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VICTÓRIA RENATA FONTOURA BENEMANN

ECOLOGIA DO FORRAGEIO E QUANTIFICAÇÃO DE MERCÚRIO NO ATOBÁ-PARDO (*SULA LEUCOGASTER*) (BODDAERT, 1783) EM DOIS ARQUIPÉLAGOS BRASILEIROS

São Leopoldo
2024

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Tese apresentada como requisito parcial para obtenção do título de Doutora em Biologia, pelo Programa de Pós-Graduação em Biologia da Universidade do Vale do Rio dos Sinos (UNISINOS).

Orientadora: Prof.ª Dra. Maria Virginia Petry

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Minha jangada vai sair pro mar
Vou trabalhar, meu bem querer
Se Deus quiser quando eu voltar do mar
Um peixe bom eu vou trazer
Meus companheiros também vão voltar
E a Deus do céu vamos agradecer

Dorival Caymmi

RESUMO

A Teoria do Forrageio Ótimo prediz que um predador ajusta suas estratégias de forrageio de modo a maximizar o ganho energético, gastando a menor energia possível para suprir suas demandas energéticas. A eficiência de forrageio é uma métrica utilizada para medir o saldo energético final resultantes das atividades de forrageio de um indivíduo, onde o ganho energético obtido pelo consumo das presas deve ser maior do que o custo energético para busca, captura e ingestão. O atobá-pardo (*Sula leucogaster*) é uma ave marinha da família Sulidae amplamente distribuída nos oceanos tropicais e subtropicais, tanto em zonas costeiras como pelágicas, e é caracterizado por apresentar uma alta plasticidade trófica. O objetivo principal desta tese é investigar o comportamento e a eficiência de forrageio do atobá-pardo em duas populações da espécie, comparando as condições ambientais e a influência antrópica em cada uma. Os objetivos específicos são (1) determinar as áreas de forrageio no arquipélago de Moleques do Sul (MS) e investigar como variáveis oceanográficas e a distribuição das frotas de pesca de arrasto influenciam o uso dos hábitats de forrageio, (2) testar diferenças intersexuais no comportamento de forrageio, (3) comparar a composição de espécies-presa e a qualidade nutricional da dieta do atobá-pardo entre os arquipélagos de MS e São Pedro e São Paulo (SPSP), (4) comparar a eficiência de forrageio entre os dois arquipélagos, e (5) determinar e comparar a concentração de mercúrio em penas de indivíduos jovens e adultos entre os dois arquipélagos. Indivíduos reprodutivos (n = 39) foram rastreados por três dias com *biologgers* programados para coletar coordenadas geográficas, dados de aceleração e profundidade durante as viagens de forrageio nos dois arquipélagos. Destes 39 indivíduos rastreados, 26 tiveram amostras de dieta coletadas através de regurgitos espontâneos para análise de dieta e composição nutricional. Para a análise da concentração de mercúrio, foram coletadas penas ventrais de 58 indivíduos: 21 em MS e 37 em SPSP. Não foi observada uma influência significativa da distribuição das frotas de pesca de arrasto na escolha por áreas de forrageio dos atobás-pardos em Moleques do Sul no período amostrado. Foi observada uma diferença significativa nos teores de proteína e lipídio, mas não na densidade energética entre as presas dos dois arquipélagos. Os atobás de MS realizaram viagens mais distantes da colônia reprodutiva e uma maior profundidade de mergulhos nas viagens de forrageio, o que resultou num gasto energético mais

alto do que em SPSP. A eficiência de forrageio do atobá-pardo foi maior em SPSP do que em MS, provavelmente devido a maior disponibilidade de presas neste arquipélago. Quanto à contaminação por mercúrio, não foram observadas diferenças significativas em relação a sexo e idade, mas sim entre os arquipélagos, onde indivíduos de MS apresentaram concentrações maiores. A presente tese apresenta novas informações sobre o comportamento de forrageio e a contaminação por mercúrio do atobá-pardo nos arquipélagos estudados, em especial para a população de MS, que representa o limite sul da distribuição da espécie no Oceano Atlântico e é ainda pouco estudada.

Palavras-chave: Plasticidade trófica; ecologia do movimento; Sulidae; estratégia de forrageio; pesca de arrasto.

ABSTRACT

The Optimal Foraging Theory predicts that a predator adjusts its foraging strategies to maximize energy gain, spending the least amount of energy possible to meet its energy demands. Foraging efficiency is a metric used to measure the final energy balance resulting from an individual's foraging activities, where the energy gain obtained by prey consumption should be greater than the energy cost of searching, capturing and ingesting it. The brown booby (*Sula leucogaster*) is a seabird of the Sulidae family, widely distributed in tropical and subtropical oceans both in coastal and pelagic zones and is characterized by exhibiting a high trophic plasticity. The main goal of this thesis is to investigate the foraging behavior and efficiency of brown boobies in two populations of the species, comparing the environmental conditions and the anthropic influence in each one. The specific goals are to (1) determine the foraging areas in the Moleques do Sul archipelago (MS) and investigate how oceanographic variables and the distribution of trawling fleets influence the foraging habitat use, (2) test intersexual differences in foraging behavior, (3) compare the prey species composition and nutritional quality of brown boobies diet between MS and São Pedro and São Paulo (SPSP) archipelagos, (4) compare foraging efficiency between the two archipelagos, and (5) determine and compare mercury concentration in feathers of juveniles and adults from the two archipelagos. Breeding adults (n = 39) were tracked for three days with biologgers programmed to collect geographic coordinates, acceleration, and depth data during foraging trips in both archipelagos. Of these 39 individuals tracked, 26 had their diet samples collected through spontaneous regurgitation to analyze diet and nutritional composition. To analyze mercury concentration, ventral feathers were collected from 58 individuals: 21 in MS and 37 in SPSP. No significant influence of trawling fleets spatial distribution was found on the choice for foraging areas in MS during the studied period. A significant difference was observed in protein and lipid contents, but not in energy density between the prey of the two archipelagos. Brown boobies from MS performed trips farther from the breeding colony and dived deeper, which resulted in higher energy expenditure than in SPSP. The foraging efficiency of brown boobies was higher in SPSP than in MS, probably due to the greater availability of prey in this archipelago. Regarding mercury contamination, no significant differences were observed concerning sex and age, but there were differences between the

archipelagos, where individuals from MS showed higher concentrations. This thesis presents new information on the foraging behavior and mercury contamination of the brown booby in the studied archipelagos, especially for the MS population, which represents the southern limit of the species distribution in the Atlantic Ocean and is still poorly studied.

Keywords: Trophic plasticity; movement ecology; Sulidae; foraging strategy; trawling.

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1 APRESENTAÇÃO

A presente tese, intitulada “Ecologia do forrageio e quantificação de mercúrio no atobá-pardo (*Sula leucogaster*) (Boddaert, 1783) em dois arquipélagos brasileiros”, apresenta seus resultados em forma de artigos científicos. Primeiramente foi apresentada uma introdução geral sobre o tema, onde são explorados os assuntos que serão abordados nos artigos, de forma a contextualizar o leitor quanto aos conceitos e informações essenciais sobre a espécie objeto de estudo, ecologia do forrageio, ecologia nutricional, problemáticas decorrentes da interação das aves marinhas com a pesca, utilização das aves como biomonitoras de poluição ambiental, e por fim sobre as áreas de estudo aqui exploradas: os arquipélagos de Moleques do Sul e São Pedro e São Paulo. Os artigos científicos resultantes dessa pesquisa foram apresentados em forma de capítulos, que estão formatados de acordo com as normas das revistas às quais foram/serão submetidos. As demais seções da tese – apresentação, introdução geral e considerações finais – estão formatadas de acordo com as normas da Academia Brasileira de Normas Técnicas (ABNT), norma de referência NBR 6023:2023.

O primeiro capítulo, intitulado “Foraging areas, diet, and habitat use of the Brown Booby *Sula l. leucogaster* breeding in the Moleques do Sul archipelago, Southern Brazil”, investiga a dieta e a influência de variáveis ambientais – naturais e de origem antrópica – na seleção de habitats de forrageio de atobás-pardos reprodutivos no Arquipélago de Moleques do Sul. Este trabalho apresenta dados inéditos sobre as áreas de forrageio utilizadas pela espécie no arquipélago, e investiga a sobreposição espacial destas áreas com as frotas de pesca de arrasto atuantes na região costeira do estado de Santa Catarina. O artigo está formatado de acordo com as normas do periódico “Marine Ornithology” (Qualis Capes B2, Fator de Impacto 0.8) e encontra-se em fase de revisão (*minor revision*) na referida revista.

O segundo capítulo, intitulado “Foraging efficiency of a generalist pantropical seabird, the brown booby (*Sula leucogaster*), in contrasting prey availability scenarios” investiga a eficiência de forrageio do atobá-pardo em duas populações sob diferentes paisagens marinhas. O artigo avalia a eficiência de forrageio desta espécie que apresenta alta plasticidade trófica através de estimativas de esforço de forrageio e ganho energético em duas populações com composições de dieta distintas. Neste estudo são abordados e testados conceitos de bioenergética e

ecologia nutricional. O artigo está formatado de acordo com as normas do periódico “Journal of Experimental Biology” (Qualis Capes A1, Fator de Impacto 2.9, Q1).

O terceiro capítulo, intitulado “Differences in mercury (THg) levels in Brown booby (*Sula leucogaster*) feathers from two environmentally distinct Brazilian archipelagos” investiga a concentração do mercúrio (Hg), um metal não-essencial tóxico, em penas de atobás-pardos adultos e juvenis nos arquipélagos de Moleques do Sul e São Pedro e São Paulo. O artigo discute potenciais fatores ambientais – geográficos, oceanográficos, geológicos e ecológicos – que podem influenciar nos resultados observados, e aborda o potencial uso de penas de aves marinhas como indicadoras dos níveis de contaminação por mercúrio no ambiente marinho. Este artigo encontra-se publicado no periódico *“Science of the Total Environment”* (Qualis Capes A1, Fator de Impacto 8,2, Q1). A versão on-line do artigo está disponível em: https://doi.org/10.1016/j.scitotenv.2024.176457.

Na seção final são apresentadas as considerações finais da tese com uma síntese dos principais resultados obtidos nos três capítulos e suas contribuições para a pesquisa científica no campo da ecologia de aves marinhas, bem como suas implicações para a conservação desses organismos. Por fim, na seção anexos, são apresentadas fotografias referentes à cada capítulo da tese para fins ilustrativos, trazendo registros das áreas de estudo, do trabalho de campo e laboratório.

2 INTRODUÇÃO GERAL

2.1 A FAMÍLIA SULIDAE E O ATOBÁ-PARDO (*Sula leucogaster*)

A família Sulidae, ordem Suliformes, compreende 10 espécies de aves marinhas de grande porte, distribuídas em três gêneros: *Morus* spp., *Papasula* sp. e *Sula* spp., comumente referidas como atobás e gansos-patola (Schreiber; Burger 2002). Estas aves se destacam por sua excelente habilidade de realizar mergulhos de forrageio em alta velocidade para capturar presas, sobretudo peixes, um comportamento facilitado por adaptações anatômicas, como corpos hidrodinâmicos e ossos robustos que oferecem proteção contra o impacto na água. Em relação à biologia reprodutiva, os atobás realizam cuidado biparental da prole e ninhadas reduzidas, tipicamente compostas por um ou dois filhotes (Nelson, 1978; Schreiber, 1979; Carboneras, 1992). São, portanto, consideradas espécies k-estrategistas, caracterizadas por adaptações evolutivas que priorizam a sobrevivência e o recrutamento da prole em detrimento de uma alta taxa de fecundação (MacArthur; Wilson 1967). As espécies da família Sulidae são amplamente distribuídas nos oceanos tropicais, subtropicais e temperados globalmente. Habitam predominantemente zonas costeiras, ilhas oceânicas e áreas de plataforma continental, onde encontram condições propícias para alimentação e reprodução (Nelson, 1978; Schreiber, 1979). Das 10 espécies da família existentes no mundo, três ocorrem em território brasileiro: o atobá-mascarado *Sula dactylatra* (Lesson, 1831), o atobá-de-pé-vermelho *Sula sula* (Linnaeus, 1766) e o atobá-pardo *Sula leucogaster* (Boddaert, 1783).

O atobá-pardo (*S. leucogaster*) é a espécie mais abundante e considerada a de hábitos mais costeiros dentre as três, reproduzindo-se tanto nas ilhas oceânicas de Fernando de Noronha, Arquipélago de São Pedro e São Paulo (SPSP), Atol das Rocas e Abrolhos, como em diversas ilhas costeiras ao longo da costa brasileira (Nunes *et al.,* 2016). Apresenta acentuado dimorfismo sexual, sendo as fêmeas em média 38% maiores do que os machos (Lewis *et al.,* 2005), bem como uma ampla variação alométrica entre populações localizadas em diferentes regiões geográficas. Estas variações são atribuídas principalmente a processos oceanográficos de pequena e mesoescala, que influenciam diretamente na oferta local de recursos (Mancini *et al.*, 2014; Nunes *et al.*, 2016). A dieta do atobá-pardo pode variar

amplamente de acordo com condições ambientais e disponibilidade de presas locais, podendo apresentar uma dieta especialista em determinados locais e amplamente generalista em outros, sendo assim considerada uma espécie com alta plasticidade trófica (Jacoby *et al.,* 2013). A plasticidade trófica é a habilidade de um organismo em ajustar sua dieta em resposta à variabilidade temporal e espacial dos recursos alimentares disponíveis (Larkin, 1956; Gerking, 1994).

Em ilhas oceânicas, como nos arquipélagos de Fernando de Noronha e de São Pedro e São Paulo, a dieta do atobá-pardo é fundamentalmente composta por cerca de 8 espécies de peixes pelágicos, predominantemente peixes-voadores da família *Exocoetidae* (Both; Freitas, 2001; Mancini *et al.*, 2014, Jacoby *et al.*, 2023). Já em ilhas costeiras localizadas sobre a plataforma continental, inseridas em ecossistemas neríticos, a dieta da espécie tende a apresentar uma dieta mais generalista, com uma maior amplitude de nicho trófico. Nos arquipélagos de Santana e Moleques do Sul, por exemplo, a dieta do atobá-pardo é composta por 22 e 39 espécies-presa, respectivamente (Branco *et al.*, 2005, Jacoby *et al.*, 2023, Mancini *et al.*, 2023). Os atobás-pardos utilizam duas principais estratégias de forrageio: o mergulho profundo (*plunge diving*) e o mergulho de perseguição (*pursuit diving*) (Nelson, 1978; Schreiber; Burger, 2002; Schreiber; Norton, 2002). No *plunge diving,* realizam mergulhos profundos, podendo atingir até 30 metros de profundidade, geralmente partindo de uma altura considerável (10 - 30 m) e entrando na água verticalmente em alta velocidade para capturar as presas. Já no *pursuit diving*, as aves perseguem as presas ativamente debaixo d'água utilizando seus pés palmados e asas como propulsores (Carboneras *et al.*, 1992; Schreiber; Burger, 2002). O status global de conservação do atobá-pardo é Pouco Preocupante, e embora a população global seja estimada em mais de 200 mil indivíduos, acredita-se que há uma tendência de declínio em consequência de distúrbios aos seus locais de reprodução e da exploração humana, em especial a caça para consumo humano e para a utilização como iscas na pesca (Carboneras *et al.*, 2018; Birdlife International, 2024).

2.2 ECOLOGIA DO FORRAGEIO: TEORIA DO FORRAGEIO ÓTIMO E A HIPÓTESE DE *JUNK-FOOD*

A teoria do forrageio ótimo (Macarthur; Pianka, 1966) prediz que a razão entre o esforço de forrageio e o ganho energético irá determinar se a escolha de uma determinada presa é ou não favorável ao predador, uma vez que o ganho energético proporcionado pelo recurso ingerido deve compensar a energia dispendida na sua captura e consumo (Macarthur; Pianka, 1966; Parker; Hawkes, 2018). Assim, predadores investiriam seus esforços de forrageio de modo que a razão E/h seja positiva, sendo: E = energia (calorias) fornecida pelo consumo da presa, e h = o tempo necessário para procura, captura, manuseio e ingestão da presa (Macarthur; Pianka, 1966). Contudo, o modelo proposto por MacArthur e Pianka (1966) foi considerado muito simplista por diversos ecólogos, tendo sofrido uma série de críticas a partir da década de 1980 (Pyke, 1984; Pierce; Ollason, 1987). Uma das críticas apontadas sobre o modelo inicial é de que este ignora necessidades nutricionais que vão além da demanda energética puramente dita (kJ), como por exemplo, a composição de micronutrientes presentes nas presas (Pyke, 1984).

A hipótese de *junk-food* (Alverson, 1992) prevê que indivíduos que consomem recursos de baixo valor nutricional e energético tendem a ter o sucesso reprodutivo reduzido, pois deficiências nutricionais da dieta afetam o crescimento e habilidades cognitivas da prole (Piatt; Anderson, 1996; Kitaysky *et al.*, 2005; Wanless *et al.*, 2005). Apesar das críticas quanto à limitação do uso da densidade energética (kJ) como proxy para qualidade de dieta, estudos demonstram que a razão proteína: lipídio representa o aspecto mais importante na avaliação da qualidade nutricional da dieta de um predador, e que o consumo de presas com teores insuficientes destes dois nutrientes pode levar a prejuízos no *fitness* de adultos reprodutivos e consequentemente no sucesso reprodutivo das populações, uma vez que uma dieta rica em proteínas e lipídios influencia positivamente no ganho de peso e sobrevivência de ninhegos de aves marinhas em fase de crescimento (Romano 1999; Anthony *et al.*, 2000; Visser, 2001; Sorensen *et al.*, 2009, González-Medina *et al.*, 2018). Enquanto uma dieta rica em lipídios fornece energia suficiente para a manutenção de indivíduos adultos, e ainda com baixo custo metabólico quando comparada a proteína, os indivíduos em fase de crescimento necessitam de uma

maior demanda deste segundo macronutriente para a síntese de tecidos nesse estágio do ciclo de vida (Roby *et al.*, 1991; Anthony *et al.*, 2000).

Eficiência de forrageio é a medida utilizada para avaliar a razão entre o esforço de forrageio e o ganho energético, e ela pode variar entre indivíduos e populações de uma mesma espécie de acordo com uma série de fatores como idade (Lescroël *et al.*, 2019) diferenças no hábitat (Werner *et al.*, 1979; Roese *et al.*, 1991), na disponibilidade local de presas (Bertrand *et al.*, 2012; Goundie *et al.*, 2015; Carlsen, 2022), interações intra e interespecíficas (Mittelbach, 1981), condições climáticas (Lescroël *et al.*, 2010; Speakman *et al.*, 2020) e adaptações comportamentais (Rubolini *et al.*, 2015; Rebstock *et al.*, 2022). Os métodos mais tradicionalmente utilizados para medir o gasto energético em animais de vida livre, isto é, sua taxa metabólica de campo (FMR, do inglês *field metabloc rate*) são o método da água duplamente marcada (DLW, do inglês *doubly labelled water*) (Speakman, 1997) e o método da frequência cardíaca (Butler *et al.*, 2004). A técnica de água duplamente marcada envolve a administração de água contendo isótopos estáveis de hidrogênio (^{2}H) e oxigênio (^{18}O) ao animal, e a medição da eliminação desses isótopos ao longo do tempo para calcular a taxa metabólica (Schultner *et al.*, 2010; Shaffer, 2011). O método DLW fornece apenas um único valor estimado com média calculada ao longo da duração do estudo e requer procedimentos invasivos para implantar registradores (Butler *et al.*, 2004). Quanto ao método da frequência cardíaca, é possível que processos cardiovasculares não relacionados ao gasto energético possam influenciar a relação entre frequência cardíaca e consumo de oxigênio e, portanto, a utilização desta técnica necessita de calibrações adicionais antes de ser aplicado em campo (Weimerskirch *et al.*, 2002; Gleiss *et al.*, 2011; Green, 2011; Elliot, 2016).

Recentemente, dados de acelerometria têm sido utilizados para investigar a bioenergética de animais de vida livre (Bennison *et al.*, 2021; Sutton *et al.*, 2023). Acelerômetros triaxiais são dispositivos que quantificam o movimento ao longo de três direções: X, Y e Z. Estes três eixos representam as três dimensões do movimento no espaço tridimensional e o sensor do dispositivo registra a aceleração do movimento nestas três direções (Shepard *et al.*, 2008). A técnica mais utilizada para estimar o gasto energético dos acelerômetros é o cálculo da aceleração corporal dinâmica vetorial (VeDBA), devido à sua correlação com outras medidas tradicionais de gasto energético, como quantificar o volume de oxigênio utilizado

pelos músculos e frequência cardíaca (Laich *et al.*, 2011; Gleiss *et al.*, 2011). Esses métodos tradicionais são considerados mais invasivos e por isso o uso da acelerometria é cada vez mais incentivado (Wilson *et al.*, 2020).

2.3 INTERAÇÕES ENTRE AS AVES MARINHAS E A PESCA

Os efeitos gerados pelo consumo de descartes da pesca sobre o *fitness* de aves marinhas são ainda pouco compreendidos e muitas vezes controversos (Bicknel *et al.*, 2013). A pesca de arrasto captura uma alta biomassa de espécies não-alvo (e.g. peixes e cefalópodes sem valor comercial), as quais são descartadas pelas embarcações em alto mar. Portanto, é comum que diversas espécies de aves marinhas de hábitos oportunistas utilizem tais descartes como fonte de alimento, os quais muitas vezes constituem a principal fonte de recursos para determinadas populações (Yorio; Caille, 1999; Bicknell *et al.*, 2013; Karris *et al.*, 2018). Sabe-se que o descarte pesqueiro pode representar uma potencial fonte de impacto, podendo causar tanto efeitos deletérios (Votier *et al.*, 2004; Wagner; Boersma, 2011; Benemann *et al.*, 2016) quanto benéficos (Copello; Quintana, 2009; Bartumeus *et al.*, 2010; Krüger *et al.*, 2017) sobre estas populações. A tendência e a extensão dos efeitos causados pelos descartes pesqueiros sobre os predadores marinhos podem variar de acordo com aspectos ecológicos, geográficos e comportamentais da espécie ou da população em questão (Bicknel *et al.*, 2013). Embora a os descartes possam representar uma fonte adicional de alimento que naturalmente não estaria acessível às aves, e ainda potencialmente diminuir o esforço de forrageio necessário para a busca e captura (Arcos; Oro, 2002; Depestele *et al.*, 2016), diversos estudos demonstram que as espécies comumente descartadas pela indústria pesqueira representam uma fonte de baixo teor nutricional quando comparadas às presas naturais destes predadores (Grémmilet *et al.*, 2008; Bicknel *et al.*, 2013), e que muitas vezes também não compensam em termos de ganho energético (Pichegru *et al.*, 2007; Le Bot *et al.*, 2019).

A interação da do atobá-pardo com a frota de pesca de arrasto, em especial a pesca direcionada à camarão, vem sendo amplamente reportada em diversos locais ao longo da costa brasileira (Branco, 2001; Branco *et al.*, 2005; Carniel; Krul, 2012) e em outros locais ao longo de sua distribuição geográfica global (Blaber *et al.*, 1995; Hill; Wassenberg, 2000). A região costeira do estado de Santa Catarina, onde está

localizado o arquipélago de Moleques do Sul, representa uma das principais zonas de atividade de frotas pesqueiras no Brasil (FAO, 2019), especialmente tratando-se da pesca de arrasto de fundo direcionada à captura do camarão-sete-barbas (*Xiphopenaeus kroyeri*) e camarão-rosa (*Farfantepenaeus* sp.) (Andrade, 1998). Devido ao fino emalhe das redes utilizadas nesta arte de pesca, e consequente sua baixa seletividade em relação aos organismos capturados, a pesca de arrasto direcionada à camarão é caracterizada por resultar em altas taxas de biomassa descartada por unidade de esforço pesqueiro (Haimovici; Mendonca, 1996; Haimovici; Martins; Vieira, 1996; Vianna *et al.*, 2000; Vianna; Almeida 2005). Em um contexto histórico, é importante ressaltar que o desenvolvimento e mecanização no setor pesqueiro nas costas Sudeste e Sul brasileiras, em especial tratando-se da pesca de arrasto direcionada ao camarão, se intensificaram a partir da década de 1940 (Valentini *et al.*, 1991; Valentini; Carodoso, 1991; Valentini *et al.*, 2006). No Arquipélago de São Pedro e São Paulo, a atividade pesqueira é muito menos intensa e direcionada à captura de peixes pelágicos de grande porte (i,e, *Thunnus albacares, Acanthocybium solandri* e *Elagatis bipinnulata*), modalidade que produz um volume muito inferior de descartes do que a pesca de arrasto (Vaske Jr. *et al.*, 2008).

