Ecological niches, movement ecology, and energetics of seabirds in the eastern Pacific

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Abstract

Understanding ecological niches of seabirds in the wild, especially how sympatric species share limited resources, maximize fitness, and cope with environmental variability in the face of large fluctuations in energy availability is important for conservation and management. In this dissertation, I aim to determine how seabirds use their ecological niches by first estimating energy expenditure and field activity budgets in one seabird species (Chapter 3), the Peruvian Booby (*Sula variegata*), one of the most abundant seabirds breeding in Peru, and a species of economic importance due to the guano industry. I used doubly labelled water to obtain daily energy expenditure in the Peruvian Booby for the first time, which resulted to be similar to other sulids. Additionally, I tested if energy expenditure can be estimated from time activity budgets and/or dynamic body acceleration. Dynamic body acceleration correlated with daily energy expenditure, showing that energy expenditure can be measured using accelerometers.

Next, in Chapter 4, I determine how nutritional state varies across two years expanding my focus to two seabird species, the Peruvian Booby and the Guanay Cormorant (*Phalacrocorax bougainvilii*), sympatric fish-eaters. Using movement and nutritional data, I examined the foraging niches of these two species and how this is reflected in their fitness (via nutritional biomarkers) in two years with differing climatic conditions. As expected, seabirds increased their foraging distance from the colony during warm, El Niño-like conditions (2018) compared to cooler conditions (2019) but there was no impact on nutritional state. Seabirds may change foraging effort but not compromise their nutritional condition, potentially by sacrificing their current reproductive output (chick survival) to save energy for the next breeding cycle. However, the two species responded differently to warm conditions, implying that each species has a different nutritional niche.

Finally, I examine how seabird isotopic niches segregate across five decades (Chapter 5), with increasing niche dimensionality from two to three to five niche dimensions. Using those approaches, I compared overlap and community-wide niche metrics of sympatric species off the coast of British Columbia. More dimensions, with careful interpretation, provided additional information on niche segregation, and revealed patterns not seen in lower dimensional approaches. This supports the Hutchinsonian idea of an n-dimensional niche in ecological communities with no overlapping species. That is, even if species appear to overlap in classic isotope biplots, they show segregation in higher dimensions.

Overall, this thesis 1) highlights how the use of different methods in wild seabirds are necessary to study complex ecological systems, 2) provides the first measurements of energy expenditure of Peruvian Boobies, 3) correlates the relationship between foraging effort and physiology for Peruvian seabirds, and 4) provides evidence on how high multidimensionality in niche descriptions can provide more accurate information on segregation patterns of seabirds. My thesis increases knowledge on ecological niches of seabirds in the Eastern Pacific and demonstrates how complex systems require refined and long-term monitoring to further address the life history of wild predators.

Résumé

Il est important pour la conservation et la gestion de la faune de comprendre les niches écologiques des oiseaux marins, en particulier la façon dont les espèces sympatriques partagent des ressources limitées, maximisent leur condition physique et font face aux variations environnementales liées à d'importantes fluctuations de la disponibilité énergétique. Dans cette thèse, je cherche à déterminer comment les oiseaux marins utilisent leurs niches écologiques en estimant leurs dépenses énergétiques et leurs budgets d'activité en milieu naturel (Chapitre 3). Ceci est réalisé sur le Fou varié (*Sula variegata*) l'un des oiseaux marins les plus abondants se reproduisant au Pérou, et est d'une grande importance économique en raison de l'industrie du guano. J'ai utilisé la méthode de l'eau doublement marquée pour obtenir la dépense énergétique quotidienne du Fou varié, une première chez l'espèce, qui s'est avérée similaire à celle d'autres sulidés. De plus, je teste si la dépense énergétique peut être estimée à partir des budgets d'activité temporelle et/ou de l'accélération corporelle dynamique. L'accélération dynamique du corps est en corrélation avec la dépense énergétique quotidienne, ce qui montre que la dépense énergétique peut être mesurée à l'aide d'accéléromètres. Ensuite, dans le chapitre 4, j'ai déterminé comment l'état nutritionnel varie entre deux années, en utilisant deux espèces d'oiseaux marins, le Fou varié et le Cormoran de Bougainville (*Phalacrocorax bougainvilii*), des piscivores sympatriques. À l'aide de données sur le mouvement et l'alimentation, j'ai examiné les niches trophiques de ces deux espèces et la façon dont cela se reflète dans leur condition physique (par le biais de biomarqueurs nutritionnels) au cours de deux années où les conditions climatiques étaient différentes. Comme prévu, les oiseaux marins ont augmenté leur distance de recherche alimentaire pendant les conditions chaudes semblables à El Niño (2018) par rapport aux conditions plus fraîches (2019), sans impacter l'état nutritionnel. Cela démontre que les oiseaux marins peuvent modifier leur effort de recherche alimentaire sans compromettre leur état nutritionnel, potentiellement en sacrifiant leur rendement reproductif actuel (survie des poussins) afin d'économiser de l'énergie pour le prochain cycle de reproduction. Cependant, les deux espèces ont réagi différemment aux conditions chaudes, ce qui implique que chaque espèce a une niche alimentaire différente. Enfin, j'ai examiné comment les niches isotopiques des oiseaux marins se séparent sur cinq décennies (chapitre 5), en augmentant la dimension des niches à deux, trois et cinq dimensions. En utilisant ces approches, j'ai comparé le chevauchement et les mesures de niche à l'échelle de la communauté d'espèces sympatriques au large de la côte de la Colombie-Britannique (Canada). Des dimensions plus importantes, avec une interprétation minutieuse, ont fourni des informations supplémentaires sur la ségrégation des niches, et ont révélé des schémas qui n'avaient pas été observés dans les approches à dimensions plus faibles. Cela confirme l'idée d'une niche d'Hutchinson à n dimensions dans les communautés écologiques où les espèces ne se chevauchent pas. En d'autres termes, même si les espèces semblent se chevaucher dans les diagrammes isotopiques classiques, elles présentent une ségrégation dans les dimensions supérieures. Dans l'ensemble, cette thèse 1) met en évidence la nécessité d'utiliser différentes méthodes pour étudier des systèmes écologiques complexes chez les oiseaux marins , 2) fournit les premières mesures de la dépense énergétique des fous variés, 3) établit une corrélation entre l'effort de recherche de nourriture et la physiologie des oiseaux marins , et 4) fournit des preuves de la façon dont la multi dimensionnalité élevée des descriptions de niche peut fournir des informations plus précises sur les schémas de ségrégation des oiseaux marins. Ma thèse contribue aux connaissances sur les niches écologiques des oiseaux marins dans le Pacifique oriental et démontre que les systèmes complexes nécessitent une surveillance précise et à long terme pour mieux comprendre le cycle biologique des prédateurs marins.

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Contribution to original knowledge

Wildlife ecology research is continuously growing all over the world but there is still an increasing need for research in the Global South to improve resource management and conservation decisions. In this thesis, I contribute to knowledge on seabird ecology in Canada and Peru, using energetics, accelerometry, GPS tracking, physiology, and compound specific isotopes, methods used to address current questions in ecological research.

Chapters 3 and 4 delve into the ecology of Peruvian seabirds, where information is still needed about their life histories. For example, in Chapter 3 I report for the first time the daily energy expenditure, activity specific budgets and activity costs for Peruvian boobies, one of the most abundant seabird species in the Peruvian coast, a highly exploited marine ecosystem. This allows us to calculate the amount of food (anchovies) removed from the system by these birds, one of the most populous predators in this highly valuable fishery.

In Chapter 4, I provide the first physiological measurements of nutritional biomarkers for guanay cormorants and Peruvian boobies, and link them to their foraging effort, comparing these values between two climatically different years. With current climate change trends likely to exacerbate El Nino phenomena, my research aims to address the lack of information on physiological fitness and foraging effort in these Peruvian seabird species. I also describe for the first time repeatability measures in the form of similarity of foraging tracks using the Earth's movers' distance, which allows to define foraging patterns without generalizations of density estimates.

Finally, in Chapter 5, I use a multidimensional approach with compound-specific (amino acids) stable isotope analysis to produce up to five-dimensional niches of five species of seabirds in the coast of British Columbia, a first attempt to incorporate an n-dimensional Hutchinsonian niche concept using multiple isotopes to seabirds. The Hutchinsonian niche concept is often recommended but rarely put in practice in ecological research, but with the aid of current Bayesian inference models for isotopic ecology, my research brings novel information to show how this concept can illuminate ecological science.

Contribution of authors

Chapter 3 has been submitted to Journal of Experimental Biology and is currently under review. Kyle Elliot and I developed the concept of the study. Kyle Elliott, Jaime Silva and I collected all the data on the field. Allison Patterson contributed heavily with R coding and advised on accelerometer data processing. I completed all the analysis and wrote the manuscript. All authors provided editorial comments on the manuscript.

Chapter 4 is formatted for submission to Marine Biology. The concept for this study was developed by Kyle Elliott and me. Kyle Elliott, Jaime Silva and I collected data on the field. Allison Patterson contributed with the R coding and analysis. I completed all the analysis and wrote the manuscript. All authors provided editorial comments on the manuscript.

Chapter 5 has been accepted in Scientific Reports. The concept of this study was developed by Kyle Elliott and Francis van Oordt. John Elliott provided the long-term isotopic dataset from ECCC-CWRC. R code for data processing and analyses was written by Antonio Cuba and me, respectively. I processed the results and wrote the manuscript. Emily Choy provided guidance in the direction of the analyses. All authors provided editorial comments on the final version of the manuscript.

Chapter 1 Introduction

For years, seabirds have been considered indicators of the marine ecosystem's status (Piatt et al., 2007) and health (Velarde et al., 2019). Seabirds are usually very visible at sea and they move along ecosystem gradients such as primary productivity (Ballance et al., 1997; Ramírez et al., 2017) and fish stocks (Crawford, 2007), and even have the potential to track fisheries (Votier et al., 2010). In recent years, with the invention of new technologies in animal tracking and biochemical analyses, researchers have delved deeper into the relationships between seabirds and their habitats, by means of isotopic studies (Newsome et al., 2007; Sydeman et al., 1997) or tracking their movements at different scales, from short local displacements (Gandini et al., 2005; Mallory & Gilbert, 2008; Rishworth et al., 2014), to long distance foraging (Weimerskirch, Le Corre, et al., 2005), and even to pole-to-pole migrations (Shaffer et al., 2006).

Using seabirds to understand complex ecological processes in the oceans has been key to increasing our knowledge of many aspects of oceans in recent years (Brisson-Curadeau et al., 2017; Thibault et al., 2019). Additionally, many seabird species face strong conservation pressures due to habitat degradation (Simeone & Bernal, 2000), mining and oiling activities (Piatt & Ford, 1996), marine traffic (Merkel et al., 2023), and overall prey depletion due to intensive fisheries (Furness, 2003). The gap of knowledge on the connection between marine systems and seabirds, especially in the neotropics, is large (Croxall et al., 2012), and is one of the reasons that motivated my doctoral research presented in this manuscript. Below, I introduce my Literature Review each of my three "data" chapters, which begin with Chapter Three following Chapter One (Introduction) and Chapter Two (Literature Review).

In Chapter Two, I do an extensive literature review on the overarching topics of my research, including niche ecology, movement and foraging ecology, and energetics. I dig deeper into isotopic niche segregation, foraging and physiological fitness, and energy expenditure budgets, with a short introduction on the two main ecosystems used for my studies.

In Chapter Three, I delve into the energetics of one of the most abundant seabirds currently in the Peruvian Humboldt Current System guano-island system, the Peruvian Booby. My first goal was to understand the energy expenditure patterns of the species, by estimating daily energy expenditure using a direct method for the first time in this bird. My second goal was to validate activity patterns (time budgets or activity-specific dynamic body acceleration) as a method for making estimates of daily energy expenditure.

In Chapter Four, I investigated the differences in foraging movements and nutritional status of two species of Peruvian seabirds along the Peruvian Humbolt Current System. My main objective was to understand how foraging effort changed in the two species in two years of differing climate, and how effort, expressed in the components of a foraging trip, correlated with nutritional status, as an indication of overall fitness, and how this adheres to the predictions of foraging theories.

In my Chapter Five, I investigated the long-term niche segregation patterns of seabirds in Western Canada, using a dataset with data from more than 50 years. My main objective was to detect how segregation patterns change using multiple isotope markers, and how increasing dimensions, as suggested by the Hutchinsonian niche concept, can reveal more refined segregation patterns overlooked in lower dimension approaches.

Chapter 2 Literature review

Wild animals procure their food using many different strategies, even switching from one strategy to another when prey or conditions change (Barbosa & Moreno, 1999; Helfman, 1990; Traniello, 1989; White, 1983). Commonly predators will change the composition of their diet to deal with changes in the environment that alter prey abundance, as their proximal strategy, but they also may change behaviours to procure their prey (Morehouse & Boyce, 2011). Additionally, often several predator species will inhabit the same areas and will aim for similar prey types or food items (Berry et al., 2017; Emmrich & Düttmann, 2011; Gulka et al., 2017). In those cases, given the additional competition, predators will be under even greater pressure to alter diet or foraging behaviour. Differences in diet composition, behaviours, and consequently energy budgets, can eventually be reflected in survival rates and fitness, especially under highly variable or strenuous conditions (Field et al., 2005; Julliard et al., 2006; Ketchum et al., 2013; Navarro et al., 2013).

This literature review will address three main topics of ecological research in seabirds: niche segregation patterns; foraging movements, ecology, and fitness; and activity and energy expenditure budgets. I will cover a broad range of elements involved in each topic and the current methods used on said topics to assess ecological patterns of seabirds. Each topic will be put into the context of the two important Eastern Pacific marine ecosystems where this research was developed: the marine ecosystems around Vancouver Island, in Canada, and the Peruvian Humboldt Current System, off the Peruvian coast.

Seabirds in Eastern Pacific Ocean Ecosystems

Canadian marine systems: marine habitats off the coast of British Columbia

Two main marine habitats surround Vancouver Island and Haida Gwaii, totalling ~42 000 km^2 island surface, both located off the southwest coast of British Columbia, in the Canadian northeast Pacific: the rich cool waters mainly influenced by the Vancouver Island Coastal Current (Thomson, 1981) on the western coast of Vancouver Island, and the marine and estuarine waters of the Salish Sea, which includes the Juan de Fuca Strait, and the Strait of Georgia (Sobocinski, 2021), on the eastern coast. The richness of the ocean off the west of Vancouver Island and Haida Gwaii greatly depends on the Juan de Fuca Strait nutrient flow, coastal upwelling, and the coastal undercurrent (Patterson et al., 2011) (Fig. 2.1). This marine area is characterized by a temperate coastal climate, dry and warm summers, and rainy and cool winters (Gurdebeke et al., 2018). The continental shelf off southwestern Vancouver Island is split by Juan de Fuca Canyon in the south, and overall possess a complex bathymetry, and upwelling center exists off the mouth of the Juan de Fuca Strait. Although, this upwelling is highly seasonal and strong in the summer months, unlike others that are more consistent through out the year (e.g. Peru's Upwelling System) (Hay, 1992).

More than 100 species of birds inhabit the surrounding waters of Vancouver Island and exploit the region for food and shelter (Duguid et al., 2019; Gaydos & Pearson, 2011; Hay, 1992; Logerwell & Hargreaves, 1996). There are roughly two assemblages of seabirds exploiting the marine environment around Vancouver Island. Among those using the Salish Sea area we have ducks, geese, shorebirds, gulls, egrets, cormorants, grebes, small numbers of alcids, among others (Gaydos & Brown, 2009; Gaydos & Pearson, 2011). The western ocean off Vancouver

Island includes some of these previously mentioned species, plus others with more pelagic habits such as: large congregations of alcids, shearwaters, and albatrosses (Hay, 1992).

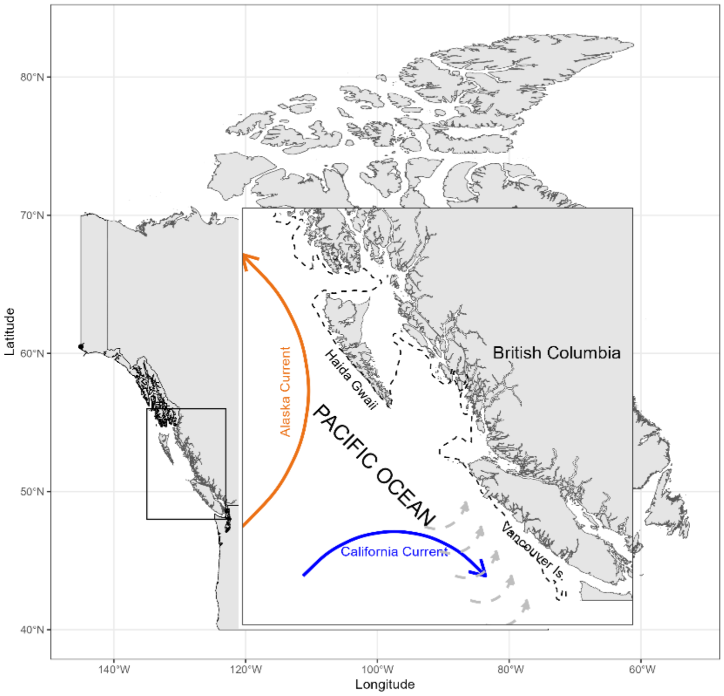

Figure 2.1. Western Coast of British Columbia depicting most important oceanic currents and islands that host seabird colonies. The dashed line represents the continental shelf limit at 140m. Note the clear difference of continental shelf extension west of Haida Gwaii Islands compared to Vancouver Island. An upwelling center is located at the southern tip of Vancouver Island (dashed grey arrows).

Those seabird species with breeding colonies along either coast of Vancouver Island are of greatest importance to study in the area because they provide insight into overall ecosystem health (Parsons et al., 2008). People have been living in the region for millennia, with pre-Columbian population densities in the region being among the highest on Earth, rivalling those in China, Europe, Middle America and the central Andes. These Haida, Tsimshiam and other First Nations were sustained by remarkably plentiful ocean resources. In the two centuries since "British Columbia" was created, many of those resources have been decimated; Pacific herring stocks have collapsed in the Salish Sea and many salmon runs have disappeared. By monitoring seabirds, we can determine levels of toxic contaminants in fish (including those consumed by humans), population levels of forage fish that are key to ecosystem health and predict future fish stocks—essential so the remarkable marine bounty of the region can sustain populations for the next millennia. Of the cormorant species in the region, double-crested cormorants inhabit coastal nearshore to inland aquatic environments, with generalist habits, feeding on benthic and mid-water fish, while pelagic cormorants feeding in deeper waters (Carter et al., 2018; Mercer et al., 2013; Robertson, 1974; Sydeman et al., 1997). Alcids, such as rhinoceros auklets and ancient murrelets, and feed on epipelagic fish (Burger et al., 1993) and zooplankton and small fish (Sealy, 1975), respectively. Leach's storm-petrels feed commonly on plankton over the continental shelf during the breeding season (Hedd & Montevecchi, 2006). By monitoring a suite of species including cormorants, alcids and storm-petrels, we can thus monitor marine ecosystems from the coast to the continental shelf.

Like many other marine ecosystems, the Salish Sea and marine areas surrounding Vancouver Island suffer from great pressures that directly or indirectly influence the ecological processes and seabird populations that inhabit them. These include degradation of forest and shoreline habitat by urbanization and house development, industrial forestry and hydroelectric dams that have destroyed salmon habitat, contamination of water and bottom sediments, overall shifts in food web interactions, increased non-native and invasive species presence with high potential to alter habitat structure and native species diversity, among others (Gaydos et al., 2008). In the last decades, several species of seabirds that inhabit the coast of British Columbia, including both pelagic and double-crested cormorants, have shown a fluctuations in populations sizes that include significant declines in the area (Carter et al., 2018, 2018; Ethier et al., 2020). Some of factors attributed to these declines are the persistence of contaminants in the marine systems off the British Columbia coast, which in turn affects survival and breeding output of seabird species (Elliott et al., 2023; Elliott & Elliott, 2016).

Also, El Nino Southern Oscillation, ENSO, has a significant impact on the seasonal upwellings around Vancouver Island (Thomson, 1981). The region is also affected by the global effects the ENSO including the interannual to multidecadal variations in its surrounding ocean's climate (Ware & Thomson, 2000). In this context, understanding the ecosystem dynamics in this region which is also affected by fisheries (Ainsworth & Pitcher, 2005; Moss & Cannon, 2011; J. Smith & Morgan, 2005) and possesses high abundance and diversity of predators, such as birds and many endangered and iconic mammals (killer whales, otters, etc., Bigg & MacAskie, (1978); Ford & Ellis (2006))

Peruvian upwelling marine system

The Peruvian Humboldt Current System (PHCS) is one of the most productive upwelling systems on the planet sustaining large biomasses of both prey and large predators. In this region, strong seasonal upwelling supports several complex food webs (Fig. 2.2). The key component of these ecosystem's food webs is the Peruvian anchovy (*Engraulis ringens*), which is the prey of most coastal predators, especially seabirds (Crawford et al., 2006; Crawford & Jahncke, 1999).

