2, P = 0.0275), while the interaction between individual Elo-rating and conspecific Elo-rating had no discernible effect (β = 0.656, Std. Error = 1.34, Z = 0.489, P = 0.625). Nonetheless, interference competition explained only a marginal proportion of the variation in the data (Marginal R^2_{GLMM} = 2.75%) compared to the influence of dolphin identity (Conditional R^2_{GLMM} = 15.7%). Finally, we found a moderate among-individual differences in contributions to the benefits accrued by fishers (R = 0.44), showing that a few dolphins made disproportionately larger contributions to the quantity of fish caught by fishers. Dolphin identity explains 44.6% of the variation in the number of fish caught by fishers, with no influence from individual dominance rank (β = 0.409, Std. Error = 0.985, Z = 0.416, P = 0.678) or interference from conspecifics (β = 1.77, Std. Error = 2.06, Z = 0.859, P = 0.391). Remarkably, the three dolphins with 95% confidence interval above the global mean were responsible for ca. 64.3% of all fish caught during the three years of sampling. Coefficients from all fit models can be found in Supplementary Material Tables S4–S6.

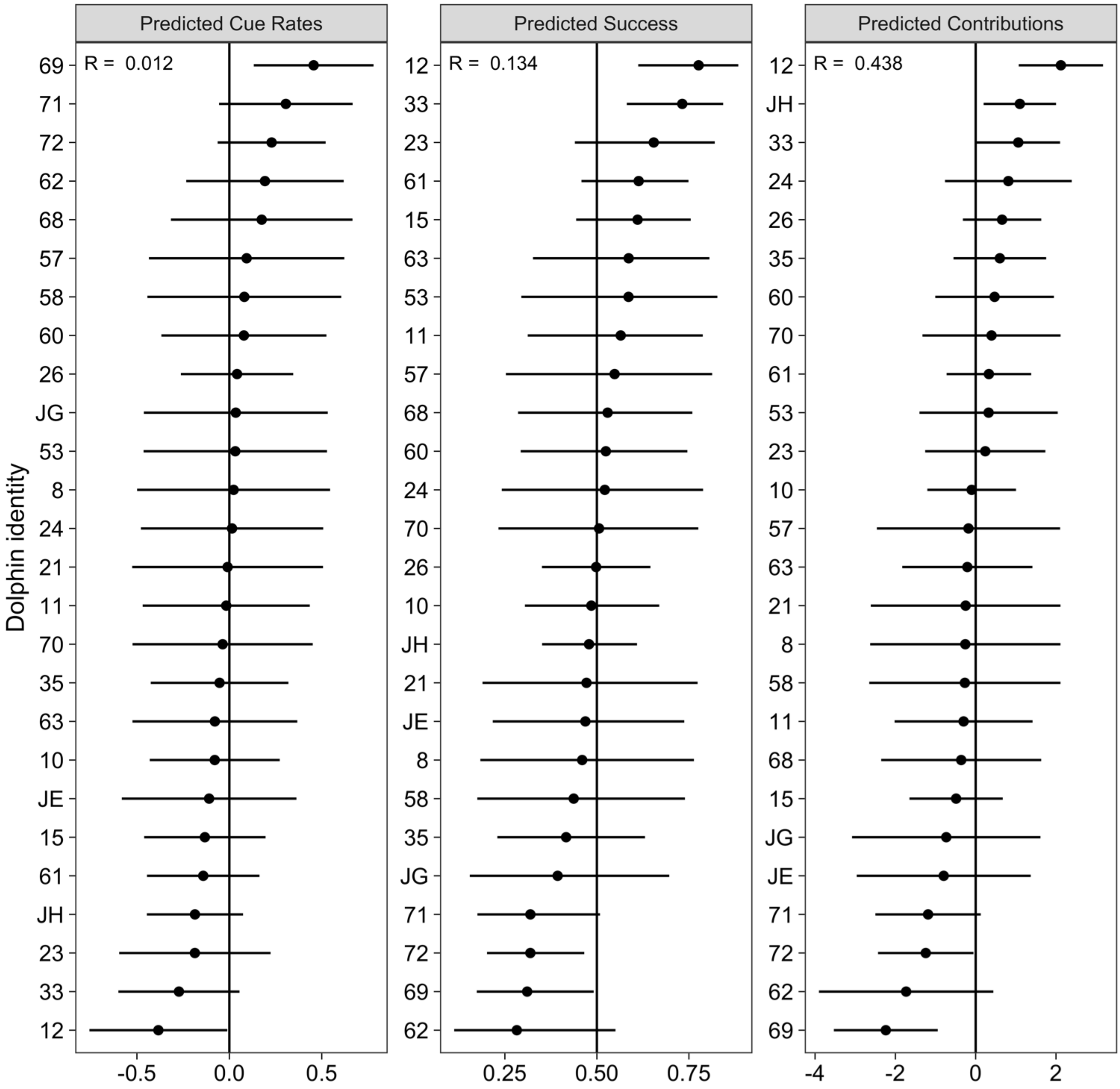

Figure 4.2: Individual differences in cue rates produced, the proportion of successful dolphin-fisher synchronous foraging events, and contributions to human partners in terms of mullet caught. Points show the random intercept estimates, and the lines depict the 95% confidence intervals for each individual. In each model, the global mean is shown by the black vertical line, and the repeatability coefficient by the R values. The estimates for the predicted success were back transformed from the logit link function and range from 0 to 1.

4.6 DISCUSSION

Our findings illustrate how individuals can disproportionately contribute to a mutualistic system. By quantifying the foraging behaviour of dolphins over time, we demonstrate that individual differences among dolphins can affect the outcomes of a dolphin-fisher social foraging interaction: only a few dolphins were responsible for producing most of the benefits accrued by fishers in terms of mullet catch. We further quantified the dolphin foraging behaviour when interacting with fishers across different dolphin group composition and show that interference competition by conspecifics does not represent a major mechanism underlying such individual differences. These findings suggest that individuals who specialize in the social foraging tactic with humans play a central role in determining the outcomes of this mutualistic system, and that intraspecific competition among dolphins does not modulate the access of conspecifics to their human partners, nor does it influence the foraging benefits accrued. Next, we discuss how other social factors, such as social learning processes, could explain why only a few dolphins specialize in the social foraging with humans.

We initially hypothesized that interference competition could be one of the main mechanisms modulating the individual differences in engagement within the human-dolphin social foraging. For instance, more dominant and better competitor individuals could potentially monopolize the fishing interaction site, thereby excluding conspecifics and leading to individual variation in engagement levels. However, our empirical data indicate that the relative importance of dominance and interference competition in influencing the outcomes of the dolphin-fisher interactions is negligible. The role of intra- and interspecific exploitative competition might be more important in this context, although the ephemeral nature of mullet schools at the dolphin-fisher interaction site as previously noted (Machado et al., *in prep*), may favour social foraging strategies, as mullet schools could leave the area faster than individuals can exploit them individually. Yet, such context-specific effects of exploitative and interference competition taking the environmental variation into account (e.g., Marshall et al., 2015) remains to be formally tested, as such as the individual variation in plasticity (e.g., Fisher & Cheney, 2023). On the fishers' side, competition for space arises, particularly in to accessing the net-casting slots in the water. This competition has prompted fishers to establish rules defining the order of access, time limits and fishing quotas, which democratize the opportunities for fishing with dolphins (Peterson et al., 2008). At the primary interaction site, for instance, a fisher who catches more than one fish with the assistance of dolphins must vacate the slot for the next fisher waiting in the queue. Dolphins might have also developed their own solution to mitigate competition for space and queuing, as individuals show different levels of fidelity to specific fishing sites (Cantor et al., 2018). With no clear evidence supporting interference competition as a possible mechanism explaining the observed variation in this mutualistic system, other social processes may be underlying individual differences.

We hypothesize that individual differences in performance can emerge from two distinctive, yet not mutually exclusive, pathways. Social learning can be one of the key processes influencing the development of social foraging tactic on both the human and the dolphin sides of this mutualistic interaction (Simões-Lopes et al., 2016). For instance, fishers can learn how to forage with dolphins either through individual trial and error or via social learning mechanisms. Fishers from local and traditional communities learn how to fish with dolphins primarily with their parents or grandparents, while fishers from open or adjacent communities may be influenced by outsiders and alternative learning processes, diverging from the cultural vertical transmission (Cantor & Santos-Silva *et al.*, *under review*[2]*)*. Dolphins may also learn how to forage with fishers from their mothers (Simões-Lopes et al., 2016), similarly to other culturally transmitted foraging specializations (e.g., Mann et al., 2012; Wild et al., 2019). Ultimately, the cultural learning process could contribute to the foraging and spatial specialization observed within the dolphin-fisher interaction, but other learning pathways cannot be definitively excluded. Dolphins learning to forage with fishers from their mothers may benefit from the expertise acquired during the parental care periods (Galef & Laland, 2005). In contrast, dolphins that learn individually or horizontally may either fail to acquire the necessary skills or simply require more practice and experience in the tactic to attain the necessary expertise (Dukas, 2019) to herd mullet schools towards fishers and synchronize their behaviour with the fishers' net-casting.

In tandem with the learning processes occurring on both dolphin and human sides of this social foraging interaction, signal quality could also underlie the observed individual differences. Individual identity can serve as an honest signal when partners can track their performance across interactions. However, fishers that learn through non-vertical transmission are prone to errors and may not accurately depict the identity of dolphins (Da Rosa et al., 2020). Thus, individual differences could emerge if fishers fail to correctly recognize dolphins' identity, leading to a potential bias in their perceptions and responses towards the cue produced

---

[2] Cantor, M., Santos-Silva, B., Daura-Jorge, F.G., Machado, A.M.S., Peterson, D., Rosa, D.X., Simões-Lopes, P.C.A., Valle-Pereira, J.V., Zank, S., Hanazaki, N. Insights from traditional knowledge on changes in the social-ecological system around a reciprocal human-dolphin relationship. *Under review at People and Nature.*

by more easily distinguishable dolphins. But given the low repeatability in cue rates produced, we suggest that fishers do not bias their response to cues from specific dolphins. Instead, fishers adopt a sit-and-wait strategy, relying on the mere presence of dolphins as a cue for initiating their foraging activities (Machado et al., *in prep*), regardless of the dolphin identity. This is consistent with the open nature of the system at the dolphin-fisher interaction site were assessed, which accommodates both amateur and professional fishers with mixed learning processes and experience levels (Santos-Silva et al., 2022; Valle-Pereira et al., 2022).

The contributions of our study are threefold. First, our findings suggest that the outcomes of this rare case of human-wildlife cooperation does not rely only on the number of cooperators in the population and their propensity to adopt a cooperative behaviour, but also on the quality of these cooperators, particularly in terms of their ability to produce the shared outcomes that underlie the dynamic of this mutualistic system. Second, by ruling out simpler mechanisms, such as competition, as drivers of individual differences and changes in the outcomes of the cooperation, our findings strengthen the thesis that social learning is an important process to the development and maintenance of this human-wildlife cooperation (Cram et al., 2023; van der Wal et al., 2022). Finally, given that a small number of key individual dolphins provide disproportional contributions to the benefits accrued by their human partners, losing these individuals due to unnatural causes might disproportionally reduce the motivation of fishers to remain engaged in this century-old fishery practice. Assessing individual variation over the long term is therefore imperative to provide new insights on the resilience of the few remaining cases of human-wildlife cooperation.

4.7 AUTHOR CONTRIBUTIONS

AMSM: study conception and design, data sampling, data processing, data analyses, visualization, writing. MC: study conception and design, data sampling, data analyses, data processing, writing, supervision, funding. DRF: study conception and design, data sampling, editing, supervision, funding. CB: data sampling, data processing, editing. FGDJ: study conception and design, data sampling, data analyses, editing, supervision, funding. All authors contributed critically to the manuscript and gave final approval for publication.

4.8 DECLARATION OF INTERESTS

We declare no conflicts of interest.

4.9 ACKNOWLEDGEMENTS

We are grateful for the teamwork effort in data collection (B. Romeu, J. Valle-Pereira, P. He, B Santos-Silva, E. Ehrdhardt, L. Rosa, C. Alves, L. Pereira, G. Oms, R. Suhs, F. Tiemy, E. Vontobel, A.C. Dotto, E. Ramalho, F. Peverari, K. Sears, T. Silva, H. Brandl, P. Simões-Lopes), logistical and field support (P. Castilho), and processing of photo-identification data (F. Peverari).

This study is part of a Brazil–Germany PROBRAL Research Program funded jointly by CAPES and DAAD (#88881.198854/2018–01), and of the SELA Long-Term Ecological Research Program (PELD CNPq #445301/2020–1). The study received further support from the Max Planck Society and the Centre for the Advanced Study of Collective Behaviour funded by DFG under Germany's Excellence Strategy (EXC 2117–422037984). AMSM received a CAPES MSc scholarship (finance code 01) and a CAPES–DAAD PROBRAL exchange scholarship; MC was supported by a CAPES postdoctoral fellowship (88881.170254/2018–01) and the Department for the Ecology of Animal Societies at the Max Planck Institute of Animal Behaviour; DRF was supported by the ERC European Union's Horizon 2020 (#850859) and an SNSF Eccellenza Professorship (#PCEFP3_187058); and FGDJ was supported by CAPES (#88887.374128/2019–00), CNPq (#308867/2019–0), and FAPESC (#TR2012000295).

4.10 REFERENCES

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267. https://doi.org/10.1080/14794802.2011.585831

Alves, L. C. P. de S., Andriolo, A., Orams, M. B., & de Freitas Azevedo, A. (2013). Resource defence and dominance hierarchy in the boto (*Inia geoffrensis*) during a provisioning program. *Acta Ethologica*, *16*(1), 9–19. https://doi.org/10.1007/s10211-012-0132-2

Bezamat, C., Castilho, P. V., Simões-Lopes, P. C., Ingram, S. N., & Daura-Jorge, F. G. (2020). Reproductive parameters and factors influencing calf survival of bottlenose dolphins that engage in a unique foraging cooperation with fishermen. *Marine Biology*, *167*(1), 1–12. https://doi.org/10.1007/s00227-019-3611-4

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brehm, A. M., Mortelliti, A., Maynard, G. A., & Zydlewski, J. (2019). Land-use change and the ecological consequences of personality in small mammals. *Ecology Letters*, *22*(9), 1387–1395. https://doi.org/10.1111/ele.13324

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Cantor, M., Farine, D. R., & Daura-Jorge, F. G. (2023). Foraging synchrony drives resilience in human–dolphin mutualism. *Proceedings of the National Academy of Sciences*, *120*(6), e2207739120. https://doi.org/10.1073/pnas.2207739120

Cantor, M., Simões-Lopes, P. C., & Daura-Jorge, F. G. (2018). Spatial consequences for dolphins specialised in foraging with fishermen. *Animal Behaviour*, *139*, 19–27. https://doi.org/10.1016/j.anbehav.2018.03.002

Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Animal Behaviour*, *103*, 223–235. https://doi.org/10.1016/j.anbehav.2015.02.019

Cram, D. L., Lloyd-Jones, D. J., Van Der Wal, J. E. M., Lund, J., Buanachique, I. O., Muamedi, M., Nanguar, C. I., Ngovene, A., Raveh, S., Boner, W., & Spottiswoode, C. N. (2023). Guides and cheats: Producer–scrounger dynamics in the human–honeyguide mutualism. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2010), 20232024. https://doi.org/10.1098/rspb.2023.2024

Cram, D. L., van der Wal, J. E. M., Uomini, N., Cantor, M., Afan, A. I., Attwood, M. C., Amphaeris, J., Balasani, F., Blair, C. J., Bronstein, J. L., Buanachique, I. O., Cuthill, R. R. T., Das, J., Daura-Jorge, F. G., Deb, A., Dixit, T., Dlamini, G. S., Dounias, E., Gedi, I. I., … Spottiswoode, C. N. (2022). The ecology and evolution of human-wildlife cooperation. *People and Nature*, *4*, 841–855. https://doi.org/10.1002/pan3.10369

Da Rosa, D. S. X. X., Hanazaki, N., Cantor, M., Simões-Lopes, P. C., & Daura-Jorge, F. G. (2020). The ability of artisanal fishers to recognize the dolphins they cooperate with. *Journal of Ethnobiology and Ethnomedicine*, *16*(30), 1–10. https://doi.org/10.1186/s13002-020-00383-3

Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D., & Simões-Lopes, P. C. (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biology Letters*, *8*(5), 702–705. https://doi.org/10.1098/rsbl.2012.0174

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. https://doi.org/10.1111/1365-2656.12013

Dukas, R. (2019). Animal expertise: Mechanisms, ecology and evolution. *Animal Behaviour*, *147*, 199–210. https://doi.org/10.1016/j.anbehav.2018.05.010

English, S., Nakagawa, S., & Clutton-Brock, T. H. (2010). Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). *Journal of Evolutionary Biology*, *23*(8), 1597–1604. https://doi.org/10.1111/j.1420-9101.2010.02025.x

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R., & Sánchez-Tójar, A. (2021). *aniDom: Inferring Dominance Hierarchies and Estimating Uncertainty* (R package version 0.1.5). https://CRAN.R-project.org/package=aniDom

Fisher, D. N., & Cheney, B. (2023). Dolphin social phenotypes vary in response to food availability but not the North Atlantic Oscillation index. *Proceedings of the Royal Society B*, *290*(20231187). https://doi.org/10.1098/rspb.2023.1187

Galef, B. G. B., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, *55*(6), 489–499.