2.4 AVES MARINHAS COMO BIOINDICADORAS DE CONTAMINAÇÃO AMBIENTAL

As aves marinhas são frequentemente utilizadas como ferramentas no monitoramento de poluição ambiental, sendo consideradas espécies sentinelas devido à sua posição elevada na teia trófica e à sua sensibilidade às mudanças nos ecossistemas marinhos (Burger; Gochfeld, 2004; Camphuysen, 2006; Carravieri *et al.*, 2013; Cusset *et al.*, 2023). Por serem espécies predadoras de topo, longevas, com amplas distribuições geográficas e áreas de vida, as aves marinhas são excelentes bioindicadoras de seus ecossistemas pois fornecem informações sobre os níveis tróficos inferiores e possibilitam o monitoramento ambiental numa larga escala espaço-temporal (Furness; Camphuysen, 1997; Helgason *et al.*, 2008; Rajpar *et al.*, 2018, Gilmour *et al.*, 2019; Mills *et al.*, 2020; Cusset *et al.*, 2023; Albert *et al.*, 2024). Por ocuparem níveis altos na cadeia trófica, estudos sobre a dieta de aves marinhas podem também contribuir para o monitoramento da poluição ambiental,

especialmente devido aos processos de biomagnificação e bioacumulação de substâncias tóxicas como metais pesados (Muirhead; Furness, 1988; Albert *et al.*, 2021; Benemann *et al.*, 2024) e poluentes orgânicos persistentes derivados de agrotóxicos (Adrogué *et al.*, 2019; Gilmour *et al.*, 2021). O processo de bioacumulação ocorre quando um organismo (indivíduo) absorve contaminantes ao longo do tempo, acumulando-os em concentrações mais altas em seus tecidos corporais ao longo do tempo. Já a biomagnificação se refere ao aumento da concentração de poluentes à medida que eles passam por diferentes níveis da cadeia trófica. Devido a esse processo, espécies predadoras de topo em geral apresentam níveis mais altos de concentração de poluentes em seus tecidos, refletindo a contaminação de suas presas (Seco *et al.*, 2021; Matias *et al.*, 2022).

O mercúrio (Hg) é um metal não-essencial tóxico naturalmente distribuído na Terra, originário de fontes naturais, como vulcões e processos geotérmicos, e antropogênicas, como a mineração e usinas de energia movidas a combustíveis fósseis (Pirrone *et al.*, 2010; Brocza *et al.*, 2024). Por ser uma substância altamente volátil, a principal via de circulação do mercúrio no ambiente é atmosférica, embora também possa ser disperso pela água, como correntes oceânicas e escoamentos fluviais (Travnikov *et al.*, 2017; Dastoor *et al.*, 2022). É considerado um dos elementos mais tóxicos para os organismos vivos, principalmente quando é submetido ao processo de metilação pela ação de microrganismos e assume sua forma orgânica metilmercúrio (MeHg) (Clarkson, 1997; Fitzgerald *et al.*, 2007). O mercúrio se acumula nos tecidos orgânicos devido à sua alta afinidade por proteínas, sendo retido nos corpos dos organismos (Kidd *et al.*, 2012). As penas são tecidos frequentemente utilizados para amostrar os níveis de mercúrio em aves por se tratarem de um método pouco invasivo e por apresentarem concentrações relativamente altas, uma vez que são uma das principais vias excretoras desse elemento não essencial no corpo de uma ave (Burger, 1994; Bottini *et al.*, 2021; Bighetti *et al.*, 2022). Elas apresentem concentrações de mercúrio significativamente maiores do que o sangue, com uma menor variação interespecífica e uma maior variação intraespecífica na concentração (Bustamante *et al.*, 2023).

Diversos efeitos negativos à saúde e ao fitness de aves já foram registrados decorrentes da contaminação por mercúrio, como alterações nos níveis de hormônios reprodutivos (Tartu *et al.*, 2015; Provencher *et al.*, 2016), comportamento parental (Tartu *et al.*, 2013), efeitos neurológicos nas regiões cerebrais responsáveis

pelas informações geomagnéticas e pelo controle biomecânico (Seewagen, 2020), e na condição corporal, como reservas de gordura (Moura *et al.*, 2018; Ackerman *et al.*, 2019). Estudos comparando as concentrações de poluentes em uma mesma espécie em diferentes localizações geográficas e condições ambientais trazem perspectivas ecológicas que contribuem ao entendimento de como estes contaminantes se dispersam e se distribuem espacialmente nos oceanos (Shoji *et al.*, 2021; Albert *et al.*, 2024).

2.5 AS ÁREAS DE ESTUDO: ARQUIPÉLAGOS DE MOLEQUES DO SUL E SÃO PEDRO E SÃO PAULO

O arquipélago de Moleques do Sul (27°51'S, 48°25'W) é um arquipélago costeiro localizado ao Sul da Ilha de Santa Catarina, a 14 km do da costa do estado de Santa Catarina. A Ilha Maior possui uma área de 9,86 ha, é formada por rochas graníticas e sua superfície é predominantemente coberta por vegetação arbustiva e herbácea (Bege; Pauli, 1989; Salvador; Fernandez, 2008). Neste arquipélago reproduzem três espécies de aves marinhas: o atobá-pardo (*Sula leucogaster*), o gaivotão (*Larus dominicanus*) e a fragata ou tesourão *(Fregata magnificens*). O arquipélago de Moleques do Sul representa o limite meridional da distribuição do atobá-pardo no Oceano Atlântico (Bege; Pauli, 1989, Branco *et al.*, 2005). A população da espécie neste arquipélago é estimada em cerca de 1700 indivíduos, e a reprodução ocorre ao longo do ano todo, com dois picos na abundância de adultos reprodutivos: um entre janeiro e fevereiro, e um entre agosto e novembro (Branco *et al.*, 2010; Branco *et al.*, 2013). São Pedro e São Paulo (00°55'N, 29°20'W) é um arquipélago pelágico localizado a 1.100 km do estado do Rio Grande do Norte e a 1.824 km da África. Possui uma área total de 1,3 ha e toda sua superfície é coberta por rochas plutônicas. No arquipélago de São Pedro e São Paulo reproduzem três espécies de aves marinhas: o atobá-pardo, o trinta-réis-escuro (*Anous stolidus*) e o trinta-réis-preto (*Anous minutus*). A reprodução do atobá-pardo ocorre ao longo do ano todo e a população é estimada em aproximadamente 600 indivíduos (Mancini *et al.*, 2016). Devido à limitação de espaço para nidificação devido ao tamanho reduzido da ilha, a colônia reprodutiva de atobá pardo apresenta alta densidade demográfica, com ninhos cerca de 1 m equidistantes, resultando em uma alta disputa por espaço entre os adultos reprodutivos (Nunes *et al.*, 2018).

As características oceanográficas dos dois arquipélagos são bastante distintas: o arquipélago de Moleques do Sul está inserido em um ecossistema nerítico, sob influência contínua da Corrente Brasileira, sazonalmente afetada pela ressurgência de águas frias da Corrente das Malvinas, e representa uma região de elevada produtividade primária (Castro; Miranda, 1998; Odebrecht; Castello, 2001). O arquipélago de São Pedro e São Paulo, por sua vez, está localizado na zona pelágica, inserido no Sistema Equatorial de Correntes Marinhas, sob influência direta da Corrente Sul-Equatorial, que flui superficialmente na direção oeste, e da Contracorrente Equatorial submersa, que flui na direção oposta (leste) a uma profundidade entre 60 e 100 m (Costa Campos *et al.*, 2005; Knoppers *et al.*, 2009). O relevo submerso acentuado do arquipélago promove áreas de ressurgência de pequena escala, gerando um aumento na concentração de nutrientes nos arredores do arquipélago (Soares *et al.*, 2012).

No Arquipélago de Moleques do Sul, 50% das espécies que compõem a dieta do atobá-pardo são atribuídas descarte da pesca (Branco *et al.*, 2005). Dentre as principais espécies consumidas, estão o mangangá-liso (*Porichthys porosissimus)*, a maria-luísa (*Paralonchurus brasiliensis*), a pescadinha (*Isopisthus parvipinnis*) e o xixarro (*Trachurus lathami*) (Branco *et al.*, 2005). Entretanto, há uma ampla variação sazonal da dieta da espécie nesse arquipélago, atribuída principalmente a eventos do ciclo de vida de suas presas e a oferta de recursos provenientes do descarte pesqueiro em determinadas épocas do ano quando a pesca camaroeira é mais intensa, em especial no verão (Krul, 2004; Branco, 2001; Branco *et al.*, 2005). Já no Arquipélago de São Pedro e São Paulo, a dieta da espécie é composta em cerca de 90% por peixes-voadores (Exocoetidae) (Both; Freitas, 2001). *Exocoetus volitans* é uma das espécies mais frequentes, chegando a representar 71% de sua dieta nos meses de verão (Naves *et al.*, 2002), e é considerada uma presa altamente proteica (Harewood *et al.*, 1993).

3 OBJETIVOS E HIPÓTESES

O objetivo geral desta tese é investigar e comparar o comportamento de forrageio do atobá-pardo (*Sula leucogaster*) em duas populações da espécie sob diferentes condições ambientais e influência antrópica. Os objetivos específicos são:

- Determinar as áreas de forrageio do atobá-pardo no arquipélago de Moleques do Sul;
- Investigar a influência de variáveis oceanográficas e da distribuição espacial das frotas de pesca de arrasto no uso de hábitats de forrageio da espécie no arquipélago de Moleques do Sul;
- Investigar diferenças intersexuais no comportamento de forrageio;
- Comparar a composição taxonômica e nutricional de presas utilizadas pelo atobá-pardo nos arquipélagos de São Pedro e São Paulo e Moleques do Sul;
- Comparar a eficiência de forrageio, em termos de esforço de forrageio versus ganho energético, entre os dois arquipélagos;
- Determinar e comparar a concentração de mercúrio total (THg) em penas de indivíduos jovens e adultos de *S. leucogaster* entre os dois arquipélagos.

A primeira hipótese desta tese é de que as atividades pesqueiras influenciam na escolha de habitats de forrageio do atobá-pardo em Moleques do Sul. A segunda hipótese é de que o consumo de presas provenientes do descarte pesqueiro pela população reprodutiva de Moleques do Sul fornece uma dieta de qualidade nutricional inferior quando comparada à dieta composta majoritariamente por peixes-voadores de São Pedro e São Paulo. A terceira hipótese é de que a eficiência de forrageio do atobá-pardo é maior em São Pedro e São Paulo do que em Moleques do Sul. A quarta hipótese é de que a concentração de mercúrio é maior em penas de indivíduos adultos do que jovens, e maior na população reprodutiva de Moleques do Sul do que na de São Pedro e São Paulo.

CAPÍTULO 1

FORAGING AREAS, DIET, AND HABITAT USE OF THE ATLANTIC BROWN BOOBY *SULA L. LEUCOGASTER* BREEDING IN THE MOLEQUES DO SUL ARCHIPELAGO, SOUTHERN BRAZIL

VICTÓRIA RENATA FONTOURA BENEMANN, DENYELLE HENNAYRA CORÁ & MARIA VIRGINIA PETRY

Laboratório de Ornitologia e Animais Marinhos, Universidade do Vale do Rio dos Sinos, Av. Unisinos, 950, São Leopoldo, Brazil, CEP 93900-000
(victoriabenemann@gmail.com)

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ABSTRACT

BENEMANN, V.R.F., CORÁ, D.H. & PETRY, M.V. 2024. Foraging areas, diet, and habitat use of the Atlantic Brown Booby *Sula l. leucogaster* breeding in the Moleques do Sul Archipelago, southern Brazil. *Marine Ornithology.*

Seabirds' selection of foraging habitats is driven by several environmental variables, including food availability, climatic and oceanographic conditions, and the presence of fishing vessels. Many seabird species are known to interact with fisheries to forage on fishing discards, but the ecological effects of these interactions are still poorly understood. We investigated the diet, foraging areas and habitat use of the Atlantic Brown Booby *Sula l. leucogaster* during the chick-rearing period in the Moleques do Sul Archipelago, Southern Brazil, using oceanographic features and trawl fishing effort as explanatory variables for foraging habitat use. Nineteen breeding adults were tracked with GPS loggers during September 2022 for three days, which results in obtaining information from 82 complete foraging trips (females = 45, males = 37). Fourteen spontaneous regurgitations were obtained during handling thus to allow diet analysis. We used an Expectation-Maximization Binary Clustering to identify foraging areas and a Generalized Linear Model to investigate how environmental variables influenced Brown Booby foraging behavior. Brown Boobies performed foraging trips with an average duration of 2 h. Females travelled farther (mean maximum distance from colony = 29 km) than males (averaging 22 km). Chlorophyll-*a* was the only significant

environmental variable (*z-value* = 12.544, $p < 0.01$) correlating with where boobies foraged, while trawl fishing effort did not contribute substantially to the model. However, our data reflects a single period of the year when trawl fisheries are less intense in the study area. Studies using tracking data at fine-scale resolutions to investigate seabird at-sea distribution and interactions with fisheries, should provide valuable insights to help improve fisheries sustainability, namely towards the reduction of fishery discards.

Keywords: trawl fishery, discards, global fishing watch, seabirds, gps tracking, ecology, Sulidae

INTRODUCTION

Seabird at-sea distribution is mainly determined by oceanographic and biological features, such as prey availability, which in turn is affected by primary productivity, seawater temperature, ocean currents and fronts, upwellings, and seabed topography --- areas of high primary productivity generally tending to be likely foraging grounds for most seabird species (Bost *et al.* 2009, Zavalaga *et al.* 2010, Cox *et al.* 2018, Evans *et al.* 2021, Wakefield *et al.* 2021, Finger *et al.* 2023). Regarding topography, bathymetric characteristics can play a role in the location of foraging areas, as turbulence along the seabed (especially if irregular) can lead to enhancement of nutrients, thus promoting increased primary production, higher phytoplankton concentration and, consequently, macrozooplankton abundance (Schneider *et al.* 1990, Zavalaga *et al.* 2010, Evans *et al.* 2004, Yen et al. 2004). The microzooplankton, in turn, are preyed up by fish. Chlorophyll-a is commonly used as a proxy of primary productivity as it measures the standing stock of phytoplankton in surface waters (), thus often reflecting indirectly the availability of prey for marine predators (Weimerskirch *et al.* 2005, Huot *et al.* 2007, Grémillet *et al.* 2008,Tremblay *et al.* 2009, Serratosa *et al.* 2020).

During the breeding season, seabirds behave as central-place foragers, being restricted to the vicinity of the colony due to their breeding duties. Thus, they use comparably narrower foraging ranges than in the non-breeding period when they are free to reach areas further away, a density-dependent factor (Orians & Pearson 1979, Furness & Birkhead 1984, Burke & Montevecchi 2009, Trevail *et al.* 2024). In addition, local prey

availability is one of the most important factors in determining foraging effort and breeding success for seabird populations (Sherley *et al.* 2013, Fayet *et al.* 2021). Finally, fishing activities also influence the distribution of seabirds at sea, positively among those species that benefit from discards but negatively among those species that compete with fisheries (e.g., Paleczny *et al*. 2015, Grémillet *et al*. 2018). Since the development of industrial fishing, this anthropogenic activity has also played an important role in the foraging movements of these predators (Sherley *et al.* 2020, De la Cruz *et al.* 2002, Montevecchi 2023).

Seabirds interact with fisheries, although the nature and intensity of these interactions varies according to species foraging behavior, local features, and fishing gear type (Bartumeus *et al.* 2010, Calado *et al.* 2021, Genovart *et al.* 2017, Patrick *et al.* 2015). Several harmful impacts have been reported, mostly caused by incidental bycatch, entanglement in fishing gears, competition for feeding resources, and consumption of fishery discards (Furness 2003, Žydelis *et al.* 2013, Benemann *et al.* 2015, Grémillet *et al.* 2018, Sherley *et al.* 2020). Fisheries discards are composed of fish offal and non-targeted organisms that are incidentally captured, and due to the lack of commercial value become discarded (Zeller *et al.* 2018). These discards can be an easy source of food supply to marine megafauna (Lewison *et al.* 2004, Bicknell *et al.* 2013), altering the trophic dynamics of marine ecosystems (Goñi 1998, Furness 2003, Bicknell *et al.* 2013, Grémillet *et al.* 2008). For instance, Cardoso *et al.* 2021 reported that in southern Brazil, 24% of all fish caught by the bottom pair trawling fishery are discarded. These discards include 64 species, mostly having no commercial value or undersized fish; discard rates and species composition have been about the same for 40 decades (Cardoso *et al.* 2021, Haimovici & Maceira 1981). Fishery discards, a main, predictable anthropogenic food subsidy (PAFS), can generate cascade effects within biological communities. These lead to ecological consequences such as decrease in temporal population variability, increase in resilience of opportunistic species, and decrease in community diversity (Oro *et al.* 2013, Heath *et al.* 2014).

The Brown Booby *Sula leucogaster* is a widely distributed pantropical seabird species, having several subspecies (e.g., Howell & Zufeld 2019) that exhibits much trophic plasticity according to local prey availability; over a hundred prey species have already been reported in their diet even in just the western South Atlantic Ocean (Jacoby *et al.*

2023). These boobies forage mainly by plunge-diving, generally up to 2 m depth; mostly they feed on bony fish, but can also on squid and crustaceans (Del Hoyo *et al.* 1996, Branco *et al.* 2005, Correia *et al.* 2021). Brown Boobies are sexually dimorphic in body size, in which females can be 38% heavier and perform longer foraging trips (Lewis *et al*. 2005, Nunes *et al.* 2017, Miller *et al.* 2018, Correia *et al.* 2021). Furthermore, the species show a wide variation of body size across populations, attributed to local environmental conditions, showing a high phenotypic diversity (Nunes *et al.* 2018). Among the Atlantic Brown Booby populations monitored in Brazil, individuals from the São Pedro and São Paulo Archipelago are larger than in any other populations in the country (Nunes *et al.* 2018). In this archipelago, there is a great availability of pelagic flying fish (family Exocoetidae), which are their main prey (Jacoby *et al.* 2023).

On the other hand, in the Moleques do Sul Archipelago, the southern boundary of the species' distribution in the South Atlantic Ocean, the Brown Booby diet fishery discards contribute ~ 50% of the diet (Branco et al. 2005). Among the main prey species reported are Atlantic Midshipman *Porichthys porosissimus*, Banded Croaked *Paralonchurus brasiliensis*, Bigtooth Corvina *Isopisthus parvipinnis*, and Rough Scad *Trachurus lathami* (Branco *et al.* 2005). Considering that Brown Booby dives are fairly shallow, those fish in the diet that are classified as demersal can be attributed to fishery discards (Branco 2001, Yoda & Kohno 2008, Mellink et al. 2014, Mancini et al. 2023). Thus, it is likely that variation in diet composition, foraging behavior and foraging areas are influenced by the spatial distribution of fisheries (Jacoby et al. 2023). Although the diet of Brown Boobies breeding in Moleques do Sul is known to show high rates of discarded fish species (Branco et al. 2005, Branco et al. 2010), there is no knowledge of how these seabird-fishery interactions occur.

Our main goals in this study were to (1) identify Brown Booby foraging areas of those nesting in the Moleques do Sul Archipelago, (2) determine the species' diet in this archipelago and (3) investigate the influence of environmental features – oceanographic and fishing-related – on the species' foraging habitats.

MATERIAL AND METHODS

Study area

Sampling was conducted on Maior Island in the Moleques do Sul Archipelago (27°50'S, 48°25'W), state of Santa Catarina, southern Brazil. Moleques do Sul is located 8.25 km from Santa Catarina Island and 14 km from the continent. Maior Island, which has an area of 9.86 ha, is formed by granite rocks and is predominantly covered by bush and herbaceous vegetation (Bege & Pauli 1989, Salvador & Fernandez 2008). Three seabird species breed on Maior Island: Kelp Gull *Larus dominicanus,* Magnificent Frigatebird *Fregata magnificens,* and Brown Booby (Branco 2003). The archipelago, a Conservation Unit, is within the Serra do Tabuleiro State Park, which is an Intangible Zone due to its importance as a seabird breeding ground and the only occurrence area of an endemic mammal, the Santa Catarina Guinea Pig *Cavia intermedia* (listed as Critically Endangered by the IUCN Red List; Roach 2016). Brown Booby breeding population size is an estimated ~1600 individuals (Branco et al. 2010).

Field sampling

During the chick-rearing period of September 2022, 20 Brown Booby individuals (females = 11, males = 9) were equipped with miniaturized GPS loggers (Axy-Trek Marine; TechnoSmart, Italy) set to store 1 fix/10 s for three days. Tag mass was 11 g, equivalent to 0.84% body weight of Brown Boobies. Individuals were captured on their nest using a hand-net during chick rearing. The loggers were attached using Tesa® tape to the three central tail feathers following Weimerskirch et al. (2005). From the 20 individuals marked, we retrieved 19 devices, which were quickly removed with a scissors. Birds were ringed with numbered metal rings provided by CEMAVE and manually released back to their nest. Fourteen spontaneous regurgitations were obtained during birds' handling and stored in plastic bags for further analysis. This study was conducted under the approval of the Ethics Committee on Animal Use CEUA 14.2019 and the Research Authorizations IMA 31562-2022 and SISBIO 73286-4.

Data analysis

Diet. Among the 14 diet samples, all prey specimens that were in a good state of conservation were identified at the species level using reference guides (Figueiredo & Menezes 1997, Fischer *et al.* 2004), measured, and weighed. We calculated the

frequency of occurrence (FO%) as the number of samples of each prey species relative to the total number of samples (regurgitations). We also calculated the Index of Relative Importance (IRI) of each prey species following the equation: IRI = FO (%W+%N), where FO represents the frequency of occurrence, %W represents the weight percentage, and %N is the abundance percentage. Species were then classified by habitat and depth occurrence range (Chao 1978, Cervigón & Fischer 1979, Whitehead 1988, Starnes 1988, Cervigón 1993; Figueiredo *et al.* 2002, Riede 2004).

Trip metrics. Using R statistics in the track2KBA package (Beal *et al.* 2021), we extracted the following foraging trip metrics: Maximum Distance from Colony (km), Cumulative Distance (km), and Trip Duration (h), using the function '*tripSummary.*' Maximum Distance from Colony means the distance from the nest to the furthest tracked point, in a straight line. Cumulative Distance means the total distance traveled during a trip. Trip Duration means the time between the first point sampled at the beginning of a trip to the return time, arriving at the colony. We used the function '*tripSplit'* to exclude points within 3 km of the colony to determine the start of foraging trips and to exclude incomplete trips from the data. The function '*estSpaceUse'* was used to estimate areas of restricted search using the First Passage Time analysis, calculating 25, 50, and 75% kernel utilization distributions (KUD) for individuals of each sex. The smoothing parameter (*h*) was calculated using the '*findScale*' function. We assumed areas of 50% utilization distribution as 'core' foraging areas, representing areas in which birds spend 50% of their time (Lascelles *et al.* 2016). We tested for intersexual differences in Maximum Distance from the Colony, Cumulative Distance, and Trip Duration using a non-parametric Wilcoxon Rank Sum test after testing data for normality using a Shapiro-Wilk test.

Classification of foraging areas. We used a trajectory segmentation analysis to identify, from the GPS locations, likely foraging locations. The Expectation-maximization binary clustering ('*EmBC*') is a general purpose, unsupervised, multivariate, clustering algorithm that uses velocity and turning angle to classify locations into four behavioral states: (1) high velocity and low turn (HL; "traveling"), (2) low velocity and low turn (LL; "resting"), (3) high velocity and high turn (HH; "extensive search"), and (4) low velocity and high turn (LH; "intensive search") (Garriga 2016). This approach has proven effective across a wide array of species with a set of benefits, such as reduced

need for supervision, fewer pre-existing assumptions, and lower computational demands (Garriga *et al.* 2016, Bennison *et al.* 2018, Denhard *et al.* 2022, Finger *et al.* 2023). For the analysis of habitat use, we used locations classified as LH and HH as foraging areas, and locations classified as LL and HL as non-foraging areas (Mendez *et al.* 2017, Zango *et al.* 2020).