Climate events, such as El Niño or Kelvin Waves, change the normal conditions of the PHCS, reducing upwelling and increasing the sea surface temperature, changing species distributions in the water column (vertically and horizontally) (Chavez & Messié, 2009). In the past few years, the PHCS has been subject to more frequent and stronger changes due to El Niño that can drastically change primary productivity levels, which then directly affects prey abundance and therefore seabird populations, behaviour, and energetics. At the same time, fisheries provide intense competition for predators in this system as well (Bertrand et al., 2012).

During periods of reduced prey abundance due to El Niño or overfishing, seabirds may need to switch foraging locations, prey types, or expend unsustainable levels of energy to obtain distant prey, eventually leading to reproductive failure and reduced fitness (Jahncke et al., 2004). Factors such environmental change and increased fishing effort greatly affect the distribution, dispersal, breeding success and overall survival of seabird species in marine ecosystems in the world (Hemery et al., 2008; Quillfeldt & Masello, 2013; A. D. M. Smith et al., 2011; Tasker, 2000; Votier et al., 2010), including cormorants, boobies, pelicans, among other species (Bertrand et al., 2012).

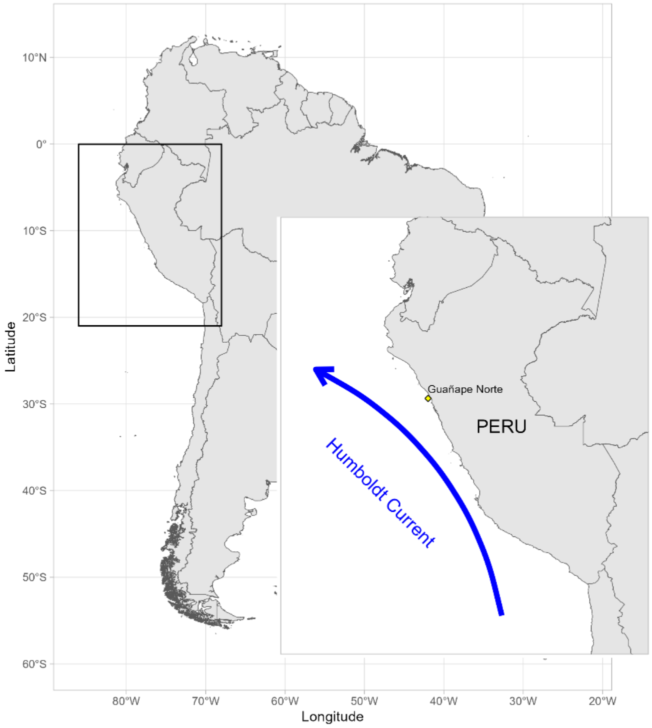

Figure 2.2. Area of influence of the Peruvian Humboldt Current System, including the location of Guañape Norte Island (yellow diamond shape). The island location coincides with one of the major upwelling centers in Peru (not depicted).

There are about 100 species of seabirds that coexist in the PHCS waters (Spear & Ainley, 2008), and about 20 of these species breed sympatrically along the Peruvian coast (Crawford et al., 2006). Among these, the well renowned "guano seabirds" are of special interest because of their high numbers, economic importance (due to the exploitation of their guano as a natural fertilizer), and their role as predators of Peruvian anchovy. Peruvian boobies (*Sula variegata*) and Peruvian pelicans (*Pelecanus thagus*) are plunge divers, that feed on Peruvian anchovy, during the day and night, respectively (Jeyasingham et al., 2013; Weimerskirch et al., 2012; Zavalaga et al., 2010, 2011). The guanay cormorant (*Phalacrocorax bougainvilii*) is the eponymous guano seabird, whose abundance has not recovered since the last population crash in the 1970s. It is a foot propelled diver feeding also exclusively on Peruvian anchovy (Weimerskirch et al., 2012; Zavalaga & Paredes, 1999).

Besides the guano seabird species, a few other seabirds make important use of the same island and areas within the island. Among them are Humbolt penguins (*Spheniscus humbolti*) and Inca terns (*Larosterna inca*) are two sympatric species to the previous three, sometimes considered also guano seabirds, because they inhabit the same inshore "guano-islands", abundances are relatively high, and feed primarily as well on Peruvian anchovy (Nelson, 2006; Taylor et al., 2002). Nesting, and primarily resident, procellariforms in the region, such as Peruvian diving-petrel and Markham's storm-petrel, may feed on lower trophic level prey items (e.g. anchovy or other small pelagic larvae) and also breed in the same coastal islands, or on the coast as well (storm-petrel) (García-Godos et al., 2002; García-Godos & Goya, 2006; Jahncke et al., 1999). Some other iconic resident seabird species that inhabit the PHCS and may play an important role in the ecological process in the system are: red-legged cormorants (*Phalacrocorax gaimardi*), neotropical cormorants (*Phalacrocorax brasilianus*), kelp gulls (*Larus dominicanus*), and Belcher's gulls (*Larus belcheri*). Conversely, many migratory species also exploit the waters of the PHCS and little to nothing is known about their roles in the trophic or energetic processes in the region, such as: waved albatross (*Phoebastria irrorata*), black-browed albatross (*Thalassarche melanophris*), white-chinned petrel (*Procellaria aequinoctialis*), sooty shearwater (*Ardenna grisea*), pink-footed shearwater (*A. creatopus*), Franklin's gull (*Leucophaeus pipixcan*), Wilson's storm-petrel (*Oceanites oceanicus*), Elliot's storm-petrel (*O. gracilis*), red phalarope (*Phalaropus fulicarius*), among many others (Spear & Ainley, 2008).

Environment and Climate Change Canada's Specimen Bank

Environment and Climate Change Canada (ECCC) is agency in change of the administration of two environmental specimen banks; the National Aquatic Biological Specimen Bank (a repository of mostly fish tissues gathered as part of ECCC Fish Contaminants Monitoring Program) and the National Wildlife Specimen Bank, which houses mainly bird tissues (collected through different monitoring programs and research studies in the country). The National Wildlife Specimen Bank is housed in the National Wildlife Research Centre (NWRC), currently located in Carleton University in Ottawa and has the capacity to hold thousands of samples in three extra-large –40°C walk-in freezer rooms for long-term storage. The samples from the National Wildlife Specimen Bank have hundreds of research studies in the last years and also Chapter 3 of this thesis, on isotopic niches of seabirds in British Columbia. But the housed in the bank range from the Atlantic, to the Arctic, and the Pacific. The National Wildlife Specimen Bank allows for the retrospective screening for new chemical compounds that otherwise would be impossible.

Energy expenditure estimations in wild animals and seabirds

Energy requirements of wild animals, determined by metabolic rates, will control many factors in their life history and survival, such as diet composition and daily amount of food needed (Nagy, 1987; Nagy et al., 1999). Basal metabolic rate (BMR), the energy expenditure in a resting or very low activity state, and field metabolic rate (FMR), energy expenditure while active [e.g. locomoting, foraging, etc.], have been commonly used to explain energetic demands in wild animals (Hudson et al., 2013). Flapping flight is energetically expensive compared to most other activities, and this is especially true in seabirds that need to travel great distances to find food in very patchy environments (Ballance et al., 1997; Weimerskirch, 2007). Many seabirds switch from air to water to locate and later catch their prey, which imposes limitations in their locomotion or the need of behavioural adjustment during foraging (Ropert-Coudert et al., 2004). This change of media implies a trade-off in optimal locomotion between both media.

Among different foraging strategies, plunge diving seabirds have high aspect ratio wings, a design better adapted for longer and more sustained flights (Van Oordt et al., 2018). However, plunge-diving seabirds do not reach great depths compared to other diving seabirds, as they do not propel themselves underwater for sustained times with their wings or legs (Ropert-Coudert et al., 2004, 2009). Conversely, foot-propelled diving seabirds, such as cormorants, are less adapted for long sustained flight and typically forage close to their colonies compared with other seabirds of a similar size (Cody, 1973; K. H. Elliott et al., 2013; Stothart et al., 2016). On the other hand, foot-propelled divers are efficient at foraging and chasing prey underwater (Harell, 2016). Thus, one might expect that plunge-divers invest their time in low energy-cost flight (therefore greater foraging range) at the expense of limited time underwater (limited foraging depth or prey availability in the water column). The transport costs (energy consumed per unit of distance travelled) and metabolic constraints of wild seabirds will have great impact in their fitness and ecology (Halsey, 2016; Halsey & White, 2010, 2019; Shaffer, 2011).

Classic methods for metabolic rate estimation include respirometry, which is performed mainly in the lab and allows us to estimate only resting metabolic rate (RMR), but with some applications in the field (K. H. Elliott, 2016). The method involves capturing animals and keeping them in a box for long periods of time and measuring the amount (volume of oxygen V_{O2}) of oxygen consumed (Shirai et al., 2013). Oxygen consumption can be expressed in watts or joules per unit of time using conversion coefficients that could be species specific or generalized from the literature, and depend on the substrate being metabolized (carbohydrate or protein) and the number of ATP generated per oxygen molecule (Shirai et al., 2013). But the need to estimate field metabolic rates (FMR) has given rise to a series of other methods that allow a measurement of caloric use while performing other activities more relevant to the actual ecology of seabirds.

One method commonly used to estimate field metabolic rate is heart rate, which consists of using a heart monitor implanted into the animal via surgery and is therefore highly invasive (Hicks et al., 2017). This method may offer a different approach to measure instantaneous effort and energy expenditure in wild animals but pose different constraints as calibrations are required to correlate heart rate frequencies and activities and volumes of oxygen consumed (Bevan et al., 1994; Weimerskirch et al., 2000). In particular, heart size and thus stroke volume will vary among individuals, and so oxygen delivered per heartbeat will be variable.

Doubly labelled water (DLW) has been used on wild animals since at least the early 1980s (Lifson & McClintock, 1966; Nagy et al., 1999) and allows the estimation of energy expenditure in the field. The method is based on the turnover rates of isotopic markers, specifically hydrogen (^{2}H or ^{3}H) and oxygen (^{18}O). Heavy water (water enriched in both isotopes, know as DLW, or even triply labelled water) can be easily injected into an animal (Speakman, 1997). Those isotopes will rapidly equilibrate with the body water of the organism (Fig. 2.3) within approximately one hour, depending on the size of the animal. Once the animal has been released and a longer amount time has passed, turnover of the labeled body water will occur due to water ingestion, exchanges with inspired oxygen and carbon dioxide production, and metabolic water production (Shaffer, 2011). As water flux is tracked via the hydrogen isotopes, the difference between oxygen flux and water flux can be estimated to determine carbon dioxide production. Assuming a known respiratory quotient, oxygen consumption rate can be estimated from carbon dioxide production. The use of this method has been validated in several species of mammals and birds, and accurately estimates an animal's field metabolic rate, rather than only basal metabolic rate obtained in the laboratory by means of respirometry (Costa & Gales, 2003; Fort et al., 2011).

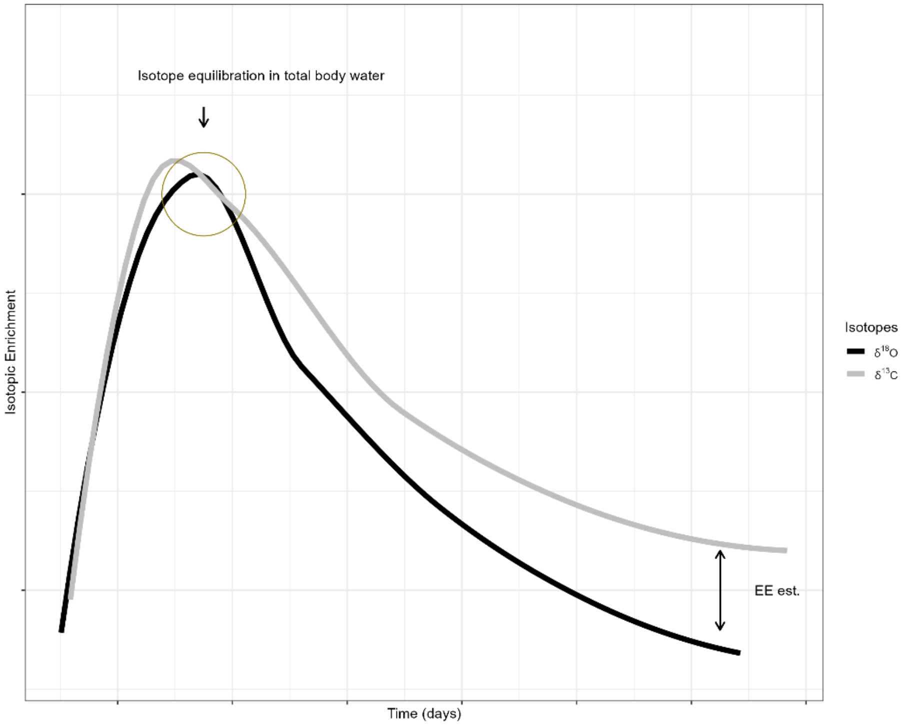

Figure 2.3. Doubly labelled water enrichment curves for $\delta^{18}O$ and $\delta^{2}H$ (deuterium) after injection. Black curve represents $\delta^{18}O$ and grey curve represents $\delta^{2}H$ (deuterium). The difference between both enrichment values after a given time can be used to estimate energy expenditure (EE est.), The circle shows the equilibration point after a given time, usually consistent between isotopes.

One of the caveats of using DLW is that it will produce one unique value for the total span of time that the animal was released and recaptured (usually ranging from one day to two or three days depending on the species and the among of water injected). Before 2 days, isotope levels are too close to initial levels, and after 3-4 days, isotope levels are too close to background, to provide a measurable signal of energy expenditure. Additionally, to accurately estimate equilibrium curves using the DLW method, it is required to hold some individuals for the expected *equilibrium time* (1-2 hours) in a closed chamber (Gabrielsen et al., 1991; Shaffer, 2011). Therefore, several blood samples are taken at different stages of the process to obtain dilution rates of isotopic markers at different times (background, at equilibrium, final measurement, Speakman 1997). Once measurements of the isotopic concentration in the water of the blood has been performed, mathematical formulae are applied to get accurate estimate of energy expenditure in joules during the sampling time (Nagy, 1987; Speakman, 1997).

Due to the overall intrusiveness of the abovementioned methods (i.e. holding an animal for 1 hour for equilibration, surgery) and the limitation of the time scale (2-3 days) for doubly-labelled water, the adoption of accelerometry as a technique for measuring energy expenditure, in humans and wild animals has increased in the last decade (Hicks et al., 2017). Because acceleration signatures should closely correlate with locomotory methods allowing identification of behaviours, and also should correlate with the energy associated with the physical work required for each behaviour, accelerometry potentially allows for the measurement of fine scale energy costs (Chivers et al., 2015; K. H. Elliott, 2016; Kokubun et al., 2015).

Dynamic body acceleration (DBA) can be calculated from tri-axial acceleration (heave, surge and sway) as the integral of acceleration over time after removing the static component associated with posture (Gómez Laich et al., 2009; Wilson et al., 2006). DBA can be expressed as Overall DBA (the raw measurement of the DBA in each activity) or Vectorial DBA (a measurement that accounts for the direction of movement), but both measurements are correlated with another(Gómez Laich et al., 2009). DBA correlates with energy expenditure during different locomotory methods (flying, walking, diving) and even resting (Gómez Laich et al., 2009; Wilson et al., 2006). Thus, energy expenditure can be estimated from DBA by means of time budgets of previously defined and classified behaviours (Patterson et al., 2019) or by summing up total DBA per activity (Stothart et al., 2016). In the first method ('time budget method'), the activity patterns observed with accelerometers can be used in combination with DLW to calculate activity costs by using a multiple regression of FMR on activity budgets with the intercept set to zero (Shaffer, 2011). In the second method ('DBA method'), the strong correlation of overall dynamic body acceleration (ODBA) with the rate of oxygen consumption (VO2) allows for estimations of activity-specific energy expenditure directly (Gómez Laich et al., 2009). The use of accelerometers to measure energy expenditure, after validation using DLW, may be an effective and less stressful method in wild birds. Moreover, this method could measure energy expenditure at a scale from seconds to years while DLW is limited to measuring energy expenditure over about 2-3 days in seabirds.

Seabird niches and segregation

In community ecology, understood as the study of the complex suite of interactions of organisms coexisting in a particular location, the way to define the ecological niche of species has puzzled researchers from more than two hundred years, as noted by Hutchinson (1959).

Although much has been said and written about ecological niches there is no unified literature about it (Pedruski et al., 2016) and definitions have shifted from habitat descriptions focusing on the physical environment (Grinnell, 1917) to more functional approaches such as the trophic roles of species (Elton, C.S., 1927), to more comprehensive definitions which consider niches as n-dimensional spaces that describe the position of species by a complex suite of variables, both physical and biological (Hutchinson, 1957).

The pattern or topology of species niches in an ecosystem can allow us to comprehend ecological processes that may have shaped community structure, such as competition or predation (Bastolla et al., 2002). Indeed, understanding the mechanisms shaping ecological niches, as well as understanding of the relationship between functional diversity (i.e. diversity of niches) and ecosystem functioning has become an important priority in community ecology (Dehling & Stouffer, 2018). Niches can partly reflect patterns of ecological segregation (De León et al., 2014; Wilson, 2010). Such segregation is expected to be the result of past competition in a way that species currently exploit resources differently to minimize use overlap and without such segregation geographic exclusion may occur (Croxall & Prince, 1980; Navarro et al., 2013; Weimerskirch et al., 1986). For example, seabird species partition their foraging space or prey in several geographic and temporal scales (Barger & Kitaysky, 2012; Ceia et al., 2015; Masello et al., 2010; Wakefield et al., 2013), or may partition nesting locations within a colony to avoid competition for space (Cody, 1973).

Optimal and central place foraging theory: link foraging, physiology and fitness

Most predators in most circumstances should obtain food by means of searching, locating, and capturing food items or prey. The energy obtained should be enough to support other activities as predators normally will not be able to perform two different tasks at the same time, such as obtaining food, mating, defending territories, or avoiding predators (Pyke, 2019). Models have a set of assumptions that determines the model's 'optimal' choice of behaviour by the predators, such as currency and physiological constraints (Stephens & Krebs, 1986). However, all 'optimal foraging models' assume that natural selection leads to animals using the most efficient strategy to balance energy gain and consumption.

Overall, optimal foraging theory focuses on four main topics of the foraging process: diet, patch choice, patch exploitation, and movement. Diet composition is variable among predators under the same conditions, as is prey quality (energy content, size, etc.), so it is expected that predators make a choice about which item to secure (Brisson-Curadeau & Elliott, 2019). Food items are not equally distributed in the surrounding environment, and thus predators need to select 'optimal' foraging grounds (Boyd et al., 2015; Shaffer et al., 2009; Weimerskirch et al., 2010; Weimerskirch, Gault, et al., 2005). Consequently, predators will remain in the select patch a certain amount of time they decide adequate until either finishing the activity or moving to another patch (Schneider, 1990; Soanes et al., 2021). For example, the marginal value theorem states that a predator should stay in a patch, consuming resources, until its subsequent capture rate in the patch (including transit) is similar to the average capture rate for patches in that habitat (Charnov, 1976; Turrin et al., 2017). The 'giving up time' is the time between when the animal last feeds and when it leaves the patch. Giving up times will be longer if patches are farther apart or current patches are poor in resources, increasing the ratio of travel cost to foraging benefit. Mathematically, the optimal time spent in a patch is given by the tangent to the resource intake curve that departs from the expected transit time value (Charnov, 1976; Turrin et al., 2017).

Central place foraging theory is an application of the marginal value theorem to organisms that need to always return to a location (central place) every time they displace to search and obtain an item for food (foraging bout), such as prey (Orians, 1979), which is the case of most seabirds during their breeding season. A foraging trip is considered to include traveling time to the patch, searching and handling time (also total foraging time), and traveling time back to the central place (Fig. 2.4). The theory suggests that foragers should travel to and select foraging patches (and prey) in which they will have the highest energy gain after balancing the expenses incurred in the trips to such patch (Burke & Montevecchi, 2009; Weimerskirch et al., 2008; Weimerskirch, Le Corre, et al., 2005).

Longer foraging trips will occur if the net energy gain at distant foraging patches (e.g., higher energy content or more prey) is higher than at closer patches (Bertrand et al., 2012; Houston & McNamara, 1985; Ropert-Coudert et al., 2004). This balance when making the decision of performing long trips and maximizing energy gain is especially important when breeding, and even more so during chick rearing, when part of the prey captured must be provided to the chicks, and the gain for parent's foraging trip is diminished (Granadeiro et al., 1998; Tveraa et al., 1998; Weimerskirch et al., 1999).

Many seabird species have adopted a dual foraging trip strategy, performing long and short trips interchangeably, to balance faster provisioning to chick with self-sustaining foraging trips (Clay et al., 2019; J. A. Phillips et al., 2023; Weimerskirch et al., 2009; Zavalaga et al., 2012). The increased effort in long trips will surely affect parental energy expenditure and potentially reduce fitness and capabilities for subsequent breeding events in the future (K. H. Elliott, O'Reilly, et al., 2014), and it is hypothesized that this decision is based solely in the current body condition of the parent (Weimerskirch, 1998), where parents with greater body condition would travel longer trips and sustain good condition at the expense of the chicks (Navarro & González-Solís, 2007).