Gazda, S. K., Connor, R. C., Edgar, R. K., & Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B*, *272*(1559), 135–140. https://doi.org/10.1098/rspb.2004.2937

Hartley, A., Shrader, A. M., & Chamaillé-Jammes, S. (2019). Can intrinsic foraging efficiency explain dominance status? A test with functional response experiments. *Oecologia*, *189*(1), 105–110. https://doi.org/10.1007/s00442-018-4302-4

Herbst, D. F., & Hanazaki, N. (2014). Local ecological knowledge of fishers about the life cycle and temporal patterns in the migration of mullet (*Mugil liza*) in Southern Brazil. *Neotropical Ichthyology*, *12*(4), 879–890. https://doi.org/10.1590/1982-0224-20130156

Irvine, A. B., Scott, M. D., Wells, R. S., & Kaufmann, J. H. (1981). Movements and activities of the atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*(4), 671–688.

Jones, E. I., Bronstein, J. L., & Ferrière, R. (2012). The fundamental role of competition in the ecology and evolution of mutualisms. *Annals of the New York Academy of Sciences*, *1256*(1), 66–88. https://doi.org/10.1111/j.1749-6632.2012.06552.x

Laskowski, K. L., Chang, C.-C., Sheehy, K., & Aguiñaga, J. (2022). Consistent Individual Behavioral Variation: What Do We Know and Where Are We Going? *Annual Review of Ecology, Evolution, and Systematics*, *53*, 161–182.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Machado, A. M. S., & Cantor, M. (2022). A simple tool for linking photo-identification with multimedia data to track mammal behaviour. *Mammalian Biology*, *102*, 983–993. https://doi.org/10.1007/s42991-021-00189-0

Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications*, *3*(1), 980–980. https://doi.org/10.1038/ncomms1983

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2015). Social effects on foraging behavior and success depend on local environmental conditions. *Ecology and Evolution*, *5*(2), 475–492. https://doi.org/10.1002/ece3.1377

Moran, N. P., Caspers, B. A., Chakarov, N., Ernst, U. R., Fricke, C., Kurtz, J., Lilie, N. D., Lo, L. K., Müller, C., R, R., Takola, E., Trimmer, P. C., van Benthem, K. J., Winternitz, J., & Wittmann, M. J. (2022). Shifts between cooperation and antagonism driven by individual variation: A systematic synthesis review. *Oikos*, *e08201*, 1–16. https://doi.org/10.1111/oik.08201

Nakano, S. (1995). Individual Differences in Resource Use, Growth and Emigration Under the Influence of a Dominance Hierarchy in Fluvial Red-Spotted Masu Salmon in a Natural Habitat. *The Journal of Animal Ecology*, *64*(1), 75–75. https://doi.org/10.2307/5828

Neumann, K. (2020). *EloRating: Animal dominance hierarchies by elo rating*. https://CRAN.R-project.org/package=EloRating.

Peterson, D., Hanazaki, N., & Simões-Lopes, P. C. (2008). Natural resource appropriation in cooperative artisanal fishing between fishermen and dolphins (*Tursiops truncatus*) in Laguna, Brazil. *Ocean & Coastal Management*, *51*(6), 469–475. https://doi.org/10.1016/j.ocecoaman.2008.04.003

Psorakis, I., Voelkl, B., Garroway, C. J., Radersma, R., Aplin, L. M., Crates, R. A., Culina, A., Farine, D. R., Firth, J. A., Hinde, C. A., Kidd, L. R., Milligan, N. D., Roberts, S. J., Verhelst, B., & Sheldon, B. C. (2015). Inferring social structure from temporal data. *Behavioral Ecology and Sociobiology*, *69*(5), 857–866. https://doi.org/10.1007/s00265-015-1906-0

R Core Team. (2021). *R: A language and environment for statistical computing.* (4.1.2). R Foundation for Statistical Computing. https://www.R-project.org/

Saito, C. (1996). Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: Effects of food patch size and inter-patch distance. *Animal Behaviour*, *51*(5), 967–980. https://doi.org/10.1006/anbe.1996.0100

Samuels, A., & Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science*, *13*(1), 70–99. https://doi.org/10.1111/j.1748-7692.1997.tb00613.x

Sánchez-Tójar, A., Schroeder, J., & Farine, D. R. (2018). A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *Journal of Animal Ecology*, *87*(3), 594–608. https://doi.org/10.1111/1365-2656.12776

Santos-Silva, B., Hanazaki, N., Daura-Jorge, F. G., & Cantor, M. (2022). Social foraging can benefit artisanal fishers who interact with wild dolphins. *Behavioral Ecology and Sociobiology*, *76*(42), 1–14. https://doi.org/10.1007/s00265-022-03152-2

Sih, A., Sinn, D. L., & Patricelli, G. L. (2019). On the importance of individual differences in behavioural skill. *Animal Behaviour*, *155*, 307–317. https://doi.org/10.1016/j.anbehav.2019.06.017

Simões-Lopes, P. C. (1998). Intraspecific agonistic behavior of *Tursiops truncatus* (Cetacea, Delphinidae) during dolphin-human cooperative fishing in southern Brazil. *Biotemas*, *11*(2), 165–171.

Simões-Lopes, P. C., Daura-Jorge, F. G., & Cantor, M. (2016). Clues of cultural transmission in cooperative foraging between artisanal fishermen and bottlenose dolphins, *Tursiops* *truncatus* (Cetacea: Delphinidae). *Zoologia (Curitiba)*, *33*(6), e20160107–e20160107. https://doi.org/10.1590/s1984-4689zool-20160107

Simões-Lopes, P. C., Fabián, M. E., & Menegheti, J. O. (1998). Dolphin interactions with the mullet artisanal fishing on southern Brazil: A qualitative and quantitative approach. *Revista Brasileira de Zoologia*, *15*(3), 709--726. https://doi.org/10.1590/S0101-81751998000300016

Stander, P. E. (1992). Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology*, *29*, 445–454.

Vail, A. L., Manica, A., & Bshary, R. (2014). Fish choose appropriately when and with whom to collaborate. *Current Biology*, *24*(17), R791–R793. https://doi.org/10.1016/j.cub.2014.07.033

Valle-Pereira, J. V. S., Cantor, M., Machado, A. M. S., Farine, D. R., & Daura-jorge, F. G. (2022). The role of behavioural variation in the success of artisanal fishers who interact with dolphins. *ICES Journal of Marine Science*, *79*(4), 1150–1158. https://doi.org/10.1093/icesjms/fsac038

van der Wal, J. E. M., Spottiswoode, C. N., Uomini, N. T., Cantor, M., Daura-Jorge, F. G., Afan, A. I., Attwood, M. C., Amphaeris, J., Balasani, F., Begg, C. M., Blair, C. J., Bronstein, J. L., Buanachique, I. O., Cuthill, R. R. T., Das, J., Deb, A., Dixit, T., Dlamini, G. S., Dounias, E., … Cram, D. L. (2022). Safeguarding human–wildlife cooperation. *Conservation Letters*, *15*, 1–18. https://doi.org/10.1111/conl.12886

Wild, S., Allen, S. J., Krützen, M., King, S. L., Gerber, L., & Hoppitt, W. J. E. (2019). Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. *Biology Letters*, *15*(7), 20190227–20190227. https://doi.org/10.1098/rsbl.2019.0227

4.11 SUPPLEMENTARY MATERIAL

Table S1: Generalized mixed-effect model to quantify the individual differences in the time spent at the interaction site. Time at the interaction site during each sampling day was fit to an intercept only model, including dolphin identity as the random intercept. Model was fit to the data using a negative binomial error structure with a log link function.

Term	Estimate	Std. Error	Z	P
Intercept	7.9355	0.1357	58.46	0
Std. Deviation of Random Intercept (dolphin ID)	0.4874			

Table S2: Generalized mixed-effect model to quantify the individual differences in the cue rates produced at the human-dolphin mutualism. The total number of cues produced by each dolphin during a sampling day was fit to an intercept only model, including dolphin identity as the random intercept. Model was fit to the data using a negative binomial error structure with a log link function and an offset term to account for the time to produce the number of cues.

Term	Estimate	Std. Error	Z	P
Intercept	-6.6681	0.08936	-74.62	0
Std. Deviation of Random Intercept (dolphin ID)	0.2694			

Table S3: Generalized mixed-effect model to quantify the individual differences in the proportion of successful outcomes on the human-dolphin mutualism. The proportion of successful and unsuccessful cooperative events that each dolphin was involved in each sampling day were fit to an intercept only model, including dolphin identity as the random intercept. Model was fit to the data using a binomial error structure with a logit link function.

Term	Estimate	Std. Error	Z	P
Intercept	-1.0319	0.183	-5.639	1.709e-08
Std. Deviation of Random Intercept (dolphin ID)	0.6898			

Table S4: Generalized mixed-effect model to quantify the individual differences in the cue rates produced at the human-dolphin mutualism. The total number of cues produced by each dolphin during a grouping event was fit against the interaction between individual Elo-rating and the maximum Elo-rating of conspecifics in the groups, including dolphin identity as the random intercept. Model was fit to the data using a negative binomial error structure with a log link function and an offset term to account for the time in the group to produce the number of cues.

Term	Estimate	Std. Error	Z	P
Intercept	-6.1623	0.1610	-38.279	0.00000
Elo-rating of conspecifics	0.6538	0.4254	1.537	0.12431
Individual Elo-rating	0.3919	0.2853	1.374	0.16951
Elo-rating of conspecifics * Individual Elo-rating	-1.4072	0.7151	-1.968	0.04909
Std. Deviation of Random Intercept (dolphin ID)	0.2721			

Table S5: Generalized mixed-effect model to quantify the individual differences in the proportion of successful outcomes on the human-dolphin mutualism. The proportion of successful and unsuccessful cooperative events that each dolphin produced during grouping events were fit against the interaction between individual Elo-rating and the maximum Elo-rating of conspecifics in the groups, including dolphin identity as the random intercept. Model was fit to the data using a binomial error structure with a logit link function.

Term	Estimate	Std. Error	Z	P
Intercept	-1.5308	0.3468	-4.4136	1.016e-05
Elo-rating of conspecifics	-0.4344	0.8098	-0.5364	5.917e-01
Individual Elo-rating	1.2523	0.5680	2.2049	2.746e-02
Elo-rating of conspecifics * Individual Elo-rating	0.6558	1.3420	0.4887	6.251e-01
Std. Deviation of Random Intercept (dolphin ID)	0.7124			

Table S6: Generalized mixed-effect model to quantify the individual differences in the contributions to the human-dolphin mutualism. The number of fish caught by fishers in grouping events with each dolphin were fit against the interaction between individual Elo-rating and the maximum Elo-rating of conspecifics in the groups, including dolphin identity as the random intercept. Model was fit to the data using a binomial error structure with a logit link function.

Term	Estimate	Std. Error	Z	P
Intercept	0.4104	0.5736	0.7154	0.4743
Elo-rating of conspecifics	-0.7722	1.2407	-0.6224	0.5337
Individual Elo-rating	0.4095	0.9853	0.4156	0.6777
Elo-rating of conspecifics * Individual Elo-rating	1.7671	2.0581	0.8586	0.3906
Std. Deviation of Random Intercept (dolphin ID)	1.2186			

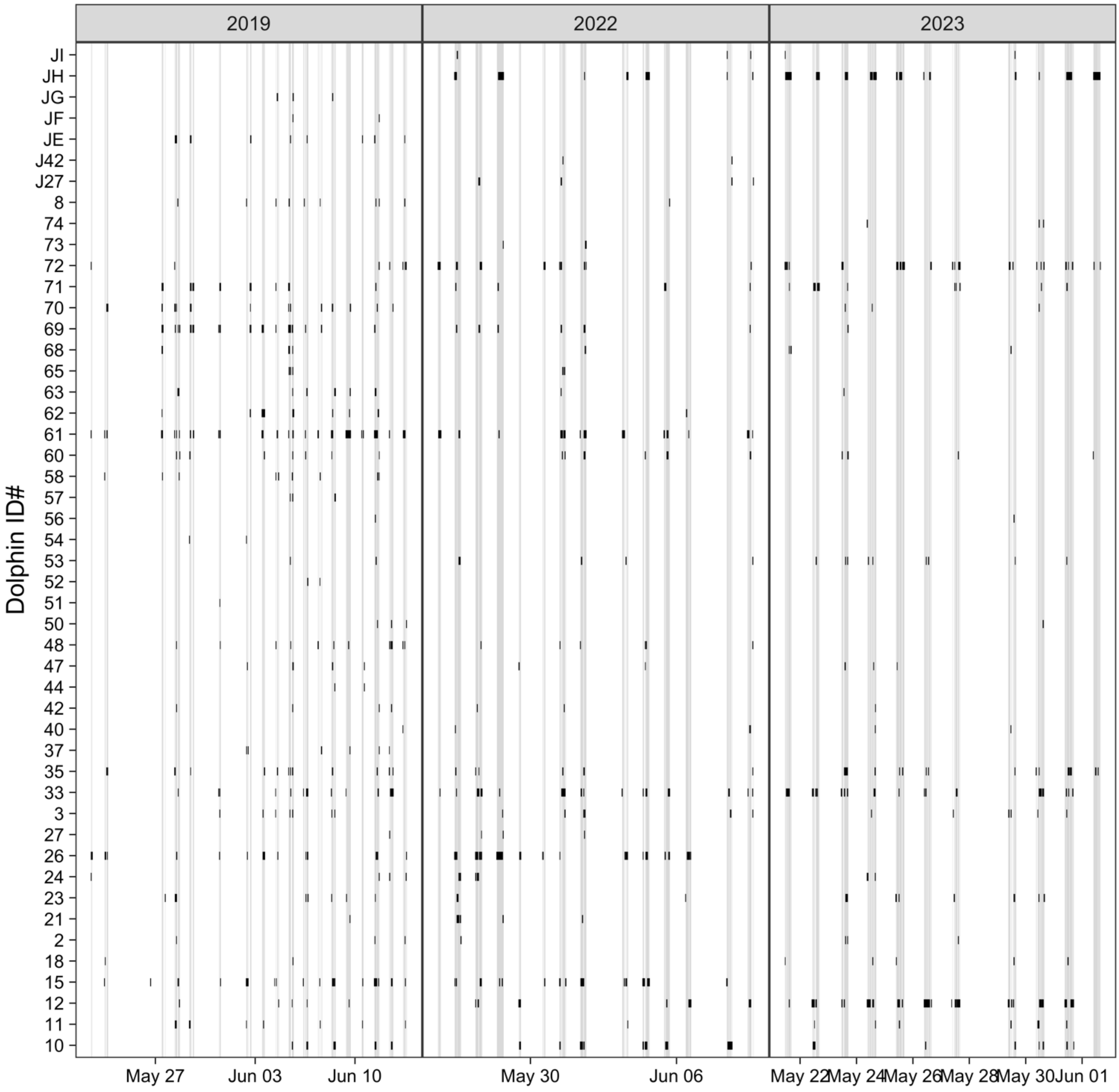

Figure S 1: Groups inferred from gaussian mixture models. Coloured rectangles highlight the group duration, and the black ticks represent a photo taken of each individual.

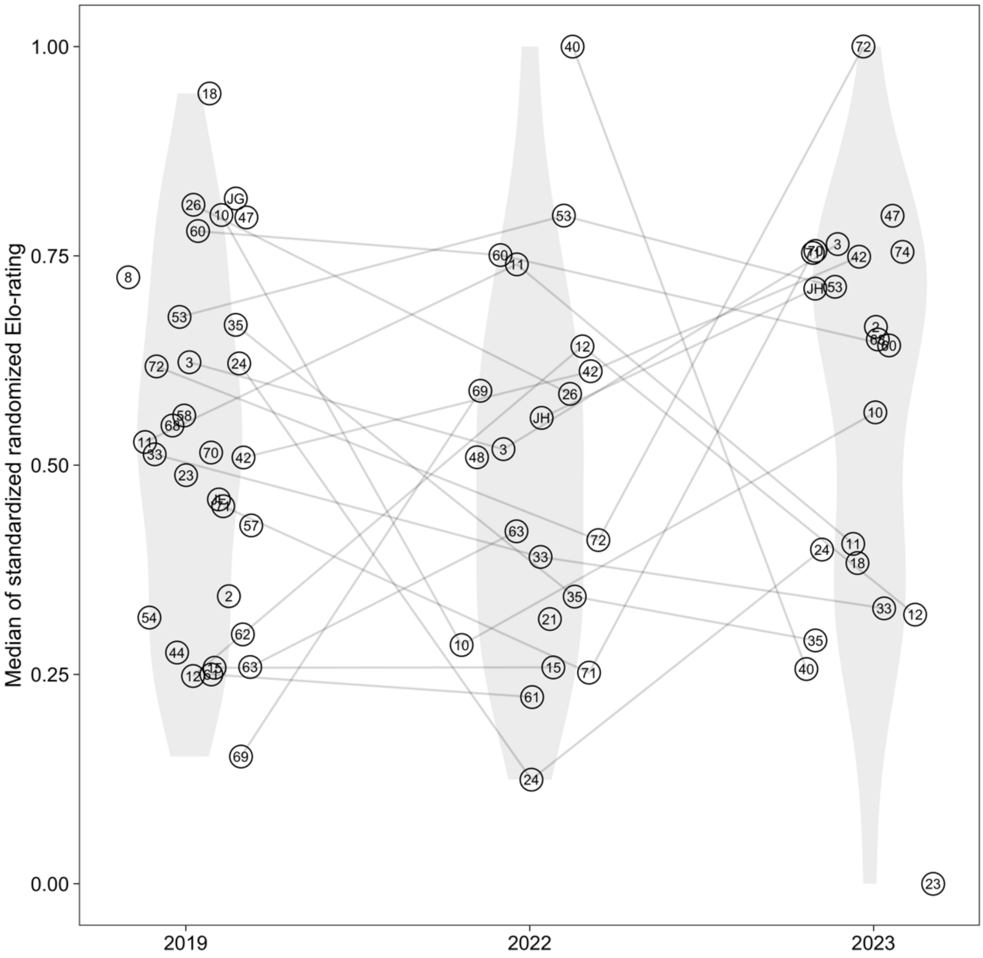

Figure S 2: Elo-scores of dolphins at the dolphin-fisher interaction site. Violin plots in grey show the distribution of Elo-Ratings scores, standardized from 0 to 1 (the highest rank). Lines connect the dolphin identity across years, showing changes in the Elo-rating score.