Environmental variables. Fishing data was extracted from the Global Fishing Watch dataset (http://globalfishingwatch.org/), which contains spatial data on daily fishing activity worldwide. This is an open-access database that provides data on the fishing effort of active vessels larger than 15 m, using remote sensing and convolutional neural networks to classify fisheries through Automatic Identification System (AIS). The latter is a very high frequency (VHF) radio-based open access tool that supports safe navigation and fisheries monitoring (Longépé *et al.* 2018, Burger *et al.* 2019). We downloaded a raster file of daily trawl fishing effort (h) at a 0.01° grid cell resolution (~ 1 km) of the exact days Brown Boobies were tracked (21-24 September 2022), filtered by gear type, using the Brazilian Exclusive Economic Zone (EEZ) as the layer for download. Procedures used for fishing data extraction can be accessed at https://www.youtube.com/watch?feature=shared&v=tUEEuR_U5Bw.
Oceanographic variables (chlorophyll-*a* and sea surface temperature) were obtained from the Giovanni Browser (https://giovanni.sci.gsfc.nasa.gov/giovanni/). Chlorophyll-*a* concentration (mg m^{-3}), a proxy for phytoplankton concentration, and sea surface temperature (°C), were downloaded for a spatial resolution of 0.04° (approx. 4 km) as a monthly mean composite for September 2022. Bathymetric data was downloaded from the ETOPO1 Global Relief Model (https://www.ncei.noaa.gov/products/etopo-global-relief-model) with a spatial resolution of 0.01° (~1 km) (Fig. 1).

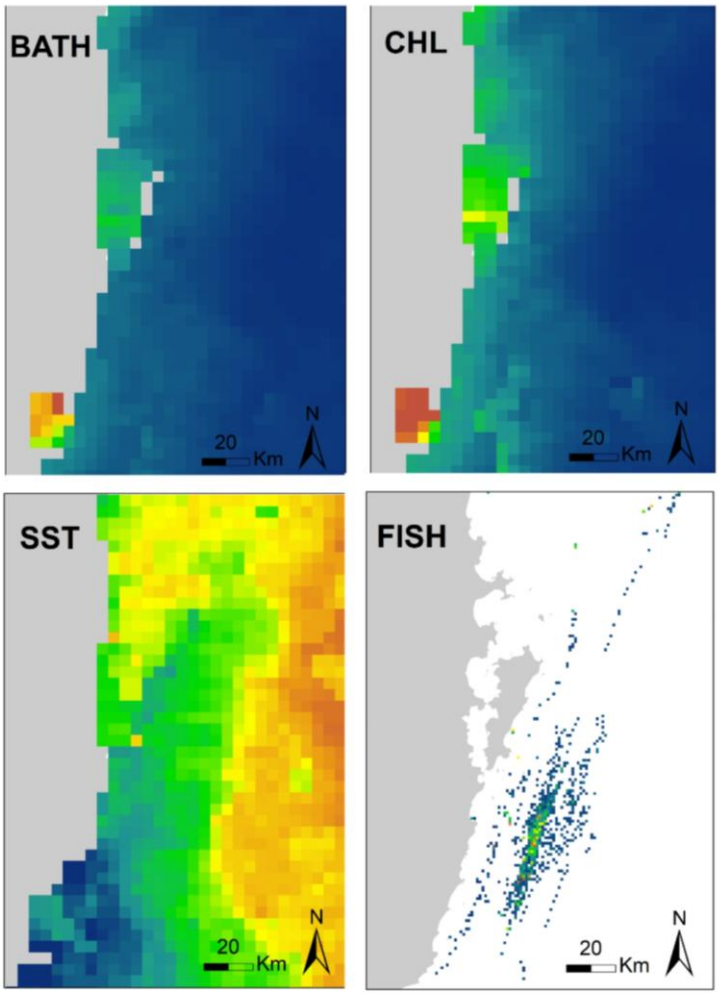


Fig. 1. Oceanographic and fishing-related variables used to model Brown Booby foraging habitat in waters of the Moleques do Sul Archipelago.

Habitat use. Firstly, we standardized predictive variables (SST, chlorophyll-*a,* bathymetry, and fishing effort) to the broader extent of 0.04°, projection, and resolution using the R package "*raster.*. Then we extracted habitat variable values from both foraging and non-foraging points previously classified by the *EmBC,* using the "*extract"* function of the "*raster*" package. We ran a binomial generalized linear model (GLM) and a binomial generalized linear mixed model (GLMM) using sex as a random effect, to fit Brown Booby foraging areas assuming (1) foraging and (0) non-foraging, using the "*glmer*" of the "*lme4*" R package. The "*scale"* function was used to normalize predictive variables. Firstly, we tested for multicollinearity among predictive variables using the "*cor*" function of the "*MASS"* R package. Then, we only included variables

not correlated with others in the models (Fishing and Chlorophyll-*a* Concentration). Additionally, we calculated Variance Inflation Factors (VIFs) using the "*vif*" function in R to ensure no significant multicollinearity between the variables used in the final model. We then ran separate models (GLM and GLMM) and chose the one with the lower AIC for the final model. Then, for the final model, we decided to use the GLM through the following equation:

behavior ~ chl + fish, family = binomial

Where: chl = chlorophyll-a concentration and fish = fishing effort.

RESULTS

Diet

We identified seven fish species despite almost half of the samples being overly digested and, therefore, identification at the species level was not possible. Scianidae was the most representative, with four species: *Isopisthus parvipinnis, Paralonchurus brasiliensis*, and *Larimus breviceps*, *Cynoscion guatucupa* (Table 1). The most frequent and important species was *I. parvipinnis* (FO% = 21.43, IRI = 10.76), followed by *C. guatucupa* (FO% = 14.29. IRI = 9.94). We also found fishes from the family Engraulidae, Mullidae, and Priachantidae. We found mostly coastal fish species derived from demersal, benthic, and estuarine habits, occurring from 1 to 200 m depth.

TABLE 1

Prey species found in Brown boobies' diet in Moleques do Sul, classified by habitat and depth range FO% = Frequency of Occurrence, IRI = Index of Relative Importance.

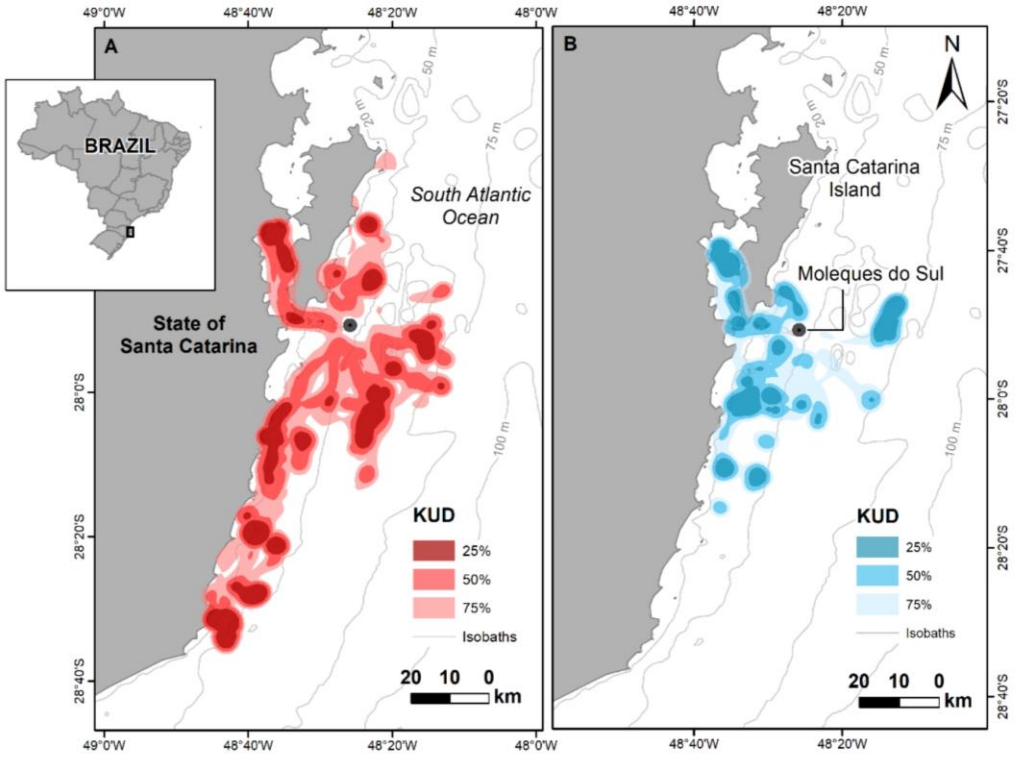
Taxon	Depth range	Habitat	Abundance	Length (cm) min-max	Biomass (g)	FO%	IRI
Osteichthyes							
Engraulidae							
Cetengraulis edentulus	10 - ? m	Pelagic/Estuarine	3	11.5 - 17.5	66.82	7.14	2.00
Scianidae							
Paralonchurus brasiliensis	? - 50 m	Estuarine/Demersal	2	17 - 17.5	103.88	14.29	4.01
Larimus breviceps	1 - 60 m	Coastal/Benthic	2	10.5 - 14	45.89	7.14	1.35
Cynoscion guatucupa	1 - 194 m	Benthopelagic	4	13.1 - 17.3	159.91	14.29	6.94
Isopisthus parvipinnis	1 - 45 m	Estuarine/Demersal	4	13.5 - 16	170.31	21.43	10.76
Mullidae							

Mullus argentinae	20 - 60 m	Demersal	3	12.4 - 14.2	63.14	14.29	3.92
Priacanthidae							
Priacanthus arenatus	10 - 200 m	Reef	2	14 - 16.5	129.15	14.29	4.58
Unidentified					753.11		

268

269 **Foraging trips**

270 We successfully tracked 82 complete Brown Booby foraging trips, 45 trips by females
271 and 37 by males (Fig. 2). Most trips lasted less than 2 h, reached about 25 km from the
272 colony, and encompassed about 50 km of cumulative distance traveled (Fig. 3). The
273 highest Cumulative Distance was reported for a female who traveled a total distance of
274 232 km, while the shortest trip was traveled by a male (21 km). Regarding mean values,
275 males showed a mean Cumulative Distance of 62.8 km and females of 83.2 km (Table
276 2). Mean Trip Duration was similar among sexes (females = 2.2 h, males = 2.0 h).
277 However, Maximum Distance was the only variable to show a significant difference
278 between sexes ($p = 0.0002$), where females (29.9 km) traveled farther from the colony
279 than males (22.8 km) (Fig. 3). Females traveled farther southwards, while males mostly
280 foraged close to the archipelago (Fig. 2).



281

Fig. 2. Foraging distribution of 19 Brown Boobies (red = females, blue = males) breeding in the Moleques do Sul Archipelago tracked for 3 d during chick rearing. Color scales represent 25, 50, 75, and 95% kernel utilization distributions (KUD).

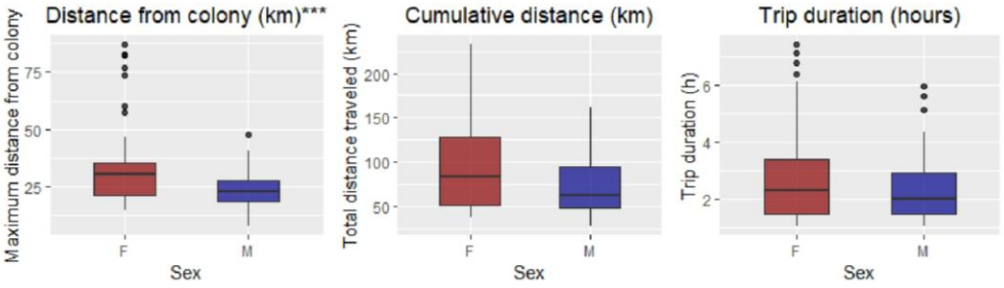


Fig. 3. Boxplots of trip metrics (Maximum distance from colony, Cumulative distance, and Trip duration) per sex (females = red, males = blue) expressed as Median [Q1-Q2]. Asterisks *** indicate significant differences.

TABLE 2

Foraging trip metrics of Brown Boobies (n = 19) Results for metrics are given as median [Q1-Q3] with range (min-max) in parenthesis

Metric	Females	Males	Statistics
Total number of trips	45	37	
Trip duration (h)	2.2 [1 – 3] (1 – 7.4)	2 [1 – 3] (1 – 5.9)	W = 910, p = 0.4751
Maximum distance (km)	29.9 [21 – 34] (14.6 – 86.9)	22.8 [18 – 47] (7.4 – 47.6)	W = 1156, p = **0.0002***
Cumulative distance (km)	83.2 [51 – 127] (37.4 – 232.2)	62.8 [47 – 94] (27 - 161)	W = 1006, p = 0.1072

Habitat use

Chlorophyll-*a* was the most important and only significant variable in our model with a positive relation with foraging probability (Table 3). The null deviance of the model was 96.732, while the residual deviance was 96.571, indicating a significant improvement in the fit with the inclusion of the predictor variables. The Akaike Information Criterion (AIC) for the adjusted model was 96.577. The variance inflation factors (VIF) for the predictor variables were 1.055 for “chl” and 1.055 for “fish”,

indicating that there are no significant multicollinearity issues in the model. Figure 4 summarizes the influence of each variable on the model.

TABLE 3

Results of the Generalized Linear Model used to fit Brown Booby foraging areas in waters of the Moleques do Sul Archipelago, Brazil (**) means significant contribution of the variable to the model.

Variable	$\beta \pm$ SE	z-value	p-value
Intercept	-1.208 ± 0.008	-151.93	**< 2e-16**
Chlorophyll-a	0.1 ± 0.008	12.544	**< 2e-16****
Fishing Effort	0.006 ± 0.008	0.699	0.485

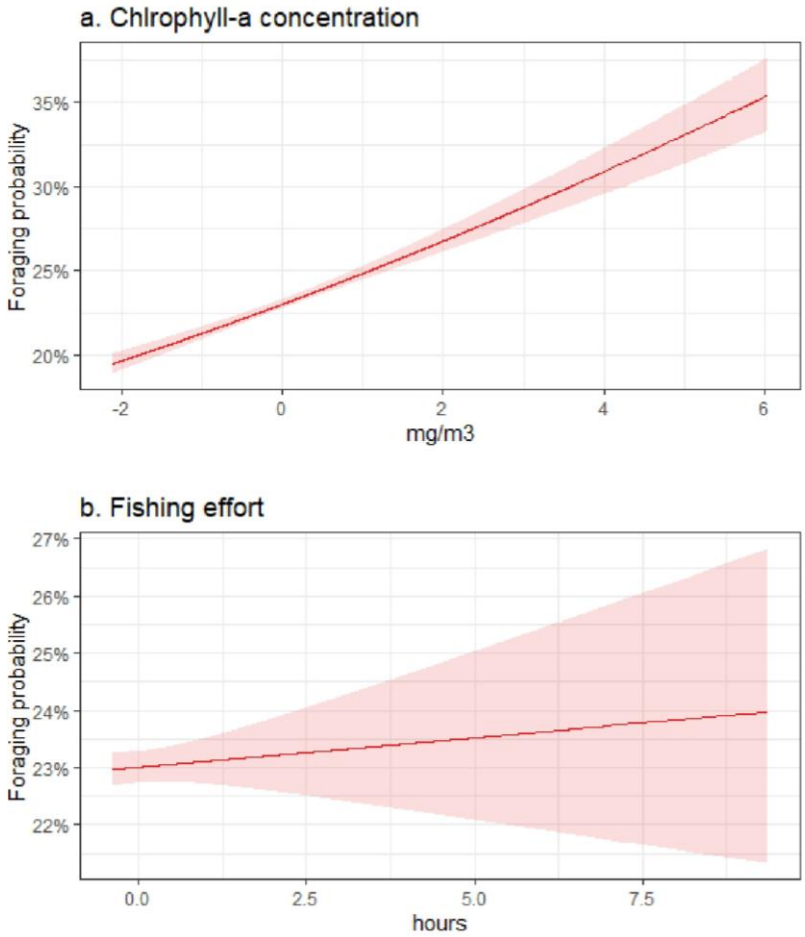


Fig. 4. Foraging probability of Brown Boobies in response to chlorophyll-*a* (A) and fishing effort (B).

Spatial overlap

Although our model showed that fishing effort was not one of the main variables influencing Brown Booby foraging behavior, we constructed a map to visualize the spatial overlap of foraging core areas (KUD 50%) and trawl fisheries operating in the study area during the period when birds were tracked (Fig. 5).

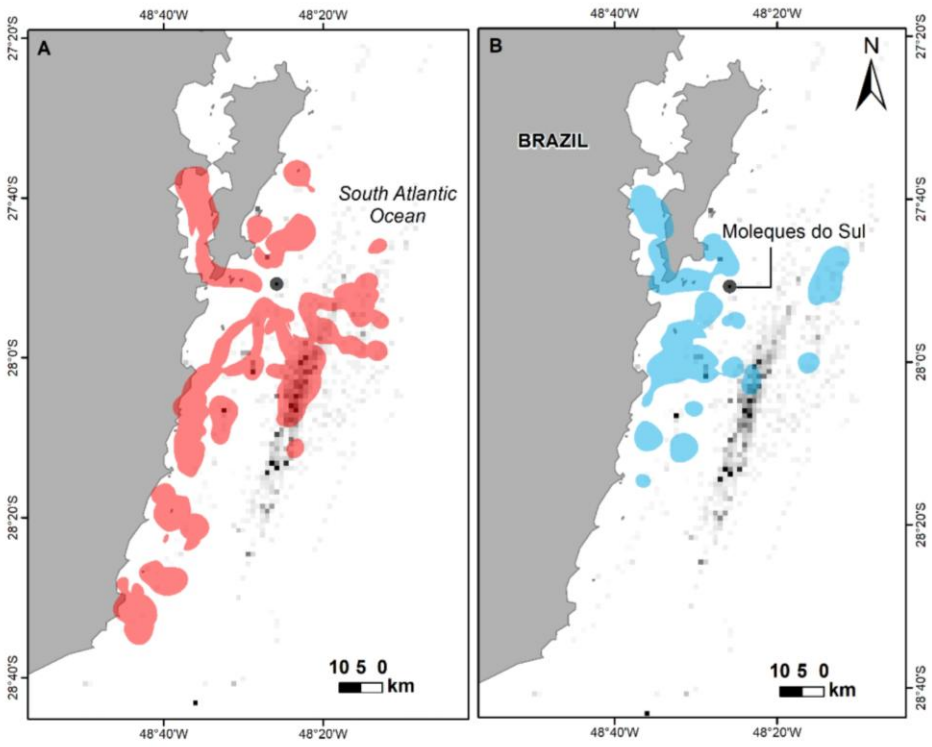


Fig. 5. Spatial overlap between Brown Booby core areas (KUD 50%) and mean trawl fishing effort during the study period. Fish intensity is expressed in grayscale and increases from light grey to black

DISCUSSION

We found that boobies undertook foraging trips averaging ~ 2.1 h, reaching an average of 29.9 km from the colony for females and 22.8 km for males. There was a significant sex-related difference, whereby females performed longer distance trips but not for trip duration nor cumulative distance. Chlorophyll-*a* was the only variable correlating with Brown Booby foraging areas. Against expectation, fishing effort was not a significant predictor of foraging areas, nor was coastal bathymetry, at depths of < 80 m. This is the first study concerning the spatial foraging behavior of the Brown Booby in Moleques do

Sul Archipelago. Previous studies mainly focused on diet, breeding biology, and demography (Branco 2004, Branco *et al*. 2005, Branco *et al*. 2013). However, these studies reported data collected before 2007, leaving a temporal gap in information of more than a decade regarding the species biology and ecology in this region of Brazil.

Diet

Our results are in accordance with previous data on Brown Booby diet in the waters of Moleques do Sul (Branco *et al.* 2005). Branco *et al.* 2005 reported *P. brasiliensis* and *C. edentulus* as the most important prey species, while in our study the most important species (highest IRI) were *C. guatucupa* and *I. parvipinnis.* Although most studies attribute the presence of demersal fishes in Brown Booby diet to trawl fishery discards, some of these species (e.g., *C. guatucupa* and *I. parvipinnis*), desspite being benthopelagic and demersal species, respectively, can occur as shallow as 1 m deep in shallow waters (Chao *et al.* 1978, Figueiredo *et al.* 2002). Mancini *et al.* (2023) also found that demersal species comprised 54% of the ingested prey of boobies in the Santana Archipelago, also reporting high Indexes of Relative Importance for *C. guatucupa* and *I. parvipinnis.* In that study, it was suggested that the presence of such demersal species in the diet is influenced by the interactions with trawl fishing vessels, reporting that Brown Boobies feed on discards throughout the year (Mancini *et al.* 2023). On the other hand, in the Cagarras Archipelago, despite the presence of trawl fisheries, the occurrence of prey species associated with discards was low, with high availability of engraulids and clupeids around the colony (Jacoby *et al.* 2023). We also found fish species that occur in estuarine areas *P. brasiliensis, I. parvipinnis* and *C. edentulus*, and despite being commonly reported species in Brown Booby diet, the estuarine habitat is not often mentioned.

Considering our results that show little spatial overlap and no significant influence of trawl fisheries on Brown Boobies foraging behavior and areas in our study (Figs. 3, 5, respectively), nor the depth range of the main prey fish species found in the diet, it is reasonable to assume that Brown Boobies can be naturally fishing demersal species rather than only obtaining it through fishery discards, as previously assumed, at least in this period of the year. The species' diet varies seasonally in this archipelago, as affected by prey life cycle events and the supply of resources from fishing discards. The

latter is more important when shrimp fishing is more intense, especially in the summer (Branco *et al.* 2005, Branco *et al.* 2013).

Foraging trips and habitat use

GPS tracking has been used widely to investigate seabird ecology and seabird-fishery interactions during the past two decades (Grémillet *et al.* 2004, Votier *et al.* 2010, Le Bot *et al.* 2018). In Brazil, there are available Brown Booby tracking data for only two locations: São Pedro e São Paulo Archipelago (0°55'N, 29°20'W) (Nunes *et al.* 2018) and Abrolhos Archipelago (17°55′S, 38°56′W) (Nunes *et al.* 2022). Brown Boobies from São Pedro e São Paulo performed trips of 1 h duration on average, with a mean maximum distance from the colony of 7 km (Nunes *et al.* 2018). The short and fast foraging trips in São Pedro e São Paulo can be explained by the great food availability – especially flying fish from the Exocoetidae family - in that region (Mancini & Bugoni 2014). In our study, Brown Boobies performed much longer trips.

On the other hand, Brown Boobies from Abrolhos traveled an average 43 km from the colony, showing a mean trip duration of 4 h (Nunes *et al.* 2022). In Tinhosa Grande, São Tomé and Príncipe, a pelagic island off the coast of western Africa, females performed foraging trips averaging 11.4 h and reaching 92.7 km from the colony, while males performed slightly shorter trips of 9.5 h, reaching 64.4 km from the colonyThe diet of Brown Boobies there was based on pelagic fish rather than species associated with fishing discards. (Correia *et al.* 2021).