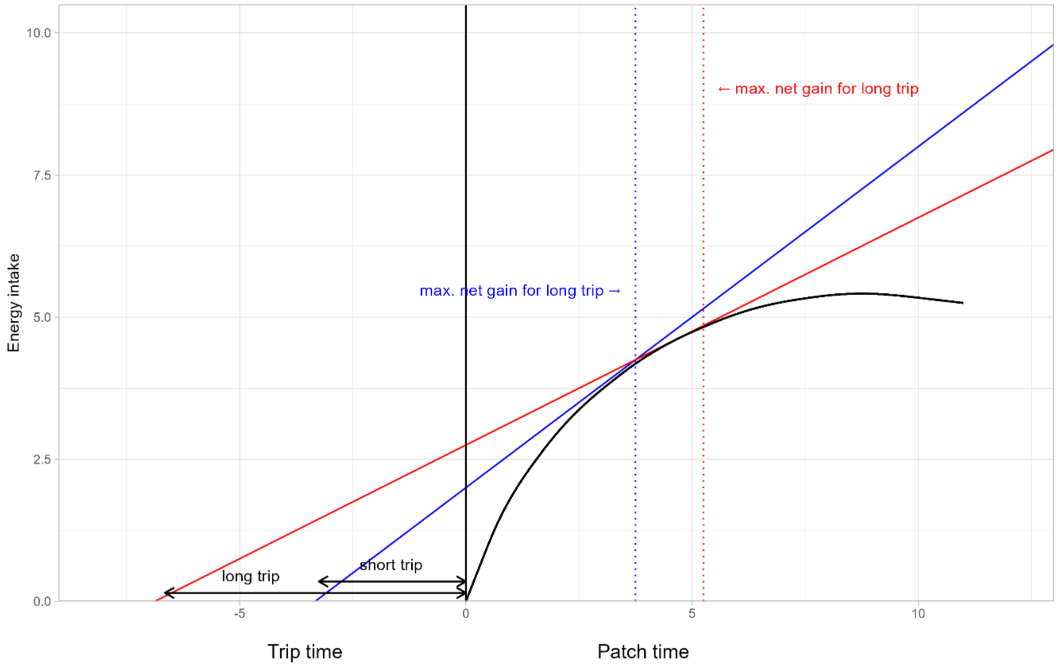

Figure 2.4. Central place foraging theory graphical representation in two hypothetical situations. The blue line represents a short trip, which should allow for maximum energy gain in a shorter time. The red line represents a long trip, which would require a longer time in the foraging patch, to maximize energy gain.

Body condition is commonly described as an organism's state (nutritional and/or physical) that influences performance to some extent (M. E. Brown, 1996; Chastel et al., 1995; Labocha & Hayes, 2012). Body mass is a common index of body condition in vertebrates and especially birds, as it represents the amount of fat reserves (energy reserves), muscle mass (protein status), as well as overall growth (specially in organisms with limited growth rates). In many animals, body mass alone is not always a good predictor of the status of the bird (eg. non-migratory birds). For this reason, in recent years, plasma metabolites (e.g. glucose, triglycerides, cholesterol, etc.) are used in tandem as they may better reflect the current overall state of the organism, or for that matter, the energy stores in the individual at time of measurement (Alonso-

Alvarez & Ferrer, 2001; Doody et al., 2008; Minias & Kaczmarek, 2013). In particular, glucose and ketones may represent how recently an animal fed, providing an index of its 'nutritional status' (Jackson et al., 2023) (Fig. 2.5).

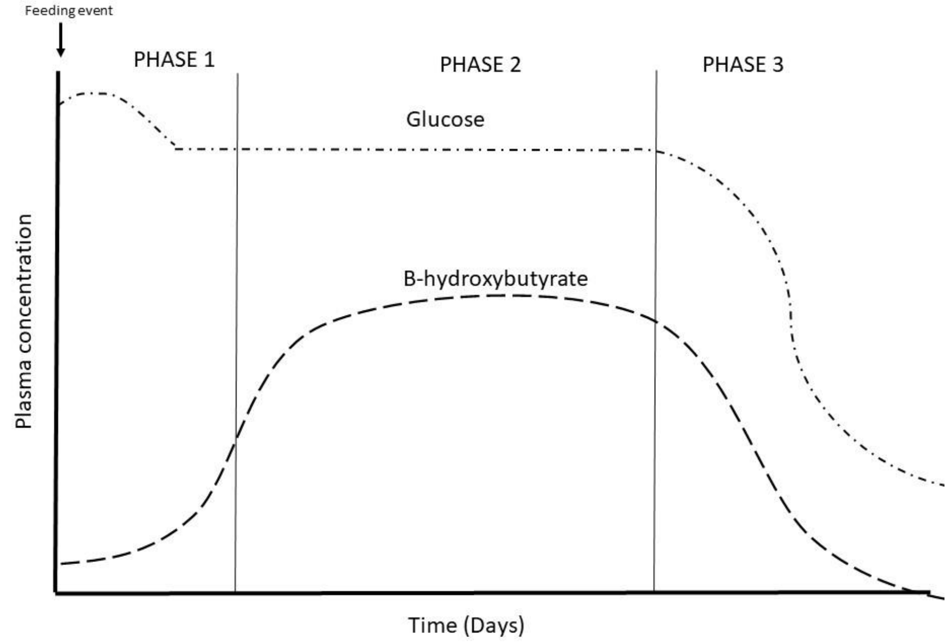

Figure 2.5. Predicted variation glucose and beta-hydroxybutyrate in plasma immediately following a feeding event and subsequently during fasting in birds. Modified from Morales et al. (2020) originally from Alonso-Alvarez and Ferrer (2001). Scale does not represent actual concentration values.

The use of several blood metabolites simultaneously allows researchers to assess changes in body condition over short-, mid-, and long-term periods. These periods can range from minutes (glucose) to hours (triglycerides and cholesterol) to days (beta-hydroxybutyrate) (Hennin et al., 2016). Foraging success should have a direct influence on these body condition indicators and therefore may represent a better proxy of fitness than body mass (Heiss et al., 2009; McNamara & Houston, 1996; Monclús et al., 2017). Although the relationship between these different metabolites is robust in all species and under all environmental conditions, there are general and accepted uses as indicators of nutritional state, and therefore the condition of the individual (Bauch et al., 2010).

During periods of abundant and stable food resources, individuals acquire food faster and with reduced energetic costs, and energy stores are greater (Jackson et al., 2023). This is reflected in higher levels of overall lipids (cholesterol and triglycerides) and glucose. Higher energy stores will reduce the risk of starvation, ultimately increasing fitness (K. H. Elliott, Le Vaillant, et al., 2014). Conversely, lower levels of these metabolites and increased levels of by-products of fat metabolism should reflect a lower body condition or lack of food supplies or starvation (Alonso-Alvarez & Ferrer, 2001). One of such by-products is beta hydroxybutyrate or ketones, which over long periods of times can show levels of starvation because of fat metabolism, and may be a good predictor of lower body condition (Storey et al., 2017). Therefore, the nutritional state can be reflected in the blood metabolites of an organism, which in time can reflect the overall body condition independent of body, may be a product of environmental variability and prey availability and the differences in foraging effort (Kitaysky et al., 2001; Stoskopf et al., 2010; Whiteman et al., 2013).

Isotopic niche: ecological use of stable isotopes

Stable isotopes are commonly used in ecological studies because many physicochemical and biochemical processes differ in the discrimination or separation of stable isotopes. In consumers, the food they ingest will result in a set of isotopes incorporated into their bodies that represent the origin of their food sources (Newsome et al., 2007; Young et al., 2010). The measures of isotope ratios $\delta^{13}C$ and $\delta^{15}N$, representing the relative proportion of ^{13}C to ^{12}C and ^{15}N to ^{14}N respectively, in tissues, are reliable indicators of diet, and consequently can be used to delineate trophic assemblages in marine ecosystems (Young et al. 2015; Espinoza et al. 2017). $\delta^{13}C$ can be used to infer feeding locations (such as pelagic or benthic/coastal), whereas $\delta^{15}N$ provides an index of trophic position (Karnovsky et al. 2012). Isotopic niche measurements can be used to describe trophic levels (range of $\delta^{15}N$), prey source ($\delta^{13}C$ signatures), niche diversification ($\delta^{13}C$ range), overall density of species packing (mean of the Euclidean distances to each species' nearest neighbor in bi-plot space), among other indexes that help describe trophic niches and relationships (Layman et al. 2015). The use of these metrics in characterizing trophic dynamics can help determine different interactions within the community such as competition (by increased trophic redundancy) or predation (increase in trophic diversity) (Layman et al. 2015).

Additionally, the use of sulfur isotopes ($\delta^{34}S$) allows to detect differences among primary producers, and may not be affected by changes in trophic levels of the food web, unlike $\delta^{13}C$ signatures. $\delta^{34}S$ is now used to identify important differences especially in marine habitats, when looking into sources such as benthic and pelagic environments (Layman et al., 2012). Several other isotopes are used to describe changes in ecological patterns or species, such as hydrogen ($\delta^{2}H$) or oxygen ($\delta^{18}O$) commonly used to describe latitudinal differences, or strontium ($\delta^{87}Sr$) to investigate migration in geological timeframes (Crowley et al., 2017; Fischer et al., 2013). Although these sets of isotopes have proven good descriptors of food webs and trophic relationships in wild animals and a broad range of ecosystems, some intricacies may not be easily solved by these isotopes alone, as for trophic isotopes ($\delta^{15}N$ and $\delta^{13}C$) baselines signals may vary as well, and obscure the potential inferences we can make from the markers (Lorrain et al., 2009; Seminoff et al., 2012). For instance, baseline $\delta^{15}N$ varies across space and time so is not necessarily representative of relative trophic position. Moreover, $\delta^{13}C$ increases with trophic position and is more negative in both offshore and terrestrial environments, meaning that it is not necessarily representative of foraging location.

More importantly, two variables cannot describe the diet of a predator with more than two prey items and food webs typically have a topology of more than two dimensions (Bowes et al., 2017). Therefore, the use of amino acid specific isotopes has increased significantly in the last decades as a solution to this problem. Trophic amino acids (e.g. glutamate) increase systematically with trophic position while non-trophic amino acids (e.g. phenylalanine) do not (Seminoff et al., 2012). The difference in $\delta^{15}N$ between trophic and non-trophic amino acids ($\delta^{15}N_{glu-phe}$) can therefore be a reliable indicator of trophic position. Similarly, essential amino acids' $\delta^{13}C$ is preserved through the food web, and can be used as a good indicator of foraging location and primary producers' source (e.g. kelp, phytoplankton, benthos) (McMahon et al., 2011; Schiff et al., 2014; Walsh et al., 2014), overcoming some of the issues in the use of carbon and nitrogen bulk isotope studies.

Food web structure and stability are two of the most important characteristics for understanding food web functioning (Rooney & McCann, 2012). Diversity, as well as the degree and number of interactions in a food web, can determine stability in a community (Dunne et al., 2002). Network analysis of isotopic values can be used to quantify connections in food webs and describe the stability and structure of the system (Lyubchich & Woodland, 2019). Many, weak interactions within a system tend to make the system more stable, but strong interactions are still needed to define the system heuristically (Csermely, 2004). Therefore, a thorough description of ecological niche metrics and network food web connections using diverse isotopic signature tools are useful tools to understand ecosystem functioning.

Climate change and shifting marine ecosystem dynamics

Changes in the sea surface temperature and atmospheric conditions are evident and increasingly important for all ecosystems throughout the world (Schmidt & Boyd, 2016). These changes in environmental variability may dramatically affect wildlife species in a short span of time (Varela et al., 2008). Climate change is affecting the distribution of seabirds in several oceans (Péron et al., 2010) or even transfer of marine subsidies to land (Molina-Montenegro et al., 2013). In particular, inter-annual variability of ocean conditions may reflect changes in foraging patterns in seabirds (Warwick-Evans et al., 2016).

Figure 2.6. Peruvian booby while chick rearing on its nest at Guañape Norte Island, Peru. Colonies are distributed along the island, located on slopes, flat terrain, cliffs, or on buildings, or on dense "guano" accumulation, and even previously used nests of cormorants.

Figure 2.7. Densely packed guanay cormorant colony at Guañape Norte Island, Peru. Colonies are normally located on slopes, and nests can be reused quickly accumulating feathers and guano through time.

Shifts in species distribution are obvious when interannual environmental variability increases, and this could result in temporal shifts of the trophic predator assemblage and how they behave and exploit the ecosystem (Yurkowski et al., 2018). Changes in diet have been reported for top predators in Arctic marine communities, such as polar bears and thick-billed murres, as a response to changing environmental temperature (McKinney et al., 2022). In the Arctic, the loss of sea-ice provides a clear ecosystem-wide impact that changes the distribution of seabirds. However, impacts are not limited to the Arctic. For example, El Niño is expected to become stronger and more frequent in tropical oceans, potentially impacting population viability in the PHCS (Shin et al., 2022).

Additionally, intense fishing activities are increasing in several ecosystems and are having impacts on communities dynamics (Sydeman et al., 2017). These impacts have been reflected in many marine communities and seabird populations, such as gannets, cormorants, and penguins population in South Africa (Crawford, 2007). The effects of strong El Niño events and climate change are already being detected via seabird behavioral changes and population trends (Anchundia et al., 2014; Jenouvrier et al., 2012; Sandvik & Einar Erikstad, 2008). Understanding how a functionally diverse group of seabirds may be affected by changes by oceanic conditions in Peru is necessary to manage such complex system affected by both climate and intensive fisheries.

Given the impacts of climate change and fisheries on seabirds, from their individual energetics to their community assemblages, the rest of the thesis examines these topics in a series of three "data chapters". Chapter 3 provides estimates of energy expenditure and field activity budgets in the Peruvian booby and validates the use of accelerometry to calculate daily energy expenditure. Chapter 5 shows how foraging effort varies across two years and two species, the Peruvian booby and guanay cormorant, and how this variation does not influence nutritional state. Finally, Chapter 5 demonstrate the effect of increasing dimension in ecological niches allows for more accurate detection of ecological segregation across five decades and five seabird species.

Chapter 3 Plunge-diving into dynamic body acceleration and energy expenditure in the Peruvian booby

Title: Plunge-diving into dynamic body acceleration and energy expenditure in the Peruvian booby

Running title: Energy expenditure of Peruvian boobies

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keywords: energy expenditure, field metabolic rate, Peruvian booby, daily activity patterns, flight costs

Summary statement

Here, we measured energy expenditure using doubly-labelled water and activity-specific budgets in Peruvian boobies and validate the use of dynamic body acceleration to determine field metabolic rates for the first time in this species.

Abstract

Energy expenditure is an essential currency for wild animals. Daily energy expenditure is the result of decisions on how to allocate time among activities, such as commuting and foraging, and the energy costs of those activities. The energy spent in such behaviours is mainly due to the costs of movement, therefore it can be measured in terms of acceleration. Dynamic body acceleration (DBA), which represents mechanical work over time in active organisms, can be used as a proxy for daily energy expenditure (DEE) on species that use such active behaviours, but has been validated only on a few of them. We used doubly-labelled water to estimate DEE and to validate the use of DBA on a plunge-diving seabird, the Peruvian booby (*Sula variegata, Tschudi, 1843*). Mass-specific DEE in boobies was 1.12 kJ/d/g, and higher in males than in females. DBA alone provided the best fitting model to estimate mass-specific DEE compared to models that included DBA partitioned per activity and time-budget models. Nonetheless, the predictive capacity of models parametrizing activity in the colony and activity outside of the colony was higher (r = 0.6) than the best fitting model. Time spent at the colony was the largest contributor to DEE as it was the most time-consuming activity and involved active nest defense. However, flight was the most power-consuming activity, and had higher costs in boobies than in other gliding seabirds, representing the cost of flapping flight and plunging. In conclusion, DBA alone was sufficient to act as a proxy for mass-specific DEE, opening avenues to measure the conservation energetics of this seabird in the rapidly-changing Peruvian Humboldt Current System.

Introduction

Energy balance in wild animals determines important outcomes in their life history, such as migration patterns (Guillemette et al., 2012), breeding strategies (Dunn et al., 2018; Viera et al., 2011), growth rates (Navarro et al., 2015), and ultimately survival (Daunt et al., 2007; Elliott et al., 2014b). These linkages occur because energy balance affects how an animal decides which activities to perform, such as foraging, flying, swimming, or running (Nagy, 1987; Nagy et al., 1999). Nonetheless, measuring energy balance, especially energy costs, in the wild can be challenging (Collins et al., 2016; Shaffer, 2011). Flapping flight is energetically expensive compared to other forms of locomotion, and this is especially true in seabirds that need to travel great distances to find food in very patchy environments (Ballance et al., 1997; Weimerskirch, 2007). Energy expenditure becomes especially important during high demand periods, such as breeding at a central place, or during food shortages, commonly caused by changing environmental conditions (Ashmole, 1963; Elliott et al., 2014b, 2009; Tremblay et al., 2022; Welcker et al., 2010).

Little is known about the energy expenditure of seabirds in the Peruvian Humboldt Current system (PHCS), one the most productive marine upwelling systems on the planet (Chavez et al., 2008). Of special importance are the guano seabird species, due to their association with the anchovy population and guano industry. Among them, Peruvian Boobies, hereafter referred to as boobies, are one the most abundant guano seabirds since the collapse of the anchovy fishery and subsequent major drop in the seabird population of the system in the 1950s (Barbraud et al., 2018; Jahncke et al., 2004). Boobies in the PHCS are plunge-divers with high aspect ratios and forage exclusively during the day (Van Oordt et al., 2018; Weimerskirch et al., 2012; Zavalaga et al., 2010). In contrast to gannets which plunge-dive and also flap their wings under the water (Ropert-Coudert et al., 2009; Sutton et al., 2023), boobies exclusively plunge-dive potentially reducing both flying and diving energy expenditure at the cost of reduced mobility underwater (Nelson, 1978).

Plunge-diving seabirds are considered efficient flyers compared to pursuit-diving birds, as their wing designs are adapted for longer and more sustained flights, they do not make deep dives, and they do not significantly use their wings to propel themselves underwater (Ropert-Coudert et al., 2009, 2004). Nonetheless, daily energy expenditure in gannets is higher than many other seabird despite low flight costs, possibly because plunging is an energetically demanding activity, especially when flapping underwater (Adams et al., 1991; Ropert-Coudert et al., 2009; Shaffer, 2011). In addition, boobies and gannets nest in densely inhabited islands and experience intraspecific aggressive behaviours that incur energetic costs additional to those of locomotion (Côté, 2000; Siegel-Causey and Hunt, 1981). To better understand why daily energy expenditure is high in plunge-diving birds including gannets, there is need to estimate activity-specific energy expenditure in plunge-diving seabirds aside from gannets (Birt-Friesen et al., 1989; Collins et al., 2016; Wilson and Culik, 1993).

The estimation of energy expenditure in the wild ("field metabolic rate") has been a difficult task in ecological research (Elliott, 2016). Several methods have been used for this purpose such as mass loss, heart rate, accelerometry, respirometry in semi-wild conditions, thermal imagery and doubly labelled water (DLW), although they all pose certain limitations or biases (Elliott, 2016; Green, 2011; Speakman, 1997). DLW is widely used to provide accurate estimates field metabolic rate animals (Shaffer, 2011). This is done by means of injecting water enriched in deuterium (^{2}H) and oxygen-18 (^{18}O), which rapidly equilibrates with the body water of the organism. Turnover of the labeled body water occurs due to water ingestion, exchanges with inspired oxygen, carbon dioxide production, and metabolic water production (Butler et al., 2004; Shaffer, 2011; Speakman, 1997). Thus, by labelling both hydrogen and oxygen, DLW produces a single integrated value of carbon dioxide production over 24-48 hours separate from water turnover. Additionally, DLW requires holding some individuals for 1-2 hours for initial calculations after isotopic water equilibrates with body water (Gabrielsen et al., 1991; Shaffer, 2011).

The most common method to calculate activity-specific field metabolic rates is by using a time budget approach (Wilson and Culik, 1993). The development of small accelerometers has led to the use of accelerometry to obtain more accurate estimates of activity budgets facilitating the time budget approach (Elliott et al., 2013; Hicks et al., 2017). The most common method for estimating activity-specific metabolic rates in wild animals is to calculate the regression of daily energy expenditure on each activity (Stothart et al., 2016; Wilson and Culik, 1993). The slope of the regression of daily energy expenditure on time spent in each activity provides the cost of the activity ("time-budget model"; Elliott et al., 2013; Navarro et al., 2015; Shaffer, 2011; Ste-Marie et al., 2022). As error in the intercept can bias estimates, such relationships are usually calculated using a multiple regression that incorporates all activities and where the intercept is consequently set to zero (Wilson and Culik, 1993). However, this approach assumes that the average cost of each activity is representative when the cost of activity can vary; for example, the cost of flight is higher when flying into a headwind than with a tailwind and the cost of "resting" is higher when preening than when sleeping (Elliott et al., 2014a; Furness and Bryant, 1996; Richman and Lovvorn, 2008). Thus, there is growing interest in whether other methods to estimate activity-specific metabolic rates during each activity can improve accuracy compared to time-budget models.