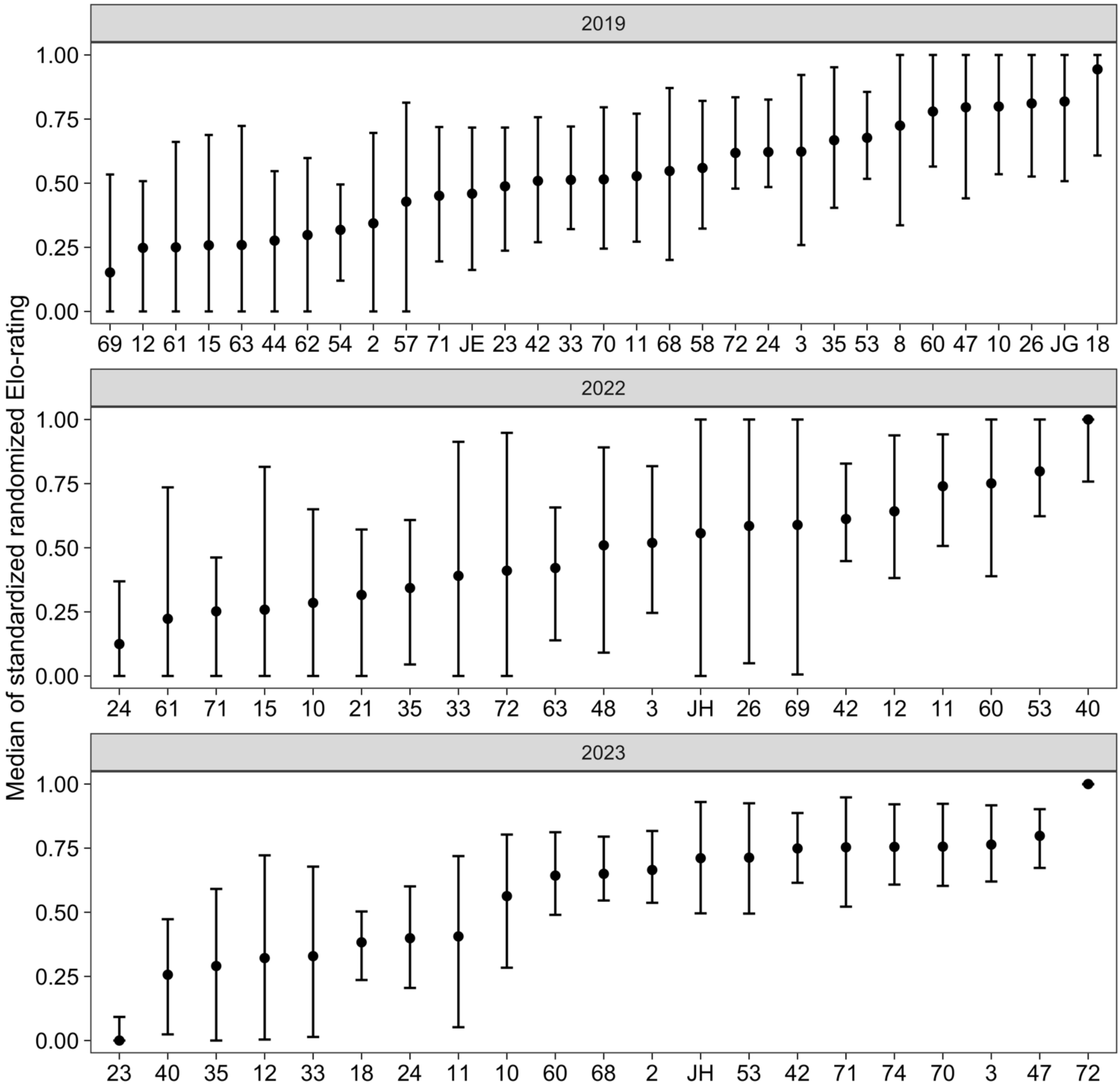

Figure S 3: Elo-rating scores of dolphins at the dolphin-fisher interaction site. Point estimates show the median Elo-score from 1000 randomizations and bars show the 95% confidence intervals. The Elo-rating is standardized, ranging from 0 to 1 (the highest rank).

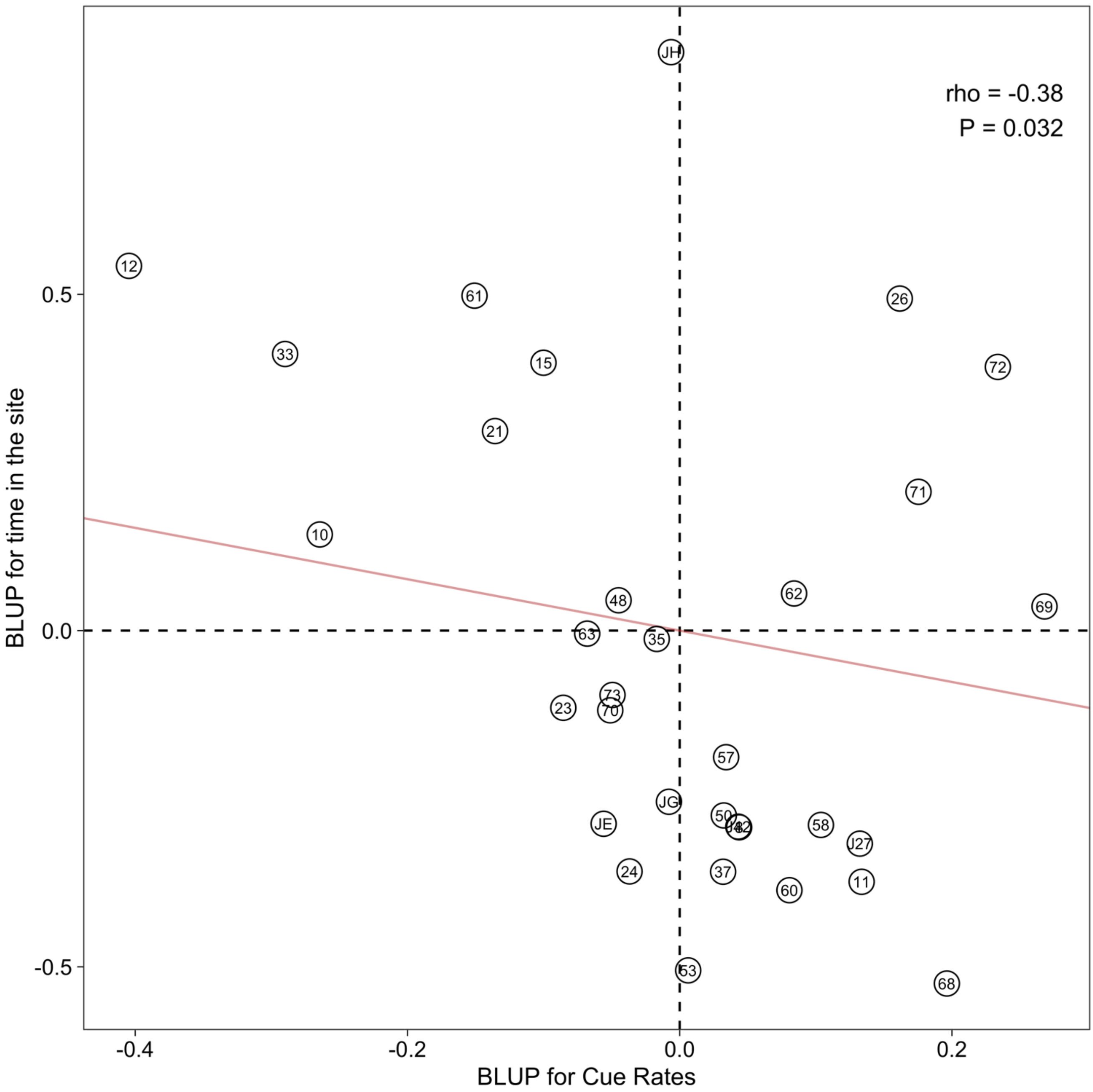

Figure S 4: Correlation between the best linear unbiased predictor of the time each individual spent at the dolphin-fisher interaction site and the cue rates produced. Red line shows the estimate from the spearman correlation and the dashed lines shows the global mean from each model.

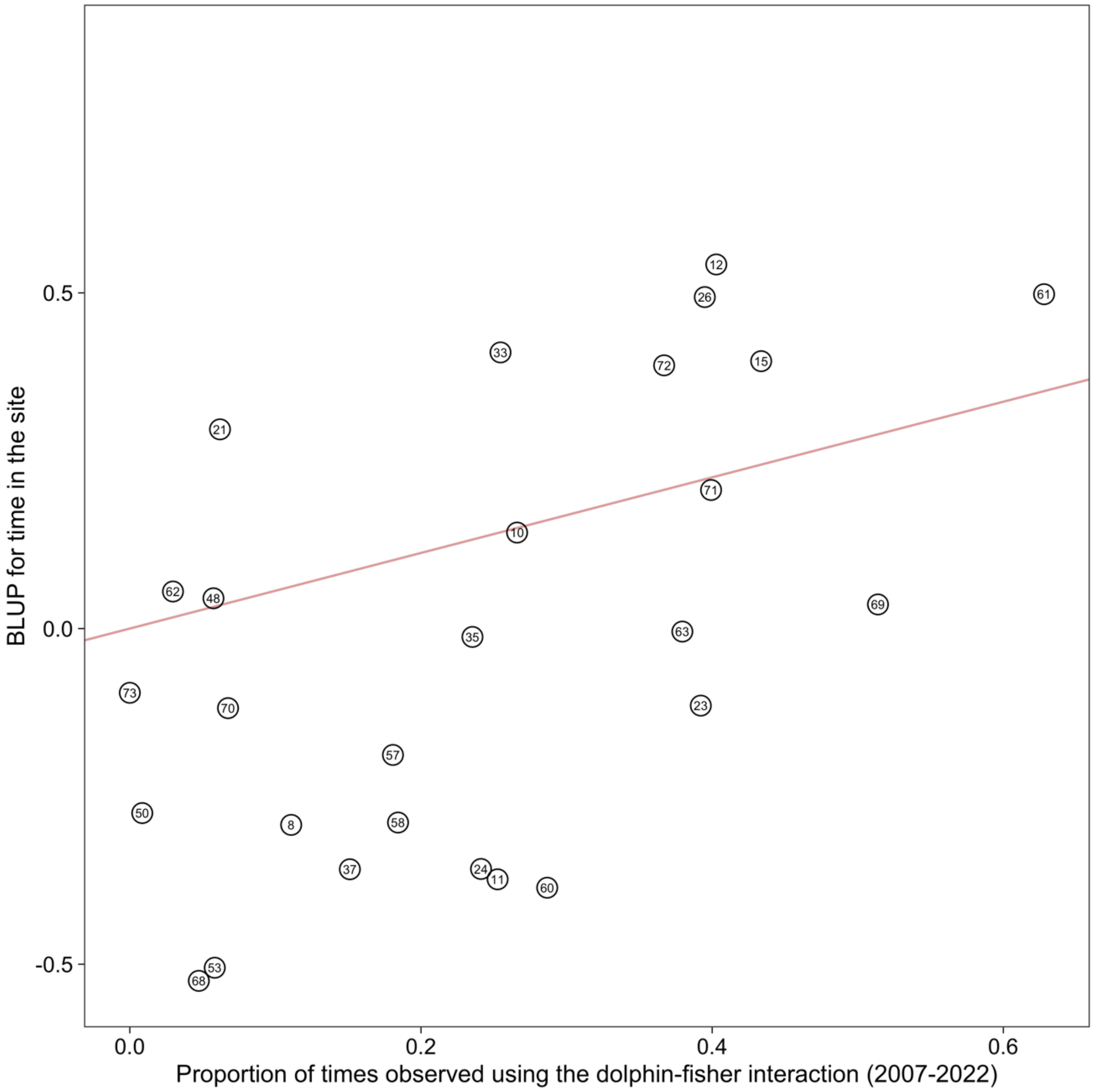

Figure S 5: Correlation between the prediction of time spent at the dolphin-fisher interaction site and the proportion of time dolphins were observed using the foraging tactic across all sites. The time at the interaction site was estimated from the photo-identification data and groups inferred with gaussian mixture models. The proportions of times seen at all interaction sites was estimated from boat surveys conducted between 2007 and 2022. The positive correlation between the two suggest that some dolphins consistently use the cooperative foraging.

5 CAPÍTULO 3: A SIMPLE TOOL FOR LINKING PHOTO-IDENTIFICATION WITH MULTIMEDIA DATA TO TRACK MAMMAL BEHAVIOUR

Alexandre M.S. Machado[1,2]
Mauricio Cantor[1,3,4,5,6]

1 Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil.
2 Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Radolfzell, Germany.
3 Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany.
4 School of Plant, Animal and Earth Sciences, University of Witwatersrand, Johannesburg, South Africa.
5 Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná, Brazil
6 Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, USA

Capítulo publicado em edição especial da revista Mammalian Biology, em 27/12/2021.

Machado, A. M. S.; Cantor, M. A simple tool for linking photo-identification with multimedia data to track mammal behaviour. **Mammalian Biology**, v. 102, p. 961–971. 2021. https://doi.org/10.1007/s42991-021-00189-0

5.1 ABSTRACT

Identifying individual animals is critical to describe demographic and behavioural patterns, and to investigate the ecological and evolutionary underpinnings of these patterns. The traditional non-invasive method of individual identification in mammals—comparison of photographed natural marks—has been improved by coupling other sampling methods, such as recording overhead video, audio and other multimedia data. However, aligning, linking and syncing these multimedia data streams are persistent challenges. Here, we provide computational tools to streamline the integration of multiple techniques to identify individual free-ranging mammals when tracking their behaviour in the wild. We developed an open-source R package for organizing multimedia data and for simplifying their processing a posteriori—"*MAMMals: Managing Animal MultiMedia: Align, Link, Sync*". The package contains functions to (i) align and link the individual data from photographs to videos, audio recordings and other text data sources (e.g. GPS locations) from which metadata can be accessed; and (ii) synchronize and extract the useful multimedia (e.g. videos with audios) containing photo-identified individuals. To illustrate how these tools can facilitate linking photo-identification and video behavioural sampling in situ, we simultaneously collected photos and videos of bottlenose dolphins using off-the-shelf cameras and drones, then merged these data to track the foraging behaviour of individuals and groups. We hope our simple tools encourage future work that extend and generalize the links between multiple sampling platforms of free-ranging mammals, thereby improving the raw material needed for generating new insights in mammalian population and behavioural ecology.

Key-words: Behavioural sampling, Hydrophone, Individual, Photo-identification, Unmanned aerial vehicle

5.2 INTRODUCTION

Natural populations change in size and composition, propelling the dynamics of ecological communities, species interactions, and energy flow through the ecosystem (Odum; Barret, 1971). At the heart of these changes, are individual animals being born, growing, behaving, and dying. Individual-based data provide the raw material to investigate the mechanics and dynamics of these natural populations, their ecological interactions and evolution (Coulson, 2020), particularly in longitudinal studies (Clutton-Brock; Sheldon, 2010). Therefore, a deep understanding of these patterns and processes in animal ecology requires identifying and tracking individual animals over time and space (Coulson, 2020).

The available invasive and non-invasive methods for sampling individual animals present trade-offs on the accuracy, content and quality of the data they provide. Invasive methods require capturing animals to mark (e.g., with collars, tattoos, tags, freeze branding; Silvy; Lopez; Peterson, 2005) or fit tracking devices (RFID, GPS, acoustic, satellite tags: e.g., Krause et al., 2013) but provide detailed information about the individuals (e.g., identity, location, behaviour, health). Actively capturing and marking animals, however, can be unfeasible, expensive or disrupt natural behaviour or physiology (Walker et al., 2011). By contrast, non-invasive identification methods, such as photographic, acoustic and video recording (Karczmarski et al., 2022a, 2022b), rely on systematic comparison of natural marks or behaviours (e.g., Karanth; Nichols, 1998; Muller et al., 2018; Longden et al., 2020) to track individuals from a distance (e.g., Clapham et al., 2020; Ferreira et al., 2020). Although efficient in providing individual identities, non-invasive methods generally provide fewer information on other biological variables (but see Toms; Stone; Och-Adams, 2020), which has motivated the simultaneous use of other multimedia sampling platforms, such as video (e.g., Raoult; Tosetto; Williamson, 2018; Francisco; Nührenberg; Jordan, 2020; Landeo-Yauri et al., 2020) and audio recordings (Cheng et al., 2012; Erbe et al., 2020). Novel technologies for identifying and tracking individuals using such multimedia data are becoming increasingly more precise in the lab or captivity (e.g., Mersch; Crespi; Keller, 2013; Dell et al., 2014; Pérez-Escudero et al., 2014; Alarcón-Nieto et al., 2018; Graving et al., 2019; Marks et al., 2021), but doing so in situ remains more challenging (e.g., Ferreira et al., 2020; Guo et al., 2020). In the field, where animals are not spatially constrained, recording data from multiple sampling platforms simultaneously, or syncing large volumes of data to then link with that of individual identification a posteriori, can be troublesome.