Issues with fishery data

Foraging behavior of seabirds is mostly shaped by density-dependent factors as well as prey availably, which results from several oceanographic processes and local conditions (Soanes *et al.* 2014, Nunes *et al.* 2017, Cox *et al*. 2018, Finger *et al.* 2023). However, it can be also influenced by anthropogenic activities such as fisheries (Weimerskirch 2007, Votier *et al.* 2010, Bertrand *et al.* 2012, Patrick *et al.* 2015). Our results show that high chlorophyll-*a* concentrations are positively related to foraging areas, but not trawl fishing effort Figure 6. In contrast to previous studies that attribute 50% of the Brown Booby diet in Moleques do Sul to the consumption of trawl fishing waste (Branco *et al.* 2005), our results revealed a low overlap between foraging areas and areas of fishing effort monitored by the AIS system. This was especially true in areas very close to the

399 coast where these vessels do not usually operate, which indicates that the birds may be
400 preying naturally on near-surface but benthic prey. However, it is important to highlight
401 that we only used data extracted from the AIS system, which comprises only vessels
402 over 24 m in length (measured from the base of the hull to the top of the superstructure)
403 by local regulations. Smaller vessels could be operating closer to shore.
404
405 Some studies have pointed out the limitations of using AIS system to monitor fishery
406 activities because it can underestimate the operation of nondeclared and/or illegal
407 fishing vessels (Weimerskirch *et al.* 2020). Navaro-Herrero *et al.* (2023), for instance,
408 found that 27% of the radar events in the Balearic, Canary and Cabo Verde islands did
409 not overlap with reported fishing vessels between June and July of 2019 and 2020. In
410 that study, three procellarid seabird species (*Calonectris diomedea*, *Calonectris*
411 *borealis*, and *Calonectris edwardsii*) were equipped with radar detector tags capable of
412 recording signals from vessels, and used as biomonitors of illegal fisheries by
413 comparing those signals with the AIS system. Considering that the consumption of
414 fishery discards may affect seabird health and breeding success (Romano *et al.* 2006,
415 Grémillet *et al.* 2008), it is mandatory for researchers to better understand the response
416 of these predators to changes in historical fishing activity. In Santa Catarina coastal
417 waters, for instance, the fishing structure has widely changed during past decades, being
418 mostly represented by otter and pair bottom trawls in the 1970s, double-rig trawls for
419 fish and shrimp, and bottom gill nets in the mid-1980s, and bottom longlines in the
420 upper slope in the early 1990s (Andrade 1998).
421
422 **CONCLUSION**
423
424 Our study provides novel data on the foraging ecology of the Brown Booby in southern
425 Brazil. Differently than expected based on the available literature, we did not find a
426 consistent influence of trawl fishing activity on foraging areas, nor a high overlap
427 between trawl fishing areas and core areas used by boobies around the Moleques do Sul
428 archipelago. We found fish prey species similar to those found in previous studies, but
429 we identify the possibility of a greater contribution of naturally caught prey than
430 previously thought, and consequently a smaller contribution of fishing discards to the
431 diet, at least in September when shrimp fishing is less intense in the region. Sustainable
432 fisheries management alternatives to deal with discards are essential to ensure biological

conservation and fisheries productivity. Several measures have already been applied to minimize the deleterious effect of discards in different parts of the world, but in Brazil, there is still a long way to go towards the sustainable exploitation of marine resources.

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AUTHOR CONTRIBUTIONS

VRF Benemann: conceptualization, sampling design, field sampling, formal analysis, software, and writing; DH Corá: field sampling and writing; and MV Petry: conceptualization, funding acquisition, supervision and writing.

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702

CAPÍTULO 2

Foraging efficiency of a generalist pantropical seabird, the Brown Booby *Sula leucogaster* (Boddaert, 1783), in contrasting prey availability scenarios

Victória Renata Fontoura Benemann[1]*, Bianca Costa Ribeiro[1], Jessica Fernanda Hoffmann[2], Maria Virginia Petry[1]

[1]Laboratory of Ornithology and Marine Animals, University of Vale do Rio dos Sinos, Av. Unisinos, 950, São Leopoldo, RS 93022-000, Brazil.

[2]Technological Institute in Food for Health, University of Vale do Rio dos Sinos, 93022-750 São Leopoldo, RS, Brazil

*Corresponding author: victoriabenemann@gmail.com

Abstract

The Optimal Foraging Theory states that animals use different strategies to maximize energy intake by balancing energy gains and costs during foraging. For seabirds, high-quality prey rich in lipids and proteins enhances foraging efficiency, critical for reproduction and survival. On the other hand, prey choices may demand differential foraging efforts and energy expenditure to obtain feeding success. We integrated movement analysis (GPS, accelerometry, time-depth recorders) with dietary data (food load and prey energy density) to evaluate the foraging efficiency of brown boobies (*Sula leucogaster*) breeding in two Brazilian archipelagos with distinct scenarios of prey availability: Moleques do Sul (MS) and São Pedro e São Paulo (SPSP). We compared (1) prey composition, food load and energy density (kJ), (2) foraging effort metrics (maximum distance from colony, cumulative distance, trip duration and diving depth), and (3) energy expenditure and energy gain of chick-rearing brown boobies during three days between the archipelagos. We observed significant differences in protein content, lipids content, and food load energy density between sites, as well as in maximum distance from colony, diving depth, energy expenditure, and energy gain between the two colonies. We conclude that brown boobies from SPSP obtained a greater foraging efficiency than those from MS, which probably reflects differences in prey availability such as abundance, taxonomic composition and spatial distribution in the water column (benthic vs. epipelagic). Accelerometry and the calculation of Vectorial Dynamic Body Acceleration (VeDBA) are increasingly used to estimate the foraging energy costs of free-

living animals, and when combined with dietary data it can provide precise information on foraging efficiency. Bioenergetic studies on foraging efficiency and feeding plasticity are crucial to understanding how seabirds adapt their diet and foraging strategies to fluctuations in prey availability and environmental challenges.

Key-words: Bioenergetics, accelerometers, VeDBA, macronutrient, energy density

Introduction

Optimal foraging theory (OFT) is a concept in ecology that focuses on explaining how animals choose their feeding habitats and resources to maximize their energy intake, usually measured by the energy gained per unit time from foraging, thus predicting the most profitable feeding strategy based on energy costs and gains during food foraging (MacArthur and Pianka, 1966). It states that the ratio between foraging effort and energy gain will determine whether the choice of a particular prey is favorable to the predator since the energy gain provided by the ingested resource must compensate for the energy expended in its capture and consumption, thus improving the foraging efficiency (Norberg, 1977). Foraging efficiency is the measure of how much food an animal gathers given the amount of energy it spends during that process, in a way that maximizes energy gain while minimizing energy expenditure (Mittelbach, 1981; Lescroël et al., 2010). It is often defined as the ratio of energy gained over energy spent while foraging and involves both the time spent searching for resources and the time spent processing or handling them (Weimerskirch et al., 2003). Efficiency is not only dependent on time but also on the energy costs associated with foraging movements, which are determined by the balance between the energy obtained from the resource and the energy expended during its searching and handling it (Elliott et al. 2009; Bennison et al., 2021; Sotillo et al., 2019; Sutton et al., 2023). Because predators may gather more with less effort, areas with abundant prey availability are typically more effective foraging grounds (Enstipp et al., 2007; Goundie et al., 2015; Waggitt et al., 2018).

The energy density and nutritional quality of prey play a crucial role in the foraging efficiency of seabirds, directly affecting their ability to meet energy demands to sustain long-distance foraging trips and to obtain breeding success (Wanless et al., 2005; Jodice et al., 2006; González-Medina et al., 2018). Prey rich in essential nutrients (e.g., lipids and proteins) enable seabirds to optimize calorie intake. Paradoxically, low-quality food resources may impose high energy costs and extended foraging time to fullfill the

63 birds' nutritional demands, potentially decreasing overall foraging efficiency (González-
64 Medina et al., 2018). Several studies demonstrate that the lipid:protein ratio represents
65 the most important aspect in assessing the nutritional quality of a predator's diet, and that
66 the consumption of prey with insufficient levels of these two nutrients can lead to losses
67 in the fitness of reproductive adults and consequently in the reproductive success of
68 populations, since a diet rich in proteins and lipids positively influences the weight gain
69 and survival of nestlings of seabirds in the growth phase (Romano 1999, Anthony et al.
70 2000, Visser 2001; Sorensen et al. 2009). While a diet rich in lipids provides sufficient
71 energy for the maintenance of adult individuals, and still with low metabolic costs when
72 compared to protein, individuals in the growth phase require a greater demand of this
73 second macronutrient for the synthesis of tissues at this stage of the life cycle (Roby et
74 al., 1991; Anthony et al., 2000).

75 The junk-food hypothesis (Alverson, 1992) states that individuals consuming
76 resources of low nutritional and energetic value tend to have reduced breeding success
77 because dietary deficiencies affect the growth and cognitive abilities of offspring (Piatt
78 and Anderson, 1996; Kitaysky et al., 2005; Wanless et al., 2005, Romano et al. 2006).
79 Several studies suggest that fisheries discards represent a nutritionally poor food supply
80 for seabirds. They often have low-calorie, protein, and lipid contents, and other essential
81 nutrients that seabirds need for optimal health, growth, and reproduction (Grémmilet et
82 al., 2008, Österblom et al., 2008). While discards may provide an easily accessible and
83 often abundant food source in areas of intense fishing activity, requiring little foraging
84 effort to catch, these discarded resources' nutritional quality can be inferior to seabirds'
85 natural prey (Pichegru et al., 2007; Bicknell et al., 2013).

86 Fishery discards are non-target fish and other marine species, captured
87 accidentally in fishing gears that do not meet commercial standards (e.g. undersized,
88 underaged specimens) and thus are discarded by fishing vessels at sea (Bartumeus et al.,
89 2010; Zeller et al., 2018; Sherley et al., 2019). Despite discards being an extra food
90 resource, several studies show that these species are nutritionally poorer than natural prey
91 (Grémillet et al., 2008; Bicknell et al., 2013), and do not compensate in terms of energetic
92 gain (Pichegru et al., 2007; Le Bot et al., 2019). The importance of fishing discards as a
93 food resource for seabirds is so great in certain locations that, for example, it is estimated
94 that in the North Sea - one of the highest discard-producing regions in the world - discards
95 are responsible for supporting more than 3 million seabirds by 2010 (Sherley et al., 2019).

The Brown Booby (*Sula leucogaster*) is a broadly distributed pantropical seabird species that exhibits a high level of trophic plasticity and can adapt its diet in response to the relative availability of prey, often considered a generalist species (Nunes et al., 2017; Jacoby et al., 2023). The interaction of this species with the trawling fleet, especially shrimp fishing, has been widely reported in several locations along the Brazilian coast (Branco, 2001; Branco et al., 2005; Carniel and Krull, 2012) and in other locations throughout its global geographic distribution (Blaber et al., 1995; Hill and Wassenberg, 2000, Cannell et al., 2022). Trawl fisheries produce the majority of global fishery discards worldwide. This occurs because trawl nets, which are dragged across the seafloor, often are made with a very fine mesh that captures great amounts of unwanted specimens, non-target species, and undersized and/or juvenile individuals (Gilman et al., 2020, Kennelly and Broadhurst, 2021; Barnes et al., 2022).

In the Moleques do Sul Archipelago (MS), Southern Brazil, 50% of brown boobies' diet composition is attributed to derive from fishing discards (Branco, 2005). The species in this archipelago exhibit significant seasonal fluctuations in its diet, primarily due to the life cycle events of its prey and the availability of resources from fishery discards during specific periods of the year, particularly during the intensified shrimp fishing season in summer (Krul, 2004; Branco 2001; Branco et al., 2005). In São Pedro e São Paulo (SPSP), a tropical archipelago also in Brazil, brown boobies feed mostly on pelagic flying fish of the family Exocoetidae, exhibiting a much narrower trophic niche than in MS (Both and Freitas, 2001; Jacoby et al., 2023). *Exocoetus volitans* is a prevalent species, constituting 71% of its diet during the summer months (Naves et al., 2002), and is regarded as protein-rich prey (Harewood et al., 1993).

The marine landscape, oceanographic characteristics, and anthropic impacts on the archipelagos differ greatly. Moleques do Sul (27°51'S, 48°25'W) is a coastal archipelago located 14 km from the South American continent (Figure 1), which is under the continuous influence of the Brazilian Current, seasonally affected by the upwelling of cold waters from the Malvinas Current (Castro and Miranda, 1998), with intense fishing activity in the surrounding area. São Pedro e São Paulo (00°55'N, 29°20'W), on the other hand, is a pelagic archipelago located within an environmental protection area at 1,100 km from South America and 1,824 km from Africa and is inserted in the Equatorial System of Marine Currents, under the direct influence of the South-Equatorial Current and the submerged Equatorial Current (Costa Campos et al., 2005; Knoppers et al. 2009).

129 The location, human activity and species composition reflected in the distinct
130 composition of prey species in the boobies' diet as well.

131 Recently, accelerometry data have been used to investigate the bioenergetics of
132 free-ranging animals with greater precision (Bennison et al., 2021; Sutton et al., 2023).
133 The most used technique to estimate energy expenditure from accelerometers is the
134 calculation of vectorial dynamic body acceleration (VeDBA) due to its correlation with
135 other traditional measures of energy expenditure such as quantifying the volume of
136 oxygen utilized by muscles and heart rates (Laich et al., 2011; Gleiss et al., 2011; Qasem
137 et al., 2012; Miuwa et al., 2015). These traditional methods are considered more invasive
138 and therefore the use of accelerometry is increasingly encouraged (Wilson et al., 2020).

139 In this study, we combined the use of movement analysis (GPS, accelerometry,
140 and time depth recorders) with dietary data (macronutrient composition) to assess the
141 foraging efficiency of brown boobies breeding in two environmentally distinct
142 archipelagos in Brazil, with contrasting scenarios of prey availability. Our main goals
143 were (1) to compare the diet and nutritional composition and energy density of brown
144 booby prey, (2) to compare foraging effort metrics (cumulative distance, maximum
145 distance from colony, trip duration, diving depth, and energy expenditure) and (3) to
146 compare the foraging efficiency (energy gain *vs.* energy expenditure) of brown boobies
147 between the two archipelagos (MS and SPSP).

148 **Material and Methods**

149 ***Field sampling***

150 We tagged 39 breeding brown boobies during chick-rearing period using Axy-
151 Trek Marine loggers set to store 1 fix/10 s for three days. The Axy-Trek Marine
152 (TechnoSmart, Italy) is a miniaturized data logger with an integrated GPS antenna, a tri-
153 axial accelerometer, and a time depth recorder (TDR), specifically engineered for marine
154 fauna. Logger's total mass was 11 g, equivalent to ~0.84% of brown boobies body weight.
155 From the 39 sampled individuals, 19 were tracked in MS (10 females, 9 males) in
156 September 2022, and 20 were tracked in SPSP (10 females, 10 males), in June 2022
157 (Figure 1). The loggers were attached using Tesa® tape to the three central tail feathers
158 following Weimerskirch et al. (2005). Birds were captured using a hand net directly from
159 the nest and measured (weight, bill length, wing length, tail length), ringed with numbered

metal rings provided by CEMAVE, and then manually released back to their nest. Spontaneous regurgitations were obtained during birds' handling, stored in plastic bags, and frozen until identification. This study was conducted under the approval of the Ethics Committee on Animal Use CEUA 14.2019 and the Research Authorizations IMA 31562-2022 and SISBIO 73286-4.

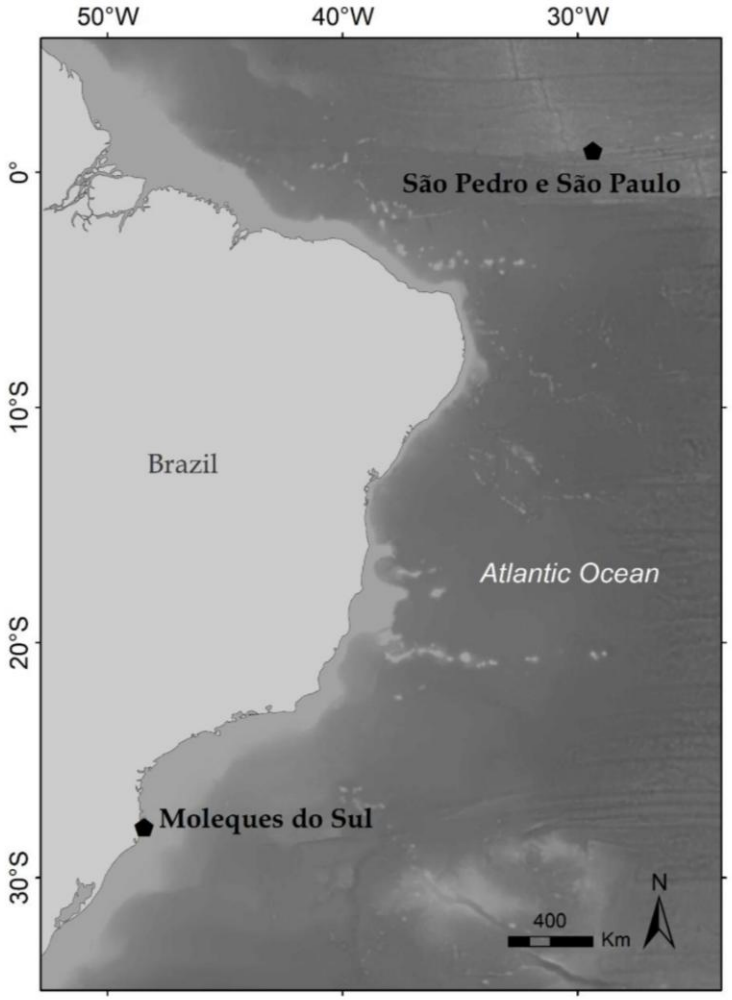


Figure 1: Location of Moleques do Sul and São Pedro e São Paulo Archipelagos, Brazil, where brown booby individuals were sampled.

Diet and macronutrient determination

Of the 39 individuals handled, we obtained 26 regurgitations: 14 from SPSP and 12 from MS. Diet samples were unfrozen, and then all prey specimens that were in a good state of conservation were identified at the species level using reference guides

(Figueiredo and Menezes, 1997; Fischer et al., 2004), measured, and weighed. For the remaining 13 tracked individuals that did not regurgitate, we used an average of food load mass for their respective sex. To obtain nutritional information, we used a pool including prey specimens of each sample. The fish in the best conservation state were crushed whole in an electric grinder. Subsequently, this biomass corresponding to the food load of each brown booby sampled was analyzed to determine the protein, lipid and water content (%). We used the Kjeldahl method for protein determination and an adaptation of the Bligh-Dyer method for lipids determination (Lutz, 1985). The water percentage was determined by drying the sample in an oven at 105 °C until constant weight. Macronutrient analyses were performed in the Technological Institute of Food for Health (itt Nutrifor) of the Universidade do Vale do Rio dos Sinos. To estimate prey energy density (kJ g-¹) from macronutrient data, we followed the method used by Anthony et al. (2000), adapted from Schmidt-Nielsen (1997), through the following equation:

$$Energy\ density\ (kJ\ g-^{1}\ wet\ mass) = (1 - WF)([LF\ .39.3] + [PF\ .17.8])$$

Where: WF is the water fraction, LF is the lipid fraction, and PF is the protein fraction of fish mass.

We then multiplied the energy density (kJ g-¹) of each sample by its total mass (g) to obtain the energy density of each food load (regurgitation).

Movement analysis

Foraging trip metrics

Utilizing R statistics within the track2KBA package (Beal et al., 2021), we derived the subsequent foraging trip metrics from the dataset: Maximum Distance from Colony (km), Cumulative Distance (km), and Trip Duration (hours) utilizing the 'tripSummary' function. *Maximum Distance from Colony (km)* refers to the straight-line distance from the deployment site within the colony nest to the furthest distant tracked location. *Cumulative Distance (km)* refers to the total distance traveled during a foraging trip. *Duration (hours)* refers to the interval from the initial sampling point at the commencement of a journey to the return time upon arrival at the colony. We employed the 'tripSplit' tool to eliminate points within 3 km of the colony, thereby identifying the beginning of foraging trips and excluding incomplete trips from the dataset. To process the diving information recorded by the TDR we used the diveMove R package (Luque,

2024). We extracted individual diving depths and calculated mean and maximum diving depths for each foraging trip (n = 182). A graphic of dives for each individual was plotted for visualization (Figure 6). We used the calculated trip metrics maximum distance from the colony (km), cumulative distance (km), trip duration (hours), mean and maximum diving depth (m) as proxies for foraging effort.

Acceleration metrics

VeDBA (Vectorial Dynamic Body Acceleration) is an emerging tool to estimate animals' energy expenditure from their movements and acceleration. This is a novel methodology in animal bioenergetics that enables the estimation of energy expenditure without the use of invasive methods, such as direct calorimetry or respirometry. VeDBA is calculated by summing the dynamic acceleration in the three directions - axes X (surge), Y (sway), and Z (heave) - resulting in a numeric value used as a proxy for energy expenditure. We calculated VeDBA from raw accelerometer data, only considering values collected within complete foraging trips (already filtered using the track2KBA package). Firstly, we calculated the average of each axis (X, Y, Z) to remove the static component of the acceleration, which is the gravitational acceleration. Then, we calculated VeDBA through the following equation:

$$VeDBA = \sqrt{X_{dynamic}^2 + Y_{dynamic}^2 + Z_{dynamic}^2}$$

VeDBA is a continuous value, and when it is equal to 0, it means that the animal is completely inactive, and then energy expenditure is zero. The higher the VeDBA value, the higher the energy expenditure is.

To estimate energy expenditure from accelerometers by converting VeDBA values to kilojoules (kJ), we followed the methods described by Bennison et al. (2021). This method assumes that the covariance between the rate of energy expenditure (kJ) and instantaneous VeDBA is linear, defined by slope k, which allows an estimate of kilojoules spent during that movement from a given VeDBA value. The process assumes that the amount of energy used during locomotion is equal to the animal's field metabolic rate (FMR) minus basal metabolic rate (BMR). The resulting value is defined as auxiliary energy expenditure (AEE), it is, the energy spent in a period of 24 hours by an animal only for movement. We obtained boobies' FMR from the FMR calculator corrected for

individual bird mass and colony latitude (Dunn et al. 2018), and BMR estimates through allometric equations proposed by Schreiber and Burger (2001) for sulids to transform VeDBA to kJ for each individual. We calculated VeDBA24 for each bird by summing VeDBA values for an entire day and then calculated a mean value for the three days, which was used in the prediction equation along with BMR and FMR estimations for the respective bird. By obtaining slopes *k* from the correlation VeDBA24 and AEE for each individual, we were able to estimate energy expenditure in kilojoules by multiplying *k* values by VeDBA24 values:

$$kJ = k * VeDBA$$

For more details on these calculations, see Bennison et al. (2021) and the Supplementary Material of this work. To evaluate the foraging efficiency, we calculated the final energy gain by subtracting food load energy density (kJ) from the energy expenditure (DBAkJ).

Statistical analysis

Diet and macronutrient

To test for significant differences in lipids (%), protein (%), energy density (kJ g^{-1}), and food load energy density (kJ) between archipelagos we used univariate tests (T-test and Mann-Whitney U) according to data distribution, after testing for normality and homogeneity of variances using Shapiro-Wilk and Levene's test, respectively. The significance level was assumed at $p < 0.05$.

Movement analysis

We tested significant differences between archipelagos for the following parameters of foraging efficiency: maximum distance from colony, cumulative distance, trip duration, mean diving depth per foraging trip, energy expenditure (DBAkJ) and energy gain (food load energy density minus energy expenditure) between archipelagos using univariate tests (T-test and Wilcoxon rank-sum test) according to data distribution, after testing for normality and homogeneity of variances using Shapiro-Wilk and Levene's test, respectively. The significance level was assumed at $p < 0.05$.

Results

Diet and macronutrients

We did not find any common prey species in the diet of the brown booby between the two archipelagos (Table 1). In MS, fish from the Scianidae family predominated, while in SPSP, fish from the Exocoetidae family predominated, both in abundance and biomass. The food load biomass was higher in SPSP ($\overline{x}$ = 163.65, σ = 83.6) than in MS ($\overline{x}$ = 98.61, σ = 33.39). We found a significant difference in the prey protein (t = -4.7995, df = 24, $p < 0.05$) and lipids (W = 124, $p < 0.05$) percentage between the archipelagos, where the protein fraction was higher in prey from SPSP and lipids in prey from MS (Figure 2). No significant difference was found when comparing the proportional energy density (kJ/g^{-1}) between prey from the two archipelagos (t = 1.6756, df = 24, $p > 0.05$), but when we considered the energy density of the total food load (kJ), a significant difference was found (t = -2.8809, df = 17.644, $p < 0,05$), where food loads from SPSP were more energetic (Figure 2). Mean and standard deviation of each nutritional parameter evaluated are expressed in Table 2.

291 Table 1: Prey species found in the brown booby diet in the archipelagos of
292 Moleques do Sul and São Pedro e São Paulo.

	Abundance	Total biomass (g)
	Moleques do Sul (n = 12)	
Osteichthyes		
Engraulidae		
Cetengraulis edentulus	3	66.82
Scianidae		
Paralonchurus brasiliensis	2	103.88
Larimus breviceps	2	45.89
Cynoscion guatucupa	4	159.91
Isopisthus parvipinnis	4	170.31
Mullidae		
Mullus argentinae	3	63.14
Priacanthidae		
Priacanthus arenatus	2	129.15
Unidentified prey		753.11
	São Pedro e São Paulo (n = 14)	
Osteichthyes		
Exocoetidae		
Cheilopogon cyanopterus	7	1790.83
Exocoetus volitans	32	2429.91
Hemiramphus balao	1	7.52
Hirundichthys affinis	1	36.69
Oxyporhamphus micropterus	11	1880.94
Prognichthys gibbifrons	3	560.93
Scrombidae		
Scomberomorus cavalla	1	11.57
Cephalopoda		
Unidentified sp.	1	8.17
Unidentified prey	33	2570.51

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298 Table 2: Mean and standard deviation of nutritional parameters of brown booby
299 prey. Asterisks mean significant difference between archipelagos.