Dynamic body acceleration (DBA) is the most commonly used metric in accelerometry to estimate energy expenditure directly as opposed to via time budgets (Wilson et al., 2006). DBA is calculated using tri-axial acceleration (heave, surge and sway) allowing for the measurement of total and fine scale activity-specific energy costs (Chivers et al., 2015; Kokubun et al., 2015; Stothart et al., 2016). DBA is the area under the accelerometer-time curve after removing the static component associated with posture (Wilson et al., 2006). Specifically, Work is equal to the integral of Force (F) over distance (x) as given by $\int Fdx = mv\int \frac{da}{dt} = mvDBA$, and therefore mass-specific energy expenditure at a constant speed (v) is proportional to DBA, provided all work is in the direction of travel (Gómez Laich et al., 2009; Stothart et al., 2016).

Because locomotion makes up a substantial proportion of an animal's energy budget, DBA and the rate of oxygen consumption (VO_2) are often highly correlated (Gómez Laich et al., 2009; Stothart et al., 2016). Nonetheless, most validations of the DEE_{DLW}-DBA relationship in diving birds have occurred on birds with high locomotory costs such us diving or larger plunger (Elliott et al., 2013; Stothart et al., 2016; Hicks et al. 2017; Sutton et al. 2021). For example, recent work on large, plunge-diving birds in cold water showed a strong relationship between these two variables (Sutton et al., 2023). However, we might expect that DEE_{DLW}-DBA relationships be weaker in smaller plunge-diving birds, such as boobies, due to the lower flight and diving costs associated with plunge-diving in warmer water. Indeed, given the importance of energy expenditure in animal ecology (Elliott, Le Vaillant, et al., 2014; Elliott, O'Reilly, et al., 2014), there is a need to better understand why the DEE_{DLW}-DBA relationship varies across different locomotory modes.

Additionally, understanding daily energy expenditure and activity budgets in seabirds, especially in Peruvian boobies, whose marine habitat is highly exploited by fisheries (Ballón et al., 2008; Chavez et al., 2008; Tam et al., 2008), can shed light on the energy landscapes of the region. In a species of seabird which seems to be highly sensitive to climatic fluctuations and prey abundance (Bertrand et al., 2012; Clark et al., 2022), there is need in understanding their energy balance as this may pose a special constraint in recovering its population size since the 1970s anchovy crash.

To address that need, we develop biologger validations for plunge-diving Peruvian boobies for both time budget and DBA approaches using accelerometers. These validations will help better understand energy limitations and consequently the impact of fisheries and El Nino-driven climate change on the PHCS (Chavez et al., 2008) and the dramatic changes in bird populations occurring in the PHCS (Jahncke et al., 2004). Specifically, we measured energy expenditure in Peruvian boobies using doubly labelled water and accelerometry. We used the accelerometers to classify activities into flying, plunge-diving, resting on land and resting away from the colony. We predicted that: 1) total daily DBA will correlate with total DLW-estimated daily energy expenditure, and 2) DBA would better predict DLW-estimated mass-specific daily energy expenditure compared to time budget approaches. These models will allow for future use of accelerometry to estimate energy expenditure in Peruvian boobies to understand the comparative energetics of the guano-seabird community in the PHCS.

Methods

Study site and species

We performed our study between 11 November and 17 November of 2019 at Guañape Norte Island (08°32’41”S, 078°57’49”W) within the Reserva Nacional Sistema de Islas Islotes y Puntas Guaneras, Peru. Thirty-one chick rearing Peruvian boobies were captured on their nests using a noose pole (>3 m long). Handling time was less than 5 minutes, both at deployment and recapture. Sex was determined in the field based on size and vocalizations (Zavalaga et al., 2009). All boobies were wrapped tightly in a fabric bag and measured on an electronic scale (±1 g). We attached Technosmart (Rome, Italy) Axy-trek accelerometers (18 g; GPS sampling = 1 per minute, sampling interval = 1 Hz for pressure; sampling interval = 50 Hz for triaxial acceleration) to the four central tail rectrices using two zip-ties, super glue, and Tesa tape. Devices, including attachment materials, weighed 30g, ranging from 1.6 to 2.9% of the body mass of our birds, which we assumed produced minimal effects on the birds (Bodey et al., 2018; Geen et al., 2019). No abandonment was detected. We used tail-mounted devices to reduce the loss of devices due to the bird's plunging behaviour, as devices detach more easily from the back (Vandenabeele et al., 2014).

Doubly labelled water and energy expenditure calculations

Using the same birds for equilibrium and final blood samples alters measurements of energy expenditure because of altered behaviours due to handling stress (Schultner et al., 2010). We used the single-sample method to minimize stress of the deployed birds (handling time <5 min for non-equilibrium birds), as described by Stothart et al. (2016) and well documented by (Speakman, 1997). Briefly, we captured two sets of birds: one set for estimation of equilibrium of isotopic concentrations, and a second set on which we deployed accelerometers (and later recaptured) and on which we calculated activity budgets.

The first set of birds consisted of 10 birds used to determine the relationship between isotopic dilution and body mass known as the equilibrium rate. We extracted blood in 3 capillary tubes (~150 μl) from all the birds' brachial veins as soon as they were captured for isotopic background value readings. We injected 1 ml of doubly labelled water (50% $H_2{}^{18}O$ and 50% D_2O; see Elliott et al. (2013) for details) and kept the birds in a dark box for 1 hour before collecting 3 new capillary tubes (~150 μl) of blood from the other wing's brachial vein. All capillary tubes obtained in the field were flame sealed for later analysis. We obtained a dilution relationship equation per isotope (deuterium and Oxygen-18) with high correlation values (Pearson's $r > 0.7$) (Fig. S3.1), so we were confident that using the single-sample technique for the second set of birds would provide accurate estimates of energy expenditure.

The second set of birds consisted of 21 individuals that were captured and injected with 1 ml of doubly labelled water (same mixture as described above) and released with GPS-accelerometers within 5 minutes of injection. All birds were recaptured ~48 h after deployment (range = 46.1 –

61.3 h, std = 3.7), except for one bird, which was recaptured ~100 h after and was not included in the energy expenditure validation analysis because the biologger turned off before recapture. Upon recapture we obtained a blood sample from the brachial vein in 2-3 capillary tubes (~150µl). Biologging devices were carefully removed to avoid the loss of feathers.

All blood samples were distilled in the lab through evaporation after 24 h on a hotplate while in flame sealed glass Pasteur pipettes. DLW analysis was performed using a Los Gatos Liquid Water Isotopic EP Benchtop Analyzer (model GLA430 LWIA-912) (hereafter LWIA). Samples were run later in batches of corresponding enrichment using DLW standards for each batch (high enrichment for initial samples and very low enrichment for background value samples, both from the first set of birds, and low enrichment for final samples from the second set of birds). Each run consisted of five preparation injections and five measured injections, which were averaged to obtain the final value for the H^2/H^1 and O^{18}/O^{16} ratios for all posterior calculations. We used a low and a high standard at the beginning and end of the run, as well one of each standard between every 2-4 samples to correct for any residual effect during the run. In the case of some unusual readings, such as low density (due to bubbles in the vials) or pressure errors, samples were rerun or redistilled when needed.

All calculations followed Speakman (1997) as described in the Appendices.

Behavioural classification and accelerometry

We used Hidden Markov Models (HMMs) with the momentuHMM package (McClintock and Michelot, 2018; Patterson et al., 2019) to classify four behavioural states of boobies: at colony, flying, plunging, and resting (Fig. 1A, and 1B for mapped track). To estimate behavioural states we included three parameters: presence at the colony based on the distance from the colony recorded by the GPS (distances ≤ 1 km of the colony = 1, distances > 1 km from the colony = 0); wing beat frequency, calculated as the peak frequency of the z axis over a 30 sec window using a Fast Fourier Transform; and diving activity based on the depth sensor (depths ≥ 0.5 m = 1, depth <0.5 m = 0). GPS locations and depth values were linearly interpolated to the same sampling rate as the accelerometer data, and after all data were sub-sampled to a 1-sec interval. Probability distributions for each data stream and starting values for each behavioural state used in the HMM are provided in Table 3.1.

Table 3.1. Probability distributions and starting values for the data streams used in Hidden Markov Models to define behavioural states.

			Behaviour			
Data	Distribution	Parameter	Colony	Flying	Foraging	Resting
Wing beat frequency	Gamma	Mean	0.01	4	4	0.01
		SD	0.01	1	0.5	0.01
		Zero-mass	0.99	0.000001	0.01	0.99
Distance to colony	Bernoulli	Probability	0.9999	0.1	0.1	$1\text{x}10^{-10}$
Diving	Bernoulli	Probability	$1\ \text{x}10^{-10}$	$1\text{x}10^{-10}$	$1-1\text{x}10^{-10}$	$1\text{x}10^{-10}$

Vectorial Dynamic Body Acceleration (DBA from now on) for daily energy expenditure models was calculated for the total deployment time as well as for each activity and averaged to a 24h period (dividing total DBA or total activity specific DBA by sampling time in hours and multiplying by 24). DBA was calculated using:

$$DBA = \sqrt{(A_x - \bar{A}_x)^2 + \left(A_y - \bar{A}_y\right)^2 + (A_z - \bar{A}_z)^2}\,, \qquad \text{Eq. 3.1}$$

Where, A_x is the acceleration measured in the antero-posterior axis (surge), A_y is the acceleration in the lateral axis (sway), A_z is the acceleration in the dorso-ventral axis (heave), and $\bar{A}_n$ represents the static component of the acceleration in each axis and calculated over a 3-sec running window (Shepard et al., 2008; Stothart et al., 2016). We then used mean DBA values for 1-sec of sampling to match the HMM classifications.

This study was approved by the McGill University Animal Care Committee.

Statistical analyses

All statistical analyses were performed using R (R Core Team, 2023). We first tested differences between sexes in total mass-specific daily energy expenditure using linear models, as boobies are sexually dimorphic in size (body mass). No deviations from normality in the model were significant. Although there were significant differences in mass- specific DEE in boobies, we grouped all individual after doing this comparison due to small sample sizes per sex, considering that males and females represented a continuum of body mass along the x-axis. Sex-specific models are still presented in Table S3.2.

We built linear regression models for all birds parametrizing activity-specific energy expenditure for flying, diving, resting, and at colony, as we expect these activities will have different energy requirements. Time-budget models were based on the full model considering all activities as follows:

$$DEE = MR_f \cdot T_f + MR_p \cdot T_p + MR_r \cdot T_r + MR_c \cdot T_c, \qquad \text{Eq. 3.2}$$

where DEE is the daily DLW-estimated energy expenditure (derived from the total sampling period), MR_f is flying metabolic rate, MR_p is foraging (plunging) metabolic rate, MR_r is resting metabolic (away from the colony), MR_c is metabolic rate at the colony (on land), T_f is time spent flying, T_p is time spent foraging (plunging), T_r is time spent resting (away from the colony), T_c is time spent at the colony (on land). The intercept was set to zero when accounting for all activities performed by the individual during the time allotted time, as suggested by Wilson and Culik (1993). All activity times were calculated using the classification from HMMs as described above.

DBA models were built likewise, following the full activity formula:

$$DEE = a \cdot DBA_f + b \cdot DBA_p + c \cdot DBA_r + d \cdot DBA_c + \propto, \qquad \text{Eq. 3.3}$$

where DBA_n is total DBA in each activity: flying, plunging, resting (away from the colony), and at colony, and $\propto$ is the intercept (i.e. DEE with no activity, representative of resting metabolic rate). In all models we calculated the daily DBA respective to each activity to be consistent with DEE in 24 hours (total $DBA_{activity}$ of deployment / total sampling time for each bird). For both modelling approaches we considered combined activities additionally to independent parametrization (e.g. Time Flying and Plunging, as one parameter) under the assumption that the DEE_{DLW}-DBA conversion parameter may be similar across some activities.

We then compared all twelve time-budget and DBA models using the corrected Akaike's information criterion (AICc) approach (see Table 3.2). The AICc ranks models penalizing them if they have increased number of parameters without improvement in fit, and it applies a sample size correction which additionally increases penalization. Best models were then plotted with marginal effects using the ggpredict() function from the ggeffects package with 95% confidence intervals.

To additionally assess the predictive capacity (Stothart et al., 2016; Sutton et al., 2023) of the best ranked models by the AICc we investigated the correlation strength between predicted values and the actual DEE values using linear regression and reporting the correlation coefficients (r). We also present the mass-specific DEE estimation values for each activity for both approaches (time-budgets and DBA) to demonstrate activity-specific metabolic rates and plot flying costs using DBA activity-specific estimates in comparison to other flying-gliding birds.

Results

Mass-specific DEE in Peruvian boobies averaged 1.12 ± 0.29 (SD) kJ/d/g, and was higher in males ($t = 4.21$, $p < 0.001$) (Table 3.1).

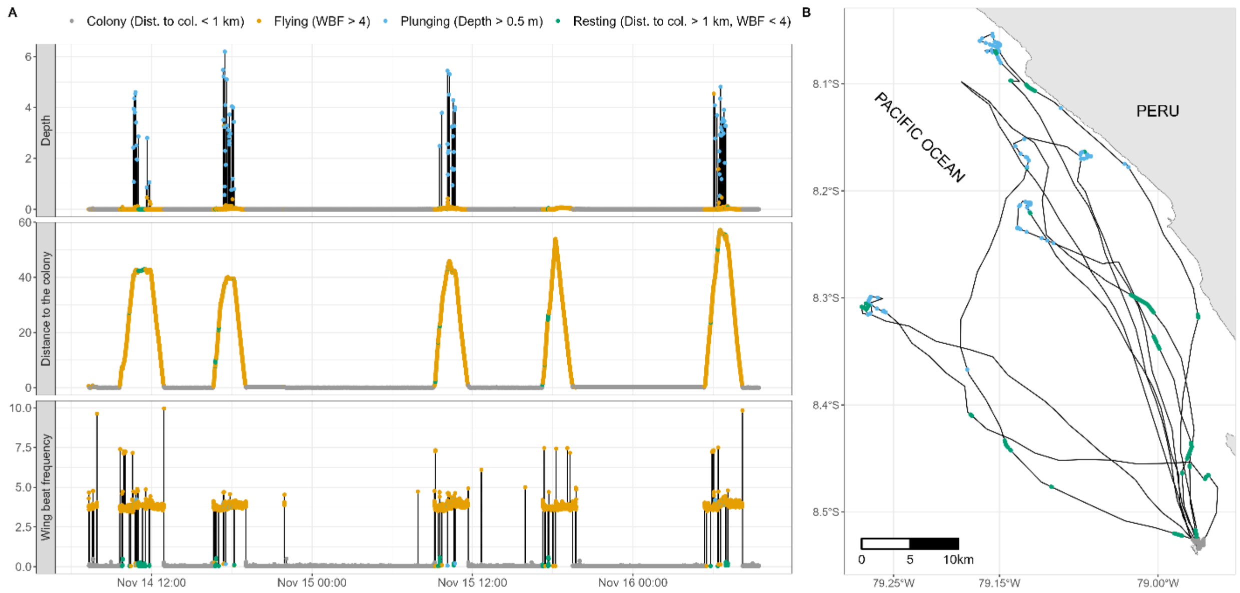

Figure 3.8. A) Sample full track of one bird with the HMM behavioural classifications showing "colony" (grey), "flying" (yellow), "plunging" (blue), and "resting" (green) for the respective values of diving depth (top left), distance to the colony (middle left panel), and wingbeat frequencies (bottom left panel), and B) mapped track with HMM behavioural classifications, where now black lines represent "flying".

Three models predicted mass-specific DEE with ΔAICc < 2. The best model to predict mass-specific DEE was daily DBA (Table 2, r = 0.57). The other two models had only two predictor variables: DBA at colony and DBA away from colony (Fig. S2, Table S3.3) or DBA at colony and resting away from the colony in one model and DBA flying and plunge-diving (Table 3.2). The model with DBA at colony and DBA away from colony (flying, plunging, resting) had strong predictive capacity (r = 0.6, p-value = 0.0049) (Fig. 3.2) and ranked better than the other two parameter model. Time at the colony (e.g. attending chicks) made up a higher proportion of all the daily time budget than all other activities (Fig. 3.3, Table S3.4). Conversely, DBA while flying was highest compared to any other activities (Table S4). DBA at the colony was weakly correlated to time spent at the colony (r = 0.53), which is the opposite as we would expect due to the "Halsey trap". In contrast, time spent away from the colony and DBA for all activities away for the colony were strongly correlated (r = 0.83), suggesting that DEE in the colony is independent of time, and associated to specific other behaviours or factors (e.g. territoriality, thermoregulation, etc.).

Table 3.2. Mass-specific DEE and mean mass (± standard deviation) for male and female chick-rearing Peruvian boobies at Guañape Norte Island in 2019 using the single sample DLW method.

	DEE_{DLW} ($kJd^{-1}g^{-1}$)				Mean Mass
Sex	Mean	SD	min.	max.	(g)
F	0.95	0.16	0.68	1.23	1526 (± 95.3)
M	1.35	0.27	1.03	1.86	1260 (± 104)

Table 3.3. Model selection results (AICc rankings) of all mass-specific DEE predictive models for time budget and DBA parameters. (subscripts represent each behaviour: *c* = colony, *f* = flying, *p* = plunging, *r* = resting).

Model structure	df	logLik	AICc	delta	weight
$DBA_{DailyMean}$	3	1.30	4.90	0.00	0.344
$DBA_{c} + DBA_{fpr}$	4	2.31	6.05	1.15	0.194
$DBA_{cr} + DBA_{fp}$	4	2.24	6.19	1.29	0.181
$T_{c} + T_{fpr}$	3	-0.36	8.23	3.33	0.065
$T_{cr} + T_{fp}$	3	-0.62	8.73	3.83	0.051
Null	2	-2.21	9.12	4.22	0.042
$DBA_{c} + DBA_{r} + DBA_{fp}$	5	2.31	9.66	4.75	0.032
$DBA_{c} + DBA_{f} + DBA_{p} + DBA_{r}$	5	2.30	9.68	4.77	0.032
$DBA_{f} + DBA_{p} + DBA_{cr}$	5	2.26	9.77	4.87	0.030
$T_{c} + T_{r} + T_{fp}$	4	-0.28	11.24	6.33	0.015
$T_{f} + T_{p} + T_{cr}$	4	-0.40	11.47	6.57	0.013
$T_{c} + T_{f} + T_{p} + T_{r}$	5	-0.1	14.48	9.58	0.003

Peruvian boobies averaged more than 19 h of the day in the colony and ~3.8 h flying, with a maximum of 6 h spent flying among the sampled birds (Fig. 3.3 and Table S3.4). Given that the proportion of time spent in plunging is so small (more than 100-fold smaller), full models showed an unexpected behaviour with negative model estimates/parameters. Therefore, we present activity specific estimates for the model that includes flying and plunging together below in Table 3.3. In both estimation approaches (time-budgets and DBA) total energy spent at the colony is highest, followed by flying, and finally resting—but only because much more total time is spent at the colony (Table S3.3). On an hourly basis, energy costs were 3.3 times higher in flight than at the colony and 2.2 times higher resting aways from the colony than at the colony.

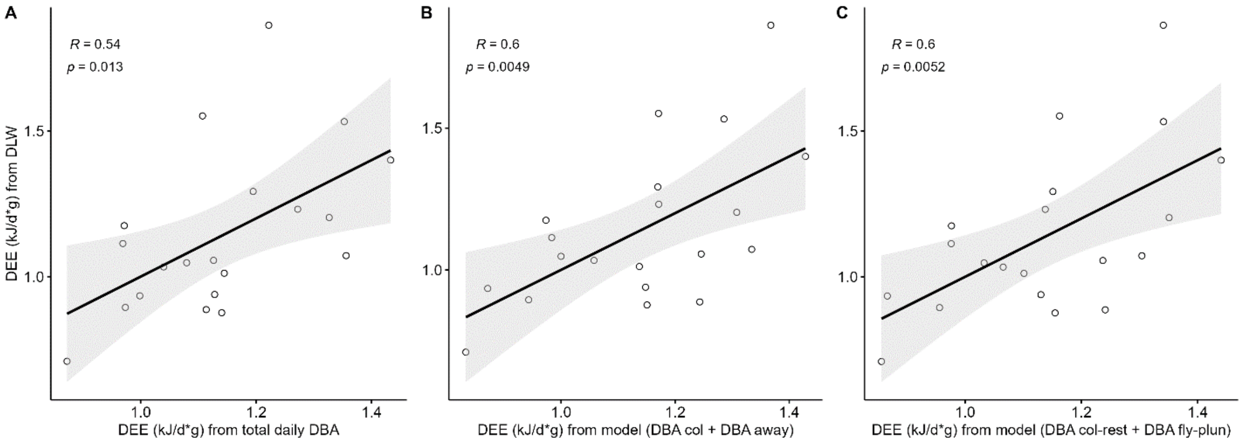

Figure 3.9. Relationship between measured DEE_{DLW} and predicted DEE values from the top three best ranking models from the AICc with the full dataset (males and females mass-specific DEE together): A) model for total mean daily DBA , B) model parametrizing mean daily DBA of activity in the colony and mean daily DBA activity away from the colony (Flying, Plunging, Resting), and C) model parametrizing mean daily DBA at colony and resting and mean daily DBA flying and plunging (n= 20).