In wild mammal research, cetacean studies exemplify the continuous development of non-invasive individual identification methods based on multimedia data. Photo-identification has been the go-to technique to recognize individual whales and dolphins in the last five decades (e.g., Würsig; Würsig, 1977; Katona; Whitehead, 1981; Hammond; Mizroch; Donovan, 1990). Since whales and dolphins can range over large areas and spend long times underwater, photo-identification has been increasingly coupled to other multimedia sampling to detect the presence of individuals and/or describe their behavioural patterns. For instance, while cameras and acoustic sampling provide invaluable underwater perspectives, the growing market of unmanned aerial vehicles (drones) has popularized the recording of behaviour, movement and health of cetaceans from an overhead view (e.g., Torres et al., 2018; Gray et al., 2019; Hartman; Van der Harst; Vilela, 2020). With few exceptions, however, these sampling techniques do not provide individual identities—but see, e.g., identification from overhead images (e.g., Payne et al., 1983; Durban et al., 2015) or acoustic signals (e.g., Janik; Sayigh, 2013). Combining traditional photo-identification sampling with hydrophones, underwater and drone cameras can resolve this limitation, but it inevitably creates another one: individual behavioural tracking from multiple platforms generates a large and multi-dimensional dataset that rapidly become unfeasible to handle manually. These technological advances have therefore produced a need for corresponding advances in computational tools to organize and process multiple data streams (e.g., Schneider et al., 2019).

Here, we introduce a free and open computational tool for aligning, linking and syncing photo-identification data with other multimedia data of free-ranging vertebrates. The R package *MAMMals—Managing Animal MultiMedia: Align, Link, Sync*—contains functions to synchronize different multimedia data streams a posteriori and so facilitate their post-processing to measure relevant biological and behavioural data. Using *MAMMals*, one can (i) extract, organize and line up the metadata of photographs, videos, audios, drone flight logs and any other timestamped text data; (ii) select, trim and export clips or stills of the footage or audio recording containing individual photo-identification; and (iii) wrangle, convert and plot data from cameras, drones, hydrophones, microphones and other timestamped data sources. In what follows, we describe the workflow for pre-processing individual photo-identification and link it to other multimedia data (Fig. 1). Next, we illustrate the utility of these tools by applying them to process and analyse empirical data on the foraging behaviour of coastal bottlenose dolphins. We conclude by discussing the caveats of our approach and how future work can alleviate them.

5.3 WORKFLOW OVERVIEW: COUPLING PHOTO-IDENTIFICATION WITH OTHER MULTIMEDIA DATA

The *MAMMals* R package targets the challenge of coupling large volumes of observational and multimedia data to traditional techniques of identifying individuals, extending therefore the possibilities for studies that use methods of focal-animal and focal-group sampling (Altmann, 1974). The minimum requirements are image files with assigned individual identification and at least one other multimedia data source. The workflow follows four steps (Fig. 1): (i) extracting the metadata of photographs and any other multimedia files available; (ii) aligning the metadata of these files to select the useful multimedia containing photo-identified individuals; (iii) linking these selected files by clipping the multimedia containing photo-identified individuals; (iv) and syncing media and text data around their intersection time. We detail each step of the *MAMMals* workflow in the next sessions, and provide instructions and examples of the input and output files in a documentation in an online tutorial (https://mammals-rpackage.netlify.app/index.html). The *MAMMals* R package can be installed from the online repository (instructions at https://bitbucket.org/maucantor/mammals/). It depends on the installation of the R environment (R Core Team, 2021) and key R packages such as *lubridate* (Grolemund; Wickham, 2011) to manage date-time formats (full list of dependencies, see the package repository), as well as external software ExifTool (https://exiftool.org) to extract the metadata of media files, and FFmpeg (https://ffmpeg.org) to clip video and audio files.

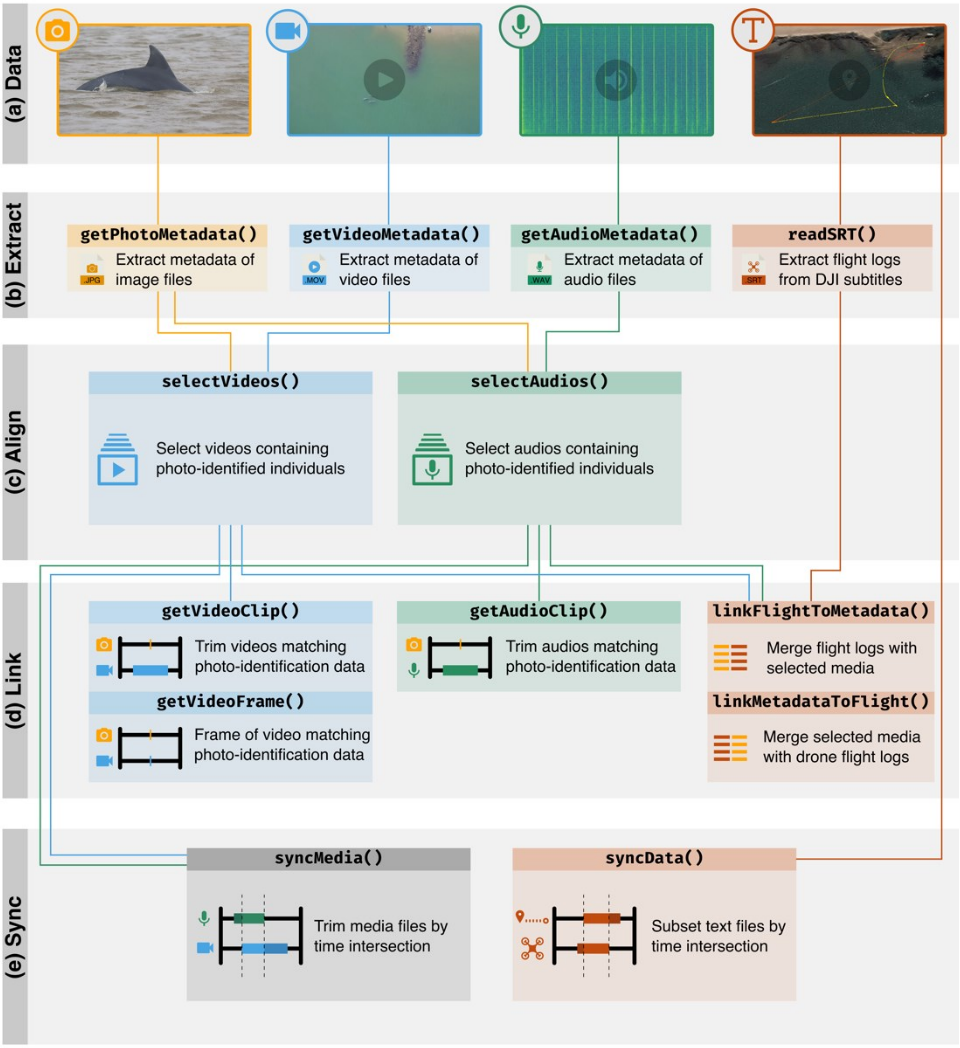

Figure 5.1: The MAMMals workflow to align, link and sync multimedia and timestamped text data. a) The inputs are files commonly produced in individual identification and behavioural sampling methods, such as images (.jpg, .tiff, .png), videos (.mov, .mp4), audios (.wav, .mp3) and/or text files (.csv, .txt, .srt). After aligning, linking and syncing the inputs, the outputs can be text files with metadata and/or synced image, audio and/or video files. The minimum requirements for the MAMMals workflow are the photo-identification data (i.e. the image files associated to individual identification text data), and at least one more multimedia data source, such as videos, audios or text files. b) The first step is to extract the metadata of all multimedia files (and flight logs, if available, or from captions in .srt files of commercially available drones). One can also export the metadata for posterior processing, such as attributing individual IDs to each photo processed by the getPhotoMetadata function, or assign individual identification from pre-processed data directly to the function getPhotoMetadata. c) The second step is to align the metadata of photographs (or timestamped field notes) with that of the other media to automatically select the video or audio files containing individual photo-identification data. d) The third step is to link the selected media by clipping the videos and audios around the information of interest (e.g. photo-identified individuals) to facilitate the post-processing of videos (getVideoClip), audios (getAudioClip) or stills from the video (getVideoFrame). If sampling includes drone videos, selected media can be linked to information from the flight, such as latitude, longitude and altitude. e) The final step is to sync media and/or text by subsetting only the time intersect between data coming from different sampling platforms. The synced multimedia and text data can be exported as a single merged file or multiple separate files.

When photographing animals for individual identification using natural marks, we recommend following the protocols for collecting, processing and organizing such data, which have been extensively detailed elsewhere (e.g., Speed; Meekan; Bradshaw, 2007; Urian et al., 2015). We highlight that using DSLR cameras equipped with GPS and digital compass can be useful when teasing apart photo-identified individuals in the field, especially when tracking them with overhead videos. For instance, when tracking multiple individuals or groups distributed in space, one can assign the photographs taken to each group recorded in the overhead footage by interpreting the GPS coordinates and shooting angle extracted from the photograph metadata. After the photographic data sampling, we recommend first processing the photo-identification data and organizing it in a plain text data frame, in which the first column contains the photograph file name and extension (e.g. ‘6Q1A8164.JPG’), and the second contains the individual (alphanumeric) identification code (e.g. ‘ID1248’).

When recording audio, we recommend using recorders that can produce timestamped files. Otherwise, one can manually check the end time of recordings after sampling and rename files accordingly with date and time. When recording videos from small drones (e.g. DJI Phantom, DJI Mavic Pro, DJI Inspire, Splash Drone) while simultaneously collecting photo-identification or audio recordings, we recommend keeping a constant flight height and point the camera straight down (i.e., drone and camera pitch = − 90°, roll = 0°) to ensure the centre of the frame matches the coordinates recorded by the drone GPS and to reduce the distortion from any measures taken from the drone footage. If measuring animals from the drone footage using photogrammetry, there will be additional requirements. In addition to the camera tilt, the aircraft altitude data are the main issues for precise and unbiased photogrammetric measurements. Off-the-shelf drones record the altitude relative to the aircraft’s take-off position (“home point”). Hence, if the aircraft takes off from the deck of a ship or a higher ground, the zero in the aircraft’s barometer does not match the sea level. To mitigate this, an object of known length can be used to calibrate a scale (details in Burnett et al., 2019). Another solution is to couple a LiDAR sensor to the drone (e.g., Dawson et al., 2017) to precisely measure the distance from the aircraft to the sea level. Correcting lens distortion and camera calibration also reduce errors in measurement estimates (see Dawson et al., 2017).

5.3.1 Step 1: extracting metadata of multimedia files

After conducting photo-identification as per standard protocols, the first step in the *MAMMals* workflow is to extract the metadata of all multimedia files (Fig. 1b) and organize them into a text database, such as an R data frame. We suggest allocating each media type in separate subfolders within the root folder of the project, then using the following functions to read and organize the metadata into a data frame where the number of rows equals the number of files, and each column corresponds to the available metadata. To extract the metadata of the photographs, access the subfolder with the image files with the function *getPhotoMetadata*, which handles many common image extensions (e.g. .jpg, .tiff, .png) and accesses the available metadata of each photograph—at least the date and time, but also the camera GPS coordinates and shooting angle, if available. The *getPhotoMetadata* function also assigns the individual ID to the full metadata of the photographs, by matching the file names with that of the simple two-column data frame containing the photo file name and the individual identification code. While we recommend having the individual identification ready prior linking and syncing with the other multimedia files, we highlight that, alternatively, one can also perform the photo-identification afterwards. In this case, the *getPhotoMetadata* function can be used to export the metadata of photographs to common text files (e.g. .csv or .txt) and to then assign individual ID to the database using any text editor or spreadsheet software (e.g. Microsoft Excel, Apple Numbers). Bear in mind, however, that issues with the date and time formats and precision are common when using spreadsheet software; thus, we suggest using plain text editors to avoid lack of precision when aligning, linking or syncing the photo-identification to the multimedia data.

For the audio subfolder, use *getAudioMetadata* to extract metadata of audio files (at least duration, initial and final time). If the audio files do not contain date and time in the metadata, initial and final time of recordings can be extracted from the filename automatically generated with date-time stamps, as exported by commonly used autonomous recorders (e.g., Whytock; Christie, 2017; Hill et al., 2019). To extract the metadata of the videos (at least duration, initial and final time), access the video subfolder with the *getVideoMetadata*. If videos were recorded with drones, additional metadata can be available (e.g. altitude, GPS coordinates) and will be extracted and organized into a text database as well. Most commercially available drones save detailed logs of every flight. Information on aircraft sensors, motors, battery, remote controller and media are logged on-board and on remote applications, often using proprietary file structures. Hobbyists (e.g. DatCon, TXTlogtoCSVtool), companies (e.g. https://airdata.com) and forensics (e.g., Clark et al., 2017) have been developing tools to decode flight logs into readable .csv files. Alternatively, the *MAMMals* R package can extract the basic flight log data recorded by DJI drones. These drones can produce timestamped subtitles (1 Hz data) logging the aircraft latitude, longitude and height (calculated from the aircraft barometer), the home point latitude and longitude, and camera settings. However, subtitles do not contain auxiliary information on the aircraft and camera roll, pitch and angle; and the accuracy of latitude and longitude is limited to 10 m. But conveniently, subtitles are natively exported from DJI drones as text files (.srt) along video files, and the *MAMMals readSRT* function can read all .srt files in a folder and return an R data frame with the formatted metadata of the DJI drone flight logs.

5.3.2 Step 2: aligning multimedia files

After extracting the metadata of the multimedia files, large volumes of multimedia data can be aligned with the *MAMMals* functions that subset media files containing photoidentification data (Fig. 1c). Use the *selectVideos* or *selectAudios* functions to get the video and audio files of interest, respectively, by aligning their metadata with the metadata of the photographs of individuals (previously generated by the functions *getVideoMetadata*, *getAudioMetadata*, *getPhotoMetadata*, respectively). The select set of functions calculates the time of the photograph in the video or audio files for all photographs taken during the sampling event, and they return an R data frame with data matching the time in the video or audio files. Then, one can export an R data frame containing only the photo-identified individuals, or other events of interest, into a .csv or .txt. We highlight that while these functions are based on photograph metadata, they also work with other text data in which events are correctly timestamped (Fig. 1c), such as observed behavioural events recorded in the field notes, and GPS positions from loggers fit to the animals.

5.3.3 Step 3: linking photographs with multimedia data

After aligning the metadata of the media files, the photoidentification data can be linked with video or audio files by trimming these media files (Fig. 1d) based on the information generated by the *selectVideos* and *selectAudios* functions. If the aim is to get a still from the video for every photo-identified individual, the *getVideoFrame* function can export a frame of the video in the moment each photo was taken. If the aim is to perform further video or audio analyses, one can export short clips around the time of each photoidentification for both video (*getVideoClip*) and audio files (*getAudioClip*). If sampling with drones, one can automatically link data from flight logs to every event exported by the *selectVideos* or *selectAudios* functions. The *linkFlightToMetadata* function returns an R data frame in which the number of lines is equal the number of photo-identification photographs, and the columns contain all available metadata. The *linkMetadataToFlight* function merges the media data with the flight data, returning an R data frame with all the flight logs, or a list with a data frame for each flight log data.

5.3.4 Step 4: syncing multimedia data

Finally, the multiple media data sources can be synchronized based on the intersection of their recording time (Fig. 1e). Using the function *syncMedia*, video and audio files that were sampled concurrently and selected by the *selectVideos* and *selectAudios* functions can be trimmed to match the time intersection, and merged into a single file or exported as separate media files. Other auxiliary text data (e.g. GPS trackers, heart rate loggers, flight logs) recorded simultaneously in the field can be synchronized based on the intersection of their sampling time and merged into a single text database using the function *syncData*, as long as the input clocks are precisely synced.

5.3.5 Auxiliary functions for post-processing multimedia data

The *MAMMals* R package was designed to streamline the pre-processing of photo-identification and multimedia data; thus its workflow does not include the post-processing of the biological data of interest. After linking the photographs with the useful parts of the videos and audios, manual or semiautomatic extraction of the target data is required. This may include video playback to quantify behavioural states and events (e.g., Torres et al., 2018), morphometry or health variables (e.g., Christiansen et al., 2020); automatic detection of species (e.g., Gray et al., 2019); or photographic comparison needed to identify individual animals (e.g., Urian et al., 2015). To efficiently measure and extract such biological data from photos, videos, and audio data, we point the reader to the growing number of computational tools available elsewhere (e.g., Abràmoff; Magalhães; Ram, 2004; Friard; Gamba, 2016; Beery et al., 2020; Schneider; Taylor; Kremer, 2018; Torres; Bierlich, 2020; Bird; Bierlich 2020; Schneider; Taylor; Kremer, 2018). We exemplify one case of post-processing behavioural data in the next section, but here we highlight that the *MAMMals* R package also contains some functions and utilities to assist with the post-processing of the linked multimedia data or auxiliary data. For instance, one can use *MAMMals* to wrangle and convert information from the drone flight log data, such as gimbal and camera angles, GPS coordinates, digital compass and barometer sensors. We conceptually divide these functions into data tools and visualization (Table 1), which are, respectively, identified by the prefixes *do* and *view*. For instance, *doCorrectAngle* can be used to correct drone yaw ranging from 0 to 180 or − 180 to 0 to 0 to 360, and the function *viewFlightPath* can be used to visualize a 2D drone flight path with photos as points, using data from the *linkMetadataToFlight*.

Tabela 5.1: Auxiliary functions provided in the MAMMals R package to assist data wrangling, conversion and visualization.