	Moleques do Sul (n = 12)		**São Pedro e São Paulo (n = 14)**		**Statistics**
	Mean	SD	Mean	SD	
Protein (%)	16.44	2.90	21.19	2.23	t = -4.7995, p < 0.05***
Lipids (%)	7.96	4.10	4.88	2.11	W = 124, p < 0.05***
Energy density (kJ g-1)	4.67	1.27	4.13	0.75	t = 1.6756, p > 0.05
Food load energy density (kJ)	429.42	173.08	736.21	405.00	t = -2.8809, p < 0,05***

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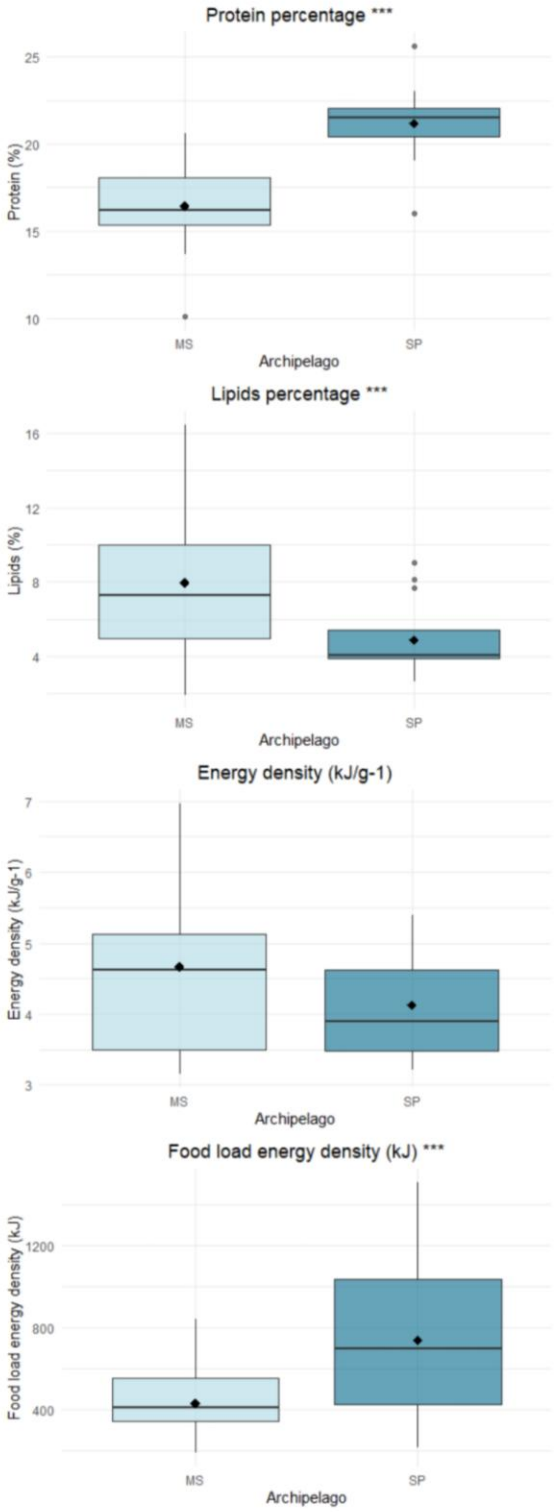


Figure 2: Differences in macronutrient composition (protein percentage, lipid percentage, energy density (kJ/g^{-1}) and food load energy density (kJ) of brown booby prey between the two studies archipelagos. Asterisks (***) represent significant differences at the significance level $p < 0,05$.

306 *Movement analysis*

307 Foraging trip metrics were, in general, similar between the archipelagos (Table 3,
308 Figure 3), with exception for maximum distance from colony and diving depth. Brown
309 boobies from MS performed significantly farther trips ($W = 5017$, $p < 0.05$), reaching a
310 maximum distance of 86.9 km from the colony (Figure 4). In comparison, in SPSP the
311 maximum distance reached was 45.3 km. Mean and maximum diving depth also varied
312 significantly ($t = 2.2365$, $p < 0.05$ and $W = 4881.5$, $p < 0.05$, respectively), where
313 individuals from MS dived deeper in both metrics (Figures 4 and 6). The median trip
314 duration was equal between archipelagos: 2.1 hours. The maximum cumulative distance
315 was also higher in MS than in SPSP (103.5 and 87, respectively), but not at a statistically
316 significant level.

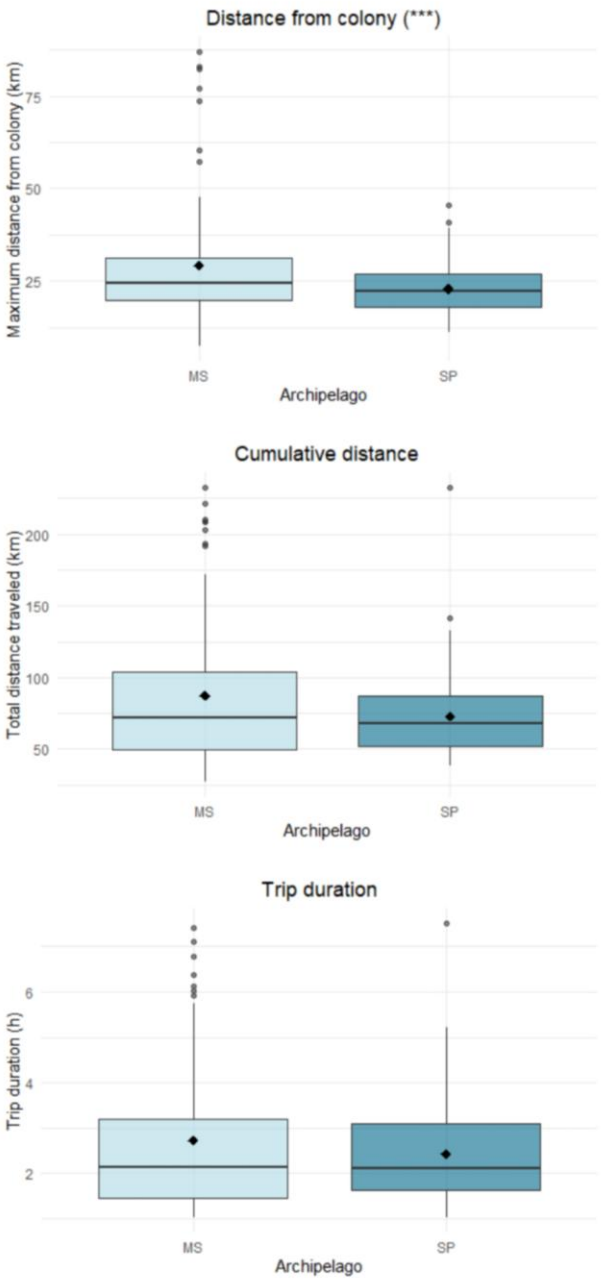
317 Table 3: Foraging trip metrics of brown boobies in the archipelagos of Moleques
318 do Sul (MS) and São Pedro e São Paulo (SPSP). Results for metrics are given as median
319 [Q1-Q3] with range (min-max) in parenthesis.

Foraging trip metric	**MS (n = 19)**	**SPSP (n = 20)**	**Statistics**
Total number of trips	45	37	
Trip duration (h)	2.2 [1 – 3] (1 – 7.4)	2 [1 – 3] (1 – 5.9)	W = 910, p = 0.4751
Maximum distance (km)	29.9 [21 – 34] (14.6 – 86.9)	22.8 [18 – 47] (7.4 – 47.6)	W = 1156, p = 0.0002*
Cumulative distance (km)	83.2 [51 – 127] (37.4 – 232.2)	62.8 [47 – 94] (27 - 161)	W = 1006, p = 0.1072
Mean diving depth (m)	2.01 [1.4 - 2.4] (0.5 - 3.1)	1.85 [1.6 - 2] (0.5 - 2.4)	t = 2.2365, df = 117.15, p < 0.05*
Maximum diving depth (m)	3.02 [2.2 - 13.5] (0.8 - 29.5)	2.62 [2.1 - 6.2] (1.2 - 17.8)	W = 4881.5, p < 0.05*

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324 Figure 3: Differences in foraging trip metrics (maximum distance from colony,
325 cumulative distance, and trip duration of brown boobies between the two studied
326 archipelagos. Asterisks (***) represent significant differences at the significance level p
327 < 0,05.

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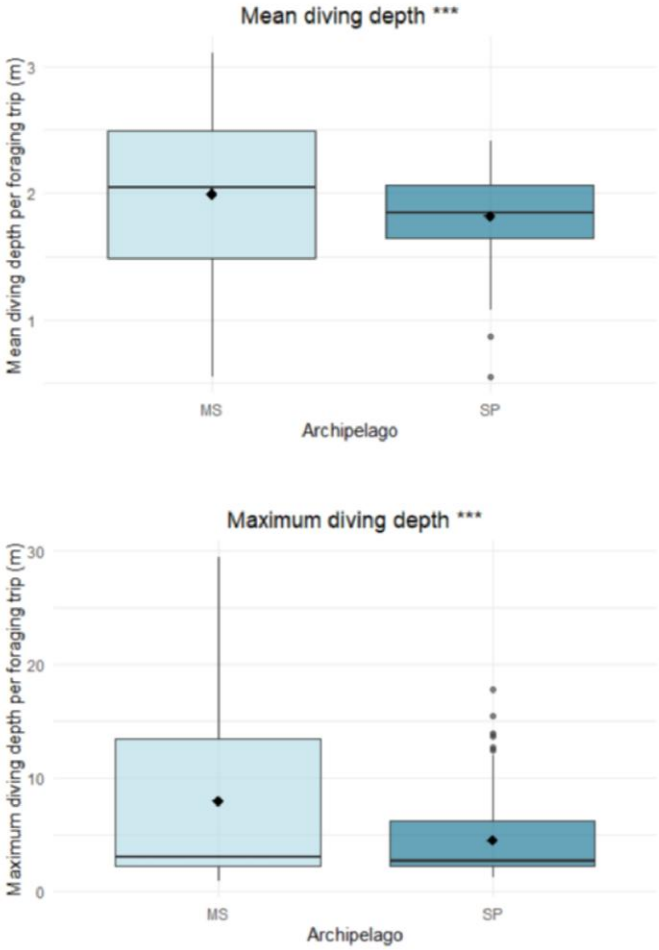
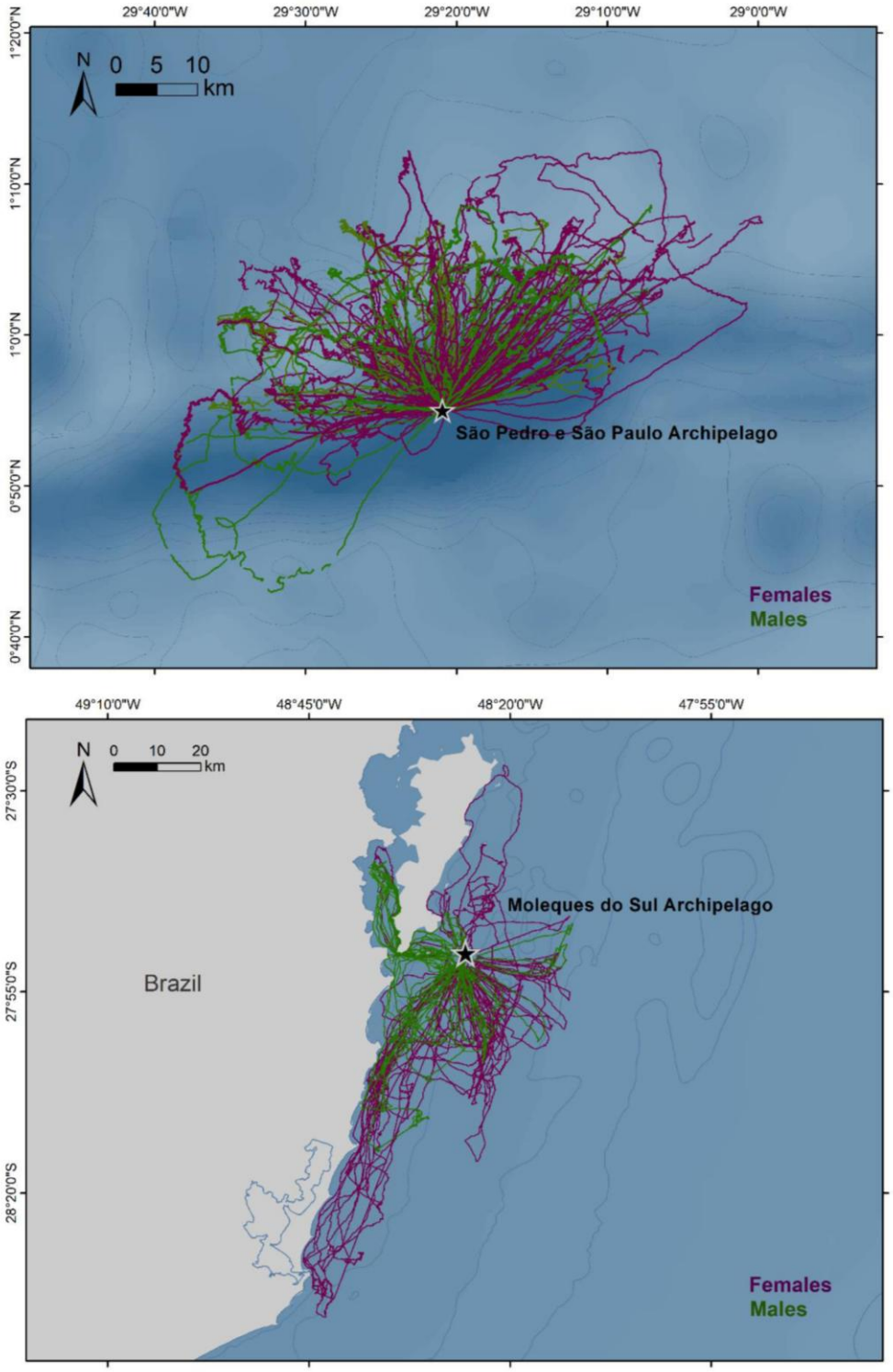
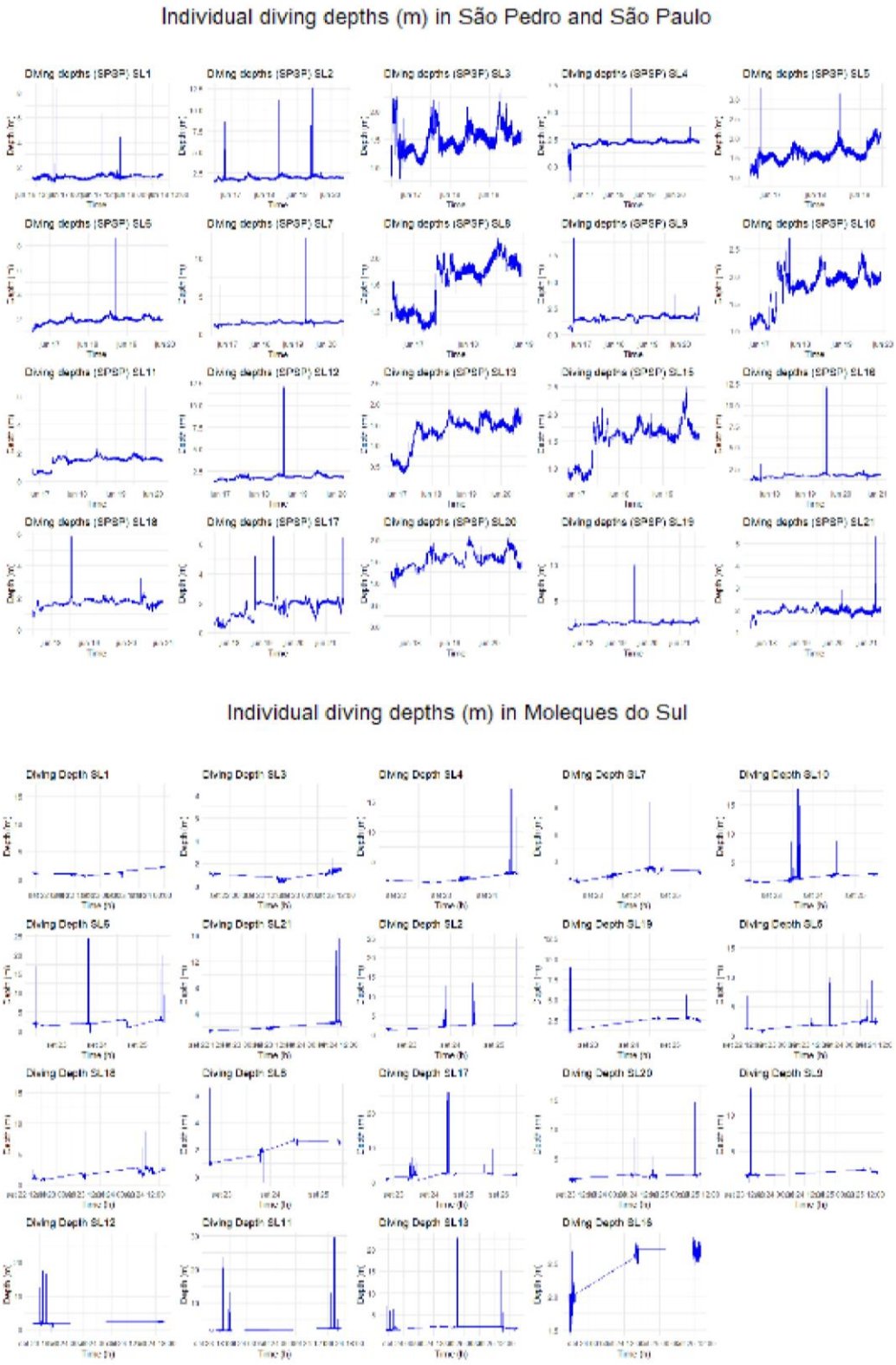


Figure 4: Differences in mean and maximum diving depths reached by brown boobies during foraging trips between the two studied archipelagos. Asterisks (***) represent significant differences at the significance level $p < 0,05$.



340

341 Figure 5: Foraging trips of brown boobies tracked for three days in the Moleques do Sul
342 archipelago (n = 19, September 2022) and São Pedro e São Paulo archipelago (n = 20,
343 June 2022).



344

345 Figure 6: Individual diving depths reached by brown in Moleques do Sul (n = 19,
346 September 2022) and São Pedro e São Paulo (n = 20, June 2022) archipelagos.

Foraging efficiency

A significant difference was found in the daily energy expenditure (kJ) of brown boobies during foraging trips between the two archipelagos ($W = 166$, $p < 0.05$), where brown boobies from MS spend much more energy on foraging than SPSP individuals. The foraging efficiency (energy gain – energy expenditure) was also significantly higher in SPSP ($t = -7.0349$, $df = 18.867$, $p < 0.05$) (Figure 5).

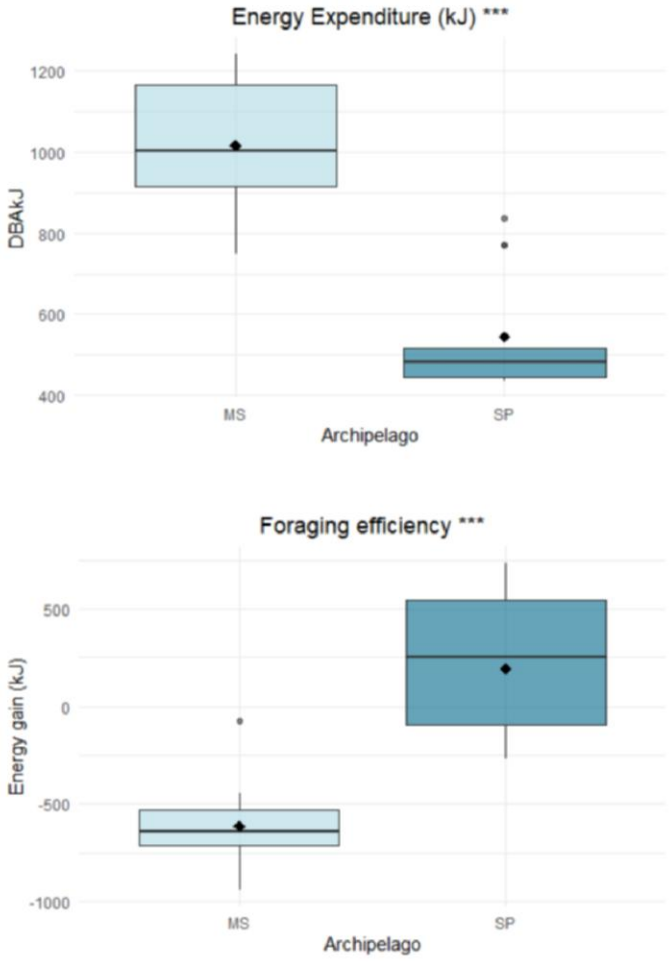


Figure 7: Differences in daily energy expenditure and foraging efficiency of brown boobies between the two studies archipelagos. Asterisks (***) represent significant differences at the significance level $p < 0,05$

Discussion

The nutritional quality of prey and the energy expended during foraging are important factors in evaluating foraging efficiency in seabirds and play a crucial role in seabird survival and breeding success, especially in challenging environments (Romano 1999, Jodice et al. 2006, González-Medina et al. 2018, Sorensen et al. 2019). We investigated the foraging efficiency of breeding Brown boobies on two oceanic islands with distinct locations, environmental and human pressure characteristics. We found significant differences in prey species, dietary parameters (protein percentage, lipid percentage, and food load energy density), and movement parameters (maximum distance from the colony, diving depth and energy expenditure) of the breeding Brown boobies in SPSP and MS. On the other hand, no significant differences were observed between the archipelagos in cumulative distance traveled, trip duration, or overall foraging efficiency.

Diet and macronutrients

The boobies from both archipelagos feed on completely different prey species. In MS, the birds primarily fed on fish from the Sciaenidae family (such as croakers, *Paralonchurus brasiliensis*), while in SPSP, they mainly consumed species from the Exocoetidae family (flying fish). Our results on the taxonomic composition of brown booby prey in MS and SPSP are in accordance with previous studies (Naves et al., 2002; Branco et al., 2005; Mancini and Bugoni, 2014; Jacoby et al., 2023). The absence of shared prey species between MS and SPSP likely reflects the geography of these islands, distinct oceanographic conditions, and differences in local human pressures. MS is located on the continental shelf and constitutes a subtropical neritic ecosystem. Neritic environments are coastal marine areas that are typically shallow and extend from the low tide mark to the edge of the continental shelf, and are considered highly productive areas (Araújo et al., 2018; Macedo et al., 2021). SPSP archipelago is inserted in an oceanic ecosystem, where the distribution of high primary productivity patches is more heterogeneous and influenced by several oceanographic patterns such as ocean circulation, convergence zones and small- scale upwellings (Soares et al., 2002; Nunes et al., 2017). The role of fishery-related prey in MS may also be highlighted. Moleques do Sul is an archipelago near the southern coast of Brazil with intense shrimp fishing activity, particularly during late spring and summer (Haimovici et al., 1996; Haimovici and Mendonça, 1996). São Pedro and São Paulo, on the other hand, is a marine protected area

where fishing activity is regulated and supervised by the Brazilian Navy within a radius of 200 nautical miles around the archipelago, when any form of predatory fishing is prohibited, thus ensuring ecological balance in the ecosystem (Brasil, 2018).