Table 3.4. Mass-specific energy expenditure model estimates per activity in Peruvian boobies. Standard error for each coefficient model is presented.

	Time-budget models		DBA models	
Activity	Coefficient $(kJd^{-1}g^{-1})$	Std. Error	Coefficient $(kJd^{-1}g^{-1})$	Std. Error
Colony	0.81	0.25	0.00058	0.00029
Flying/Plunging	2.67	1.36	0.00020	0.00010
Resting	1.79	1.46	0.00030	0.00084

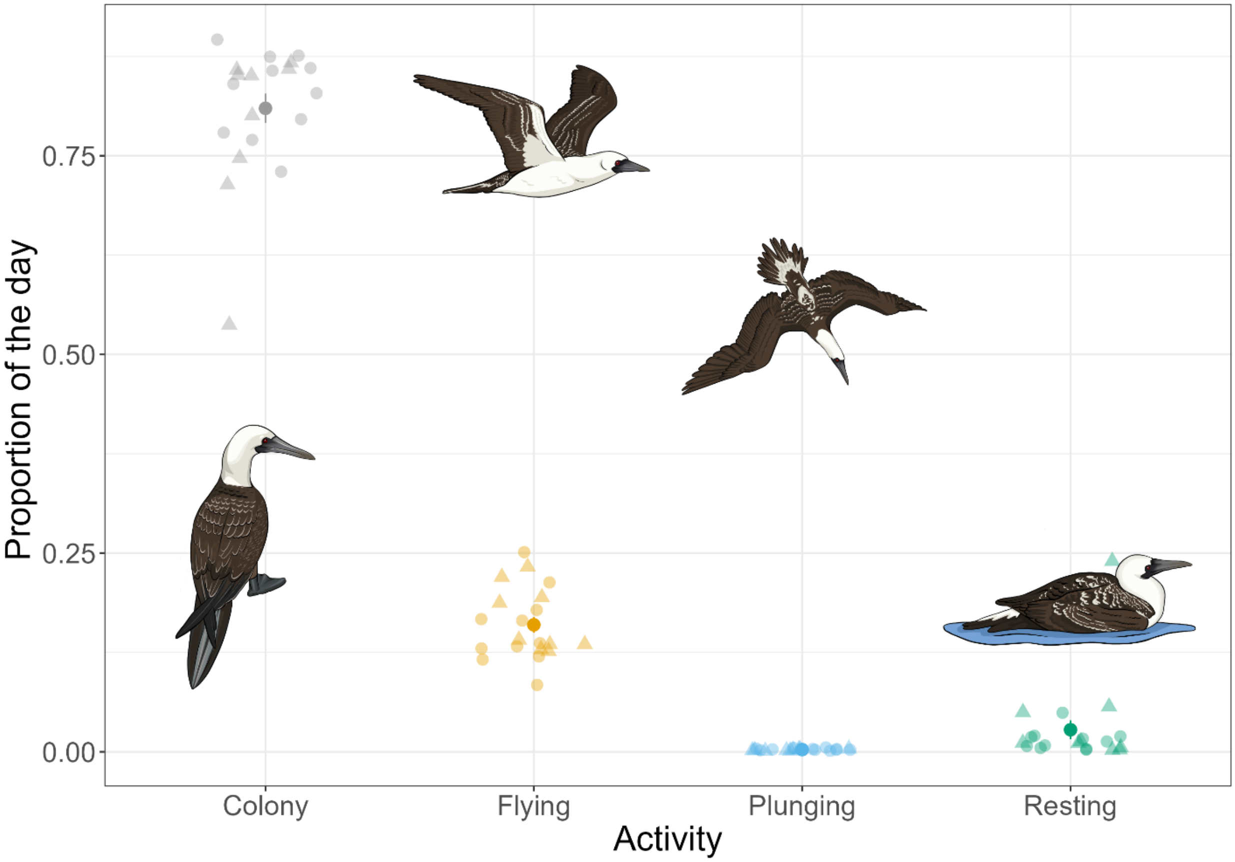

Figure 3.10. Mean daily proportion of time spent in each activity by Peruvian Boobies in Guañape Norte Island in 2019. Solid dots represent means, and semi-transparent dots are the individual values. Error bars represent standard error (n= 20). Males are represented by semi-transparent triangles (▲) and females by circles (•).

Discussion

Dynamic body acceleration (DBA) predicted daily energy expenditure in a flap-gliding seabird, the Peruvian booby. Interestingly, whereas most other studies have found that DBA in flight and diving partitioned separately from other activities (Ste-Marie et al., 2022; Stothart et al., 2016), in our study the most parsimonious model predicted DEE from DBA alone, or perhaps with colony partitioned separately. Moreover, this means that DEE can be estimated in wild plunge-diving birds from a single metric, DBA, across many different locomotory modes. Unlike in (Sutton et al., 2023), that found that the predictive capacity increased with the incorporation of other movement metrics (e.g. total distance travelled), our DBA-only models achieved a predictive capacity within the range of their best models (from 0.6 to 0.8).

We present the first estimate of energy expenditure in Peruvian Boobies using a direct method (DLW). The need to calculate daily energy expenditure of seabirds in the highly productive and over-exploited PHCS has been noted since the late 1960s, yet most approaches use approximations from basal metabolic rates and other methods (Boyd et al., 2014; Laugksch and Duffy, 1984). Our calculated energy expenditure values are similar to those of other sulids, such as red-footed boobies (~1 $KJd^{-1}g^{-1,}$ from Ballance (1995)) and northern gannets (~1-1.5 $KJd^{-1}g^{-1}$, from (Birt-Friesen et al., 1989; Pelletier et al., 2020)), but are slightly higher than those presented by Laugksch and Duffy (1984), who tried to estimate energy requirements in a larger ecosystem level analysis. Conversely, Boyd et al., (2014) modelled energy expenditure of Peruvian boobies by means of allometric equations, and found a DEE of ~0.8 $KJd^{-1}g^{-1}$, much lower than our DLW direct estimation (even lower than males alone, see Table 1), demonstrating the need for specific estimated of field metabolic rates.

During chick rearing, Peruvian boobies spent about ~80% of their time in the colony, mainly while attending their nest, except for some birds that might have stayed at a different location within the colony but not at the nest. Unlike other similarly sized seabirds in the PHCS (cormorants or gulls), boobies spend most of their time away from the colony flying (not diving or resting on the water), and individual foraging bouts are short due to their plunge diving habits (Fig. 3.1, 3.3). As expected in diurnal, chick rearing birds, time budgets showed a high bias toward time in the colony (Collins et al., 2016). On the other hand, DBA was significantly higher when flying, which explains the importance of DBA models on DEE. Unlike in other sulids (e.g. northern gannets), foraging trips in boobies are fairly short, hence the high amount of time spent at the colony, but energy expenditure values are fairly close to other species that are present at the colony only 50% of the day (Sutton et al., 2023).

The importance of DBA may be because of the high amount of time spent at the colony where metabolic rate is closely associated with activity. Densely populated seabird colonies like those of Peruvian boobies are prone to having intense aggressive interactions that imply higher than expected energy costs (Viera et al., 2011). Peruvian boobies, especially males, show highly aggressive behaviour toward other individuals in-transit to their nests or scouting for females.

This behaviour may occur in Peruvian boobies, as in other sulids, like in Nazca boobies, that commonly perform aggressive non-parental adult visits to chicks (Müller et al., 2011). This could explain why DBA models, rather than time budget models, and more especially the model with DBA in the colony as a separate parameter from other activities, ranked better at predicting mass-specific DEE. A larger sample size of males would help to understand this relationship better.

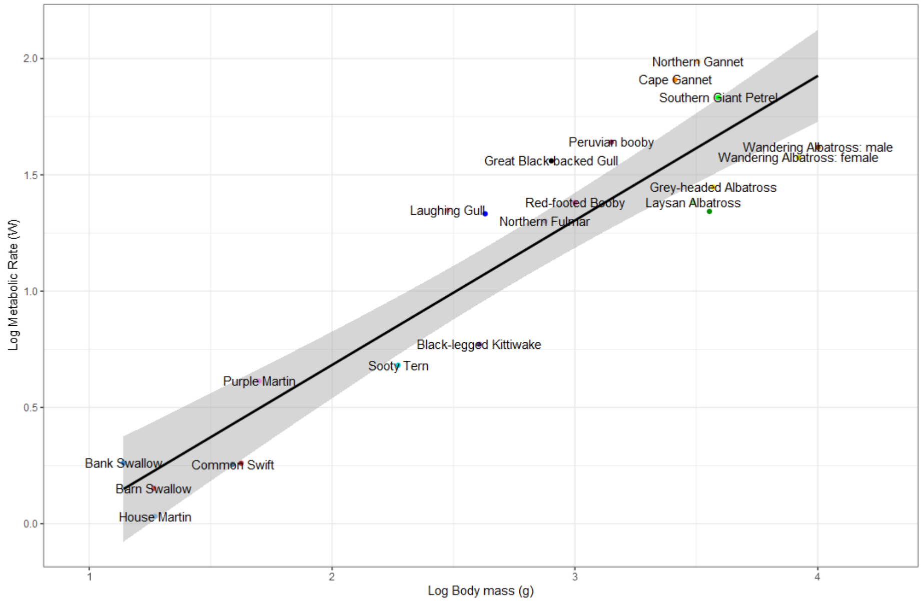

Figure 11. Multispecies comparison of flight costs of twenty-two primarily gliding bird species as defined in Guigueno et al. (2019; in Watts). The metabolic costs of flight are expressed in in Watts (kJ h^{-1} / 3.6) and are calculated from activity-specific time budgets. All data is $\log_{10}$-transformed. Shaded area represent the confidence intervals.

As observed in other plunge-diving seabirds such as gannets, Peruvian boobies' flight metabolic rate estimated from daily time-budgets was higher than those of pure gliders relative to body mass (Fig. 3.4). However, boobies' flight costs seemed to be closer to the glider line than those of gannets, implying that they are more efficient flyers, perhaps because they do not flap underwater allowing them to specialize in flying (Fig. 3.4).

Our behavioural classification appeared to reliably partition the daily activity patterns in Peruvian boobies in the PHCS using accelerometry. We restricted our classification to four behaviours thought to be the most important energetically. Potentially, a more refined classification could be achieved by increasing behaviours (searching, resting on water, resting on land, aggressive behaviour at colony, resting at colony, etc.). Nonetheless, our best model included three grouped behavioural parameters (flying, plunging, and resting away from the colony) of our four initial independent set, which may indicate that modeling DEE may not improve with a greater set of parameters as indicated by Stothart et al. (2016).

Although assumed to be efficient flyers, we found that in Peruvian boobies, as expected, flight is the most demanding activity per unit of time, even with the relatively short foraging trips that Peruvian boobies perform. Moreover, energy expenditure at the colony is high due to very close proximity to conspecifics when nesting. Although Peruvian boobies are considered to be numerous with a stable population, their high energy requirements, especially flight and plunging costs, would explain the slow recovery of their population prior to their collapse in the seventies. Future population models and projection should include accurate energetic requirements for boobies, as well as the energetics demands associated with climate change and fisheries, which pose a threat to their population stability, recovery, and management.

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Competing interests.

The authors declare no competing or financial interests.

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Data availability

Data is available in DRYAD. R code is available at https://github.com/francisvolh/axxy_depth_peru.

Author contributions

The concept of this study was developed by K.E. and F.V.O. F.V.O., K.E. and J.S. collected field data. F.V.O. processed the results and wrote the manuscript. A.P. and F.V.O. wrote the R code for data processing and analyses. All authors designed the study, discussed analysis and results, edited manuscript text, and gave final approval for publication.

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Appendices

Additional Methods

Results from the LWIA distilled water sample runs were converted into part per million (ppm) before calculations. We then calculated mean isotope turnover rate for both isotopes, deuterium and oxygen, respectively, (k_d and k_o) with:

$$k_n = \left[\ln\left(I_{initial} - I_{background}\right) - \ln\left(I_{final} - I_{background}\right)/Time\right] \qquad \text{Eq. A3.2}$$

where k_n is the turnover rate for each corresponding isotope, $I_{background}$, $I_{initial}$, and I_{final} represent the isotopes ratios for the corresponding samples, and *Time* corresponds to the total sampling time in decimal hours (time between initial and final samples). Because we used the one-sample technique, we deducted the average time of equilibrium from the total sampling time. We then calculated the birds' isotope dilution space of both deuterium and oxygen (N_d and N_o) using:

$$N_n = \frac{Mol_{inj}(I_{initial} - I_{inj})}{(I_{background} - I_{initial})} \qquad \text{Eq. A3.3}$$

where N_n is the pool for each corresponding isotope, Mol_{inj} represents the total mols of the DLW injected into the bird and I_{inj} represents the enrichment in ppm of the injectate for each isotope. We assumed a single-pool model for the estimation of CO_2 production as recommended by (Speakman, 1997), with boobies being less than 4kg, using the following reduced formula:

$$rCO_2 = N(0.48123 \cdot k_o - 0.48743 \cdot k_d) \qquad \text{Eq. A3.4}$$

where rCO2 is the production of carbon dioxide in millimoles per hour (mmol/h), N is the average of N_o and final dilution space, N_f (estimated using the "percentage mass" method described by Speakman (1997)). We then converted the resulting value into mL of CO_2 per hour by multiplying by 2240 and used the caloric equivalent of 27.3 kJh^{-1} assumed for seabirds with diets rich in protein (piscivores) to obtain daily energy expenditure in J. We used daily values instead of total energy values because the latter overestimate relationships ("Halsey's time trap"; Halsey, 2017). Lastly, as suggested by Stothart et al. (2016) we used mass-specific daily energy expenditure (DEE/mass in grams) values for posterior analyses.

Linking statement

In Chapter 3, I used a direct method to measure energy expenditure of Peruvian boobies and validated the use of activity specific time-budgets and dynamic body acceleration to estimate energy expenditure in this species. Boobies had high daily energy expenditure compared to other seabird species, with flight being the costliest activity, unexpectedly from their "efficient" flying morphology and strategies. This positions Peruvian boobies in a high energy demanding niche. Energy budgeting is one of the most crucial processes in wild animals, as this energy balance will define survival and secure fitness. In the next chapter, I will investigate how Peruvian boobies and guanay cormorants link foraging movements and their nutritional status, as a proxy for fitness, and how this nutritional/movement niche shifts under different climatic conditions.

Chapter 4 Drivers of change in foraging movements of Peruvian Boobies and Guanay cormorants governed by extrinsic factors other than physiology

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Abstract

Seabird movement is commonly driven by a series of factors, both extrinsic and intrinsic, such as climate changes or food availability, and breeding status or physiology, respectively. In the Peruvian Humboldt Current systems, a highly productive upwelling system, two seabird species, Peruvian Boobies and Guanay Cormorants are the most abundant and prey mainly on Peruvian Anchovy, a cold-water schooling fish species. Climatic conditions in the last decades have been shifting towards warm years with stronger El Niño events hitting the Peruvian coast which should be affecting seabird behaviour and overall fitness. We aimed to understand the relationship between extrinsic and intrinsic factors affecting foraging movements by means of biologging and analyzing metabolite concentrations of both species in two different climatic-condition years (warm and normal). We found differences in foraging behaviour between species with further trips done by Peruvian boobies compared to Guanay Cormorants. Foraging trips were also longer during warmer years, as expected due to reduced prey availability and increased depletion near the colony and potentially increased competition under rough conditions. Against our predictions, metabolites showed no clear pattern, and even the opposite pattern was seen in ketone concentration in boobies between normal and warm conditions, as a potential strategy to cope with lack of food and avoid full commitment to breeding. Finally, spatial similarity of foraging trips and clustering had also no relationship with nutritional condition. These foraging strategies and physiological adaptations may show how highly adapted Peruvian seabirds are to the climatic changing conditions of the Humboldt Current system and their flexible energy budgeting in breeding strategies.

Keywords: Peruvian seabirds, foraging movements, physiology, spatial clustering, fitness

Introduction

Seabird foraging movements have been the focus of study for the last decades as they shed light on several important aspects of the ecosystem, such as habitat quality (C. Burger et al., 2019; Kavelaars et al., 2020), ocean pollution (Finkelstein et al., 2006; Ito et al., 2013), fisheries stocks depletion (Bertrand et al., 2012), climate change (Fromant et al., 2021), among others. Understanding how seabirds use resources in a variable environment while minimizing competition and increasing energy gain has allowed for the proposal of several hypotheses that explain changes in foraging behaviour (Brisson-Curadeau et al., 2017; Elliott et al., 2009; Wakefield et al., 2013; Weber et al., 2021). These changes in foraging behavior, such as variations in foraging movements, may be governed then by several extrinsic (environmental variability, prey availability, wind conditions, etc. affecting behaviour) or intrinsic factors (physiology, sex, age, etc.). Consequently, changes in foraging movements and energy acquisition will ultimately affect seabird's fitness (Daunt et al., 2006; De Pascalis et al., 2020).

The Humboldt Current System (HCS) is a highly productive upwelling ecosystem that supports exceptionally high biomass of Peruvian Anchovy (Chavez et al., 2008; Moron et al., 2019) and other marine predators such as seabirds (Crawford et al., 2006; Crawford & Jahncke, 1999; Jahncke et al., 2004). The HCS is susceptible to drastic climatic fluctuation due to El Niño events (Chavez et al., 2003; Grados et al., 2018) and additionally it subject to strong fisheries pressure (Bakun & Weeks, 2008). Seabirds in this region are subject then to these environmental disturbances and, as expected, these pressures impact foraging performance and fitness (Angelier et al., 2007; Grémillet et al., 2016), especially during energy demanding periods, such as incubation or chick rearing (Colominas-Ciuró et al., 2022; Velando & Alonso-Alvarez, 2003). Peruvian boobies *Sula variegata* and Guanay cormorants *Phalacrocorax bouganvillii* are the two most abundant anchovy eating (Crawford et al., 2006) seabirds in the region and hold a high economic value as guano (natural fertilizer) producing seabirds (Plazas-Jiménez & Cianciaruso, 2020).

These two species of seabirds overlap at breeding colonies in most all of their range, increasing the potential for competition. Competition may pose a greater risk for nest failure due to increased numbers at the colony, slow chick growth (Grémillet et al., 2016) and loss of body or nutritional condition (Toge et al., 2011). To minimize competition, different species often segregate in space, prey, and foraging strategies, increasing energy gain (Lee et al., 2021). Increased warming events and fishing pressure reduce available food sources for seabird species in the HCS and therefore reduce the quality or size of patches and increase chances of overlapping foraging areas and prey (Bertrand et al., 2008). To understand whether interspecific competition is truly driving segregation, it is necessary to demonstrate that individual variants that forage in an overlapping manner have reduced fitness (Elliott et al., 2008; Woo et al., 2008). Different degrees of intraspecific competition may drive either stabilizing or disruptive selection in foraging traits, favoring segregation if competition is low, such as in highly productive systems like the HCS (R. Burger, 2002; Martin & Pfennig, 2012).

Foraging success under these variable environmental conditions, specially during warm years, may affect energy input and overall fitness, reflected in physiological stress (Angelier et al., 2007; Doody et al., 2008; Kitaysky et al., 2001). Plasma metabolites can be used to quantify nutritional condition of wild animals (Alonso-Alvarez & Ferrer, 2001), seabirds included, and correlate them with other behavioural patterns such as foraging movements (Colominas-Ciuró et al., 2022; Eby et al., 2023). Little information exists on the nutritional condition of wild seabirds, especially in the tropics and no reports are known to the authors on Peruvian boobies and

Guanay cormorants. Moreover, the connection between foraging effort and physiological parameters has been rarely reported in tropical seabirds.

Environmental variability may influence prey availability and therefore may directly or indirectly affect physical condition of wild animals via acute or chronic stress (Kitaysky et al., 2001; Stoskopf et al., 2010; Whiteman et al., 2013). Because body mass alone is sometimes not a good predictor of energy stores, plasma metabolites (e.g. glucose, triglycerides, cholesterol, etc.) are commonly used to provide an additional index of energy stores (Alonso-Alvarez & Ferrer, 2001; Doody et al., 2008; Minias & Kaczmarek, 2013). By employing multiple measures, researchers can assess variation in condition over scales ranging from minutes (glucose) to hours (triglycerides and cholesterol) to days (beta-hydroxybutyrate) (Hennin et al., 2016). These indicators of body condition could represent a better proxy of fitness than body mass, as a consequence of greater foraging success and breeding success (Heiss et al., 2009; McNamara & Houston, 1996; Monclús et al., 2017). During periods of high and predictable resource availability, individuals expend less energy to gain food, and will have high levels of energy stores, which can be detectable as high levels of lipids and glucose. Over longer time scales, individuals will metabolize other compounds as fuels, such as beta hydroxybutyrate or cholesterol. Higher energy stores reduce the risk of starvation, ultimately increasing fitness (Elliott et al., 2014).