Function	**Description**
doConvertAngle	Convert angle in degrees ranging from 0 to 180 for the right side and − 180 to 0 for the left side, and return angle in degrees ranging from 0 to 360
doCorrectCameraYaw	Correct camera yaw relative to drone yaw in degrees relative to geographical North
doFilterDroneHeight	Filter drone data to data in height equal or above a value in meters
doFilterGimbalPitch	Filter drone data to when the camera is pointing straight down, i.e. pitch = − 90º
doCalcDistanceX and doCalcDistanceY	Calculate horizontal (*doCalcDistanceX*) or vertical (*doCalcDistanceY*) distance of an object marked in any image tool (e.g. ImageJ). This distance will be used to transform the marked object into a GPS position using the origin point as reference.
doNewLatitude	Calculate latitude of an object given the distance and angle to a reference point using photogrammetry data
doNewLongitude	Calculate longitude of an object given the distance and angle to a reference point using photogrammetry data
doAngleToDec	Convert the degree-min-sec format (e.g. 28º 29' 44.77" S) into degree decimals
doCalcRadiusEarth	Calculate radius of Earth at any given latitude and altitude
viewFlightPath	Plot drone flight path and relate with photo-identification data, if available

5.4 AN ILLUSTRATIVE CASE STUDY

To illustrate the utility of the *MAMMals* R package, we used individual and behavioural data collected from a coastal bottlenose dolphin population in Laguna, southern Brazil, where some individual dolphins forage near the coast with net-casting fishers (Simões-Lopes; Fabián; Menegheti, 1998). To explore the dolphins' foraging behaviour, we combined standard photo-identification with overhead video, recorded using a commercially available drone (DJI Mavic Pro) with a built-in high-resolution camera mounted on a gimbal. We hovered the drone over the study area above 60 m to minimize potential disturbance to the dolphins (Fettermann et al., 2019), and follow all safety flight guidelines (Fiori et al., 2017; Raoult et al., 2020). The drone camera covered an area of ca. 7,500 m^2, including the coast where the fishers wait for dolphins and ca. 60 m of the lagoon canal. Simultaneously, two photographers registered the dolphins' dorsal fins for posterior individual identification based on nicks, notches, scars and skin lesions, following photo-identification protocols (Hammond; Mizroch; Donovan, 1990). One photographer positioned ashore used a DSLR Canon 60D camera equipped with a 100–400 mm lenses to photograph all dolphins in the video footage area, while the second photographer stood on a 1.5 m platform 3 m behind the fishers and used a DSLR Canon 7D MkII with built-in GPS and digital compass and a 70–300 mm lenses to identify the individual dolphins that approach the fishers to interact. This photographer was always captured in the drone footage and used a flash (Yongnuo) pointing up, so the timing of the photographs taken could be verified in the video to double-check if the clocks of the camera and drone were properly synced.

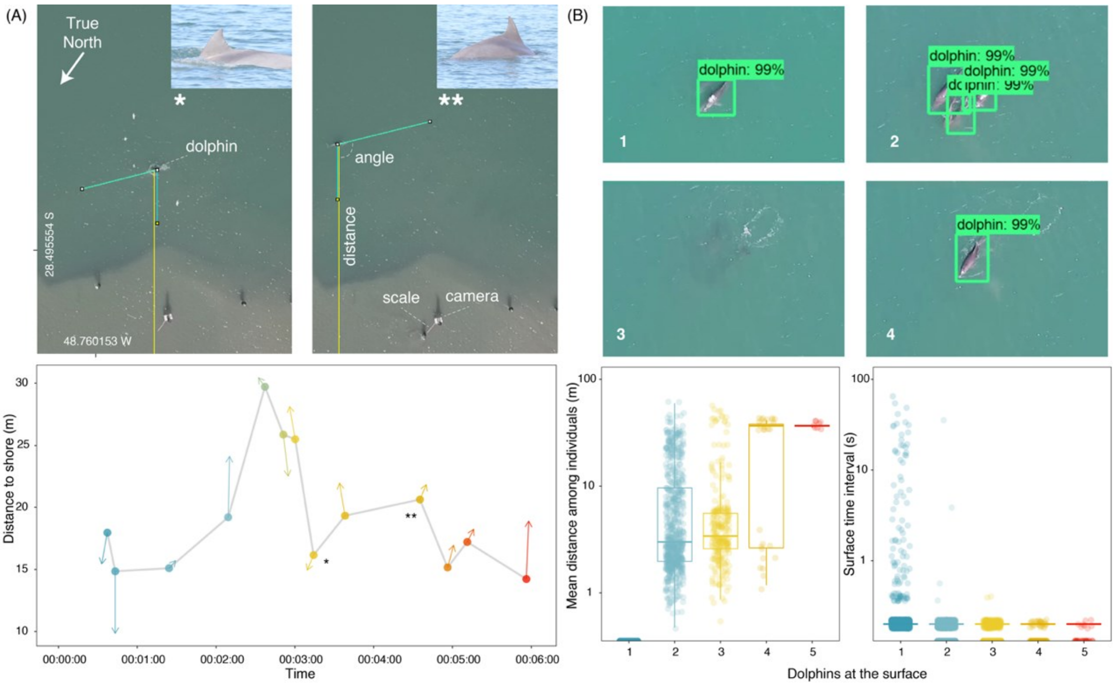

Figure 5.2: **Examples of individual- and group-level behaviour of photo-identified mammals extracted from overhead videos.** a) Tracking the foraging behaviour of individual coastal dolphins, in terms of distance and angle to the shore. The MAMMals package was used to automatically select and clip a video containing a solitary photo-identified dolphin (inset photo-identification). The video was then post-processed, when dolphins' distances (yellow lines in the picture; y-axis in the plot) and angles (cyan lines in the picture, with the middle point centred on the dolphin; arrows in the plot, whose colours indicate temporal sequence) relative to shore were measured each time they surfaced to breath. Distances measured in pixels were converted to meters based on a 1-m scale placed behind the photographer; angles measured in degree relative to the shore, were converted to radians, considering the True North as a reference. b) Group cohesion and dive synchrony of photo-identified bottlenose dolphins, in terms of relative distance to each member and timing of surfacing. The MAMMals R package was used to select the photographs with the dolphins' dorsal fins for posterior identification of the 5 group members. The group of 5 dolphins were then tracked over time with a custom computer vision model trained to detect dolphins in drone videos. Cohesion was estimated as the average Euclidean distances among the centroids of all dolphins detected (i.e. the green rectangles with detection scores) every 0.2 s and converted to meters using a known 1-m scale captured in the video (not shown here). Synchrony was estimated as the time difference between detections. Pictures 1–4 illustrate a case of diving sequence of a subgroup of 5 dolphins, in which 1 individual is detected first, followed by three that surfaced simultaneously, and then by the fifth individual after a 2-s lag. Box plots present the distribution of mean distances and breath intervals (y-axes) across different number of simultaneous detections (circles) of dolphins at the surface (x-axes) during a ~ 20-min drone video.

To illustrate two types of behavioural data that can be measured from the merged video and photo-identification dataset, we tracked (i) the foraging behaviour of individual dolphins in terms of distance and heading angles relative to the coast over time (Fig. 2a); and (ii) the foraging behaviour of a group of dolphins in terms of spatial cohesion and diving synchrony (Fig. 2b). In both cases, we used the *MAMMals* R package to automatically select examples of drone videos containing photo-identified dolphins from a total of 56.6 h of footage and 3,614 photographs of 21 identified individual dolphins. First, we used the functions *getPhotoMetadata* and *getVideoMetadata* to extract and organize the metadata of photographs and videos, extracted the drone flight logs and used some of the auxiliary functions to correct angles of drone footage (*doConvertAngle*, *doCorrectCameraYaw*) and filter off flights that were too low (*doFilterDroneHeight*) or in which the camera was not pointed straight down (*doFilterGimbalPitch*).

To describe (i) the individual-level foraging, we then used the function *selectVideos* to identify drone videos taken when there were 1 or 2 dolphins at the interaction site, and the function *getVideoClip* to crop 6-min video clips around the photographs taken. Next, we manually processed these clips with the open-source software *imageJ* (Abràmoff; Magalhães; Ram, 2004); each time the photo-identified dolphin surfaced to breath, we used the 'straight line' tool to measure the distance of the dolphin from shore, and the 'angle' tool to measure the angle between the dolphin's heading and the shore. In videos with more than one dolphin at the site, we distinguished photo-identified dolphins recorded in the video at the same time but in different places using the angle (available in the metadata of the photographs) between the dolphin and the camera equipped with built-in compass used for photo-identification. Finally, we converted the distances measured in pixels to meters based on a 1-m scale captured in the drone video, and converted the angles measured in degrees relative to the shore to radians, considering the True North as a reference. In Fig. 2a, we present an example of these data on the distances and angles of a photo-identified individual dolphin foraging close to shore.

To describe the group-level foraging, we used the functions *selectVideos* and *getVideoClip* to select the photographs of all dolphins foraging in groups and trim the complete 20-min drone video into a shorter video around the time that the photos were taken. We first photo-identified individuals manually, and then measured group cohesion and dive synchrony, in terms of relative distance to each member of the group and timing of surfacing. To do that, we have used a convolutional neural network object detection classifier (He et al., 2016) to automatically detect and count dolphins in the drone footage. We have re-trained a TensorFlow pre-trained classifier with Faster-RCNN model architecture (Ren et al., 2015) using 838 drone video frames in which dolphins were manually labelled using LabelImg (Tzutalin, 2015), and 200 other such images for testing the model. We then applied this supervised learning computer-vision model to detect and count the number of dolphins at every 0.2 s of the drone video, i.e. every 5 frames of a 25 FPS video (for a similar approach, see Guo et al., 2020). We highlight that although we have used machine learning to post-processes the video clips, this procedure could also be done manually. For instance, one can extract short .avi clips with a framerate of 1 fps using the *getVideoClip* function, and then import the clip to *imageJ* to measure the inter-individual distances and surface timing. To estimate the group cohesion, we calculated the relative time between each dolphin detection, considering greater cohesion when individuals are closer together; to estimate diving synchrony, we calculated the lag between dolphin surfacing times, considering greater synchrony when their breath intervals were shorter. We measured the group cohesion as the average Euclidean distance, in pixels, between the centroids of all dolphins detected in each frame, and converted these distances into meters based on a known 1-m scale recorded in the drone video. We measured the diving synchrony as the time lag between detections, considered the group to be in synchronous diving when more than one dolphin was detected in the same video frame. In Fig. 2b, we present these data on group cohesion and dive synchrony as the distribution of mean distances and breath intervals among different number of dolphins at the surface.

5.5 CAVEATS

The tools herein presented assist the organization of simultaneous sampling methods, but caveats exist. First, the level of detail of the outputs—be them the merged databases or the cropped and synced media—may depend on the accessibility of the study system. We have illustrated how the *MAMMals* tools work when recording and tracking coastal dolphins, but these tools could be used to process multimedia of mammals individually identifiable from photographs taken from the ground or sea level (e.g., sperm and humpback whale caudal fins, or blue whale pigmentation; Hammond; Mizroch; Donovan, 1990) and from overhead (e.g., head of right whales, or other identifiable body parts of marine and terrestrial mammals; Landeo-Yauri et al., 2020; Maeda et al., 2021). However, in our example, we had the advantage of keeping the photographer in the overhead video frame at all times for recording the position of the GPS-equipped camera as a reference point, and for double-checking the synchrony between the video and photograph data streams. This setup is rather unusual for studies of free-ranging mammals, and require the sampling design to be adapted to fit the reality of other study systems. For example, boat-based focal follows of cetaceans could aim to keep the boat close to the group most of the time to allow the photographer to be in the overhead video frame, or overhead behavioural sampling of terrestrial mammals can be focused on a relatively small open area.

The second limitation of our tools is that the precision of the link between the photo-identification and the other multimedia can be dependent on group size and group cohesion. In our example, we tracked solitary and small groups of animals that can be easily photo-identified, but mismatches in individual identification can occur when collecting data from multiple individuals at the same time, such as in large and tight groups. Our drone videos can contain multiple individuals, leading to the possibility that an individual photographed at a given time could be linked to multiple individuals that appear in the drone video at that time. We have resolved this by keeping the photographer in the overhead video frame and relying on the angle of the built-in digital compass of the camera to tease apart individuals in the overhead footage. However, these decisions become increasingly more difficult to make as the group size, and the rate of pictures taken, increase, and/or the groups become tighter and closer to the photographer. In such situations, our tools could still help defining the timestamps of sampling events to extract group-level (but not individual) data or identify subgroups of animals.

5.6 CLOSING REMARKS

Our tools to streamline the use of multimedia data with traditional individual identification methods are steps toward the integration of multiplatform behavioural sampling on free-ranging mammals. We acknowledge there is room for improvement and, to encourage further development of these tools collectively, we provide all the code of the *MAMMals* package in an open repository (https://bitbucket.org/maucantor/mammals/). We hope to inspire further collective work in the scientific community to generalize the process of linking multiple sampling platforms to refine the collection and processing of data of individual animals. More importantly, we hope these computer tools improve the raw material needed to promote new insights on the population dynamics, ecological interactions and behaviour of free-ranging animals.

5.7 APPENDIX

The *MAMMals* R Package can be downloaded and installed from its open repository https://bitbucket.org/maucantor/mammals/. Please visit the *MAMMals* R Package website at https://mammals-rpackage.netlify.app for list of all functions and a step-by-step guide on (i) extracting metadata of multimedia files; (ii) aligning multimedia files; (iii) linking photographs with multimedia data; and (iv) syncing multimedia data.

5.8 SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s42991-021-00189-0.

5.9 ACKNOWLEDGEMENTS

We are grateful to FG Daura-Jorge and DR Farine for the insightful discussions, field logistics and support during the development of these tools. We also thank all researchers involved in data sampling for their hard work (FG Daura-Jorge, C Bezamat, B Romeu, DR Farine, JVS Valle-Pereira, PV Castilho, BS Silva, N da Silva, LF da Rosa, CF Alves), and FG Daura-Jorge, DR Farine, JVS Valle-Pereira and ED Strauss for thoughtful comments on the manuscript.

5.10 AUTHOR CONTRIBUTIONS

Both authors contributed to the study conception and design, to the development of the computational tools and the R package, to data sampling and analyses. The manuscript was written, read and approved by both authors.

5.11 FUNDING

Open Access funding enabled and organized by Projekt DEAL. This study is part of the Long-term Ecological Research Program ‘Sistema Estuarino de Laguna e Adjacências’ (SELA-PELD) funded by the Conselho Nacional de Pesquisa e Desenvolvimento Tecnológico (CNPq Brazil #445301/2020-1), and by the Brazil-Germany PROBRAL Research Grant (#23038.002643/2018-01) from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Deutscher Akademischer Austauschdienst (DAAD). Fieldwork was further supported by the National Geographic Society (Discovery Grant WW210R-17), The Society for Marine Mammalogy, and The Max Planck Society (granted to MC) and The Animal Behaviour Society (granted to AMSM). AMSM received doctoral scholarship by CAPES Brazil (Finance Code 001) and an exchange scholarship from CAPES-DAAD PROBRAL Grant. MC received post-doctoral fellowship from CNPq (#153797/2016-9), CAPES (#88881.170254/2018- 01), and the Department for the Ecology of Animal Societies at the Max Planck Institute of Animal Behaviour.

5.12 DECLARATIONS

5.12.1 Conflict of interest

There are no competing interests with this study.

5.12.2 Data availability

We provide all the code and data to reproduce the analyses in the open-access repository https://bitbucket.org/maucantor/mammals/src/master/.

5.12.3 Code availability

All the code is available in the open-source R package (*MAMMals*) at https://bitbucket.org/maucantor/mammals/src/master/. We also provide a step-by-step tutorial at https://mammals-rpackage.netlify.app/index.html.

5.13 REFERENCES

Abràmoff, M. D.; Magalhães, P. J.; Ram, S. J. Image Processing with ImageJ. **Biophotonics international**, v. 11, n. 7, p. 36–42, 2004.

Alarcón-Nieto, G. et al. An automated barcode tracking system for behavioural studies in birds. **Methods in Ecology and Evolution**, v. 9, n. 6, p. 1536–1547, 2018.

Altmann, J. Observational Study of Behavior: Sampling Methods. **Behaviour**, v. 49, n. 3/4, p. 227–267, 1974.

Beery, S. et al. **Context R-CNN: Long Term Temporal Context for Per-Camera Object Detection**. 2020 IEEE/CVF Conference on Computer Vision and Pattern Recognition (CVPR). In: 2020 IEEE/CVF CONFERENCE ON COMPUTER VISION AND PATTERN RECOGNITION (CVPR). 2020.

Bird, C. N.; Bierlich, K. C. CollatriX: a GUI to collate MorphoMetriX outputs. **Journal of Open Source Software**, v. 5, p. 2328, 2020.

Burnett, J. D. et al. Estimating morphometric attributes of baleen whales with photogrammetry from small UASs: A case study with blue and gray whales. **Marine Mammal Science**, v. 35, n. 1, p. 108–139, 2019.

Cheng, J. et al. A comparative study in birds: call-type-independent species and individual recognition using four machine-learning methods and two acoustic features. **Bioacoustics**, v. 21, n. 2, p. 157–171, 2012.

Christiansen, F. et al. Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. **Marine Ecology Progress Series**, v. 640, p. 1–16, 2020.

Clapham, M. et al. Automated facial recognition for wildlife that lack unique markings: A deep learning approach for brown bears. **Ecology and Evolution**, v. 10, n. 23, p. 12883–12892, 2020.

Clark, D. R. et al. DROP (DRone Open source Parser) your drone: Forensic analysis of the DJI Phantom III. **Digital Investigation**, v. 22, p. S3–S14, 2017.

Clutton-Brock, T. H.; Sheldon, B. C. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. **Trends in Ecology and Evolution**, v. 25, n. 10, p. 562–573, 2010.

Coulson, T. Ecology and Evolution Is Hindered by the Lack of Individual-Based Data. In: Dobson, A.; Tilman, D.; Holt, R. D. (Eds.). **Unsolved Problems in Ecology**. Princeton University Press, 2020. p. 107–114.