Considering the difference in the taxonomic composition of brown booby prey between MS and SPSP, it was expected that lipids and protein composition of prey would also vary between the two archipelagos. Prey from MS exhibited higher lipid content, while prey from SPSP showed a higher protein content. Both lipids and proteins have significant ecological implications for measuring the energy density and nutritional quality of prey, directly influencing ecological aspects of seabirds, such as fitness (Anthony et al., 2000; Sorensen et al., 2009; Albano et al., 2011). Lipids, for example, are considered an important component of prey nutritional quality for seabirds, as they provide a dense and efficient energy source during periods of high demand, such as movement, breeding, or molting (Anthony et al., 2000; Romano et al., 2006; Seaman et al., 2005; Lamb et al., 2017; González-Medina et al., 2018). The lipid content was significantly higher in prey from MS ($\overline{x}$ = 7.96, σ = 4.1) compared to prey from SPSP ($\overline{x}$ = 4.88, σ = 2.11), and the mean energy density was 4.67 kJ g-1 for MS prey (mostly Scianidae) and 4.13 kJ g-1 for SPSP prey (mostly Exocoetidae). The protein content, on the other hand, was significantly higher in SPSP prey ($\overline{x}$ = 21.19, σ = 2.23) than in MS ($\overline{x}$ = 16.44, σ = 2.9). The role of protein content in seabirds' health is poorly studied, and most studies regarding the nutritional quality of diet only address the percentage of protein only to calculate energy density, without discussing the direct effects of this nutrient on seabirds' health, growth and breeding success (Wanless et al., 2005; Jodice et al., 2006, Lamb et al., 2017, Miller et al., 2018). Protein reserves are especially important when individuals reach their minimum critical body mass due to feeding restrictions when they begin to use protein rather than fat reserves (Weimerskirch et al. 2003).

Shifts in the nutritional quality and availability of local prey can disrupt marine ecosystems and affect predator populations (Wanless et al., 2005). On the west coast of South Africa, for example, a decline in the Cape gannet (*Morus capensis*) population was attributed to reduced availability of lipid-rich fish prey such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) (Mullers et al., 2009). In that study, fish discarded by fisheries (*Merluccius* sp.) had a lower energy content (4.07 kJ/g-1) and fat content (2.5%) than anchovy (6.74 kJ/g-1 and 4.2%) and sardines (8.59 kJ/g-1 and 4.8%).

These findings highlight how variations in prey quality, as observed in our study, can influence predator populations by affecting their energy intake and overall fitness. Although the prey from MS (mainly croakers and other Sciaenidae species) showed higher fat values than the prey from SPSP (flying fish), we emphasize that these results should be interpreted with caution, as optimal foraging is evaluated based on the balance between foraging effort and energy gain. In other words, although birds from SPSP consume prey with lower lipid values, this outcome must be assessed alongside the food load mass, the effort expended during foraging activity, and the positive energy balance achieved.

Energy density x Food Load Energy Density

The total food load energy density was significantly higher in SPSP (736.21 kJ) compared to MS (429.42 kJ), despite prey from MS exhibiting a greater proportional energy density (4.67 kJ g^{-1}) than prey from SPSP (4.13 kJ g^{-1}). This difference can be attributed to the larger food load biomass observed in SPSP ($\overline{x}$ = 163.65 g, σ = 83.6) compared to MS ($\overline{x}$ = 98.61 g, σ = 33.39). The higher food load energy density in SPSP indicates that prey abundance may compensate for the lower proportional energy density. This can suggest that the foraging strategy of brown boobies in SPSP is shaped by the availability of protein-rich prey, allowing them to gather sufficient energy through larger food loads. In contrast, the higher proportional energy density of MS prey reflects a reliance on lipid-rich prey, which provides efficient energy for adult metabolic demands but is delivered in smaller quantities due to lower prey abundance. The low food load regurgitated by brown boobies during this study is in accordance with the results found by Branco et al. 2005, who reported a seasonal fluctuation in regurgitations biomass with lower values during spring and autumn compared with summer and winter. Our sampling was conducted in September (early spring) when trawl fishing effort is lower on the coast of Santa Catarina, being more intense during late spring and summer (Haimovici et al., 1996; Haimovici and Mendonça, 1996). It is possible that during periods of intense trawl fishing the prey availability for brown boobies increases, as well as the foraging effort decreases, since it is known that the species feeds intensely on fishing discards in the region (Branco, 2001; Branco et al., 2005).

This trade-off between prey quality and quantity highlights how local ecological conditions influence foraging strategies and energy intake. From a fitness perspective, the

greater food load energy density in SPSP could confer advantages during the chick-rearing period, ensuring that sufficient energy is delivered to support offspring growth (Wanless et al., 2005; Romano et al., 2006; Albano et al., 2011; González-Medina et al., 2018), These findings emphasize the importance of balancing energy acquisition with foraging effort, demonstrating that both prey quality and availability play crucial roles in shaping the foraging ecology of brown boobies.

Foraging effort, Energy expenditure and Foraging efficiency

The significantly higher daily energy expenditure observed in brown boobies from MS compared with SPSP suggests that individuals in MS face greater energy costs during foraging. This is further supported by the significantly higher maximum distance reached in MS during foraging trips, where birds traveled up to 86.9 km from the colony, compared to a maximum of 45.3 km in SPSP. The difference in diving depths between the two archipelagos also explains the observed difference in energy expenditure. Brown boobies from MS reached significantly higher mean dive depths ($\bar{x}$ = 2, σ = 0.6) and maximum dive depths (29.5 m) during foraging trips than in SPSP ($\bar{x}$ = 1.8, σ = 0.3, maximum 17.8 m) (Figures 4 and 6). These findings likely reflect the ecological and geographical differences between the archipelagos.

In MS, lower prey availability may force individuals to forage farther from the colony, and the predominance of demersal and benthic fish as feeding options may impose the need to dive deeper and consequently expend more energy to catch prey. In contrast, the great abundance of flying fish in the surroundings of SPSP allows individuals to forage within a more restricted range, to catch prey on the water surface and at lower depths thus minimizing foraging energy expenditure. Interestingly, despite the greater maximum foraging distance in MS, the median trip duration was similar between the archipelagos, at 2.1 hours. This can suggest that birds in MS may target fewer but higher-quality prey to offset the energetic costs of their longer trips.

Nunes et al. 2018 also tracked brown boobies in SPSP and reported mean foraging trip durations at 1 h, and a mean maximum distance from colony of 7 km. In the Abrolhos archipelago (17°55′S, 38°56′W), Nunes et al. 2022 reported foraging trips of 4 h on average, reaching 43 km far from the colony. In Dog Island, Caribbean Sea, brown boobies reached a mean maximum depth of 39.7 km in foraging trips performed in shallow waters, with 5.9 h of duration on average (Soanes et al., 2016). In the pelagic archipelago Tinhosa Grande in western Africa, females traveled a mean of 92.7 km from

the colony in foraging trips averaging 11.4 h, while males traveled a mean of 64.4 km from the colony in foraging trips lasting ~9.5 h (Correia et al., 2021). Shorter foraging trips in SPSP may reflect the great food availability in that region (Mancini and Bugoni, 2014).

Jodice et al. 2006 found differences in the daily energy expenditure of a seabird, the black-legged kittiwakes (*Rissa tridactyla*), between two colony in different locations of Prince William Sound, Alaska, and attributed a higher energy expenditure to a localized increase in the density of a high-quality prey, the Pacific herring *Clupea pallasi,* where high levels of breeding effort and success coincided with increased availability of age 1+ herring. For wandering albatrosses (*Diomedea exulans*), Weimerskirch et al. (2005) did not find differences in foraging efficiency among water masses or between oceanic and shelf-slope waters. Van Oordt (2024) found an increase of ~20% in daily energy expenditure of peruvian boobies (*Sula variegata*) during years with harsh environmental conditions in the eastern Pacific. Australasian gannets (*Morus serrator*) expended more energy in foraging trips (higher vectorial dynamic body accelerations) during years of poorer breeding success, but within the same foraging range, indicating that they had more difficulty in obtaining foraging success in these years, probably due to low prey availability (Angel et al., 2015). For other gannet species, the northern gannet *(Morus bassanus*), Bennison et al. 2021 found a higher energetic cost to perform pursuit dives rather than plunge dives, which may be the case of our results, where brown boobies from MS dived deeper and had a higher energy expenditure in foraging trips. Machovsky-Capuska et al. (2011) reported higher feeding success in pursuit dives in Australasian gannets. Plunge dives are characterized by an almost immediate rise to the surface after entering underwater, while a pursuit dive is characterized by chasing prey underwater (Shreiber and Burger, 2002).

Conclusion

Based on our results, we conclude that the foraging efficiency of brown boobies is higher in SPSP than in MS, possibly due to greater prey availability in that region. Such conclusions are supported by greater maximum distances reached from the colony, deeper dives, and higher energy expenditure (higher VeDBAs) reported for boobies from MS, suggesting a higher foraging effort. The similar cumulative distances traveled, slightly higher in MS, further reflect this balance in foraging effort. Prey energy density, even

521 higher in prey from MS, does not compensate for the total energy intake due to a reduced
522 food load compared with SPSP. This variation in foraging strategies demonstrates the
523 plasticity of the species in adapting to varying environmental conditions and prey
524 availability scenarios. With a positive energy gain relative to expenditure, individuals in
525 SPSP may be better positioned to meet the demands of chick-rearing and maintain body
526 condition during the breeding season. In contrast, the lower foraging efficiency in MS
527 highlights the challenges posed by resource-limited environments, where increased
528 foraging effort and energy expenditure may constrain the resources available for
529 reproduction and survival. These findings emphasize the critical role of local prey
530 availability and spatial distribution in shaping the energy budgets and fitness of seabird
531 populations.

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785 **Supplementary Material**

Table S1: Raw data used to calculate brown booby energy gain. FMR = Field Metabolic Rate, BMR = Basal Metabolic Rate, AEE = Axuxiliary Energy Expenditure, DBAkj = VeDBA converted to kJ. For more details on calculations, see the supplementary material of Bennison et al. 2021.

id	island	sex	body mass (g)	protein (%)	lipids (%)	density (kJ/g)	food load mass (g)	food load density (kJ)	vdba24	FMR	BMR	AEE	k	DBAkj	Energy gain (kJ)
SP1	SP	M	1250	16.00	3.93	3.22	230.60	742.30	429.15	927.47	492.49	434.98	1.01	434.98	307.32
SP2	SP	F	1550	20.28	5.39	4.27	124.06	530.11	416.47	1358.56	587.87	770.69	1.85	770.69	-240.58
SP3	SP	M	1250	21.54	4.05	3.90	124.45	485.12	354.82	927.47	492.49	434.98	1.23	434.98	50.13
SP4	SP	F	1550	22.03	9.06	5.39	279.18	1505.91	159.06	1358.56	587.87	770.69	4.85	770.69	735.22
SP5	SP	M	1300	21.57	3.97	3.83	100.10	383.81	208.83	954.12	508.65	445.48	2.13	445.48	-61.67
SP6	SP	F	1700	19.06	2.66	3.40	124.06	422.20	289.78	1149.81	634.31	515.50	1.78	515.50	-93.31
SP7	SP	F	1500	20.45	4.49	3.95	54.04	213.67	293.41	1055.34	572.22	483.12	1.65	483.12	-269.45
SP8	SP	M	1300	23.02	7.69	5.19	194.43	1009.61	103.33	954.12	508.65	445.48	4.31	445.48	564.13
SP9	SP	F	1500	20.49	3.88	3.73	62.53	232.97	288.17	1055.34	572.22	483.12	1.68	483.12	-250.15
SP10	SP	M	1300	21.06	2.93	3.43	202.45	695.30	513.92	954.12	508.65	445.48	0.87	445.48	249.83
SP11	SP	F	1700	21.76	2.73	3.48	334.32	1163.09	694.87	1149.81	634.31	515.50	0.74	515.50	647.58
SP12	SP	M	1500	22.53	8.16	5.22	197.78	1031.95	275.90	1055.34	572.22	483.12	1.75	483.12	548.83
SP13	SP	F	1850	25.62	4.55	4.62	249.77	1154.71	557.94	1518.14	680.02	838.12	1.50	838.12	316.59
SP15	SP	M	1100						388.16	826.41	443.31	383.10	0.99	383.10	
SP16	SP	F	1550						431.97	1358.56	587.87	770.69	1.78	770.69	
SP17	SP	F	1500						270.01	1055.34	572.22	483.12	1.79	483.12	
SP18	SP	M	1250						274.11	927.47	492.49	434.98	1.59	434.98	
SP19	SP	M	1300						424.99	954.12	508.65	445.48	1.05	445.48	
SP20	SP	F	1700						220.77	1149.81	634.31	515.50	2.34	515.50	
SP21	SP	M	1250						137.66	927.47	492.49	434.98	3.16	434.98	
MS1	MS	F	1535	18.05	4.98	4.21	138.13	581.13	538.74	1607.84	583.19	1024.66	1.90	1024.66	-443.53
MS2	MS	M	1250	15.17	9.98	5.13	66.82	342.69	370.71	1408.27	492.49	915.78	2.47	915.78	-573.10
MS3	MS	F	1740	13.63	7.30	4.12	134.03	552.54	399.13	1866.73	646.56	1220.17	3.06	1220.17	-667.63
MS4	MS	F	1590	16.22	16.46	6.97	63.31	441.08	346.70	1766.23	600.33	1165.90	3.36	1165.90	-724.82
MS5	MS	M	1330	20.08	6.90	4.74	63.56	301.11	460.77	1467.85	518.29	949.56	2.06	949.56	-648.45
MS6	MS	M	1405						259.74	1523.29	542.22	981.07	3.78	981.07	
MS7	MS	F	1465	10.09	6.78	3.38	55.31	186.81	427.05	1562.68	561.21	1001.47	2.35	1001.47	-814.66
MS8	MS	M	1250	16.03	13.15	6.34	132.58	840.77	108.45	1408.27	492.49	915.78	8.44	915.78	-75.01
MS9	MS	F	1780	15.36	3.53	3.15	131.08	413.00	322.88	1899.86	658.77	1241.09	3.84	1241.09	-828.09
MS10	MS	F	1740	16.53	4.27	3.50	160.91	563.12	975.02	1866.73	646.56	1220.17	1.25	1220.17	-657.05
MS11	MS	M	1310						650.82	1454.34	511.86	942.48	1.45	942.48	
MS12	MS	M	1250	19.12	1.90	3.30	109.88	363.15	460.86	1408.27	492.49	915.78	1.99	915.78	-552.63
MS13	MS	M	1465	20.62	12.02	6.49	56.62	367.48	695.29	1562.68	561.21	1001.47	1.44	1001.47	-634.00
MS16	MS	M	1205	17.28	7.93	4.72	85.89	405.45	155.78	1372.21	477.85	894.36	5.74	894.36	-488.91
MS17	MS	F	1370						898.27	1500.01	531.08	968.93	1.08	968.93	
MS18	MS	F	1505						488.96	1588.59	573.79	1014.80	2.08	1014.80	
MS19	MS	M	1165	15.49	8.20	4.62	48.52	224.08	284.96	1212.06	464.76	747.30	2.62	747.30	-523.23
MS20	MS	F	1530						297.03	1604.64	581.62	1023.02	3.44	1023.02	
MS21	MS	F	1305						216.46	1450.95	510.25	940.70	4.35	940.70	-940.70

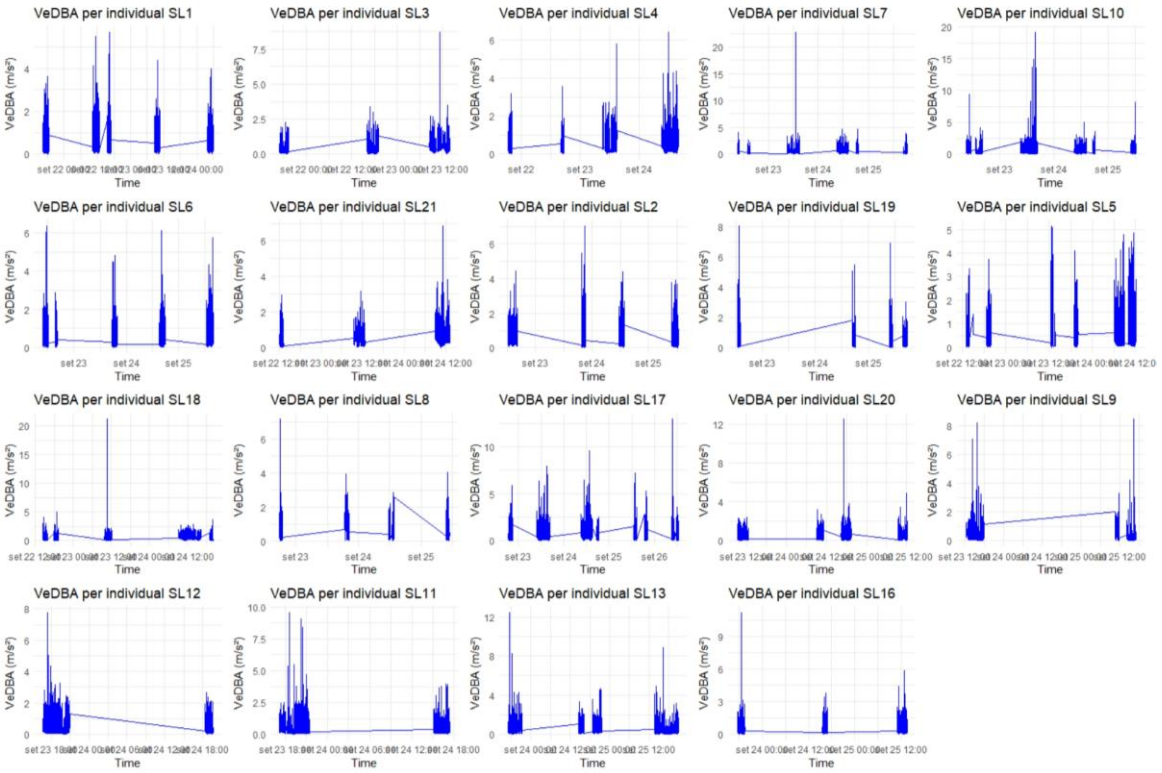


Figure S1: Individual Vectorial Dynamic Body Accelerations of brown Boobies from MS.

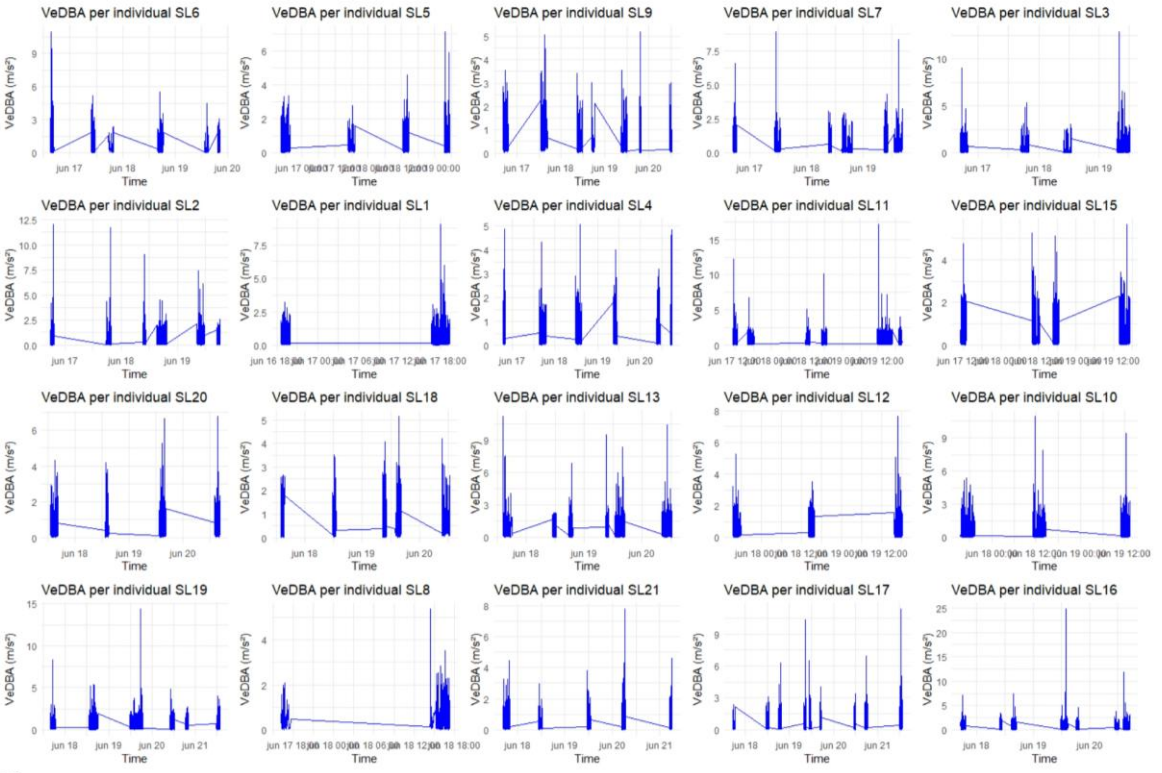


Figure S2: Individual Vectorial Dynamic Body Accelerations of brown Boobies from SPSP.

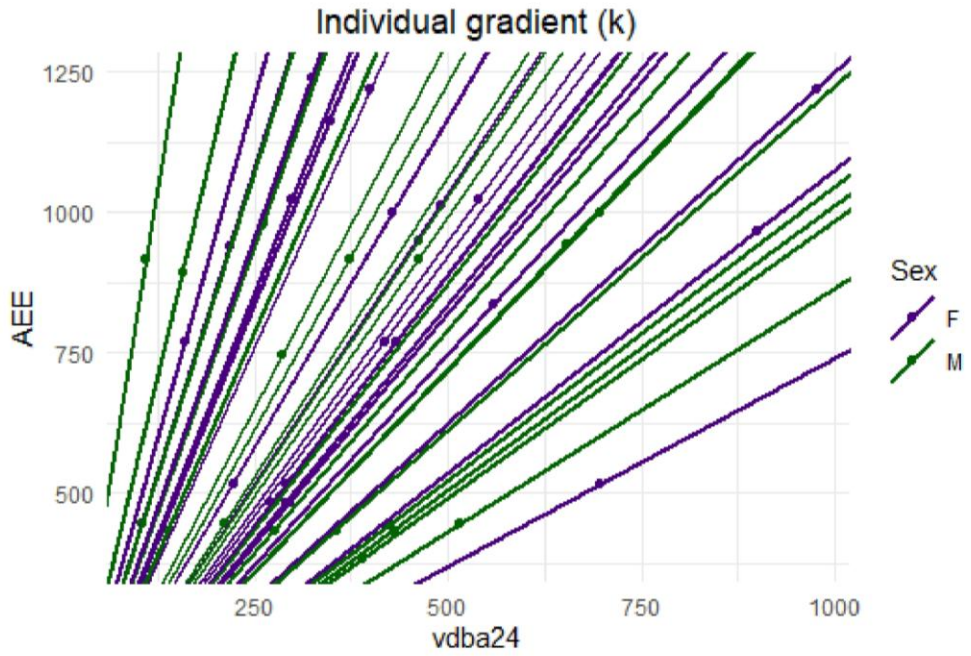


Figure S3: Relationship between vectorial dynamic body acceleration (VeDBA) and kilojoules (kJ) as described in the methods proposed by Bennison et al. 2021. The straigh line relationship enables the prediction of kilojoules expended for a given value of VeDBA.

CAPÍTULO 3

Differences in mercury (THg) levels in Brown booby (*Sula leucogaster*) feathers from two environmentally distinct Brazilian archipelagos

Given name: Victória Renata
Family name: Fontoura Benemann[1]*,

[1]Laboratório de Ornitologia e Animais Marinhos, Universidade do Vale do Rio dos Sinos, Av. Unisinos, 950, São Leopoldo, RS 93022-000, Brazil. *Corresponding author: victoriabenemann@gmail.com

Given name: Bianca
Family name: Costa Ribeito[1],

[1]Laboratório de Ornitologia e Animais Marinhos, Universidade do Vale do Rio dos Sinos, Av. Unisinos, 950, São Leopoldo, RS 93022-000, Brazil

Given name: Edson
Family name: Moreira Gonçalves[2]

[2] Instituto de Pesquisas Energéticas e Nucleares, IPEN/CNEN, Av. Prof. Lineu Prestes, 2242 - Butantã, São Paulo, Brazil.