We hypothesized that foraging movements are driven ultimately by intrinsic factors (physiology) triggered by extrinsic factors (environment). Therefore, first, we expected that climatic conditions (warm or normal-year differences) will affect foraging in both species, showing greater effort in warm years. Second, this effect should be driven by physiological changes, as seen in changes metabolite concentration (glucose, triglycerides, cholesterol, and ketones). Third, we expected that variation in physiology (metabolite concentrations) will be explained by a varying foraging effort according to the effect of climatic change, where short term foraging effort (previous 1-trip) will correlate with metabolite concentration. Finally, we hypothesized that trip similarity (per individual) to other birds would also correlate with nutritional condition (metabolite concentration) as a response to competitive interaction in foraging overlapping areas.

Methods

Study site and species

We collected data between mid-November and early-December of 2018 and 2019 at Guañape Norte Island (08°32′41″S, 078°57′49″W) within the Reserva Nacional Sistema de Islas Islotes y Puntas Guaneras, Peru. Guañape Norte is a rocky island of about 62 km² and 10 km from the mainland, with large amounts of seabird guano accumulated in varying degrees on all the surface of the island, as management of the island due ongoing guano extraction aims leaves some areas untouched in each campaign.

Peruvian Boobies breeding patches cover different sectors of the island, including areas around the buildings for the guano extraction process. Guanay Cormorants breed commonly in two very conspicuous sectors of island (north-eastern and south-western ridges). Both species were breeding during both field seasons. Birds rearing chicks on the nest were selected haphazardly in the different sectors of the breeding patches along the island and captured on the nest using a noose pole. All birds were captured and handled without harming them and processing lasted on average less than 5 minutes, both at deployment and recapture.

Movement Data collection

We deployed several device types during the two field seasons due to difficulty of recapturing cormorants in 2018 (Table 4.1). Overall GPS sampling rate was set to 1 minute in 2018 and 1 or 3 min in 2019 (for boobies and cormorants, respectively. The 3-minute sampling rate was used for Ecotone devices which were solar powered and remote download).

Table 4.1 Devices deployed on Peruvian Boobies and Guanay Cormorants at Guañape Norte Island during 2018 and 2019.

Field Season	Species	Device	Model	Features
2018	Guanay Cormorant	igotu	GT-120	GPS
	Peruvian Booby			
2019	Guanay Cormorant	Ecotone	URIA-300 LPS	GPS/GPS-TDR
		Technosmart	Axy-trek 3	GPS/TDR/Acc
	Peruvian Booby	igotu	GT-120	GPS
		Technosmart	Axy-trek 3	GPS/TDR/Acc

We deployed devices on many more birds in 2019 than 2018 (Table 4.2) because a large number of birds were abandoning their nests in 2018 possibly due to an increase of sea surface temperature (e.g. “El Niño”-conditions). In 2018, we stopped deployments considering the success of recapture and the well-being of the birds. Devices were attached with Tesa tape and zip ties on the tail feathers of all birds. Deployments lasted between 2 hours and several days (for the remote-download devices on some cormorants or birds that proved difficult to recapture).

Table 4.2. Total effective deployments and trip numbers per species and year, and individuals blood sampled in both seasons.

Field Season	Species	Deployed	Retrieved	Trips	Blood
2018	Guanay Cormorant	6	2	13	2
	Peruvian Booby	10	6	47	7
2019	Guanay Cormorant	14	10	95	11
	Peruvian Booby	50	38	151	31

Blood sampling

We blood-sampled (~1.5 mL) birds that were deployed for at least 1 full day (and no more than 4 days) (Table 4.2) to assess physiological state using Point of Care devices, which have been validated in many wild species (Morales et al., 2020), to analyze several metabolites on site. Cardiochek® was used to measure glucose, triglycerides, and cholesterol. Nova Max Plus® was used to measure ketones. All birds were sampled at recapture, to reduce disturbance and increase chances of successful recapture. The only exception was eight cormorants in 2019 that were deployed with remote download Ecotone devices. These eight birds were considered a different subset and were excluded from the foraging effort analysis. A few capillary tubes were used for the metabolite analyses (most blood was stored for isotopic analyses for other aspects of the project). Nest reference locations were also recorded for future movement calculations. All blood sampling occurred in early hours of the morning, and metabolites were plotted against time of the day to check for any sign of sampling effect. No corrections were needed (all $r < 0.5$).

Movement data processing

All GPS tracks were cleaned and processed using R (R Core Team, 2021). All fixes with speeds higher 110 km/h were systematically deleted assuming satellite/detection errors. Fixes that were closer than 30 s were considered logger error and discarded. We then calculated distance, speed, and time interval between all subsequent GPS fixes, as well as distance to the nest. Distance between fixes was estimated with the *pointDistance()* function from the *raster* package. GPS fixes were initially inspected for errors: each bird plotted on a map and "distance to colony and time" graphs were produced to detect important gaps. We then identified a *trip* as movement for all individuals that left the colony further than a 1 km threshold. After careful evaluation we trimmed out all trips that were shorter than 5 km and less than 0.5 hour, considering these as "grooming trips" or "splash-down" because in such trips where we also had data from TDRs recorded no dives and hence they were unlikely foraging trips. Two trips in which GPS reception ended about 20km before arriving to the colony, were included by adding one point right before the 1 km threshold to better estimate trip metrics. Although Peruvian Boobies and Guanay Cormorant are sexually dimorphic (body size) previous research in foraging parameter has shown no significant differences between sexes (Bertrand et al., 2012; Weimerskirch et al., 2012), so we pooled sexes in the analyses. We then calculated the following metrics for each trip: total trip time, total trip path, maximum distance travelled from the colony, and sinuosity (a function of the mean cosine of turning angles, as a proxy of search effort, calculated with the *trajr* package (McLean et al., 2018)). Trips with 10 GPS or less fixes or that GPS signal ended before the bird started the return to the colony, were eliminated. To asses track similarity between individuals last trips we used the *move* package through the *emd()* function, producing clusters of tracks and averaging the similarity of pairs track for each individual. Complete foraging trip track matched with diving locations (not analysed on this work) (SI Fig. 4.2).

Statistical analyses

We used the lme4 (Bates et al., 2015) and nlme (Pinheiro et al., 2023) packages to calculate linear mixed effect models for all trip metrics (total trip time, total trip path, maximum distance travelled from colony, and sinuosity). Year (2018 and 2019; warm and normal-conditions, respectively according to the ICEN; ENFEN, 2012) and species were fixed effects, with individuals as random effect. The nlme package was used when we needed to account for within-group heteroscedasticity, even after log transformation. We checked all best models for normality assumptions and found no outstanding deviations. We also performed a Principal Component Analysis on all trip foraging metrics to group correlated variables and group the ones associated to horizontal displacement. PC1 grouped total trip duration, total trip path, and maximum distance travelled from the colony with 63% of the variance, whereas PC2 was loaded mainly on sinuosity (28% variance). We then ran a PCA only on total trip duration, total trip path, and maximum distance travelled and used PC1 (83% of the variance, SI Fig. 4.1) for the subsequent analysis. After selecting the variables, we ran a linear mixed effect model to assess the differences in foraging effort (PC1) between 2018 and 2019 and species (fixed factors) and individuals as random factor, while accounting for search effort with sinuosity as a covariate. In both scenarios (variables independently and variables from PCA) we compared models using AICc dredge() function from MuMIn package (version 1.47.5, Barton (2023)) and selected the most parsimonious model within 2 ΔAIC.

To detect differences in metabolite concentrations between species and years as predictors, we modelled each metabolite independently using linear models. If assumptions of homogeneity of variances were not met, we accounted for different variances using the lme() function, as described above. Because sample sizes were small in 2018, specially for cormorants, we split the models and tested for species differences in 2019 only, and differences between years only for boobies in 2018 and 2019. Each metabolite model was then compared with the null model using

AICc through the MuMIn, model.sel() function, and considered a supported if each model differed in more that 2 ΔAICc from the null.

To assess the relationship between nutritional condition and foraging effort (PC1) and accounting for search effort (sinuosity) in Peruvian boobies we first used linear models to find differences in metabolite concentration in years, through a Welch Two Sample t-test. When years did not differ in metabolite concentration, we grouped them together for that metabolite. If different, we excluded 2018 from the analyses, because the small sample size would overfit the model to predict a relationship with foraging effort for that year. We also included a latency term (time between sampling and return to the nest from the last trip evaluated from GPS data). Because of small sample size we ran several small model combinations as shown in SI Table 4.1, including foraging effort (PC1), sinuosity, year (when appropriate) as predictors, and their interactions. As before, we compared models using AICc dredge() function from MuMIn package and selected the most parsimonious model within 2 ΔAIC. All models were run with the full data, or removing outliers, which yielded no difference in results.

Additionally, we also evaluated the similarity of foraging trips of all 37 birds (both species and years) using the Earth's Movers Distance (EMD) with the track for the last trip before blood sampling, to detect potential spatial clusters of track similarity and assess similarity (either mean similarity or clusters of tracks) in relation with each bird's physiological parameters (concentrations log transformed). The EMD analysis produces a kernel distribution for each trip (under a set of parameters that included trips with 20 gps fixes or more) and it estimates the amount of deformation needed to change into another track, producing a pair-wise comparison matrix. Because of small sample sizes in 2018 for cormorants and differences in ketone concentration between year, the subsequent analysis was done only on boobies for 2019. We used two approaches to look how track similarity may affect physiology: first we averaged all the values of the EMD similarity matrix per trip, to obtain an average similarity value and regressed against each metabolite concentration. Secondly, we classified each track trip after clustering the similarity matrix, and tested differences of metabolite concentrations with cluster as a factor using a one-way ANOVA.

Results

Foraging effort changed in cormorants and boobies under different climatic conditions

Both species had greater foraging effort (total trip duration, total trip path, maximum distance from the colony, sinuosity) during the warm-conditions year, when assessed independently, especially birds spent longer times away from the colony in 2018 (Fig. 4.1 A). Boobies travelled greater distances than cormorants overall (Fig. 4.1: B, C, SI Table 4.2). Search effort (sinuosity of trip) between species behaved differently under the two climatic conditions (Fig. 4.1 D, SI Table 4.2). During the warm-condition year, cormorants increase trip sinuosity, compared to boobies, and the opposite happened during the normal-condition year, where boobies increased sinuosity. Both species show a significant relationship of increased sinuosity and reduced foraging effort (Fig 2), which can be simply explained by longer foraging trips having overall reduced sinuosity due to the longer straight path to a furthest distance point, and not a considerable increase in search patterns.

Overall foraging effort changes between species and years, as expressed in Principal component 1 (PC1) of foraging parameters, and accounting for search effort (sinuosity), showed a similar pattern as the independent variables. Effort was greater in 2018 for both species (red lines in Fig. 4.2), and decreased with increased searching effort (sinuosity). This relationship was more pronounced in boobies with a greater slope between years (Fig. 4.2).

Table 4.3. AICc rankings for models of foraging metrics: total trip duration, total trip path, maximum distance travelled from the colony, and sinuosity. Only models with ΔAIC greater than 4 and the null are shown in the table. Most parsimonious model within 2 ΔAIC, if not including the null model, were interpreted as most supported.

	Inter.	Sp	Year	Sp:Year	df	logLik	AICc+-	delta	weight
Total trip duration	0.87		+		7	-214.07	442.52	0.00	0.655
	0.86	+	+		8	-214.04	444.57	2.06	0.234
	0.93	+	+	+	9	-213.81	446.23	3.72	0.102
	0.61				6	-219.73	451.74	9.22	0.007
Total trip path	3.97	+	+		8	-244.17	504.83	0.00	0.430
	3.82	+			7	-245.48	505.33	0.50	0.334
	4.08	+	+	+	9	-243.76	506.13	1.30	0.224
	4.02				6	-250.58	513.45	8.62	0.006
Max. distance from colony	3.07	+			7	-219.99	454.35	0.00	0.477
	3.14	+	+		8	-219.59	455.67	1.32	0.247
	3.24	+	+	+	9	-219.21	457.03	2.68	0.125
	3.18				6	-222.62	457.52	3.18	0.097
Sinuosity	-3.20	+	+	+	9	-147.34	313.28	0.00	0.985
	-3.79				6	-170.31	352.89	39.62	<0.0001

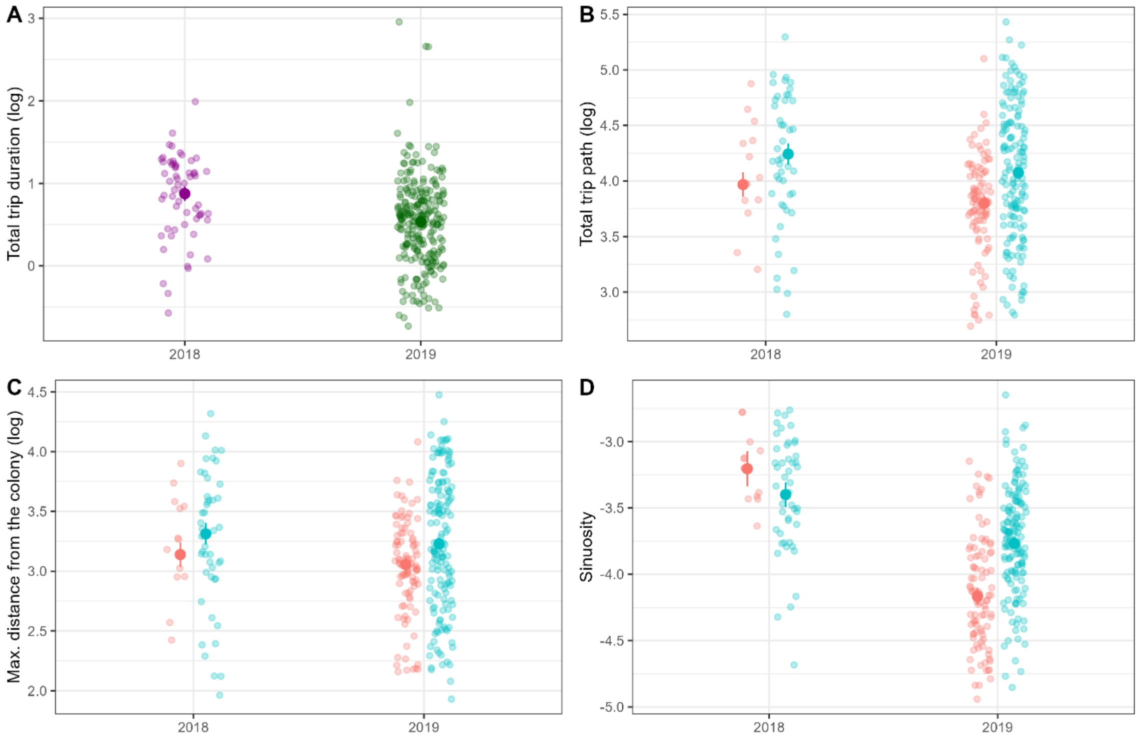

Figure 4.1. Foraging metrics model results from AIC classification: A) total trip duration; B) total trip path; C) maximum distance travelled from the colony; and D) sinuosity. Model predicted values and standard errors are plotted. Peruvian boobies in blue and Guanay cormorants in red. Solid dots and bars, represent model means and confidence intervals, respectively.

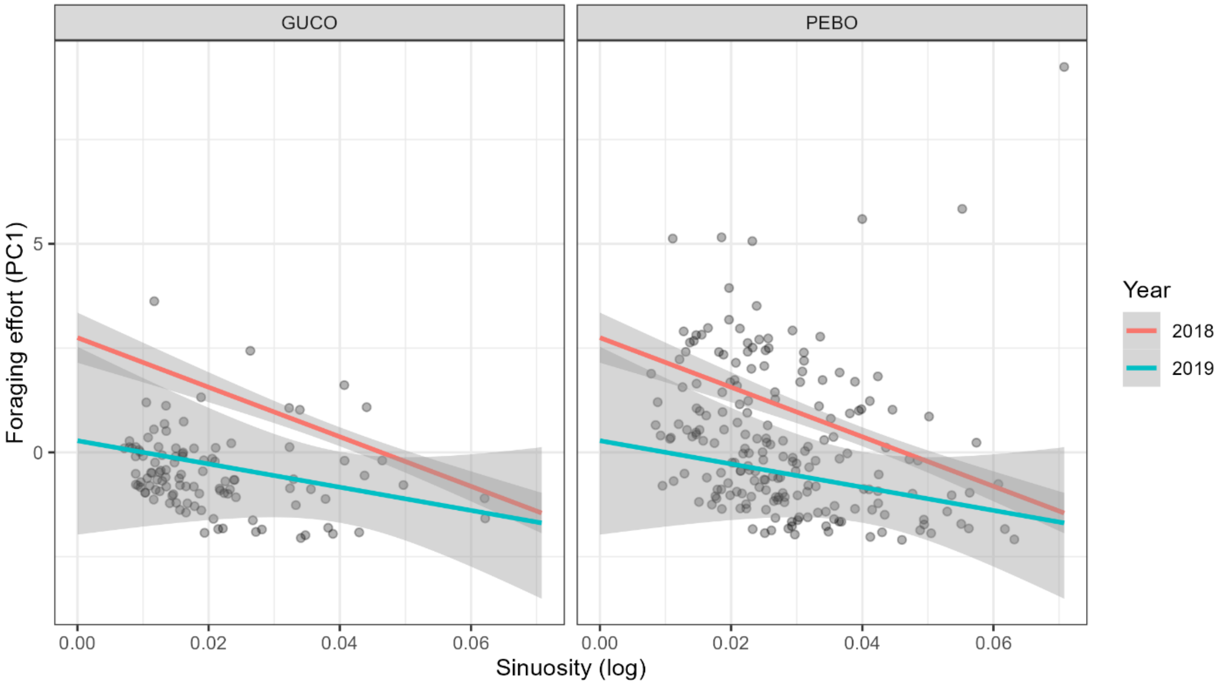

Figure 4.2. Foraging effort (PC1 including total trip duration, total trip path, and maximum distance travelled from the colony) and sinuosity for cormorants and boobies during 2018 and 2019 (warm and normal conditions, respectively). Shaded areas represent confidence intervals at 95%, with random factor set as zero.

Table 4.4. AICc rankings for foraging effort (PC1) accounting for search effort (sinuosity). Only models with ΔAIC less than 4 and the null model are shown in the table. Most parsimonious model within 2 ΔAIC, if not including the null model, were interpreted as most important.

Inter.	log(sin)	Sp	Yr	log(sin):Sp	log(sin):Yr	Sp:Yr	log(sin):Sp:Yr	df	logLik	AICc	delta	w
-6.75	-2.17	+	+		+	+		11	-502.28	1027.45	0.00	0.53
-7.50	-2.40	+	+	+	+	+		12	-502.00	1029.06	1.60	0.24
-9.59	-3.06	+	+	+	+	+	+	13	-501.60	1030.44	2.99	0.12
-0.03								6	-538.55	1089.38	61.92	<0.01

Physiological differences between cormorants and boobies in 2019

All metabolites differed between species in 2019, except cholesterol (Fig. 4.3, Table 4.5, SI Table 4.3). Glucose and triglycerides were higher in boobies than cormorants, whereas ketones showed the opposite trend, with cormorants having the higher values.

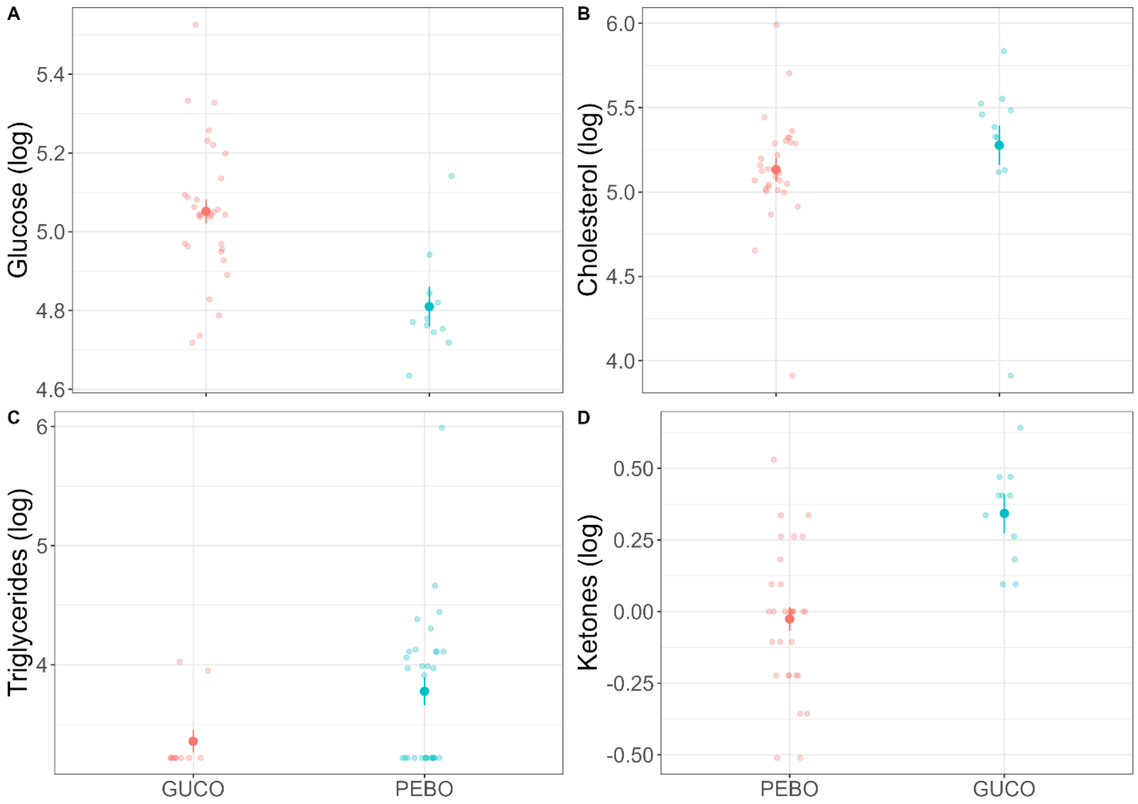

Figure 4.3. Metabolite concentration differences between cormorants and boobies in 2019. Solid dots and bars represent model predicted values and confidence intervals, respectively.