Dawson, S. M. et al. Inexpensive Aerial Photogrammetry for Studies of Whales and Large Marine Animals. **Frontiers in Marine Science**, v. 4, n. November, p. 1–7, 2017.

Dell, A. I. et al. Automated image-based tracking and its application in ecology. **Trends in Ecology & Evolution**, v. 29, n. 7, p. 417–428, 2014.

Durban, J. W. et al. Photogrammetry of killer whales using a small hexacopter launched at sea. **Journal of Unmanned Vehicle Systems**, v. 3, n. 3, p. 131–135, 2015.

Erbe, C. et al. Matching Signature Whistles with Photo-Identification of Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) in the Fremantle Inner Harbour, Western Australia. **Acoustics Australia**, v. 48, n. 1, p. 23–38, 2020.

Ferreira, A. C. et al. Deep learning-based methods for individual recognition in small birds. **Methods in Ecology and Evolution**, v. 11, n. 9, p. 1072–1085, 2020.

Fettermann, T. et al. Behaviour reactions of bottlenose dolphins (*Tursiops truncatus*) to multirotor Unmanned Aerial Vehicles (UAVs). **Scientific Reports**, v. 9, n. 1, p. 8558–8558, 2019.

Fiori, L. et al. The Use of Unmanned Aerial Systems in Marine Mammal Research. **Remote Sensing**, v. 9, n. 6, p. 543–543, 2017.

Francisco, F. A.; Nührenberg, P.; Jordan, A. High-resolution, non-invasive animal tracking and reconstruction of local environment in aquatic ecosystems. **Movement Ecology**, v. 8, n. 1, p. 1–12, 2020.

Friard, O.; Gamba, M. Boris: a free, versatile open-source event-logging software for video/audio coding and live observations. **Methods in Ecology and Evolution**, v. 7, n. 11, p. 1325–1330, 2016.

Graving, J. M. et al. DeepPoseKit, a software toolkit for fast and robust animal pose estimation using deep learning. **eLife**, v. 8, p. 620245–620245, 2019.

Gray, P. C. et al. Drones and convolutional neural networks facilitate automated and accurate cetacean species identification and photogrammetry. **Methods in Ecology and Evolution**, v. 2019, n. January, p. 1490–1500, 2019.

Grolemund, G.; Wickham, H. Dates and Times Made Easy with lubridate. **Journal of Statistical Software**, v. 40, n. 3, p. 1–25, 2011.

Guo, S. et al. Automatic Identification of Individual Primates with Deep Learning Techniques. **iScience**, v. 23, n. 8, p. 101412–101412, 2020.

Hammond, P. S.; Mizroch, S. A.; Donovan, G. P. **Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters.** Reports of the International Whaling Commission, special issue, 12.

Hartman, K.; Van der Harst, P.; Vilela, R. Continuous Focal Group Follows Operated by a Drone Enable Analysis of the Relation Between Sociality and Position in a Group of Male Risso's Dolphins (*Grampus griseus*). **Frontiers in Marine Science**, v. 7, n. May, p. 1–13, 2020.

He, K. et al. Deep Residual Learning for Image Recognition. **Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition (CVPR)**, p. 770–778, 2016.

Hill, A. P. et al. AudioMoth: A low-cost acoustic device for monitoring biodiversity and the environment. **HardwareX**, v. 6, 2019.

Janik, V. M.; Sayigh, L. S. Communication in bottlenose dolphins: 50 years of signature whistle research. **Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology**, v. 199, n. 6, p. 479–489, 2013.

Karanth, K. U.; Nichols, J. D. Estimation of tiger densities in India using photographic captures and recaptures. **Ecology**, v. 79, n. 8, p. 2852–2862, 1998.

Karczmarski, L. et al. Individual identification and photographic techniques in mammalian ecological and behavioural research—Part 2: Field studies and applications. **Mammalian Biology**, v. 102(4), n. Special Issue, 2022a.

Karczmarski, L. et al. Individual identification and photographic techniques in mammalian ecological and behavioural research—Part 1: Methods and concepts. **Mammalian Biology**, v. 102(3), n. Special Issue, 2022b.

Katona, S. K.; Whitehead, H. P. Identifying humpback whales using their natural markings. **Polar Record**, v. 20, n. 128, p. 439–444, 1981.

Krause, J. et al. Reality mining of animal social systems. **Trends in Ecology & Evolution**, v. 28, n. 9, p. 541–551, 2013.

Landeo-Yauri, S. S. et al. Using small drones to photo-identify Antillean manatees: A novel method for monitoring an endangered marine mammal in the Caribbean Sea. **Endangered Species Research**, v. 41, p. 79–90, 2020.

Longden, E. G. et al. Mark–recapture of individually distinctive calls—a case study with signature whistles of bottlenose dolphins (*Tursiops truncatus*). **Journal of Mammalogy**, p. 1–13, 2020.

Maeda, T. et al. Aerial drone observations identified a multilevel society in feral horses. **Scientific Reports**, v. 11, n. 1, p. 71–71, 2021.

Marks, M. et al. Deep-learning based identification, tracking, pose estimation, and behavior classification of interacting primates and mice in complex environments. **bioarXiv**, 2021.

Mersch, D. P.; Crespi, A.; Keller, L. Tracking Individuals Shows Spatial Fidelity Is a Key Regulator of Ant Social Organization. **Science**, v. 340, n. 6136, p. 1090–1093, 2013.

Muller, Z. et al. Giraffe social preferences are context dependent. **Animal Behaviour**, v. 146, p. 37–49, 2018.

Odum, E. P.; Barret, G. W. **Fundamentals of Ecology**. 5th. ed.

Payne, R. et al. External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. In: **Communication and behavior of whales**. Westview Press, Boulder, CO, 1983. p. 371–445.

Pérez-Escudero, A. et al. IdTracker: Tracking individuals in a group by automatic identification of unmarked animals. **Nature Methods**, v. 11, n. 7, p. 743–748, 2014.

R Core Team. **R: A language and environment for statistical computing.** Vienna, AustriaR Foundation for Statistical Computing, 2021. https://www.R-project.org/

Raoult, V. et al. Operational Protocols for the Use of Drones in Marine Animal Research. **Drones**, v. 4, n. 4, p. 64–64, 2020.

Raoult, V.; Tosetto, L.; Williamson, J. E. Drone-based high-resolution tracking of aquatic vertebrates. **Drones**, v. 2, n. 4, p. 1–14, 2018.

Ren, S. et al. **Faster R-CNN: Towards Real-Time Object Detection with Region Proposal Networks**. Advances in Neural Information Processing Systems. Curran Associates, Inc., 2015. https://proceedings.neurips.cc/paper/2015/hash/14bfa6bb14875e45bba028a21ed38046-Abstract.html

Schneider, S. et al. Past, present and future approaches using computer vision for animal re-identification from camera trap data. **Methods in Ecology and Evolution**, v. 10, n. 4, p. 461–470, 2019.

Schneider, S.; Taylor, G. W.; Kremer, S. **Deep Learning Object Detection Methods for Ecological Camera Trap Data**. 2018 15th Conference on Computer and Robot Vision (CRV). 2018.

Silvy, N. J.; Lopez, R. R.; Peterson, M. J. Wildlife marking techniques. In: **Techniques for wildlife investigations and management**. The Wildlife Society, Bethesda, MD, 2005. p. 339–376.

Simões-Lopes, P. C.; Fabián, M. E.; Menegheti, J. O. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. **Revista Brasileira de Zoologia**, v. 15, n. 3, p. 709–726, 1998.

Speed, C. W.; Meekan, M. G.; Bradshaw, C. J. A. Spot the match - Wildlife photo-identification using information theory. **Frontiers in Zoology**, v. 4, n. 2, p. 1–11, 2007.

Toms, C. N.; Stone, T.; Och-Adams, T. Visual-only assessments of skin lesions on free-ranging common bottlenose dolphins (*Tursiops truncatus*): Reliability and utility of quantitative tools. **Marine Mammal Science**, v. 36, n. 3, p. 744–773, 2020.

Torres, L. G. et al. Drone Up! Quantifying Whale Behavior From a New Perspective Improves Observational Capacity. **Frontiers in Marine Science**, v. 5, n. September, p. 1–14, 2018.

Torres, W.; Bierlich, K. MorphoMetriX: a photogrammetric measurement GUI for morphometric analysis of megafauna. **Journal of Open Source Software**, v. 5, n. 45, p. 1825–1825, 2020.

Tzutalin. **LabelImg**, 2015. https://github.com/tzutalin/labelImg

Urian, K. et al. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. **Marine Mammal Science**, v. 31, n. 1, p. 298–321, 2015.

Walker, K. A. et al. A review of the effects of different marking and tagging techniques on marine mammals. **Wildlife Research**, v. 39, n. 1, p. 15–30, 2011.

Whytock, R. C.; Christie, J. Solo: an open source, customizable and inexpensive audio recorder for bioacoustic research. **Methods in Ecology and Evolution**, v. 8, n. 3, p. 308–312, 2017.

Würsig, B.; Würsig, M. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). **Science**, v. 198, n. 4318, p. 755–756, 1977

6 CONCLUSÃO GERAL

Nesta Tese, buscou-se compreender como variações no ambiente e entre os indivíduos podem afetar interações de natureza mutualística. Utilizando como modelo a interação boto-pescador—um dos raros casos ainda ativos de cooperação entre humanos e animais não-humanos—, os resultados desta Tese suportam a ideia de que as variações interindividuais são importantes para a manutenção de interações ecológicas positivas. Primeiro, sugere-se que, na interação boto-pescador, a coocorrência e sincronia de ambos os predadores é necessária para a manutenção dos benefícios gerados. Dessa forma, botos e pescadores se beneficiam das interações sincrônicas no forrageio social como uma estratégia para superar os desafios impostos pela natureza efêmera da principal presa, as tainhas migratórias. Além disso, a importância dos indivíduos nessa interação foi reforçada ao revelar que alguns poucos botos contribuem desproporcionalmente para o total de tainhas capturadas pelos pescadores. Essas diferenças nas contribuições dos indivíduos do boto-da-tainha não parecem ser um produto da capacidade competitiva dos indivíduos, o que reforça a contribuição de outros mecanismos individuais e sociais no estabelecimento desta especialização. No entanto, esse alto grau de especialização de alguns poucos indivíduos pode limitar a capacidade de adaptação desses indivíduos às mudanças no ambiente. Perder esses poucos indivíduos pode comprometer não só a viabilidade da pequena população de *Tursiops truncatus gephyreus* de Laguna, mas também a viabilidade da cultura centenária de uma pesca cooperativa que gera valores materiais e imateriais para a comunidade humana local.

No primeiro capítulo desta Tese, teve-se a rara oportunidade de testar empiricamente os efeitos das condições ambientais e da disponibilidade de presas em um caso de forrageio social entre dois predadores—a pesca cooperativa entre botos e pescadores. Múltiplas plataformas de amostragem foram combinadas para quantificar simultaneamente os componentes deste sistema cooperativo. As condições de maré, vento e temperatura da água, bem como o número de botos e pescadores, foram continuamente registrados, e um sonar de imageamento frontal subaquático foi utilizado para quantificar a abundância de tainha, a principal presa capturada na interação boto-pescador. Então, as imagens de sonar foram processadas com técnicas de aprendizado de máquina para quantificar a variação na abundância de tainhas momento-a-momento, na fina escala da interação boto-pescador. Testou-se as relações entre os componentes deste sistema por meio de um modelo confirmatório de análise de caminhos e os resultados confirmam duas vias não-exclusivas que podem levar a maiores capturas de tainha pelos pescadores. Primeiro, os pescadores tendem a capturar mais tainhas quando essas estão mais abundantes. No entanto, variações nas condições ambientais locais não correspondem às variações na abundância de tainha ao alcance dos pescadores. Segundo, os botos tendem a aparecer mais durante os períodos de maré enchente, e um aumento no número de botos corresponde a um aumento no número de pescadores. Essa correspondência no número de botos e pescadores aumenta as chances de interações síncronas ocorrerem, o que, por sua vez, gera mais capturas de tainha.

Os resultados do primeiro capítulo demonstram que a coocorrência e a sincronia no forrageio social entre botos e pescadores é mais importante para o número de tainhas capturadas do que a própria abundância de tainhas disponíveis localmente. O mais relevante, no entanto, é que tanto a abundância de presas quanto a coocorrência dos predadores são independentes das condições ambientais locais. Nesse contexto, os pescadores utilizam a presença dos botos como pistas para a presença das tainhas. Portanto, os resultados sugerem que, através do forrageio social, botos e pescadores podem dissociar seu sucesso de forrageio das condições ambientais subjacentes que afetam a disponibilidade de presas, o que pode ser particularmente benéfico em sistemas dependentes de presas efêmeras.

No segundo capítulo, testou-se a hipótese de que as diferenças individuais podem determinar os produtos de uma tática de forrageio social. Primeiro, dados observacionais e de fotoidentificação foram combinados para quantificar diferenças individuais entre os botos-da-tainha com relação ao tempo que cada indivíduo permanece na área de interação, o número de comportamentos estereotipados produzidos por cada indivíduo e a proporção de interações com algum sucesso para os pescadores ao longo de 45 dias de amostragem distribuídos em três anos. Utilizando modelos generalizados de efeitos mistos, observou-se maiores diferenças individuais no tempo de permanência na área de interação e nas chances de sucesso. Depois, testou-se a hipótese de que a competição por interferência poderia ser um dos possíveis mecanismos subjacentes às diferenças individuais, avaliando as consequências das interações entre botos para os benefícios obtidos pelos pescadores. Os resultados sugerem que alguns botos podem ser considerados indivíduos-chave, gerando contribuições desproporcionais para os benefícios acumulados pelos pescadores em termos de tainhas capturadas. Ainda, o efeito da competição intraespecífica nessas diferenças entre botos parece ser negligenciável. Isto é, ao sugerir que mecanismos ecológicos mais simples, como a competição, não podem explicar plenamente as diferenças individuais na tática de forrageio cooperativa, esses resultados suportam a ideia de que outros processos individuais e sociais podem ser mais importantes. Por exemplo, os indivíduos podem ter desenvolvido diferentes habilidades de forrageio pela forma de aquisição desse comportamento através de processos de aprendizagem individual ou social. Nesse sentido, esses resultados se alinham à expectativa de que o aprendizado social deve ser um mecanismo importante para a manutenção de cooperações entre animais humanos e não-humanos. No entanto, as diferentes vias de transmissão dessa tática de forrageio especializada ainda não foram formalmente contrastadas e testadas.

No terceiro capítulo, foi desenvolvida uma contribuição técnica para combinar ferramentas tradicionais de identificação individual com amostragens observacional, videográfica e acústica. Apesar da ampla utilização de dados multimídia na etologia e na ecologia de predadores, combinar múltiplas plataformas de amostragem com a identificação individual *in situ* ainda é um desafio. Por isso, apresenta-se um *software* livre e de código aberto para a linguagem R—amplamente adotada na Ecologia. O objetivo foi criar ferramentas para alinhar dados observacionais com múltiplas plataformas multimídia. Essas ferramentas devem auxiliar na continuidade da coleta e processamento desses dados em longo prazo, idealmente combinando os dados de disponibilidade de tainha (capítulo 1) com os dados de variação individual (capítulo 2) para testar se as variações individuais são consistentes em diferentes contextos ou se há alguma variação contexto-específica na resposta à disponibilidade de presa e competição.

As contribuições dessa tese podem ter dois desdobramentos. De um ponto de vista teórico, o sistema boto-pescador se consolida como um bom modelo para avaliar as dimensões da variação individual—em ambos os predadores—apesar dos desafios metodológicos. Isso abre espaço para responder perguntas importantes sobre a variação individual na cooperação e como seus efeitos podem escalar para a população e outros níveis do sistema, sobre o papel do desenvolvimento individual e do aprendizado social, sobre os efeitos da competição e cooperação intraespecífica nos mutualismos, e sobre o papel das mudanças ambientais na resistência e resiliência de formas de cultura animal. Localmente, a conservação da população de botos-da-tainha de Laguna e da interação boto-pescador enfrenta desafios impostos por atividades humanas, como a poluição química e sonora, e capturas acidentais em redes de pesca. A perda desses indivíduos ocupando posições-chave por mortes não naturais poderia afetar a frequência e a qualidade dos benefícios obtidos pelos pescadores nessa interação, o que poderia desmobilizar a participação dos pescadores nessa atividade cultural centenária. Apesar de que novos indivíduos podem entrar na população e participar da interação boto-pescador, ainda é incerto quanto tempo é necessário para uma substituição desses indivíduos por outros de performance equivalente. A continuação dessa avaliação de dados individuais é imperativa para compreensão dos mecanismos de aprendizado da tática especializada e da resiliência desse caso remanescente de cooperação entre humanos e animais não-humanos.

REFERÊNCIAS

ALARCÓN-NIETO, G. et al. An automated barcode tracking system for behavioural studies in birds. **Methods in Ecology and Evolution**, v. 9, n. 6, p. 1536–1547, 2018.

ALLEN, S. J.; BEJDER, L.; KRÜTZEN, M. Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? **Marine Mammal Science**, v. 27, n. 2, p. 449–454, 2011.

ALVES, L. C. P. DE S. et al. Resource defence and dominance hierarchy in the boto (*Inia geoffrensis*) during a provisioning program. **Acta Ethologica**, v. 16, n. 1, p. 9–19, 2013.

ANSMANN, I. C. et al. Dolphins restructure social system after reduction of commercial fisheries. **Animal Behaviour**, v. 84, n. 3, p. 575–581, 2012.