Given name: Maria Virginia
Family name: Petry[1]

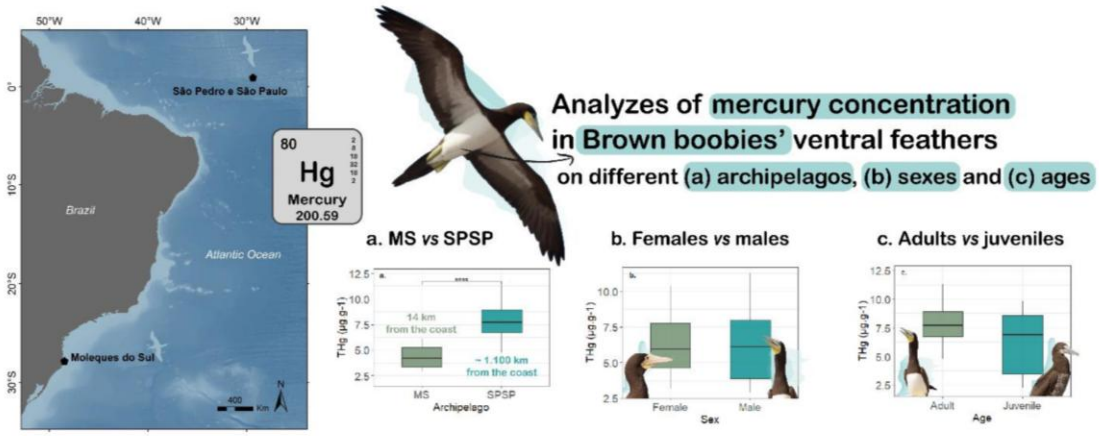
[1]Laboratório de Ornitologia e Animais Marinhos, Universidade do Vale do Rio dos Sinos, Av. Unisinos, 950, São Leopoldo, RS 93022-000, Brazil

Differences in mercury (THg) levels in Brown booby (*Sula leucogaster*) feathers from two environmentally distinct Brazilian archipelagos

Highlights

- We investigated mercury levels in Brown booby feathers from two archipelagos.
- We also tested for intersexual and age-related differences in mercury levels.
- Higher mercury concentrations were found in the tropical/oceanic archipelago.
- No significant differences were found concerning sex or age.
- Differences were attributed to environmental features and local diet.

Graphical Abstract



Abstract

Mercury pollution is a matter of global concern due to its detrimental effects on ecosystems and human well-being. Seabirds generally occupy high levels within trophic chains and are often used as valuable indicators of marine pollution, including mercury contamination. We examined the concentrations of total mercury (THg) in the ventral feathers of Brown boobies (*Sula leucogaster*) from two distinct Brazilian archipelagos: one coastal and subtropical (Moleques do Sul) and one tropical and oceanic (São Pedro and São Paulo). We hypothesized that there would be differentiation in mercury levels

between these archipelagos due to differences in geographical location and environmental conditions, where higher Hg levels would be found in Brown boobies from the coastal one since they are more exposed to anthropogenic sources from the continent. Additionally, we also investigated whether there were any differences in mercury levels based on sex and age. We found significantly higher THg levels in Brown boobies from São Pedro and São Paulo compared to those from Moleques do Sul, indicating differential levels of exposure to mercury sources. No significant differences between sexes or age classes, although juvenile individuals showed the lowest values. We suggest that the THg higher levels found in individuals from São Pedro e São Paulo can be due to the geological peculiarities of this archipelago, formed by mantle peridotites considered mercury hotspots. Our findings emphasize the importance of considering spatial and environmental factors in mercury biomonitoring and highlight the potential use of seabird feathers as a proxy for mercury contamination in marine environments.

Keywords: Seabirds, Heavy metals, Coastal, Oceanic, Atlantic Ocean

1 Introduction

Mercury (Hg) is a non-essential metal naturally distributed worldwide, originating from both natural (e.g. volcanoes, geothermal) and anthropogenic (e.g. fossil fuel-fired power plants, mining) sources (Pirrone et al. 2010; Travnikov et al. 2017; Dastoor et al. 2022). Despite human activities having accelerated the redistribution of metals in the environment, especially since the Industrial Revolution, the main determinants of metal distribution over the Earth's surface are still natural geochemistry processes of the underlying and local rocks (Garret 2000). Globally, mercury accumulation is concentrated in areas with specific geological and tectonic features

(Gustin et al. 2000). These include plate tectonic boundaries (Yin et al. 2024), recent volcanic activity (Geyman et al. 2023), precious and base metal mineralization and areas of increased heat flow in the Earth's crust (Gustin et al. 2000). Areas of arc crustal rocks and mantle peridotites are considered mercury hotspots (Canil et. al. 2015, Yin et al. 2024).

Furthermore, anthropogenic sources also play an important role in the geographical distribution of mercury emissions. In the year 2000, for instance, total mercury emissions from all anthropogenic sources worldwide were approximately 2,190 tons, two-thirds of which came from the burning of fossil fuels (Pacyna et al. 2006). Africa and Asia together produce more than half of global mercury emissions from anthropogenic sources (Pirrone et al. 2010). In South Africa there is intense activity of gold mining and coal combustion in power plants (Dabrowski et al. 2008, Leaner et al. 2009), while in Asian countries (e.g. China, India), other activities such as non-ferrous production, stationary combustion, electrical and electronic manufacturing industry are also expressive sources of mercury emission into the atmosphere (Streets et al. 2005, Mukherjee et al. 2009, Pirrone et al. 2010).

Due to its volatility, atmospheric circulation is the main pathway for Hg transportation, although it can also be dispersed through water, such as ocean currents and river runoffs (Travnikov et al. 2017; Dastoor et al. 2022). It is considered one of the most toxic elements to living organisms, especially when it is subjected to the methylation process by microorganisms' action and assumes its organic form methylHg (MeHg) (Clarkson 1997, Fitzgerald et al. 2007). In food webs, Hg biomagnifies from low to high trophic levels, occurring at higher levels in predator species such as seabirds. It incorporates into food webs through particulate organic matter (POM). It accumulates in organic tissues due to its high affinity for protein, being retained in organisms' bodies

rather than excreted, thus accumulating throughout the following levels of the trophic web (Bloom 1992, Kidd et al. 2012, Calle et al. 2015, Seco et al. 2021, Matias et al. 2022). For instance, several studies have reported a positive relationship between nitrogen stable isotopes ratios – a common proxy for trophic level and trophic width niche used in ecology – and Hg concentration, indicating that species occupying higher levels in the trophic chain are likely to exhibit higher mercury levels in their tissues (Bisi et al. 2012, Di Beneditto et al. 2012, Coelho et al. 2013, Hilgendag et al. 2022), as well as a larger and more variable Hg concentrations in generalist species (wider trophic niche) than in specialist ones (narrower trophic niche) (Pinzone et al. 2019).

Seabirds, as wide-ranging predator species, are often used as monitors of the marine environment since they reflect the conditions of the previous trophic levels within the food chain (Furness and Camphuysen 1997, Rajpar et al. 2018). They play a crucial role in regulating food webs and can also provide information on the ecosystem's quality, such as pollution levels in ecosystems (Burger and Gochfeld 2000, Camphuysen 2006, Carravieri et al. 2013, Cusset et al. 2023). Feathers are commonly used to sample Hg levels because they are non-invasive and useful biotracers of Hg exposure since they are one of the main excretory pathways of this non-essential element in a bird's body (Burger 1994, Bottini et al. 2021, Bighetti et al. 2022). As they are inert tissue, they represent contamination at the time they were synthesized by the bird, during the short period of feather growth when it is connected to the bloodstream (Burger and Gochfeld 2000). Feathers are likely to show significantly higher Hg concentrations than blood, with a narrower range of values at the interspecific scale and a higher variation at the specific scale (Bustamante et al. 2023). Molting in most seabirds occurs annually and alternates between parts of the body, so evaluating different types of feathers (i.e.

120 ventral, dorsal, wing) provides information on the contamination levels at different
121 periods of the bird's annual cycle (Carravieri et al. 2013, Bighetti et al. 2022).

122 The contamination of seabirds by Hg occurs through the ingestion of
123 contaminated prey. It may cause damage to animal health, as it can cause neurological
124 and endocrine disruptions, as well as negatively affect the immune system (Tartu et al.
125 2013, Mallory and Braune 2018, Chastel et al. 2022, Ibañez et al. 2024). Chastel et al.
126 2022 proposed toxicity benchmarks for seabird feathers by converting previously
127 established parameters for blood (Ackerman et al. 2016) to other tissues, and categorized
128 health risk values into the following categories: no risk (<1.62 μg g^{-1}), low risk (1.62 –
129 4.53 μg g^{-1}), moderate risk (4.53 – 9.14 μg g^{-1}), high risk (9.14 – 10.99 μg g^{-1}), and
130 severe risk (>10.9 μg g^{-1}). For comparison, the threshold exposure recommended by the
131 World Health Organization (2007, 2008) for scalp human hair (pregnant woman) is < 1
132 μg g^{-1}.

133 It has been demonstrated that Hg contamination could lead to a decline in
134 gonadotropin-releasing hormone (GnRH) release, which is involved in gonadal
135 maturation, sex steroid secretion, and the onset of reproduction, thus impairing seabird
136 breeding behavior (Tartu et al. 2013, Provencher et al. 2016). Moreover, in some
137 Antarctic seabirds, it was observed that high Hg concentrations influence parental
138 behavior, leading to a lower commitment to incubate eggs (Tartu et al. 2015).
139 Neurotoxic effects of Hg on seabird brain regions responsible for geomagnetic
140 information and biomechanics control can also affect navigation, flight, and ultimately
141 migration performance (Seewagen 2020). Hg contamination can also cause negative
142 effects on body condition in some bird species, such as fat stores and body mass relative
143 to individual's size (Moura et al. 2018, Ackerman et al. 2019), which are known to be

144 determinant biological traits influencing migration performance and breeding success
145 for seabirds (Chastel et al. 1995, Duijns et al. 2017)

146 The Brown booby *Sula leucogaster* (Boddaert, 1783) is a widely distributed
147 pantropical seabird that breeds on islands between 27°S and 25°N (Birdlife International
148 2024). The species exhibit a high degree of trophic plasticity according to local prey
149 availability (Jacoby et al. 2023), and a high degree of sexual dimorphism in body size,
150 where females can be up to 38% heavier than males (Nelson 1978, Lewis et al. 2005,
151 Nunes et al. 2017) and perform longer foraging trips (Miller et al. 2018; Correia et al.
152 2021). Foraging behavior consists mainly in plunge-dives, generally up to 2 m depth,
153 feeding mostly on bony fish, and to a lesser extent on squids and crustaceans (Del Hoyo
154 et al. 1996; Branco et al. 2005; Correia et al. 2021). In this study, we aimed to determine
155 and compare total mercury (THg) concentration in feathers of Brown boobies from two
156 environmentally distinct Brazilian archipelagos, as well as to test for intersexual and
157 age-related differences. We hypothesize that (1) Brown boobies from the coastal
158 archipelago would show higher Hg levels since they are more exposed to anthropogenic
159 sources from the continent, (2) females would show lower Hg levels since they excrete
160 part of the mercury burden through egg production and laying and (3) adults would show
161 higher levels than juveniles since they accumulate Hg in their tissues for a longer time
162 due to the bioaccumulation process.

163 **2 Material and Methods**

164 *2.1 Study area*

165 Moleques do Sul (MS) (27°51'S, 48°25'W) is a coastal archipelago located 14
166 km from the South American continent. Maior Island, where samples were collected,
167 has an area of 9.86 ha and is formed by granite rocks, overall alkaline granitoids of post-

168 tectonic nature, and has its surface predominantly covered by bush and herbaceous
169 vegetation (Bege and Pauli 1989; Salvador and Fernandez 2008, Tomazzoli e Pellerin
170 2015, Corrêa 2016). Granite is an intrusive igneous rock, formed primarily by the slow
171 solidification of magma beneath the Earth's surface (Schimidt et al. 2023). Although
172 granite itself is not a significant source of mercury, some of the minerals that may be
173 present in it, such as quartz and certain feldspars, may contain traces of mercury, and
174 weathering of exposed granites can release mercury contained in tiny amounts in the
175 minerals (Gerlach 1989; Stein et al. 1996; Zhu et al. 2001).

176 São Pedro e São Paulo (SPSP) (00°55'N, 29°20'W) is a pelagic archipelago
177 located 1,100 km from South America and 1,824 km from Africa, has a total area of 1.3
178 ha and its entire surface is covered by plutonic rocks. It is the only archipelago in the
179 Atlantic Ocean that is not formed by volcanic rocks, but by rocks originating from the
180 Earth's mantle and the only one in the world that maintains a direct link with the Earth's
181 mantle. Bonatti (1990) describes SPSP archipelago not as a sample of the sub-oceanic
182 mantle but as a genuine remnant of the subcontinental mantle. This remnant was left behind
183 and subsequently tectonically uplifted during the opening of the Equatorial Atlantic Ocean.
184 Belmont Island, where this study was conducted, comprises Peridotite mylonites and
185 Serpentized Peridotite mylonites (Campos et al. 2022).

186 Whereas MS is under the continuous influence of the Brazilian Current,
187 seasonally affected by the upwelling of cold waters from the Malvinas Current, SPSP is
188 inserted in the Equatorial System of Marine Currents, under the direct influence of the
189 South-Equatorial Current, which flows superficially in the EW direction, and the
190 submerged Equatorial Current, which flows in the opposite direction (WE) at a depth
191 between 60 and 100 m (Castro and Miranda 1998, Costa Campos et al. 2005, Knoppers
192 et al. 2009).

193 *2.2 Sampling*

194 We sampled ventral feathers from a total of 58 Brown boobies: 21 in MS, in
195 September 2022, and 37 in SPSP, in June 2022. From MS, all sampled individuals were
196 breeding adults during chick rearing (11 females and 10 males). From SPSP, 21
197 individuals (10 females, 11 males) were breeding adults during chick rearing, and 16
198 were juveniles. Birds were captured directly from the nest using a hand net and 8 ventral
199 feathers were sampled manually from each individual and then stored in plastic bags
200 until chemical analysis. We chose to sample ventral feathers following Bighetti et al.
201 (2022), which demonstrated that ventral feathers are the most appropriate for this
202 analysis because they show the highest Hg concentration and do not impair the seabird's
203 flight. Bird sampling and manipulation were approved by a federal license SISBIO
204 73286-4, state license IMA 31562-2022 and by the Ethics Committee on Animal Use
205 CEUA 14.2019.



206

207 Figure 1: Location of Moleques do Sul/BR and São Pedro e São Paulo/BR
208 archipelagos, where Brown booby (*Sula leucogaster*) feathers were sampled in
209 September 2022 and June 2022, respectively. The blue shade represents bathymetry
210 (lighter = shallower, darker = deeper).

211 *2.3 Sample preparation*

212 Feathers were initially subjected to a washing process being rinsed with
213 abundant distilled water inside a glass Petri dish to remove any remaining external
214 residue from the sampling site. After washing, feathers were dried in a laboratory oven

215 at 25°C overnight and then stored in ziploc plastic bags at room temperature, protected
216 from light until analyses for mercury determination.

217 *2.4 Analytical techniques for quantifying trace elements*

218 Analyses for mercury determination were performed in the Research Reactor
219 Center (CERPq) at IPEN/CNEN (Instituto de Pesquisas Energéticas e Nucleares). Due
220 to their small size, feathers were not cut before analyses. We weighed approximately
221 0.05 g aliquots of ventral feathers and 0.10 g aliquots of the certified reference materials
222 IAEA 085 (Human Hair), IPEN TM-1 (Mussel tissue), and IPEN CO-1 (Fish tissue) in
223 perfluoroalkoxy (PFA) digestion vessels, using an analytical balance with 0.0001-g
224 resolution. Then, we added 10 mL of concentrated P. A. nitric acid (HNO_3) and kept it
225 at rest for approximately seven hours at room temperature in a laboratory hood. We also
226 prepared a regent blank, consisting of 10 mL HNO_3, for every digestion batch. The
227 samples were taken to the microwave oven (MARS-6/CEM) and digested using the
228 equipment pre-established Animal Tissue method. The method uses a technology to
229 control temperature and pressure inside the digestion vessels, adjusting the power output
230 from 900 to 1050 W in order to keep samples at 200°C for 15 min. After complete
231 digestion and cooling of the digestion vessels at room temperature, the samples were
232 increased to 25 mL with Milli-Q water, in order to have a less concentrated acid solution
233 in a known volume. To quantify Hg in each sample, we used a 2-mL aliquot of the
234 digested solution diluted to 10 mL with Milli-Q water. This procedure is necessary to
235 favor the redox reaction that occurs in the spectrometer. Then we quantified THg by
236 Cold Vapor Generation Atomic Absorption Spectrometry (CV AAS) in the Perkin-
237 Elmer FIMS spectrometer (*Flow Injection Hg System*) using a 3% (m/v) $SnCl_2$ solution
238 as the Hg^{2+} reducing agent. We used a calibration curve prepared using five Hg solutions
239 (Perkin Elmer) from 0.5 to 5.0 ng mL^{-1} to calculate sample concentrations. Accuracy

240 was checked by assessing the following certified reference materials (CRM): IAEA 085
241 (Human Hair), (23.6 ± 3.5 μg g^{-1}); IPEN CO-1 (Fish tissue), (1.02 ± 0.06 μg g^{-1}); and
242 IPEN TM-1 (Mussel tissue), (0.14 ± 0.03 μg g^{-1}). These results are mean values and
243 standard deviations of four determinations. Recovery values were 115%, 85% and
244 116%, respectively.

245 *2.5 Statistical analyses*

246 We tested mean values of THg concentrations for significant differences
247 according to archipelago, sex, and age. To assess differences between archipelagos, we
248 used only adult individuals to avoid age bias. For evaluating intersexual differences, we
249 used all adult individuals from both archipelagos who were visually sexed during
250 sampling. We tested for intersexual differences separately for each archipelago, as well
251 as for all individuals from both archipelagos together. To assess differences between
252 adults and juveniles, we only used individuals from SPSP to avoid biased results from
253 asymmetric age ratios. Prior to analysis, we tested data for normality and homogeneity
254 of variances using Shapiro-Wilk and F tests, respectively. Then, we ran Student's t-test
255 and Welch's t-test to evaluate significant differences between groups. All statistical
256 procedures were performed in R 4.3.0 using the packages "dplyr" and "rstatix", and
257 graphics were produced through the packages "ggpubr" and "ggplot2" (R Core Team
258 2021).

259 **3 Results**

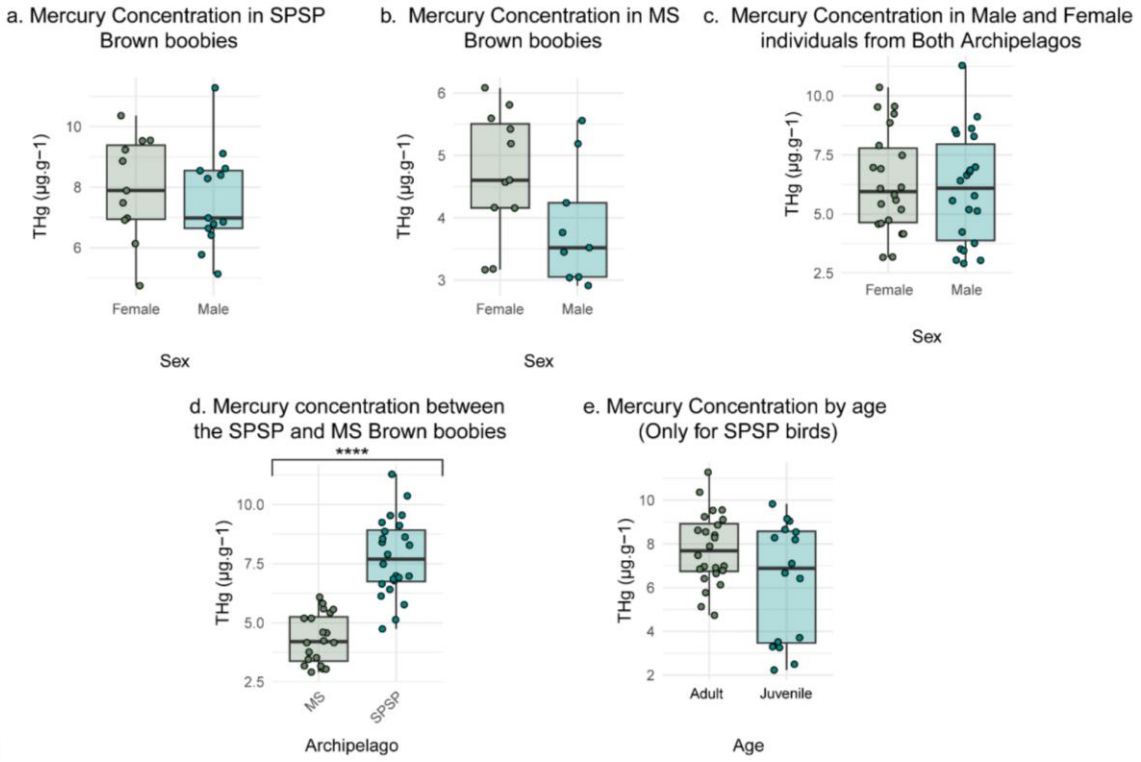
260 Mercury (THg) concentration in Brown booby feathers ranged between 2.23 and
261 11.28 μg g^{-1}, with a mean of 6.29 ± 2.31 μg g^{-1}. The THg concentration means observed
262 for each archipelago, sex, and age can be found in Table 1. We found significant
263 differences between adult individuals from the two archipelagos, where Brown boobies

264 from SPSP showed higher THg levels ($t = -8.06$, $df = 42$, $p < 0.05$). Brown boobies from
265 SPSP showed a mean of 7.18 ± 2.18 μg g^{-1}, while those from MS showed a mean of
266 4.33 ± 1.07 μg g^{-1} (Figure 1). However, we found no significant differences between
267 males and females nor for individuals from both archipelagos together ($t = 0.40$, $df = 42$, $p > 0.05$), nor separately for individuals from SPSP ($t = 0.53$, $df = 21$, $p > 0.05$) and
268 from MS ($t = 1.96$, $df = 17$, $p > 0.05$). We also found no significant differences between
269 adults and juveniles from SPSP ($t = 1.97$, $df = 22$, $p > 0.05$).
270

271 Table 1: Total mercury (THg) concentration in ventral feathers of Brown boobies
272 (*Sula leucogaster*) from São Pedro e São Paulo (n = 37) and Moleques do Sul (n = 21)
273 archipelagos in Brazil, sampled in June and September 2022, respectively. Values are
274 expressed as mean ± standard deviation (μg g^{-1}).

	Adults (n = 42)			Juveniles (n =16)
	Males	Females	Both sexes	
Moleques do Sul	3.86 ± 0.96	4.72 ± 1.00	4.33 ± 1.05	-
São Pedro e São Paulo	7.60 ± 1.64	7.97 ± 1.71	7.76 ± 1.64	7.11 ± 2.39
Both archipelagos	6.05 ± 2.20	6.20 ± 2.22	6.20 ± 2.22	-

275



276

277 Figure 2: Boxplots of total mercury (THg) concentration in ventral feathers of
278 Brown boobies (*Sula leucogaster*) from the Moleques do Sul (n = 21) and São Pedro e
279 São Paulo (n = 37) archipelagos in Brazil. a. Comparison between sexes from SPSP
280 individuals; b. Comparison between sexes from MS individuals; c. Comparison between
281 sexes of individuals from both archipelagos; d. Comparison between adult individuals
282 from both archipelagos and e. Comparison between adults and juveniles from SPSP.
283 The asterisks (****) represent a statistically significant difference ($p < 0.01$).

284 **4 Discussion**

285 The Hg levels in Brown booby feathers found in this study are the highest
286 concentrations among studies carried out on Brazilian islands to date (Table 2). We
287 attribute, in general, such high levels to (1) the type of feather analyzed and (2) the

288 geographic location of SPSP compared to other Brazilian islands, and (3) the geological
289 formation of the archipelagos.

290 Table 2: THg mercury concentrations found in Brown booby feathers from
291 Brazilian islands. Values are expressed as mean ± standard deviation (when available)
292 and ordered by latitude (from South to North).

Author (year)	Archipelago	Coordinates	Sampling year	Feather	Hg ($\mu g.g^{-1}$)
This Study	Moleques do Sul	27°51'S, 48°25'W	2022	ventral	4.33 ± 1.07
Bighetti et al. 2022	Santana	22°24'S, 41°42'W	2019	ventral	6.46 ± 1.19
Bighetti et al. 2022	Santana	22°24'S, 41°42'W	2019	wing S1	5.85 ± 1.10
Bighetti et al. 2022	Santana	22°24'S, 41°42'W	2019	tail R6	2.94 ± 0.45
Bighetti et al. 2022	Santana	22°24'S, 41°42'W	2019	dorsal	4.52 ± 1.33
Bighetti et al. 2021	Santana	22°24'S, 41°42'W	2018	S1, contour	2.68 ± 0.78
Nunes et al. 2022	Abrolhos	17°59'S, 38°42'W	2011	contour	2.34 ± ?
Nunes et al. 2022	Abrolhos	17°59'S, 38°42'W	2019	contour	0.03 ± ?
Bauer et al. 2024	Abrolhos	17°59'S, 38°42'W	2019-2022	contour	0.94 ± 1.31
Benedetti et al. 2022	São Pedro e São Paulo	00°55'N, 29°20'W	2017	P1, S8, breast	2.60 ± 3.50
This Study	São Pedro e São Paulo	00°55'N, 29°20'W	2022	ventral	7.77 ± 2.18

293

294 *4.2 Differences between archipelagos*

295 We found a significant difference in THg concentration between adult Brown
296 boobies from MS and SPSP, where birds from the latter showed the highest values. Such
297 results may be explained by two main factors: (1) distinct environmental features (e.g.
298 oceanographic, atmospheric) from these two locations and (2) differences in Brown
299 booby diet between these two archipelagos.