Table 4.5. AICc rankings for each physiological measure for boobies and cormorant in 2019. Asterisks denote significant models.

	Inter.	Species	df	logLik	AICc	delta	weight
*Glucose	4.81	+	3	16.73	-26.82	0.00	1.00
	4.99		2	9.25	-14.20	12.62	0.00
Cholesterol	5.17		2	-18.63	41.57	0.00	0.64
	5.28	+	3	-18.04	42.74	1.16	0.36
*Triglycerides	3.36	+	5	-33.74	79.18	0.00	0.79
	3.54		4	-36.35	81.80	2.62	0.21
*Ketones	0.34	+	3	3.39	-0.16	0.00	1.00
	0.07		2	-5.50	15.31	15.47	0.00

Physiological changes in boobies in 2018 and 2019

There was a significant difference only in ketone concentration in Peruvian boobies between years, whereas glucose, cholesterol, and triglycerides showed no significant different concentration between years (Fig. 4.1, Table 4.6, SI Table 4.4).

Table 4.6. AICc rankings for each physiological measure for boobies 2018 and 2019. Asterisks denote significant models.

	Inter.	Year	df	logLik	AICc	delta	weight
Glucose	5.05		4	2.62	3.96	0.00	0.87
	4.98	+	5	2.01	7.85	3.89	0.13
Cholesterol	4.62	+	5	-16.28	44.50	0.00	0.59
	5.11		4	-18.00	45.26	0.75	0.41
Triglycerides	3.83		2	-35.39	75.15	0.00	0.64
	4.10	+	3	-34.77	76.29	1.15	0.36
*Ketones	-1.77	+	5	-8.73	29.40	0.00	0.99
	-0.03		4	-14.41	38.07	8.67	0.01

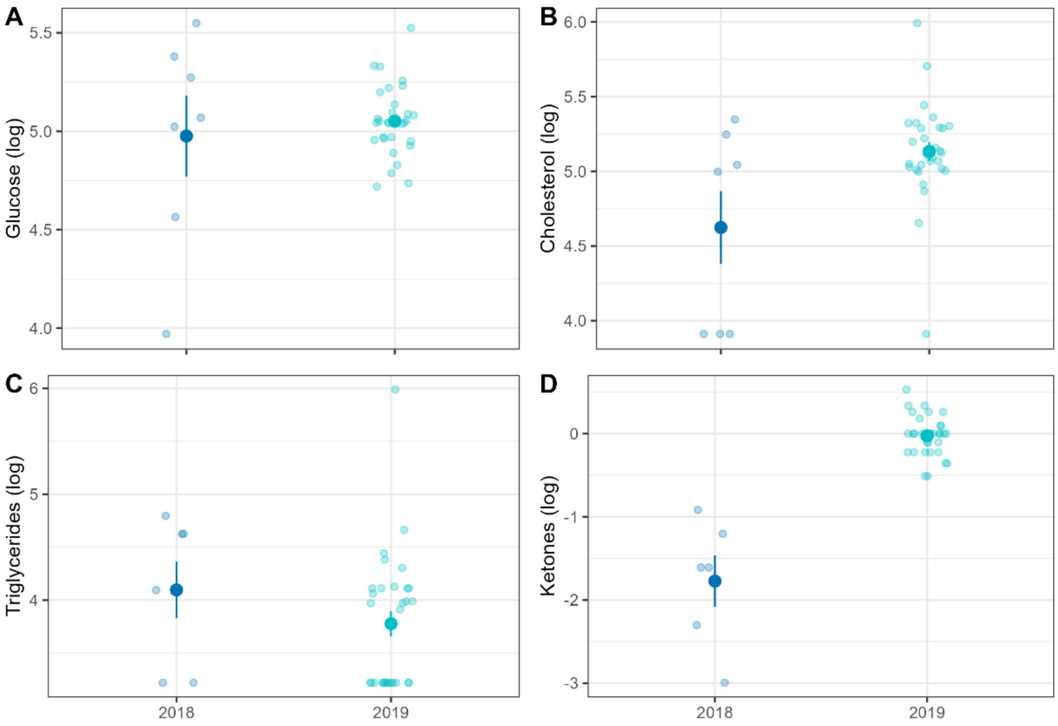

Figure 4.4. Metabolite concentration differences in boobies between 2018 and 2019. Solid dots and bars represent model predicted values and confidence intervals, respectively.

Changes in nutritional condition and effort in boobies in 2018 and 2019

Glucose, cholesterol, and triglycerides did not differ between years, so to investigate the relationship between foraging effort (PC1) and metabolite concentration all data points were grouped. Of these three metabolites, only triglycerides showed a relationship with the latency value (the time between the last trip evaluated and blood sampling) (Fig. 4.5, Table 4.7). Ketone concentration showed differences between years, but there was no relationship between ketone values and foraging effort.

Table 4.7. AICc rankings modelling triglyceride concentration as a function of foraging and search effort in boobies (2018-19) (PC1 and sinuosity) and latency (lat). Values are log -transformed as modelled. Abbreviations: trip sinuosity (sin), PCA1 (principal component 1 for foraging metrics), sampling latency (lat). Only models with ΔAIC less than 4 and the null are shown in the table. Most parsimonious model within 2 ΔAIC, if not including the null model, were interpreted as most important.

Inter.	log(sin)	PC1	log(sin):PC1	log(lat)	log(lat):PC1	df	logLik	AICc	delta	weight
4.21		-0.04		-0.28	+	5	-20.65	53.53	0.00	0.54
4.19				-0.23		3	-23.53	53.89	0.36	0.45
5.83	0.53					3	-29.96	66.75	13.22	0.00

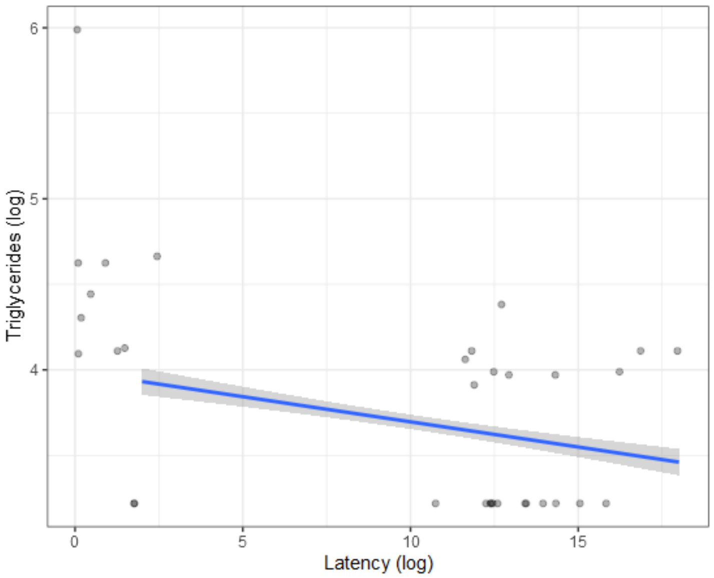

Figure 4.5. Triglyceride concentration as a function sampling latency (time between last trip and blood sampling time). Solid lines and shaded areas represent model estimates and confidence intervals.

Track Similarity and nutritional condition

We compared similarity of 37 tracks in both years and species using Earth's Movers Distance (EMD) to investigate spatial similarities of individual Peruvian seabirds' trips and address differences in physiological condition of individuals. Clustering at 50 000 (meters) showed 4 clear clusters (southern, eastern, close-northern, and far-northern areas) shown in Fig. 4.6.

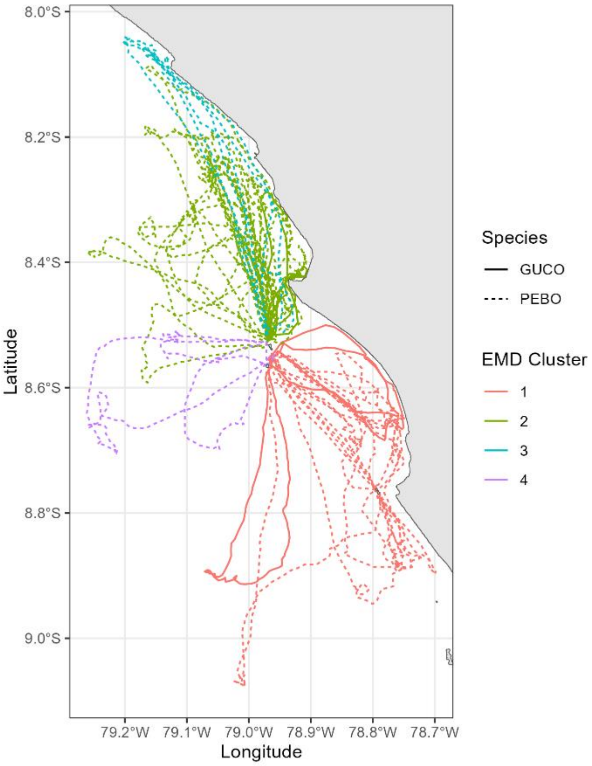

Figure 4.6. Clustering results from the EMD algorithm of 37 individual trips of Peruvian seabirds. Recognized clusters show 4 areas which we described as: southern (red), offshore (purple), close-north (green), and far-north (cyan). Peruvian boobies are represented by dotted lines (--) and guanay cormorants by solid lines (–).

We found no relationship between metabolites and mean similarity distance EMD (averaged for unique trip) or differences in metabolite concentration among cluster for boobies in 2019 (SI Figure 4.3, 4.4) (cormorant were excluded because of small sample sizes in 2018 and pre-trip blood sampling).

Discussion

Regardless of climatic conditions Peruvian boobies flew farther from the colony and followed longer trips path compared to Guanay cormorants. Weimerskirch et al. (2012) found no difference in total trip path and distance travelled from the colony between boobies and cormorants in Isla Pescadores, about 600 km south of our site, but there was a trend of boobies flying farther from the colony and following longer trip paths as expected from their greater flight capabilities and greater energy efficiency in flight, which is concurrent with our results.

Foraging effort changes in cormorants and boobies in warm vs. normal years

Seabirds breeding sympatrically show variable foraging patterns, often minimizing overlap at sea both within and across species, as the breeding period is a time when foraging competition is intensified because of chick provisioning (Gulka et al., 2019; Kappes et al., 2011; Rosciano et al., 2016). Upwelling ecosystem are normally prey rich environments in which multi-species seabird flocks have evolved to feed in large numbers together. However, their dynamics are affected by warming ocean conditions which then impact seabirds' foraging effort and energy input, leading to lower reproductive success (Chiu-Werner et al., 2019; Osborne et al., 2020; Patrick et al., 2021). As reported for other seabird species that exploit upwelling systems, foraging effort (longer or farther trips, increased search time) increases with localized or regional warming (Fromant et al., 2021; Kidawa et al., 2015; Osborne et al., 2020). In general, seabirds outperform ectotherms (fish), whether as prey or competitors, when conditions are cooler (Cairns et al. 2008). This is also the case for the Peruvian Humboldt Current System during warming events such as El Niño and other localized phenomena (eddies, Kelvin wave, etc.). Seabird reproductive output and population growth decreases during warmer condition years off the Peruvian coast due to decreased anchovy availability (Passuni et al., 2016, 2018). Anchovy schools may be farther from shore, deeper or more dispersed (Xu et al., 2013). In our study, warmer conditions (2018) increased total trip duration and sinuosity (searching). This impact was greater in cormorants, with cormorants having higher sinuosity than boobies in 2018 but the reverse in 2019 (Fig. 4.1) —which is consistent with cormorants failing rapidly in 2018. As seen in other seabird species, like albatrosses, penguins, and diving petrels, foraging is correlated with prey distribution and indirectly with sea surface temperature (Evans et al., 2021). These impacts are likely exacerbated by intense fishing seasons in the Humboldt System, results in increasing foraging effort by seabirds (Bertrand et al., 2012). Fishing activity did not overlap with most of our sampling, except in the last few days of 2019, in which we could see a little increase in foraging effort by both species.

Overall, blood plasma metabolites of boobies showed no consistent patterns between the normal and warm year, consistent with feeding or fasting conditions (Alonso-Alvarez & Ferrer, 2001). Perhaps individuals abandoned before their own condition deteriorated. Only ketones were lower in the warm year (2018) compared to the normal year (2019). This pattern was not expected as ketones should reflect worse mid/long term body condition. The same inverse pattern (ketones higher in good years) occurred in chick rearing common murres where an increase of ketones in good years may be the result of delayed weight loss (Storey et al., 2017) compared to bad years. There is no information on the physical and physiological changes in guano seabirds, but it seems like a plausible option.

Nutritional condition in cormorants and boobies in 2019

Plasma metabolites in Peruvian seabirds have not been studied extensively, especially so for Peruvian boobies and Guanay cormorants. Cormorants showed lower glucose and triglycerides plasma concentrations than boobies (during the normal year), and conversely, higher ketone concentrations. Differences in metabolite concentration are expected among sympatric species as physiological processes may differ, and correlate with a variety of factors (foraging strategies, metabolic processes, energy expenditure, parental effort, etc.) (Fossi et al., 1995; Moura et al., 2018). In our case, the lower physiological condition of cormorants than boobies (higher glucose/triglycerides; lower ketones/cholesterol) is consistent with conditions in 2018 being more challenging for cormorants than boobies. Physiological costs of cormorant species, as other foot propelled divers, tend to be high (Elliott et al., 2013; Ridgway, 2010), and so they are likely to experience stronger costs if anchovies are farther away whereas boobies may experience stronger costs if anchovies are deeper.

Although there can be an argument of causality, foraging effort of Peruvian Boobies showed no strong relationship with metabolites except triglycerides, which were influenced by sampling latency (time of last trip and time of sampling). This may indicates that nutritional condition at the time of sampling was not influenced yet by the effect of foraging effort. Similar patterns have been seen in other seabirds, such as Little Auks (*Alle alle*), which foraged under different oceanographic conditions with no change in nutritional condition was detected (Jakubas et al., 2011). Those authors suggested that Little Auks from this region did not reach the threshold that would force them to abandon breeding. Something similar may be happening with Peruvian Boobies, as boobies will abandon their eggs or chicks at any time on the breeding season in response to environmental conditions (higher than observed temperatures or lack of prey due to fisheries) (Burga-Domínguez et al., 2020; Tovar Serpa & Cabrera, 1985). Although increased foraging may impact the nutritional condition of seabirds, our analysis to answer this specific question was done only on a good year, due to lack of sampled individuals in the warm year, so little effect might have been expected. Also, we acknowledge the need of multiple metabolite values through time to more adequately understand the effect of foraging on nutrition. Nonetheless our results are one of the first estimations of this relationship.

Peruvian guano seabird's foraging tracks clustered clearly into four different areas around the colony: southern, eastern, close-northern, and far-northern areas (Figure 6). These represented fundamentally different foraging strategies, with some individuals foraging closer, others farther, some coastal and others offshore. The lack of response to trip mean similarity or clustering may be associated with the general colonial foraging strategies and may not affect the bird's nutritional condition due to competition as may in other species.

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Linking statement

In Chapter 4, I assessed the relationship between nutritional condition and foraging effort of two seabird species, the Peruvian booby and the guanay cormorant, under climatically different years, normal and El Nino-conditions. Although foraging effort differed significantly during an El Nino-year, with birds foraging farther away from the colony, and there was clear relationship between foraging effort and physiology. Thus, the nutritional/movement niche of these species differed in the short-term (two years), but the shift happened only on certain dimensions and mainly during harsh conditions. In Chapter 4, I will investigate the ecological niche of a larger assemblage of seabirds during a longer period of time, and try defining segregation patterns under different dimensional approaches, to demonstrate how increasing the variables analyzed, also known as niche dimensions, allows for the detection of patterns otherwise undetected.

Chapter 5 Amino acid-specific isotopes reveal changing five-dimensional niche segregation in Pacific seabirds over 50 years

Amino acid-specific isotopes reveal changing five-dimensional niche segregation in Pacific seabirds over 50 years

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Hutchison's niche theory suggests that coexisting competing species occupy non-overlapping hypervolumes, which are theoretical spaces encompassing more than three dimensions, within an n-dimensional space. The analysis of multiple stable isotopes can be used to test these ideas where each isotope can be considered a dimension of niche space. These hypervolumes may change over time in response to variation in behaviour or habitat, within or among species, consequently changing the niche space itself. Here, we use isotopic values of carbon and nitrogen of eleven amino acids, as well as sulphur isotopic values, to produce multi-isotope models to examine niche segregation among an assemblage of five coexisting seabird species (ancient murrelet *Synthliboramphus antiquus*, double-crested cormorant *Phalacrocorax auritus*, Leach's storm-petrel *Oceanodrama leucorhoa*, rhinoceros auklet *Cerorhinca monocerata*, pelagic cormorant *Phalacrocorax pelagicus*) that inhabit coastal British Columbia. When only one or two isotope dimensions were considered, the five species overlapped considerably, but segregation increased in more dimensions, but often in complex ways. Thus, each of the five species occupied their own isotopic hypervolume (niche), but that became apparent only when factoring the increased information from sulphur and amino acid specific isotope values, rather than just relying on proxies of δ^{15}N and δ^{13}C alone. For cormorants, there was reduction of niche size for both species consistent with a decline in their dominant prey, Pacific herring *Clupea pallasii,* from 1970 to 2006. Consistent with niche theory, cormorant species showed segregation across time, with the double-crested demonstrating a marked change in diet in response to prey shifts in a higher dimensional space. In brief, incorporating multiple isotopes (sulfur, PC1 of δ^{15}N [baselines], PC2 of δ^{15}N [trophic position], PC1 and PC2 of δ^{13}C) metrics allowed us to infer changes and differences in food web topology that were not apparent from classic carbon-nitrogen biplots.

Ecological niches are n-dimensional spaces or hypervolumes that describe the position of species by a complex suite of variables, both physical and biological [1]. The dimensions in an n-dimensional hypervolume usually include environmental factors that affect organismal performance, physiological limits, or morphological traits, as well as food resources or specific habitat needs, and can partly reflect important ecological patterns. N-dimensional niches have now been widely used to describe biological systems [2,3] and explain functional diversity [4], species morphological differences and taxonomy [5], among other ecological variables. Often the aim of constructing communities' niches is to detect patterns such as ecological segregation among species or groups within species (e.g. age classes or sexes) [6,7], which is critical to modelling niche shifts caused by anthropogenic factors including habitat loss, pollution and particularly climate change [8,9]. Such segregation is expected to be the 'ghost' of past competition such that species currently exploit resources or have minimized competition under most circumstances [10–12]. For example, some sympatric seabird species segregate their foraging space or prey at several geographic and temporal scales [13–16].

The principle of competitive exclusion states that complete competitors (with completely overlapping niches) cannot coexist [17–19]. Niche segregation, derived from differentiation, leading to coexistence among species and within species has been observed in a range of taxa, from plankton to songbirds [20–23]. If we consider a species' hypervolume within Hutchinson's n-dimensional niche space, then niche segregation implies that there is limited overlap of that hypervolume with coexisting species [7]. Seabirds are intriguing in this regard because they often include large populations of several species with apparently overlapping habitats, diets and foraging areas [24,25]. However, recent tools have shed light on how seabirds partition their foraging habitat, diet, and other components of their niche hypervolume [15,26].