ARAÚJO, M. S.; BOLNICK, D. I.; LAYMAN, C. A. The ecological causes of individual specialisation. **Ecology Letters**, v. 14, n. 9, p. 948–958, 2011.

ARMSTRONG, J. B. et al. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. **Ecology**, v. 97, n. 5, p. 1099–1112, 2016.

BAKER, I. et al. Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations. **Marine Mammal Science**, v. 34, n. 2, p. 458–457, 2018.

BARKER, J. L. et al. Synthesizing perspectives on the evolution of cooperation within and between species. **Evolution**, v. 71, n. 4, p. 814–825, 2017.

BELL, A. M.; HANKISON, S. J.; LASKOWSKI, K. L. The repeatability of behaviour: a meta-analysis. **Animal Behaviour**, v. 77, n. 4, p. 771–783, 2009.

BERGMÜLLER, R.; SCHÜRCH, R.; HAMILTON, I. M. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 365, n. 1553, p. 2751–2764, 2010.

BERGMÜLLER, R.; TABORSKY, M. Animal personality due to social niche specialisation. **Trends in Ecology and Evolution**, v. 25, n. 9, p. 504–511, 2010.

BEZAMAT, C. et al. The influence of cooperative foraging with fishermen on the dynamics of a bottlenose dolphin population. **Marine Mammal Science**, v. 35, n. 3, p. 825–842, 2019.

BEZAMAT, C. et al. Reproductive parameters and factors influencing calf survival of bottlenose dolphins that engage in a unique foraging cooperation with fishermen. **Marine Biology**, v. 167, p. 1–12, 2020.

BEZAMAT, C. et al. Dolphin population specialized in foraging with artisinal fishers requires zero-bycatch management to persist. **Aquatic Conservation: Marine and Freshwater Ecosystems**, v. 31, n. 11, p. 3133–3145, 2021.

BOLNICK, D. I. et al. The ecology of individuals: incidence and implications of individual specialization. **American Naturalist**, v. 161, n. 1, p. 1–28, 2003.

BOLNICK, D. I. et al. Why intraspecific trait variation matters in community ecology. **Trends in Ecology and Evolution**, v. 26, n. 4, p. 183–192, 2011.

BREHM, A. M. et al. Land-use change and the ecological consequences of personality in small mammals. **Ecology Letters**, v. 22, n. 9, p. 1387–1395, 2019.

BRENT, L. J. N. et al. Ecological Knowledge, Leadership, and the Evolution of Menopause in Killer Whales. **Current Biology**, v. 25, n. 6, p. 746–750, 2015.

BRONSTEIN, J. L. Our Current Understanding of Mutualism. **The Quarterly Review of Biology**, v. 69, n. 1, p. 31–51, 1994.

BROWN, C. R.; BROWN, M. B.; SHAFFER, M. L. Food-sharing signals among socially foraging cliff swallows. **Animal Behaviour**, v. 42, n. 4, p. 551–564, 1991.

BSHARY, R. et al. Interspecific communicative and coordinated hunting between groupers and giant moray eels in the red sea. **PLoS Biology**, v. 4, n. 12, p. 2393–2398, 2006.

BUSNEL, R.-G. Symbiotic relationship between man and dolphins. **Transactions of the New York Academy of Sciences**, Series II. v. 35, n. 2, p. 112–131, 1973.

CANTOR, M. et al. Multilevel animal societies can emerge from cultural transmission. **Nature Communications**, v. 6, 8091, 2015.

CANTOR, M.; FARINE, D. R.; DAURA-JORGE, F. G. Foraging synchrony drives resilience in human–dolphin mutualism. **Proceedings of the National Academy of Sciences**, v. 120, n. 6, p. e2207739120, 2023.

CANTOR, M.; SIMÕES-LOPES, P. C.; DAURA-JORGE, F. G. Spatial consequences for dolphins specialised in foraging with fishermen. **Animal Behaviour**, v. 139, p. 19–27, 2018.

CANTOR, M.; WHITEHEAD, H. The interplay between social networks and culture: theoretically and among whales and dolphins. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 368, n. 1618, 20120340, 2013.

CARTER, A. J. et al. Personality predicts the propensity for social learning in a wild primate. **PeerJ**, v. 2, p. e283, 2014.

CARTER, A. J.; ENGLISH, S.; CLUTTON-BROCK, T. H. Cooperative personalities and social niche specialization in female meerkats. **Journal of Evolutionary Biology**, v. 27, n. 5, p. 815–825, 2014.

CLEASBY, I. R.; NAKAGAWA, S.; SCHIELZETH, H. Quantifying the predictability of behaviour: Statistical approaches for the study of between-individual variation in the within-individual variance. **Methods in Ecology and Evolution**, v. 6, n. 1, p. 27–37, 2015.

CLUTTON-BROCK, T. H. Cooperation between non-kin in animal societies. **Nature**, v. 462, n. 7269, p. 51–57, 2009.

CONNOR, R. C. et al. Social Relationships in a Fission-Fusion Society. Em: MANN, J. et al. (Eds.). **Cetacean Societies: Field Studies of Dolphins and Whales**. Chicago: University of Chicago Press Chicago, IL, 2000. p. 91–126.

CONNOR, R. C.; KRÜTZEN, M. Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. **Animal Behaviour**, v. 103, p. 223–235, 2015.

COSTA, A. P. B. et al. Offshore and coastal common bottlenose dolphins of the western South Atlantic face-to-face: What the skull and the spine can tell us. **Marine Mammal Science**, v. 32, n. 4, p. 1433–1457, 2016.

COULSON, T. et al. Estimating individual contributions to population growth: Evolutionary fitness in ecological time. **Proceedings of the Royal Society B: Biological Sciences**, v. 273, n. 1586, p. 547–555, 2006.

COULSON, T. Ecology and evolution is hindered by the lack of individual-based data. Em: DOBSON, A.; TILMAN, D.; HOLT, R. D. (Eds.). **Unsolved problems in ecology**. Princeton: Princeton University Press, 2020. p. 107–114.

CRAM, D. L. et al. The ecology and evolution of human-wildlife cooperation. **People and Nature**, v. 4, p. 841–855, 2022.

DALL, S. R. X. X. et al. An evolutionary ecology of individual differences. **Ecology Letters**, v. 15, n. 10, p. 1189–1198, 2012.

DALL, S. R. X. X.; HOUSTON, A. I.; MCNAMARA, J. M. The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. **Ecology Letters**, v. 7, n. 8, p. 734–739, 2004.

DARWIN, C. **On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life**. London: John Murray, 1859.

DAURA-JORGE, F. G. et al. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. **Biology Letters**, v. 8, n. 5, p. 702–705, 2012.

DAURA-JORGE, F. G.; INGRAM, S. N.; SIMÕES-LOPES, P. C. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. **Marine Mammal Science**, v. 29, n. 2, p. 293–311, 2013.

DAVIES, J. R.; GARCIA-PELEGRIN, E. Bottlenose dolphins are sensitive to human attentional features, including eye functionality. **Scientific Reports**, v. 13, n. 1, p. 12565, 2023.

DEACY, W. et al. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. **Ecology**, v. 97, n. 5, p. 1091–1098, 2016.

DECHMANN, D. K. N. et al. Experimental evidence for group hunting via eavesdropping in echolocating bats. **Proceedings of the Royal Society B: Biological Sciences**, v. 276, n. 1668, p. 2721–2728, 2009.

DELL, A. I. et al. Automated image-based tracking and its application in ecology. **Trends in Ecology & Evolution**, v. 29, n. 7, p. 417–428, 2014.

DEVOS, R. V.; BARBOSA, G. C.; VEDANA, V. Fish news: perceptual skills, technique and distributed cognition in mullet fishing. Vibrant: Virtual Brazilian Anthropology, v. 16, p. 1–23, 2019.

DINGEMANSE, N. J. et al. Behavioural reaction norms: animal personality meets individual plasticity. **Trends in Ecology and Evolution**, v. 25, n. 2, p. 81–89, 2010.

DINGEMANSE, N. J.; DOCHTERMANN, N. A. Quantifying individual variation in behaviour: mixed-effect modelling approaches. **Journal of Animal Ecology**, v. 82, n. 1, p. 39–54, 2013.

DORNHAUS, A. et al. Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. **Behavioral Ecology and Sociobiology**, v. 63, n. 1, p. 43–51, 2008.

DYER, J. R. G. et al. Shoal composition determines foraging success in the guppy. **Behavioral Ecology**, v. 20, n. 1, p. 165–171, 2009.

ENGLEBY, L. K.; POWELL, J. R. Detailed observations and mechanisms of mud ring feeding by common bottlenose dolphins (*Tursiops truncatus truncatus*) in Florida Bay, Florida, U.S.A. **Marine Mammal Science**, v. 35, n. 3, p. 1162–1172, 2019.

ERMAK, J.; BRIGHTWELL, K.; GIBSON, Q. Multi-level dolphin alliances in northeastern Florida offer comparative insight into pressures shaping alliance formation. **Journal of Mammalogy**, v. 98, n. 4, p. 1096–1104, 2017.

ESTES, J. A. et al. Individual variation in prey selection by sea otters: Patterns, causes and implications. **Journal of Animal Ecology**, v. 72, n. 1, p. 144–155, 2003.

ESTES, R. D.; GODDARD, J. Prey Selection and Hunting Behavior of the African Wild Dog. **The Journal of Wildlife Management**, v. 31, n. 1, p. 52–70, 1967.

FERREIRA, A. C. et al. Deep learning-based methods for individual recognition in small birds. **Methods in Ecology and Evolution**, v. 11, n. 9, p. 1072–1085, 2020.

FISHER, D. N.; CHENEY, B. Dolphin social phenotypes vary in response to food availability but not the North Atlantic Oscillation index. **Proceedings of the Royal Society B**, v. 290, n. 20231187, 2023.

FOSSILE, T. et al. Pre-Columbian fisheries catch reconstruction for a subtropical estuary in South America. **Fish and Fisheries**, v. 20, p. 1124–1137, 2019.

FRÈRE, C. H. et al. Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. **Animal Behaviour**, v. 80, n. 3, p. 481–486, 2010.

FRIARD, O.; GAMBA, M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. **Methods in Ecology and Evolution**, v. 7, n. 11, p. 1325–1330, 2016.

FRUET, P. F. et al. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. **Conservation Genetics**, v. 15, n. 4, p. 879–895, 2014.

FUSTER, F.; TRAVESET, A. Importance of intraspecific variation in the pollination and seed dispersal functions of a double mutualist animal species. **Oikos**, v. 129, n. 1, p. 106–116, 2020.

GALEZO, A. A.; KRZYSZCZYK, E.; MANN, J. Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. **Behavioral Ecology**, v. 29, n. 2, p. 377–386, 2018.

GAZDA, S. et al. The importance of delineating networks by activity type in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida. **Royal Society open science**, v. 2, p. 140263–140263, 2015.

GAZDA, S. K. et al. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. **Proceedings of the Royal Society B**, v. 272, n. 1559, p. 135–140, 2005.

GENDE, S. M.; QUINN, T. P. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. **Canadian Journal of Zoology**, v. 82, n. 1, p. 75–85, 2004.

GERBER, L. et al. Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins. **Behavioral Ecology**, v. 31, n. 2, p. 361–370, 2020.

GERBER, L. et al. Cooperative partner choice in multi-level male dolphin alliances. **Scientific Reports**, v. 11, 6901, 2021.

GERO, S. et al. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. **Canadian Journal of Zoology**, v. 83, n. 12, p. 1566–1573, 2005.

GIRALDEAU, L.-A.; CARACO, T. **Social Foraging Theory**. Princeton University Press, 2000. p. 362

GRAVING, J. M. et al. DeepPoseKit, a software toolkit for fast and robust animal pose estimation using deep learning. **eLife**, v. 8, p. 620245–620245, 2019.

GREENFIELD, M. R. et al. Associates from infancy influence postweaning juvenile associations for common bottlenose dolphins (*Tursiops truncatus*) in Florida. **Journal of Mammalogy**, v. 103, n. 6, p. 1290–1304, 2022.

GUO, S. et al. Automatic Identification of Individual Primates with Deep Learning Techniques. **iScience**, v. 23, n. 8, 101412, 2020.

HAMILTON, R. A. et al. Bottlenose dolphin communication during a role-specialized group foraging task. **Behavioural Processes**, v. 200, n. June, p. 104691–104691, 2022.

HANSEN, M. J. et al. Mechanisms of group-hunting in vertebrates. **Biological Reviews**, v. 98, n. 5, p. 1687-1711, 2023.

HARTMAN, K.; VAN DER HARST, P.; VILELA, R. Continuous Focal Group Follows Operated by a Drone Enable Analysis of the Relation Between Sociality and Position in a Group of Male Risso’s Dolphins (*Grampus griseus*). **Frontiers in Marine Science**, v. 7, p. 1–13, 2020.

HERBST, D. F.; HANAZAKI, N. Local ecological knowledge of fishers about the life cycle and temporal patterns in the migration of mullet (*Mugil liza*) in Southern Brazil. **Neotropical Ichthyology**, v. 12, n. 4, p. 879–890, 2014.

HERTEL, A. G. et al. A guide for studying among-individual behavioral variation from movement data in the wild. **Movement Ecology**, v. 8, n. 1, p. 30–30, 2020.

HORTON, T. W. et al. Doctor Drone: Non-invasive Measurement of Humpback Whale Vital Signs Using Unoccupied Aerial System Infrared Thermography. **Frontiers in Marine Science**, v. 6, p. 1–11, 2019.

HUGHES, A. R. et al. Ecological consequences of genetic diversity. **Ecology Letters**, v. 11, n. 6, p. 609–623, 2008.

HUSTON, M.; DEANGELIS, D.; POST, W. New Computer Models Unify Ecological Theory. **BioScience**, v. 38, n. 10, p. 682–691, 1988.

JAAKKOLA, K. et al. Bottlenose dolphins can understand their partner’s role in a cooperative task. **Proceedings of the Royal Society B: Biological Sciences**, v. 285, n. 1887, 20180948, 2018.

JENSEN, F. H. et al. Detecting narwhal foraging behaviour from accelerometer and depth data using mixed-effects logistic regression. **Animal Biotelemetry**, v. 11, n. 1, 2023.

JOLLES, J. W.; KING, A. J.; KILLEN, S. S. The role of individual heterogeneity in collective animal behaviour. **Trends in Ecology & Evolution**, p. 1–14, 2019.

KEITH, S. A. et al. Macrobehaviour: behavioural variation across space, time, and taxa. **Trends in Ecology & Evolution**, v. 38, n. 12, p. 1177-1188, 2023.

KOHLES, J. E.; O’MARA, M. T.; DECHMANN, D. K. N. A conceptual framework to predict social information use based on food ephemerality and individual resource requirements. **Biological Reviews**, v. 97, n. 6, p. 2039–2056, 2022.

KOKKO, H. **Modelling for field biologists and other interesting people**. Cambridge University Press, 2007. p. 242

KREBS, J. R.; DAVIES, N. B. **An Introduction to Behavioural Ecology**. Blackwell Scientific Publications, 1981.

KREBS, J. R.; KACELNIK, A.; TAYLOR, P. Test of optimal sampling by foraging great tits. **Nature**, v. 275, n. 5675, p. 27–31, 1978.

KRÜTZEN, M. et al. Cultural transmission of tool use in bottlenose dolphins. **Proceedings of the National Academy of Sciences of the United States of America**, v. 102, n. 25, p. 8939–43, 2005.

LANG, S. D. J.; FARINE, D. R. A multidimensional framework for studying social predation strategies. **Nature Ecology & Evolution**, v. 1, n. 9, p. 1230–1239, 2017.

LANG, S. D. J.; MANN, R. P.; FARINE, D. R. Temporal activity patterns of predators and prey across broad geographic scales. **Behavioral Ecology**, v. 30, n. 1, p. 172–180, 2019.

LASKOWSKI, K. L. et al. Consistent Individual Behavioral Variation: What Do We Know and Where Are We Going? **Annual Review of Ecology, Evolution, and Systematics**, v. 53, p. 161–182, 2022a.

LASKOWSKI, K. L. et al. The emergence and development of behavioral individuality in clonal fish. **Nature Communications**, v. 13, n. 1, p. 6419, 2022b.

LAWTON, J. H. Are there general laws in ecology? **Oikos**, v. 84, n. 2, p. 177–192, 1999.

LEBRETON, J.-D. et al. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: a Unified Approach With Case Studies. **Ecological Monographs**, v. 62, n. 1, p. 67–118, 1992.

LEGENDRE, P. Numerical Ecology: Developments and Recent Trends. Em: FELSENSTEIN, J. (Ed.). **Numerical Taxonomy**. NATO ASI Series. Berlin, Heidelberg: Springer, 1983. p. 505–523.

LEMOS, V. M. et al. Migration and reproductive biology of *Mugil liza* (Teleostei: Mugilidae) in south Brazil. **Journal of Fish Biology**, v. 85, n. 3, p. 671–687, 2014.

LEMOS, V. M. et al. Tracking the southern Brazilian schools of *Mugil liza* during reproductive migration using VMS of purse seiners. **Latin American Journal of Aquatic Research**, v. 44, n. 2, p. 238–246, 2016.

LEWIS, J. S.; SCHROEDER, W. W. Mud Plume Feeding, A Unique Foraging Behavior of the Bottlenose Dolphin in the Florida Keys. **Gulf of Mexico Science**, v. 21, n. 1, 2003.

LINQUIST, S. et al. Yes! There are resilient generalizations (or “laws”) in ecology. **The Quarterly review of biology**, v. 91, n. 2, p. 119–131, 2013.

LOUIS, M. et al. Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. **Proceedings of the Royal Society B: Biological Sciences**, v. 281, n. 1795, 2014.

LOUIS, M. et al. Selection on ancestral genetic variation fuels repeated ecotype formation in bottlenose dolphins. **Science Advances**, v. 7, p. eabg1245, 2021.