300 *4.2.1 Environmental features*

301 São Pedro and São Paulo Archipelago and the Moleques do Sul Archipelago are
302 located in different hemispheres (Northern and Southern, respectively) and are
303 consequently inserted in different oceanographic/atmospheric systems that can reflect
304 on the transport and availability of mercury. SPSP is a tropical pelagic archipelago
305 located near the equator in the North Atlantic Ocean (00°55'N, 29°20'W), which is under
306 the direct influence of the South-Equatorial Current in its surface waters and the
307 Equatorial Current at depths between 60 and 100 m (Castro and Miranda 1998, Costa
308 Campos et al. 2005, Knoppers et al. 2009). Lamborg et al. (2014) show evidence that
309 North Atlantic waters are more enriched in Hg than South Atlantic waters at the
310 thermocline zone (100-1000 m depth), and anomalously enriched relative to deep waters
311 of the South Atlantic, Southern, and Pacific oceans, probably due to anthropogenic
312 mercury inputs. Furthermore, some studies suggest that oceanic regions can show higher
313 levels of Hg when compared to coastal regions due to atmospheric deposition and
314 oceanic circulation, and although the mercury cycle is similar in coastal and oceanic
315 environments, there are more chemical species of mercury dissolved in oceanic waters
316 (Fitzgerald et al. 2007, USEPA 2020).

317 Atmospheric deposition is the main pathway of mercury into the ocean, so
318 knowledge of atmospheric circulation patterns is crucial to better understanding
319 mercury dispersion across oceanic regions (Dastoor and Larocque 2004, Lamborg et al.
320 2014, Soerensen et al. 2014). Soerensen et al. (2014) found higher mean Hg^0 (an
321 elemental form of mercury) concentration in the northern hemisphere in both
322 atmospheric and oceanic environments, with a pronounced peak at lower latitudes (near
323 the Equator), a pattern consistent with other studies reporting enrichment of atmospheric
324 mercury in the northern hemisphere deriving from anthropogenic sources (Fitzgerald

1986, Slemr et al. 1996, Kuss et al. 2011). The SPSP is under the influence of the Intertropical Convergence Zone (ITCZ), where northeast and southeast trade winds converge (Soares et al. 2009). Both northeast and southeast trade winds come from zones of high anthropogenic mercury emission rates (e.g. South Africa, China, and India) deriving from activities such as coal and oil combustion, artisanal gold mining, non-ferrous metal production, and cement production (Streets et al. 2005, Dabrowski et al. 2008, Leaner et al. 2009, Mukherjee et al. 2009, Pirrone et al. 2010).

Another issue that must be considered to explain the high Hg concentration found in Brown booby feathers from SPSP is the geological composition of this archipelago, which may represent a natural source of mercury. The SPSP archipelago is formed by mantle peridotite rocks originating from the subcrustal oceanic mantle, where the oceanic mantle is exposed directly on the surface without any coverage by the oceanic crust of basaltic composition (Motoki et al. 2009). The mantle is considered the largest Hg reservoir on Earth, since it represents ~67% of the planet's mass (Looders and Fegley, 1998), therefore it could represent a significant source of mercury emissions in the SPSP archipelago. Heavy metals are considered geogenic contaminants, that is, harmful elements that occur naturally in geological materials and originate from natural processes such as weathering, erosion, and geologic formations (Gwenzi 2021). Peridotite mylonites and Serpentized Peridotite mylonites, which are the mantle-originated rocks that compound the archipelago, are known as geogenic hotspots (Canil et al. 2015, Yin et al. 2024). Furthermore, natural environmental processes such as weathering (the process by which rocks and minerals break down or dissolve over time) and mercury biogeochemical cycling (the transferring mechanisms of mercury across the atmosphere, ecosystems, and the lithosphere) enhance Hg distribution and availability from these natural sources (Yin et al. 2024). However, knowledge about

mercury and other heavy metals concentrations in the peridotite rocks of the SPSP archipelago is still unavailable.

The mercury concentrations found in our study for SPSP Brown boobies (7.77 ± 2.18 $\mu g.g^{-1}$) were higher, but closer to those found in ventral feathers of Brown boobies in the Santana archipelago by Bighetti et al. (2022) (6.46 ± 1.19 $\mu g.g^{-1}$). Located in southeastern Brazil (closer to the mainland, < 10 km from the coast), the Santana Archipelago is primarily composed of metamorphic rocks (gneiss and amphibolite), pegmatite dikes (plutonic rock) and diabase (subvolcanic rock) (Silva 2007). A geological report published in 2010 by Geological Service of the State of Rio de Janeiro for the Santana Archipelago highlighted the presence of natural erosive processes on the metamorphic rock outcrops of Ilha do Francês. It is known that rock erosion is one of the natural sources of mercury into the environment, however, the rock formation and erosion does not appear to be the main source of mercury for the Santana Archipelago Brown boobies, because igneous rocks can contain low traces of mercury since their formation, usually ranging from 0.04 ppm to 0.5 ppm (Aston and Riley 1972). In this case, perhaps the proximity to the continent and anthropogenic sources of mercury due to human activities may be exerting more influence on the amount found in the boobies.

The studies conducted in the Abrolhos Archipelago (Nunes et al., 2022, and Bauer et al., 2024), located in Northeast Brazil (70 km from the mainland) and characterized by volcanic rocks such as basalts and pyroclastic rocks, found much lower concentrations than those presented in this study, but this seems to be more related to the type of feather used (contour feathers), and therefore cannot be directly compared with the results found here from SPSP e MS (ventral feathers, known to be the type of feather with the highest concentrations of Hg in Brown boobies). Therefore, we highlight here that the results of mercury concentration in different populations of

boobies must be analyzed using an integrated approach of (i) ecological factors (molting period, type of feather analyzed and movement of individuals in the population), (ii) geological (origin of the archipelago, rock composition) and (iii) geographic (location and influence of different ocean currents or anthropogenic pollution input).

Bighetti et al. (2022) tested differences in THg concentrations among ventral, dorsal, wing, and tail Brown booby feathers and found the highest concentrations in ventral ones, suggesting the use of these as suitable proxies of mercury concentration for the species, because despite showing expressive levels of the element, ventral feathers are easy to sample and do not impair flight performance. The molting strategy of Brown boobies' wing feathers is classified a as complex basic molt with a stepwise strategy (Howell 2010). The molt of primaries and rectrices begins after chicks' hatch, but the molting schedule for body feathers including the ventral ones is not well-known (Howell 2010, Schreiber and Norton, 2020). Due to the wide variation in THg concentration between feather types from the same individual, it is challenging to compare values among different locations or environments, impairing the comprehension of whether the source of variation is more related to local environmental factors or whether this variation is mostly derived from the type of feather evaluated in each study (Furness et al. 1986, Peterson et al. 2019, Low et al. 2020).

Brown booby at sea movements outside the breeding period are not known in most of their colonies. Kohno et al. (2019) tracked eight individuals with geolocators during the non-breeding period on Nakanokamishima island, Japan, and reported the shortest direct maximum distance from the colony varying from 574–4,988 km, where 5 from the eight tracked individuals traveled less than 2000 km. For the Red-footed booby (*Sula sula*), a congener species, the mean maximum distance from colony reported in Raso Islet, Cabo Verde, during the non-breeding period was 55 km for males and 63 km

400 for females (Almeida et al. 2021). In the same study, the mean maximum distance from
401 the colony reported for Brown boobies was 42 km for males and 24 for females, but for
402 this species, individuals were tracked during the breeding period, chick rearing
403 specifically.

404 Considering that ventral feathers' molting period is not known (Howell 2010,
405 Schreiber and Norton, 2020), it is not possible to infer exactly when and where they
406 were formed, and therefore the location at which these feathers reflect mercury
407 exposure. However, since SPSP archipelago is a region with high prey availability for
408 Brown boobies in the surroundings of the colony (Nunes et al. 2018), and since
409 individuals do not travel long foraging trips during the breeding period when compared
410 to other archipelagos. For instance, the mean maximum distance from colony reached
411 by Brown boobies in SPSP was 7 km, while in different locations such as the Gulf of
412 California and the in the Caribbean the mean maximum distances from colony reported
413 were much higher: 28 km and 48 km, respectively (Weimerskirch et al. 2009, Soanes et
414 al. 2015, Nunes et al. 2018). In the MS archipelago, the mean maximum distance from
415 colony reported was 30 km (Benemann et al. Unpublished results). Thus, besides the
416 absence of available information, we hypothesize that individuals from SPSP do not
417 travel very long distances during the non-breeding period as well, but non-breeding
418 movements of MS individuals completely unknown.

419 *4.2.2 Diet related differences*

420 Another factor that must be considered to evaluate the difference found in THg
421 concentration between the two archipelagos is their diet. Brown booby diet varies
422 widely between the two studied archipelagos: In MS, the species exhibits a high
423 generalist foraging behavior, feeding on a wide variety of species from different taxa

424 and inhabiting different strata of the water column (e.g. benthic, demersal, epipelagic),
425 while in SPSP, Brown boobies are practically specialists on flying fish from the family
426 Exocoetidae (Jacoby et al. 2023). In MS, which is a coastal archipelago, the diet of
427 Brown boobies is predominantly based on fish from the Scianidae family, such as the
428 Banded croaked (*Paralonchurus brasiliensis*), the Bigtooth corvina (*Isopisthus*
429 *parvipinnis*) and the Stripped weakfish (*Cynoscion guatucupa*) (Branco et al. 2005,
430 Benemann et al. Unpublished results). On the other hand, the main species that
431 compound Brown boobies' diet in SPSP are the pelagic fish species Tropical two-wing
432 flyingfish (*Exocoetus volitans*) and the Margined flyingfish (*Cheilopogon cyanopterus*)
433 (Naves et al. 2002, Mancini and Bugoni 2014; Benemann et al. Unpublished results).

434 When we look at the trophic level of the species mentioned above, we can observe
435 that, in general, fish from the Scianidae family occupy a higher trophic level than flying
436 fish. Using an isotopic approach in ecology, the trophic level of a species is often
437 inferred through nitrogen ratios (δ^{15}N), where higher values indicate higher trophic
438 positions (Post 2002). In a study carried out in the Southwest Atlantic Ocean, it was
439 reported δ^{15}N values from 16.1 ‰ to 18.5 ‰ (mean ± SD = 17.6 ± 0.5 ‰) for *C.*
440 *guatucupa* (Viola et al. 2018). For *E. volitans* from the SPSP, Mancini and Bugoni
441 (2014) reported δ^{15}N values varying from 9.7 ‰ to 10.4 ‰ (mean ± SD = 10.2 ± 0.5
442 ‰), suggesting that this flying fish species occupies a lower trophic level than *C.*
443 *guatucupa.* Based on the Ecopath with Ecosim (EwE) model (Polovina 1984), which is
444 a tool for marine ecosystems modeling that is used, among other purposes, to estimate
445 trophic levels, the trophic level of the Scianidae species *C. guatucupa, P. brasiliensis,*
446 and *I. parvipinnis* were estimated at mean 3.7 ± 0.6, mean 3.4 ± 0.3 and mean 4.0 ± 0.4,
447 respectively, while the Exocoetidae species *E. volitans* and *C. cyanopterus* were
448 estimated at mean 3.0 ± 0.09 and mean 3.3 ± 0.38. respectively (FishBase 2024). These

449 estimates are based on Matthews (1993) where trophic level 1 is assigned to primary
450 producers and detritus and represents further evidence that the fish consumed by Brown
451 boobies from MS occupy higher trophic levels than those from SPSP. Controversially,
452 such results are not in accordance with the premise that species occupying higher trophic
453 levels in the trophic chain would exhibit higher Hg levels due to biomagnification (Kidd
454 et al. 2012, Seco et al. 2021). Probably, local environmental factors exert a greater
455 influence than prey trophic level; to test this hypothesis, an approach using stable
456 isotopes would be interesting and could provide important results to relate mercury
457 levels to prey trophic level and their relationship with the island's biotic and abiotic
458 factors.

459 *4.2 Sexual differences*

460 Males and females had similar average concentrations of THg, which led us to reject
461 the second research hypothesis. It was expected that female Brown boobies would show
462 lower Hg concentrations since one of the main mercury excretion pathways is through
463 egg production and laying (Robinson et al. 2012, Becker et al. 2002, Mills et al. 2022).
464 Our results regarding the absence of sexual differences in Brown boobies' mercury
465 levels are in accordance with Bighetti et al. (2021), which suggested that females'
466 greater body mass (Lewis et al. 2005) and consumption of relatively larger prey than
467 males (Bighetti et al. 2021) would compensate the amount of Hg excreted through eggs.
468 Mancini et al. 2022, on the other hand, reported males foraging on prey of higher trophic
469 positions than females in the Santana archipelago, which may indicate that males are
470 consuming larger prey than females based on the assumption of a positive relationship
471 between fish size and trophic position within the food chain (Romanuk et al. 2011).
472 Benedetti et al. 2022 also found no differences in THg concentration between Brown

473 booby sexes in the SPSP, attributing these results to the similarity in foraging behavior
474 between males and females.

475 Despite the absence of significant differences between sexes, the difference in THg
476 values between sexes was higher in the MS archipelago (Figure 2, a and b). This result
477 may be related to greater differentiation in diet between males and females in MS, since
478 in this archipelago Brown boobies exhibit a much wider trophic niche than in SPSP, and
479 although intersexual differences in diet were not tested yet in MS, females showed a
480 wider trophic niche than males in the Santana archipelago, in which Brown boobies'
481 diet is similar (Branco 2005, Mancini et al. 2021). Bustamante et al. 2023 also reported
482 significantly higher $\delta^{13}C$ and $\delta^{15}N$ values for females than males in blood Clipperton
483 Island, Pacific Ocean, suggesting that females feed on higher trophic level prey and in
484 different areas than males in that island.

485 *4.3 Age-related differences*

486 In our study there were also no significant differences between adult and juvenile
487 individuals, despite the assumption that adults would show higher concentrations due to
488 bioaccumulation throughout the living years. These results contrast with those found by
489 Bighetti et al. (2021) and Bighetti et al (2022), who reported significantly higher THg
490 and MeHg concentrations in adult Brown boobies. In a study conducted in Sinaloa,
491 Mexico, Blue-footed booby (*Sula nebouxii*) nestlings showed higher Zinc (Zn)
492 concentrations than adults, and the concentration decreased gradually with age (Lerma
493 et al. 2020). The study by Padilha et al. (2018) also did not find significant differences
494 in other bioaccumulative heavy metals (Cd and Cu) between adult and juvenile Brown
495 boobies in the Cagarras archipelago. Despite our results indicating no significant
496 differences in THg concentration between adult and juvenile Brown boobies, the lowest

497 THg values were reported for juveniles, and we can observe a wider variance in THg
498 concentrations in juvenile individuals than in adult ones (Figure 2, Table 1). In this
499 sense, the lack of significant difference in THg concentration between adults and
500 juveniles in our study may be due to a small sample size (n = 16 juveniles).

501 **5 Conclusion**

502 We found no significant differences in THg concentration in Brown boobies'
503 feathers between sexes and age classes, but rather between the two studied archipelagos.
504 Higher values were found in feathers of Brown boobies from the SPSP, which is a
505 tropical archipelago far from the coast off Brazil. While we present significant
506 differences in mercury concentrations in Brown booby across different archipelagos and
507 hemispheres, we understand that there are some limitations in the study that should be
508 considered, such as the lack of knowledge about the molting period and movement
509 during the non-breeding season of *Sula leucogaster*. That said, research is needed to
510 investigate the molting and movement of Brown booby in the SPSP and MS
511 Archipelagos so that we can better understand where these birds are becoming
512 contaminated and whether this contamination reflects the surrounding areas of the
513 archipelago or not. Our hypothesis is that the Hg concentrations found in the present
514 study reflect exposure to Hg near the breeding colonies of the respective archipelagos.

515 Brazil is one of the signatory countries of the Minamata Convention, which is a
516 global treaty aimed at protecting human health and the environment from the adverse
517 effects of mercury. The conservation and sustainable use of the oceans and marine
518 resources, for example, is one of the 17 Sustainable Development Goals of the United
519 Nations (ODS 14) which foresees a series of actions including the reduction and
520 prevention of marine ecosystems, to which Brazil is also committed. The high volatility

and great potential for dispersion of mercury are intrinsic features that challenges its environmental monitoring once it can reach areas far from the emission sources. Seabirds show great potential as biomonitors of mercury in marine environments, and future studies should prioritize the standardization of methods to enable comparisons between different populations.

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4 CONSIDERAÇÕES FINAIS

Este estudo apresenta novas informações sobre a ecologia do forrageio do atobá-pardo nos arquipélagos estudados, especialmente quanto a contribuição de descartes da pesca de arrasto na dieta da espécie no arquipélago de Moleques do Sul. Ao contrário do que se esperava com base na literatura disponível sobre a dieta das espécie neste arquipélago, a distribuição das frotas de pesca de arrasto nas proximidades de Moleques do Sul não influenciaram significativamente na seleção de áreas de forrageio, pelo menos no mês de setembro quando a pesca de arrasto na região é menos intensa. Embora as espécies de presas encontradas na dieta do atobá-pardo neste estudo sejam semelhantes às encontradas em estudos anteriores realizados na população reprodutiva de Moleques do Sul, e que tais espécies-presa sejam de fato amplamente descartadas pelas embarcações de pesca camaroeira, é provável que os atobás-pardos estejam obtendo essas presas naturalmente através de predação ao invés do consumo de descartes como se acreditava. Tais conclusões também são corroboradas pelos resultados obtidos nos sensores de profundidade, através dos quais se observou que as aves realizam mergulhos de forrageio de até 30 m de profundidade em Moleques do Sul, indicando comportamentos de mergulho de perseguição (*pursuit diving*) e mergulho de imersão (*plunge diving*) para a captura de presas. Desta forma, a primeira hipótese da tese, de que as atividades pesqueiras influenciam na escolha de habitats de forrageio do atobá-pardo em Moleques do Sul, não foi corroborada pelos resultados.

Em relação à qualidade nutricional das presas consumidas pelo atobá-pardo entre os dois arquipélagos estudados, foi observado um maior teor de proteína nos peixes de São Pedro e São Paulo e um maior teor de lipídios nas presas de Moleques do Sul. Embora não tenha sido observada uma diferença significativa na densidade energética por grama, segunda hipótese desta tese, quando associada à massa total de presas regurgitadas (*food load*), observou-se uma maior densidade energética nos conteúdos regurgitados pelos atobás-pardos de São Pedro e São Paulo. Desta forma, concluímos que a abundância e disponibilidade - e não a composição nutricional das presas em si - são fatores mais determinantes para que as aves obtenham uma maior eficiência de forrageio durante o período de guarda dos ninhegos, quando a demanda energética é mais alta devido às necessidades da prole.

A eficiência de forrageio dos atobás-pardos de São Pedro e São Paulo foi significativamente maior do que em Moleques do Sul, corroborando a terceira hipótese da tese. O ganho energético total foi maior devido à uma maior massa do conteúdo regurgitado, e o gasto energético nas viagens de forrageio menor, provavelmente devido à um maior esforço para a captura das presas em Moleques do Sul. Os atobás-pardos deste arquipélago realizaram viagens mais longas (distância máxima da colônia) e mergulharam em maiores profundidades (média e máxima) do que os de São Pedro e São Paulo, o que pode ser um reflexo da disponibilidade e distribuição espacial das presas nestes dois locais: predominantemente de espécies bentônicas e demersais (família Scianidae) em Moleques do Sul, e de espécies epipelágicas (família Exocoetidae) em São Pedro e São Paulo. As diferenças observadas no comportamento e na eficiência do forrageio do atobá-pardo entre os dois arquipélagos ressaltam a plasticidade trófica desta espécie, capaz de moldar amplamente sua dieta de acordo com as condições ambientais locais, o que pode conferir uma boa capacidade adaptativa à espécie em situações ambientais adversas.

Em relação à contaminação por mercúrio, não foram observadas diferenças significativas entre os sexos nem entre indivíduos adultos e juvenis, embora a concentração nas penas de adultos tenha sido ligeiramente maior e menos variável. Uma diferença significativa foi, entretanto, encontrada entre indivíduos dos dois arquipélagos. Ao contrário do que foi hipotetizado *a priori*, baseando-se na premissa de que ilhas mais próximas à costa estariam mais expostas à contaminação por mercúrio devido à proximidade com fontes de emissão de origem continental, os atobás-pardos de Moleques do Sul apresentaram concentrações de mercúrio menores em suas penas do que os de São Pedro e São Paulo. Foi discutido que esta diferença nas concentrações de mercúrio pode estar relacionada a características geológicas dos arquipélagos e a diferenças na dieta do atobá-pardo nestas duas localidades. Os resultados deste capítulo enfatizam a importância de considerar fatores espaciais e ambientais no biomonitoramento de mercúrio, e destacam uso potencial de penas de aves marinhas como biotraçadores em ecossistemas marinhos.

Sobretudo, cabe ressaltar a importância de estudos sobre dieta, ecologia trófica, interações com a pesca e contaminação por poluentes para a conservação das aves marinhas, uma vez que nos trazem informações essenciais para entender

como essas espécies respondem a alterações ambientais, seja de origem natural ou antrópica, e como estas alterações podem impactar sua sobrevivência e sucesso reprodutivo. Conhecer o comportamento de forrageio das aves marinhas nos ajuda a identificar seus hábitats críticos para alimentação e reprodução, fornecendo embasamento para a criação de áreas protegidas e estratégias para garantir que estas espécies tenham disponibilidade de alimento suficientes para as demandas energéticas em suas áreas de vida. Compreender a ecologia trófica, ou seja, como as aves se inserem nas cadeias alimentares marinhas, permite prever os impactos de mudanças ambientais, como as provocadas por alterações climáticas, sobre esses animais. Por fim, os estudos sobre contaminação por elementos tóxicos como o mercúrio em predadores de topo podem nos ajudar a compreender a distribuição e dispersão desses poluentes nos ecossistemas, bem como os processos de bioacumulação e biomagnificação dentro das teias tróficas.

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APÊNDICE A — FIGURAS DOS ARTIGOS

Os registros fotográficos apresentados nessa seção têm caráter ilustrativo e foram obtidos durante as coletas em campo e o processamento das amostras em laboratório. As Figuras 1-4 fazem referência ao capítulo 1, as Figuras 5-7 fazem referência aos capítulos 2 e 3.

Figura 1 — Arquipélago de Moleques do Sul, localizado na região costeira do estado de Santa Catarina, Brasil



Fonte: Elaborado pela Autora (2022).

Figura 2 — Ninho de *Sula leucogaster* monitorado no Arquipélago de Moleques do Sul em setembro de 2022



Fonte: Elaborado pela Autora (2022).

Figura 3 — Colocação do dispositivo de GPS Axy-Trek nas penas caudais de Sula leucogaster no Arquipélago de Moleques do Sul



Fonte: Fernando Farias (2022).

Figura 4 — Embarcações pesqueiras comumente utilizadas para pesca de arrasto (traineiras de arrasto de portas) fundeadas próximo ao Arquipélago de Moleques do Sul



Fonte: Elaborado pela Autora (2022).

Figura 5 — Colônia de *Sula leucogaster* no Arquipélago de São Pedro e São Paulo



Fonte: Elaborado pela Autora (2022).

Figura 6 — Fêmea de *Sula leucogaster* com GPS Axy-Trek fixado nas penas caudais no Arquipélago de São Pedro e São Paulo



Fonte: Bianca Costa Ribeiro (2022).

Figura 7 — Ninho de *Sula leucogaster* no Arquipélago de São Pedro e São Paulo. A espécie apresenta dimorfismo sexual no tamanho corporal, onde as fêmeas são maiores, e na coloração do bico e patas, que apresentam coloração rosada nas fêmeas e azulada nos machos.



Fonte: Elaborado pela Autora (2022).