LOUIS, M. et al. Ancient dolphin genomes reveal rapid repeated adaptation to coastal waters. **Nature Communications**, v. 14, n. 1, p. 4020, 2023.

LUSSEAU, D.; NEWMAN, M. E. J. Identifying the role that animals play in their social networks. **Proceedings of the Royal Society B**, v. 271, n. Suppl. 6, p. S477–S481, 2004.

MACHADO, A. M. S. et al. Alternative data sources can fill the gaps in data-poor fisheries. **ICES Journal of Marine Science**, v. 78, n. 5, p. 1663–1671, 2021.

MACHADO, A. M. S.; CANTOR, M. A simple tool for linking photo-identification with multimedia data to track mammal behaviour. **Mammalian Biology**, v. 102, p. 983–993, 2022.

MACHADO, A. M. S. et al. Homophily around specialized foraging underlies dolphin social preferences. **Biology Letters**, v. 15, n. 4, p. 20180909–20180909, 2019.

MAI, A. C. G. et al. Microsatellite variation and genetic structuring in *Mugil liza* (Teleostei: Mugilidae) populations from Argentina and Brazil. **Estuarine, Coastal and Shelf Science**, v. 149, p. 80–86, 2014.

MAI, A. C. G. et al. Coastal zone use and migratory behaviour of the southern population of *Mugil liza* in Brazil. **Journal of Fish Biology**, v. 95, p. 1207–1214, 2019.

MANN, J. et al. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. **Behavioral Ecology**, v. 11, n. 2, p. 210–219, 2000.

MANN, J. et al. Why do dolphins carry sponges? **PLoS ONE**, v. 3, n. 12, e3868, 2008.

MANN, J. et al. Social networks reveal cultural behaviour in tool-using dolphins. **Nature Communications**, v. 3, n. 1, p. 980–980, 2012.

MARSHALL, H. H. et al. Exploring Foraging Decisions in a Social Primate Using Discrete-Choice Models. **The American Naturalist**, v. 180, n. 4, p. 481–495, 2012.

MATTSON, D. J.; REINHART, D. P. Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975 – 1989. **Canadian Journal of Zoology**, v. 73, n. 11, p. 2072–2079, 1995.

MAYR, E. **The growth of biological thought**. Cambridge: Harvard University Press, 1982.

MCBRIDE, A. F.; HEBB, D. O. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. **Journal of Comparative and Physiological Psychology**, v. 41, n. 2, p. 111–123, 1948.

MCCOMB, K. et al. Matriarchs As Repositories of Social Knowledge in African Elephants. **Science**, v. 292, n. 5516, p. 491–494, 2001.

MENEZES, N. A. et al. Taxonomic review of the species of *Mugil* (Teleostei: Perciformes: Mugilidae) from the Atlantic South Caribbean and South America, with integration of morphological, cytogenetic and molecular data. **Zootaxa**, v. 3918, n. 1, p. 1–38, 2015.

METHION, S.; DÍAZ LÓPEZ, B. Individual foraging variation drives social organization in bottlenose dolphins. **Behavioral Ecology**, v. 31, n. 1, p. 97–106, 2019.

MODLMEIER, A. P. et al. The keystone individual concept: An ecological and evolutionary overview. **Animal Behaviour**, v. 89, p. 53–62, 2014.

MOIRON, M.; LASKOWSKI, K. L.; NIEMELÄ, P. T. Individual differences in behaviour explain variation in survival: a meta-analysis. **Ecology Letters**, v. 23, n. 2, p. 399–408, 2020.

MOORE, B. L. et al. Acoustic coordination by allied male dolphins in a cooperative context. **Proceedings of the Royal Society B: Biological Sciences**, v. 287, n. 1924, 20192944, 2020.

MOYES, K. et al. Exploring individual quality in a wild population of red deer. **Journal of Animal Ecology**, v. 78, n. 2, p. 406–413, 2009.

NOREN, D. P. et al. Echolocation is cheap for some mammals: Dolphins conserve oxygen while producing high-intensity clicks. **Journal of Experimental Marine Biology and Ecology**, v. 495, n. February, p. 103–109, 2017.

NOWAK, M. A. Five Rules for the Evolution of Cooperation. **Science**, v. 314, n. 5805, p. 1560–1563, 2006.

O'DEA, R. E.; NOBLE, D. W. A.; NAKAGAWA, S. Unifying individual differences in personality, predictability, and plasticity: a practical guide. **Methods in Ecology and Evolution**, v. 13, p. 278–293, 2021.

ODUM, E. P.; BARRET, G. W. 1971. **Fundamentals of Ecology**. 5th. ed.

PARTRIDGE, L. Individual differences in feeding efficiencies and feeding preferences of captive great tits. **Animal Behaviour**, v. 24, n. 1, p. 230–240, 1976.

PATTERSON, E. M.; KRZYSZCZYK, E.; MANN, J. Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. **Behavioral Ecology**, v. 27, n. 2, p. 401–410, 2016.

PÉREZ-MANRIQUE, A. et al. The study of aggression and affiliation motifs in bottlenose dolphins' social networks. **Scientific Reports**, v. 12, n. 1, p. 19672, 2022.

PETERS, R. H.; PETERS, R. H. **A critique for ecology**. Cambridge University Press, 1991.

PETERSON, D.; HANAZAKI, N.; SIMÕES-LOPES, P. C. Natural resource appropriation in cooperative artisanal fishing between fishermen and dolphins (*Tursiops truncatus*) in Laguna, Brazil. **Ocean & Coastal Management**, v. 51, n. 6, p. 469–475, 2008.

PIEROTTI, R.; FOGG, B. R. **The First Domestication: How Wolves and Humans Coevolved**. Yale University Press, 2017.

PIROTTA, E. et al. Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. **Functional Ecology**, v. 28, n. 1, p. 206–217, 2014.

PITMAN, R. L.; DURBAN, J. W. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. **Marine Mammal Science**, v. 28, n. 1, p. 16–36, 2012.

PRYOR, K.; LINDBERGH, J.; MILANO, R. A dolphin-human fishing cooperative in Brazil. **Marine Mammal Science**, v. 6, n. 1, p. 77–82, 1990.

PYKE, G. H. Optimal foraging theory: a critical review. **Annual review of ecology and systematics**, v. 15, n. 1, p. 523–575, 1984.

RÉALE, D. et al. Integrating animal temperament within ecology and evolution. **Biological Reviews**, v. 82, n. 2, p. 291–318, 2007.

REEVES, I. M. et al. Ancestry testing of "Old Tom," a killer whale central to mutualistic interactions with human whalers. **Journal of Heredity**, v. 114, n. 6, p. 598–611, 2023.

RIDGWAY, S. et al. On doing two things at once: Dolphin brain and nose coordinate sonar clicks, buzzes and emotional squeals with social sounds during fish capture. **Journal of Experimental Biology**, v. 218, n. 24, p. 3987–3995, 2015.

ROMEU, B. et al. Bottlenose dolphins that forage with artisanal fishermen whistle differently. **Ethology**, v. 123, n. 12, p. 906–915, 2017.

ROSSMAN, S. et al. Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. **Oecologia**, v. 178, n. 2, p. 415–425, 2015.

SADOWSKI, V.; ALMEIDA DIAS, E. R. Migração da tainha (*Mugil cephalus* Linnaeus, 1758, sensu latu) na costa sul do Brasil. **Boletim do Instituto de Pesca**, v. 13, n. 1, p. 31–50, 1986.

SAMPAIO, E. et al. Octopuses punch fishes during collaborative interspecific hunting events. **Ecology**, v. 102, n. 3, p. e03266, 2021.

SAMUELS, A.; GIFFORD, T. A quantitative assessment of dominance relations among bottlenose dolphins. **Marine Mammal Science**, v. 13, n. 1, p. 70–99, 1997.

SÁNCHEZ-TÓJAR, A.; MOIRON, M.; NIEMELÄ, P. T. Terminology use in animal personality research: a self-report questionnaire and a systematic review. **Proceedings of the Royal Society B: Biological Sciences**, v. 289, n. 1968, 2022.

SANDOVAL GALLARDO, S. et al. 150 years of anthropogenic impact on coastal and ocean ecosystems in Brazil revealed by historical newspapers. **Ocean & Coastal Management**, v. 209, n. March, p. 105662–105662, 2021.

SANTOS, M. L.; LEMOS, V. M.; VIEIRA, J. P. No mullet, no gain: cooperation between dolphins and cast net fishermen in southern Brazil. **Zoologia**, v. 35, p. 1–13, 2018.

SANTOS-SILVA, B. et al. Social foraging can benefit artisanal fishers who interact with wild dolphins. **Behavioral Ecology and Sociobiology**, v. 76, n. 42, p. 1–14, 2022.

SARGEANT, B. L. et al. Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). **Canadian Journal of Zoology**, v. 83, n. 11, p. 1400–1410, 2005.

SARGEANT, B. L.; MANN, J. Developmental evidence for foraging traditions in wild bottlenose dolphins. **Animal Behaviour**, v. 78, n. 3, p. 715–721, 2009.

SHELDON, B. C.; KRUUK, L. E. B.; ALBERTS, S. C. The expanding value of long-term studies of individuals in the wild. **Nature Ecology & Evolution**, v. 6, n. 12, p. 1799–1801, 2022.

SHEPPARD, C. E. et al. Intragroup competition predicts individual foraging specialisation in a group-living mammal. **Ecology Letters**, v. 21, n. 5, p. 665–673, 2018.

SHEPPARD, C. E. et al. Individual foraging specialization in group-living species. **Animal Behaviour**, v. 182, p. 285–294, 2021.

SIH, A.; BELL, A. M.; JOHNSON, J. C. Behavioral syndromes: An ecological and evolutionary overview. **Trends in Ecology and Evolution**, v. 19, n. 7, p. 372–378, 2004.

SIH, A.; SINN, D. L.; PATRICELLI, G. L. On the importance of individual differences in behavioural skill. **Animal Behaviour**, v. 155, p. 307–317, 2019.

SIH, A.; WATTERS, J. V. The mix matters: behavioural types and group dynamics in water striders. **Behaviour**, v. 142, p. 1417–1431, 2005.

SIMÕES-LOPES, P. et al. Bottlenose dolphin ecotypes of the western South Atlantic: the puzzle of habitats, coloration patterns and dorsal fin shapes. **Aquatic Biology**, v. 28, p. 101–111, 2019.

SIMÕES-LOPES, P. C. Intraspecific agonistic behavior of *Tursiops truncatus* (Cetacea, Delphinidae) during dolphin-human cooperative fishing in southern Brazil. **Biotemas**, v. 11, n. 2, p. 165–171, 1998.

SIMÕES-LOPES, P. C.; DAURA-JORGE, F. G.; CANTOR, M. Clues of cultural transmission in cooperative foraging between artisanal fishermen and bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae). **Zoologia (Curitiba)**, v. 33, n. 6, p. e20160107–e20160107, 2016.

SIMÕES-LOPES, P. C.; FABIÁN, M. E.; MENEGHETI, J. O. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. **Revista Brasileira de Zoologia**, v. 15, n. 3, p. 709–726, 1998.

SMITH, B. D. et al. Catch composition and conservation management of a human-dolphin cooperative cast-net fishery in the Ayeyarwady River, Myanmar. **Biological Conservation**, v. 142, n. 5, p. 1042–1049, 2009.

SMOLKER, R. A. et al. Sex differences in patterns of association among indian ocean bottlenose dolphins. **Behaviour**, v. 123, n. 1, p. 38–69, 1992.

SOLEDADE LEMOS, L. et al. Intra- and inter-annual variation in gray whale body condition on a foraging ground. **Ecosphere**, v. 11, n. 4, 2020.

SPOTTISWOODE, C. N.; BEGG, K. S.; BEGG, C. M. Reciprocal signaling in honeyguide-human mutualism. **Science**, v. 353, n. 6297, p. 387–389, 2016.

SPOTTISWOODE, C. N.; WOOD, B. M. Culturally determined interspecies communication between humans and honeyguides. **Science**, v. 382, n. 6675, p. 1155–1158, 2023.

STANDER, P. E. Cooperative hunting in lions: the role of the individual. **Behavioral Ecology and Sociobiology**, v. 29, p. 445–454, 1992.

STEPHENS, D. W.; KREBS, J. R. **Foraging theory**. Princeton: Princeton University Press, 1986. p. 247

STILLMAN, R. A.; CALDOW, R. W. G.; ALEXANDER, M. J. Individual variation in intake rate: the relative importance of foraging efficiency and dominance. **Journal of Animal Ecology**, v. 69, p. 484–493, 2000.

STOFFEL, M. A.; NAKAGAWA, S.; SCHIELZETH, H. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. **Methods in Ecology and Evolution**, v. 8, n. 11, p. 1639–1644, 2017.

SUTHERLAND, W. J. et al. Identification of 100 fundamental ecological questions. **Journal of Ecology**, v. 101, n. 1, p. 58–67, 2013.

THOMPSON, J. W. et al. finFindR: Automated recognition and identification of marine mammal dorsal fins using residual convolutional neural networks. **Marine Mammal Science**, v. 38, n. 1, p. 139–150, 2022.

TINKER, M. T.; MANGEL, M.; ESTES, J. A. Learning to be different: Acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. **Evolutionary Ecology Research**, v. 11, n. 6, p. 841–869, 2009.

TORRES, L. G. et al. Drone Up! Quantifying Whale Behavior From a New Perspective Improves Observational Capacity. **Frontiers in Marine Science**, v. 5, n. September, p. 1–14, 2018.

TORRES, L. G.; READ, A. J. Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. **Marine Mammal Science**, v. 25, n. 4, p. 797–815, 2009.

TOSCANO, B. J. et al. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. **Oecologia**, v. 182, n. 1, p. 55–69, 2016.

TSAI, Y. J. J.; MANN, J. Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. **Marine Mammal Science**, v. 29, n. 2, p. 261–279, 2013.

URIAN, K. et al. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. **Marine Mammal Science**, v. 31, n. 1, p. 298–321, 2015.

VAIL, A. L.; MANICA, A.; BSHARY, R. Fish choose appropriately when and with whom to collaborate. **Current Biology**, v. 24, n. 17, p. R791–R793, 2014.

VALLE-PEREIRA, J. V. S. et al. The role of behavioural variation in the success of artisanal fishers who interact with dolphins. **ICES Journal of Marine Science**, v. 79, n. 4, p. 1150–1158, 2022.

VAN DER WAL, J. E. M. et al. Safeguarding human–wildlife cooperation. **Conservation Letters**, v. 15, p. 1–18, 2022.

VERMEULEN, E. et al. 2019. *Tursiops truncatus* ssp. *gephyreus*, Lahille’s Bottlenose Dolphin. **The IUCN Red List of Threatened Species**.

VIEIRA, J. P. Juvenile Mullets (Pisces: Mugilidae) in the Estuary of Lagoa dos Patos, RS, Brazil. **Copeia**, v. 2, p. 409–418, 1991.

VIEIRA, J. P.; GARCIA, A. M.; GRIMM, A. M. Evidences of El Niño effects on the mullet fishery of the Patos Lagoon estuary. **Brazilian Archives of Biology and Technology**, v. 51, n. 2, p. 433–440, 2008.

VINDENES, Y.; LANGANGEN, Ø. Individual heterogeneity in life histories and eco-evolutionary dynamics. **Ecology Letters**, v. 18, n. 5, p. 417–432, 2015.

WELLS, R. S.; SCOTT, M. D. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). Em: RIDGWAY, S. H.; HARRISON, R. (Eds.). **Handbook of marine mammals: the second book of dolphins and the porpoises**. Academic Press, 1999. v. 6p. 137–182.

WELLS, R. S.; SCOTT, M. D. Common Bottlenose Dolphin: *Tursiops truncatus*. Em: PERRIN, W. F.; WÜRSIG, B.; THEWISSEN, J. G. M. (Eds.). **Encyclopedia of Marine Mammals (Second Edition)**. London: Academic Press, 2009. p. 249–255.

WEST, S. A.; GRIFFIN, A. S.; GARDNER, A. Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. **Journal of Evolutionary Biology**, v. 20, n. 2, p. 415–432, 2007.

WHITFIELD, D. P. Individual Feeding Specializations of Wintering Turnstone *Arenaria interpres*. **Journal of Animal Ecology**, v. 59, n. 1, p. 193–211, 1990.

WILD, S. et al. Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. **Biology Letters**, v. 15, n. 7, p. 20190227–20190227, 2019.

WILD, S. et al. Integrating Genetic, Environmental, and Social Networks to Reveal Transmission Pathways of a Dolphin Foraging Innovation. **Current Biology**, v. 30, n. 15, p. 3024- 3030.e4, 2020.

WILSON, D. S. Adaptive individual differences within single populations. **Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences**, v. 353, n. 1366, p. 199–205, 1998.

WILSON, E. O. The Evolution of Caste Systems in Social Insects. **Proceedings of the American Philosophical Society**, v. 123, n. 4, p. 204–210, 1979.

WISNIEWSKA, D. M. et al. Buzzing during biosonar-based interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. **Journal of Experimental Biology**, v. 217, n. 24, p. 4279–4282, 2014.

WISZNIEWSKI, J.; LUSSEAU, D.; MÖLLER, L. M. Female bisexual kinship ties maintain social cohesion in a dolphin network. **Animal Behaviour**, v. 80, n. 5, p. 895–904, 2010.

WOLF, M.; WEISSING, F. J. Animal personalities: Consequences for ecology and evolution. **Trends in Ecology and Evolution**, v. 27, n. 8, p. 452–461, 2012.

WÜRSIG, B.; WÜRSIG, M. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). **Science**, v. 198, n. 4318, p. 755–756, 1977.