In predators that show high inter- and intra-specific competition dietary partitioning is an important component of niche diversification [27]. The study of trophodynamics, within marine communities allow us to understand changes in time and space of such niche diversification and trophic relationships [28]. Direct diet sampling can be invasive (i.e., killing animals to sample stomachs) or be biased due to differential digestion of prey items, while behavioural observations can also be biased and difficult for marine species that forage over large areas offshore [29]. Stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), representing the relative proportion of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in tissues, have proven to be reliable indicators of diet, and consequently can be used to delineate trophic assemblages in marine ecosystems [28,30–32]. In particular, $\delta^{13}C$ can be used to infer feeding habitat (such as pelagic or benthic/coastal), whereas $\delta^{15}N$ is commonly used to provide an index of trophic position [33]. However, both bulk isotopic values are unable to reflect the influence of baseline values of the ecosystem, therefore careful interpretation if often needed[34]. Layman metrics can be used to describe trophic levels (range of $\delta^{15}N$), niche diversification ($\delta^{13}C$ range), overall density of species packing (mean of the Euclidean distances to each species' nearest neighbor in bi-plot space), among other indices that help describe trophic niches and relationships [35]. The use of these metrics in characterizing trophic dynamics can help detect different interactions within the community such as competition (by increased trophic redundancy) or high predation levels (increase in trophic diversity) [36].

However, most studies of niche partitioning using stable isotopes have only employed $\delta^{13}C$-$\delta^{15}N$ biplots [35,37,38]. In some cases, "δ-spaces" can be converted into "p-spaces" using mixing models to quantitively assign diet proportions [32]. However, two variables are unlikely to be able to resolve complex food webs [39]. The use of additional isotopes provides additional degrees of freedom especially when trying to identify prey sources with the use of the above-mentioned mixing models. The addition of a third dimension in community ecology analysis can provide important information overlooked with only two isotopic dimensions [40]. Three -dimensional approaches to look at isotopic niche segregation, such as incorporating sulphur ($\delta^{34}S$), have proven to be efficient in detecting segregation in marine species [41]. This has been reported also in seabirds when marine epipelagic species are more enriched in $\delta^{34}S$ compared to benthic or coastal species, proving to good indicator independent of trophic level (unlike bulk carbon isotopes)[42]. The use of compound specific isotopic analysis, such as using carbon and nitrogen isotopes of amino acids, overcomes some biases present in bulk analysis of $\delta^{13}C$ and $\delta^{15}N$ [43,44]. Moreover, current tools to look at n-dimensional niches are increasing in the literature, including re-sampling and Bayesian methods to produce metrics for isotopic niches [45]. Incorporating amino acid specific isotopic values into ecological studies provides new levels of information that allows to differentiate trophic and baseline signals in the trophic webs that would otherwise be masked in bulk isotopic values [43,46]. The use of trophic indicators such as nitrogen isotopic values of glutamic acid (Glx) may allow to discriminate baseline shifts and also improve predictions trophic position. Such tools allow for testing of hypotheses about how niches vary across dimensions (e.g., changes in overlap and segregation patterns, more distant centroids, smaller volumes).

Niches change over time due to natural and anthropogenic changes. In particular, niche segregation may only be apparent when resources are limited; during resource pulses, all species may be able to take advantage of the same abundant food sources [47,48]. In marine habitats, overfishing [49], marine pollution [50], and other stressors [51] could cause variation in isotopic niches that could reflect important changes in species populations. Stable isotopes allow tracking of diet over long time scales due to archived specimens and may provide insights on important trophic changes [52]. These changes may occur over very long periods, hundreds of years or decades [49,53], or shorter periods, such as seasons or consecutive years [30,54,55]. Thus, isotope measurements in historical samples link population trends with diet shifts across time. Nonetheless, most studies examine only one (δ^{14}N) or two (δ^{13}C and δ^{15}N) isotopes, which may mask niche variation occurring in other dimensions. Therefore, producing clear niche metrics and understanding fine patterns of niche shifts in seabird assemblages through time may allow for better management and conservation of species due to these current threats (e.g. increasing pollutant loads in oceans, climate change, etc.)

Here, we incorporate an n-dimensional approach, comparing 1, 2, 3, and 5-dimension models, to build isotopic niches with δ^{13}C and δ^{15}N of 11 amino acids in an assemblage of five coexisting seabirds (ancient murrelet, double-crested cormorant, Leach's storm-petrel, rhinoceros auklet, pelagic cormorant) that breed along the southern coast of British Columbia. We test the idea that seabirds overlapping in δ^{13}C and δ^{15}N biplots will differ in segregation patterns when using multiple stable isotopes in higher dimensions (2, 3, and 5 dimensions). Especially, trophic relationships will be more apparent when using amino acid specific nitrogen values as indicators, e.g. reflecting higher trophic level for cormorants, compared to storm-petrels or auklets. Moreover, we expect that in higher dimensions, most Layman community metrics should differ as all five species may change patterns of segregation from each other, but relative niche volume among species should remain constant. As the prey base of cormorants changed over time, we predicted that niche centroids would vary, and overlap would decrease, but overall niche size would remain constant in higher dimensions.

Methods

Dataset and study species

We studied five species (ancient murrelet, double-crested cormorant, Leach's storm-petrel, rhinoceros auklet, pelagic cormorant) using whole eggs collected since 1969 and archived at the National Specimen Bank (National Wildlife Research Centre [NWRC], Ottawa, Ontario) as part of the long-term contaminants monitoring program initiated in 1968 by the Canadian Wildlife Service (see Table 5.S1 for final egg sample numbers per species). Seabird eggs are commonly used as a relatively non-invasive sampling source to represent the contaminant and dietery composition in the female adult prior to and during the egg-laying period. Double-crested cormorants *Phalacrocorax auratus* are generalist seabirds, inhabiting coastal nearshore to inland aquatic environments across North America [56]. They feed on diverse benthic and mid-water schools of fish in the British Columbia coast. Pelagic cormorants *Phalacrocorax pelagicus* forage mainly in deeper water on the continental shelf during the breeding season [57–59]. Rhinoceros auklets *Cerorhinca monocerata* (hereafter auklets) inhabit temperate waters of the northern Pacific [60,61] and feed on epipelagic fish [62]. Ancient murrelets *Synthliboramphus antiquus* (hereafter murrelets) are offshore, sub-surface feeders and prey on zooplankton and small, schooling fish [63]. Leach's storm-petrels *Oceanodrama leucorhoa* (hereafter storm-petrels) are planktivorous surface feeders found in the northern Atlantic and Pacific Oceans [64]. While breeding, they feed closer to the colony on the continental shelf, whereas they feed hundreds of kilometres away when not breeding [64]. Eggs were sampled from islands and coastal sites on the Pacific coast of British Columbia, Canada: Cleland Island (storm petrels and auklets), Langara Island (murrelets), Lucy Island (auklets), Mandarte Island (cormorant), Mitlenatch Island (pelagic cormorants), Thomas Island (storm-petrels), and Thorton Island (storm-petrels) (Figure 5.S1). Maps were produced with the gpplot2 [65] and sf [66,67] packages, and shapefiles from gadm.org. We followed the methods already presented in contaminant research [42,68–70]. Sampling effort (frequency and sites sampled) varied since 1970 due to cost and logistics, and in some cases, eggs were collected during spring and early summer (late April to early July). Some egg samples were pooled into 1g sub-samples from a total of 15, 5, or 3 samples after homogenization as described in work by Miller et al.[70]. Briefly, 1.5 g wet weight of aliquots were homogenized after removal from the eggshell and then subsampled into aliquots for preservation.

Stable isotope analysis

Stable isotope analysis for bulk carbon, nitrogen, and sulphur was carried out using sub-samples of 1 mg freeze-dried eggs, loaded into tin, using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (IRMS; Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility at the University of California, Davis (http://stableisotopefacility.ucdavis.edu). Delta values were provided in parts per thousand (‰) and δ13C values have been lipid normalized [71]. Carbon and nitrogen stable isotopes of ten specific amino acids, both essential and non-essential (alanine, valine, glycine, isoleucine, leucine, proline, aspartic acid, phenylalanine, glutamic acid (Glx), lysine) were also analyzed at UC Davis Stable Isotope facility via GC-C-IRMS as described in [42,68–70]. Sulfur isotope we performed in a Europa Roboprep-20/20 EA-IRMS (lipids were not extracted from homogenates as lipid extraction is known to alter δ^{34}S and lipids should not contain sulfur) as described by Elliott et al. [71]. Samples for specific amino acids were analyzed with an isotope cube elemental analyzer (Elementar, Germany) interfaced with a Finnigan DeltaPlus XP isotope ratio mass spectrometer (Thermo Germany) coupled with a ConFlo IV (Thermo Germany). Amino acids were liberated via acid hydrolysis and derived by methyl chloroformate. Methoxycarbonyl amino acid methyl esters were then injected in splitless (^{15}N) mode and separated on an Agilent DB-23 column (30 m × 0.25 mm ID, 0.25 µm film thickness). Once separated, the esters were converted to N^2 in a combustion reactor at 1000 ◦C. Water was subsequently removed through a nafion dryer. During the final step of the analysis, N2 entered the IRMS. Pure reference N^2 was used to calculate provisional δ- values of each sample peak. Next, isotopic values were adjusted to an internal standard (e.g. norleucine) of known isotopic composition. Final δ-values were obtained after adjusting the provisional values for changes in linearity and instrumental drift such that correct δ-values for laboratory standards were obtained. Laboratory standards were custom mixtures of commercially available amino acids that had been calibrated against IAEA-N1, IAEA-N2, IAEA-N3, USGS-40, and USGS-41. A final subset of 63 samples (Table 5.S1) for five species of seabirds with a complete set of sulphur isotopes, and carbon and nitrogen amino acid isotopes was used for all analyses.

Statistical methods

All data processing and analyses were performed using the R software[72]. Because studies have found less support for the Glx-Lys difference in high consumers[73], we tried a different approach that was agnostic to the meaning of δ^{15}N in amino acids by using all the variance of the isotopic values of each compound by means of principal component analysis (PCA). PCA were performed on the 63-sample subset for both sets of carbon and nitrogen amino acid-specific isotopic values, independently using the prcomp() function, with scaling, in base R. We used the first principal component (PC) of the nitrogen amino acids (PC1-Nss) for one-dimensional analyses, as δ^{15}N is a classic basic indicator of trophic level segregation among sympatric predators[39]. We used the first PCs of carbon and nitrogen amino acids (PC1-Css and PC1-Nss) for the two-dimensional analyses. We included the standardized value of sulphur (referred to as *stdDeltaS*) to these previous two dimensions for the 3-dimensional approach and incorporated the second PC of both carbon and nitrogen amino acid stable isotope values for the 5-dimensional approach (see **Error! Reference source not found.**). PC1-Css and PC1-Nss s howed a strong correlation with bulk independently measured isotope values of carbon and nitrogen [39], and therefore PC1 values of amino acids were considered also as proxies of bulk carbon and nitrogen isotopes.

The dimensions produced from the PCA analyses proved to be a good proxy for isotopic values of carbon and nitrogen. Scores of PC1 of carbon (PC1-Css) were equally loaded in all amino acids (ranging from 6.16 to 12.32%) and strongly correlated with bulk carbon values (r =-0.88) (

Table 5.S2). PC2-Css had the highest loading for proline (50.18%), a non-essential amino acid. PC1 of Nitrogen (PC1-Nss) was mainly loaded on alanine, isoleucine, leucine, and valine (14.96 to 16.32%), the first three being trophic amino acids, and highly correlated with bulk nitrogen isotope values (r =0.57). PC2-Nss was loaded on aspartame, and phenylalanine (23.67 and 30.57 respectively), trophic and source amino acids, respectively. Additionally, to confirm our approach, we contrasted the first two PCA components of the δ^{15}N values in amino acids with several trophic indices (Glx-Lys, Glx-Phe, and two trophic position indexes for single and mean amino acid values[74–76]), and found strong correlations with either PC2 (r > |0.6| in all cases, see Fig. 5.S2). We could assume that PC1Nss was an indicator of baseline nitrogen values, and PC2Nss closely reflected trophic level. Similarly, we checked for the the correlation of the PC1

raw carbon (uncorrected) values and the PC1 of corrected δ values of amino acids for Suess effect for the Gulf of Alaska region, using the SuessR package[77], and found a very strong correlation (r = 0.998, also Fig. 5.S2).

Table 5.8. Components incorporated in each dimensional approach. Principal components of amino acids are labelled with the corresponding isotope for carbon and nitrogen (e.g. PC1-Css for carbon isotope values in amino acids, or PC1-Nss for nitrogen isotope values in amino acids)

Model approach	Dimensional components
1-dimensional	PC1 of δ^{15}N in amino acids (PC1-Nss)
2-dimensional	PC1 of δ^{13}C and PC1 of δ^{15}N in amino acids (PC1-Css, PC1-Nss)
3-dimensional	PC1 of δ^{13}C and PC1 of δ^{15}N in amino acids, and standardized δ^{36} S (PC1-Css, PC1-Nss, stdDeltaS)
5-dimensional	PC1 and PC2 of δ^{13}C in amino acids, PC1 and PC2 of δ^{15}N in amino acids, and standardized δ^{36} S (PC1-Css, PC1-Nss, stdDeltaS, PC2-Css, PC2-Nss)

The package nicheROVER [45] was used to model the distribution of the different niche isotopic components using a Bayesian inference framework, incorporating uncertainty into the analysis, and a method insensitive to sample size (therefore the increase of sample size will not cause random increases in niche region). The default 'non-informative' priors were used in nicheROVER. We sampled 100 000 posterior distributions to calculate centroid locations and probability percentiles for all species and overall community metrics (described below) to be used in comparing dimensional approaches. The nicheROVER package also produces estimations for niche size (described as the probability in n-dimensional space) and niche overlap (the 95% probability of one species falling into the niche of another). Overlap estimates incorporated 95% of the data.

To compare differences between independent dimension centroids and niche sizes between species, we calculated the Bhattacharyya Coefficient [78]. This coefficient estimates the probability of overlap between two posterior distributions. To identify if niches of each species had different positions in isotopic space the posterior estimates μ were divided into a null (n) and test (t)

equally sized distributions [41]. We used those estimates to produce a conservative probability estimate that the centroid locations differ between species, by calculating the probability that the distance between two centroid values in the test distributions (μ_{1t} and μ_{2t}) was greater than the distance between the test and null distributions for μ_1 and μ_2, respectively:

$$P[D\mu 1, \mu 2] > 0 = \frac{\Sigma(D[\mu_1,\mu_2] - D[\mu_{1t},\mu_{2t}] - D[\mu 2t,\mu 2n] > 0)}{total\ number\ of\ posterior\ estimates\ in\ null\ or\ test\ distributions} \qquad \text{Eq. 5}$$

We used the 100 000 draws from the posterior distribution extracted from the nicheROVER models, and calculated isotopic range for each tracer, representing the different mean of diversification in trophic level or niche, centroid distance (CD), representing species spread in space, nearest neighbour distance (NND), the density of species packing or niche redundancy, and standard deviation of the nearest neighbor distance (SDNND) following the methods of [35], to assess at how increasing dimensionality may influence the representation of community structure.

A spider chart was used to plot independent centroid locations for each dimension and all species. 3-dimensional plots were produced with the mean values of sigma and mu (covariance and means posteriors) following [41]. Boxplots of the probability distribution of CD, NND, SDNND, and ranges for all variables for the whole community in all dimensional approaches are presented.

We additionally evaluated the changes in cormorant (the two species with the largest sample sizes that allowed for such comparison) niches for 2D, 3D, and 5D dimensional approaches only between the periods of 1970-1989 and 1990-2006.

Results

The use of stable isotopic values to describe ecological segregation in communities or assemblages is gaining momentum [36,79]. Moreover, ecological patterns and segregation often times need more than just two indicators to describe observable differences and pattern shifts in time [40,41]. The use of Layman metrics in a high-dimensional approach to get a better approximation to the n-dimensional ecological niche, described by Hutchinson, should allow for better observation of ecological patterns. Of the Layman metrics analysed here, centroid locations of niches for each species and niche sizes were fairly consistent in all dimensional approaches, but overlap (and therefore segregation) patterns changed not only in proportion to dimensionality when comparing lower (1D and 2D) to higher dimensional approaches (3D and 5D) (Table 5.9,Table 5.10; Figure 5.8, 5.Figure 5.9).

Species centroid locations in 2D, 3D, 5D

Species relative values for each dimension were preserved from 2D to 5D (Figure 5.18, Table 5.S3). Storm-petrels tended to be positioned the farthest from the rest of the species, whereas the two cormorant species, were consistently close to each other, but not always overlapping significantly (Table 5.S4). The two alcids differed in only two axes, PC1-Css and sulphur (std-$\delta^{36}S$) (Bhattacharyya coefficient probability of 0.95 and 0.63), as expected from their different diets. Overall, no species coincided in all dimensions with another species, indicating community segregation.

All species showed different overall centroid locations. All species occupied a different location in the iso-space across all dimensional approaches (Table 5.S5: A, B, C). The difference between centroid locations was somewhat consistent among dimensions, with some interesting shifts that can be seen in Table 5.S5:D-E-F. For example, storm-petrels and double-crested cormorants were more distant to each other than any other pair of species in all dimension approaches. Conversely, both cormorants were the closest species in 2D and 5D; but not in 3D, where pelagic cormorants and auklets were the closest species to each other. Interestingly, we can see a clear shift in species in PC1Nss and PC2Nss, reflecting important differences in baseline and trophic signals. For example, storm-petrel had highest values of PC1Nss (baseline), but lowest values of PC2Nss (trophic position) together with the rhinoceros auklet, and double-crested cormorant had higher trophic level.

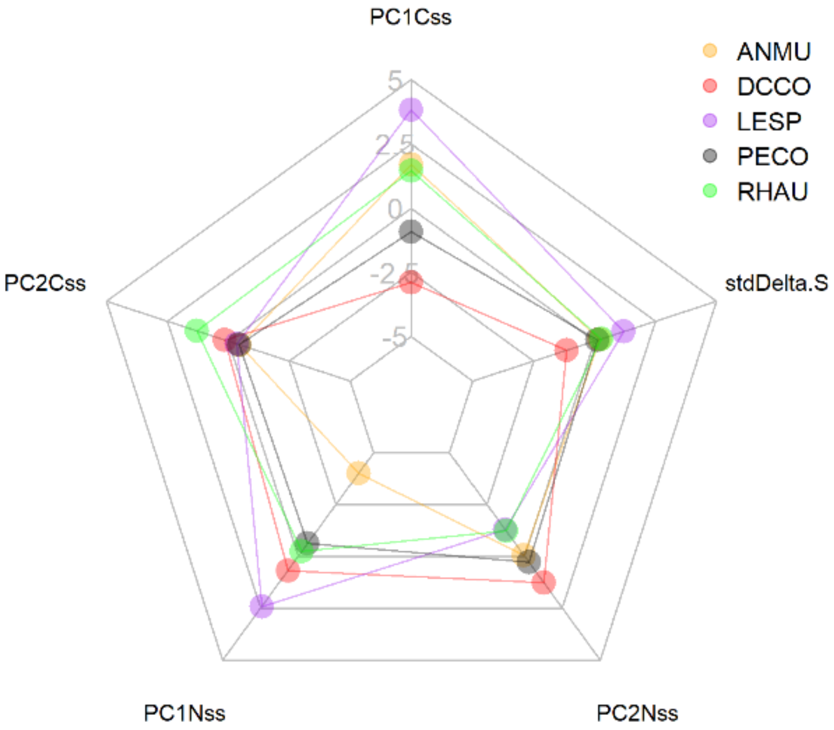

Figure 5.18. Average centroid locations for all species in 5 dimensions from 100 000 samples drawn from the posterior distribution (where PC1Css, PC2Css, PC1Nss, and PC2Nss are the first and second principal component of carbon and nitrogen isotope values of amino acids, respectively. stdDeltaS is the standardized value of sulphur values). Ancient murrelet = ANMU, double-crested cormorant = DCCO, Leach's storm-petrel = LSPE, pelagic cormorant = PECO, Rhinoceros Auklet = RHAU. These are relative positions when comparing one species to another and polygons do not represent niche size or shape (the PCA axes were not rotated).

Niche sizes in 1D, 2D, 3D, 5D

Relative niche size remained relatively constant from 2D to 5D (Table 5.9). Double-crested cormorants had the largest 2D niche, though similar in size to alcids (niche size 31.24 and 41.36, Bhatt coef. prob. = 0.89, Table 5.S6, Figure 5.S2). By a statistically significant margin (>0.8 probability), the double-crested cormorants were found to have the largest niche size in higher dimensional approaches, followed by auklets, and pelagic cormorants. Storm-petrels had the smallest niche in 2D and 3D, but not in 1D or 5D, where murrelets had the smallest niche size. Niche sizes were very similar in lower dimensions, with almost half of the pairs of species having overlapping niche sizes with a probability greater than 80% (for niche size overlapping probabilities see Table 5.S6). Niches sizes increased in higher dimensions, with only storm-petrels and murrelets having overlapping niche sizes in 3D. No pair of species had overlapping niche sizes in 5D (Table 5.9 and Table 5.S6).

Table 5.9. Niche sizes for five species of seabirds on the coast of British Columbia. Mode and 5% and 95% quantiles of the posterior distribution from 100 000 samples are shown. Bolded values are those representing shifts in increasing trend size of niches into higher dimensional approaches. See Figure 1 for species abbreviations.

	1D	2D	3D	5D
Leach's Storm petrel	4.38 (2.94-6.75)	18.02 (12.67-33.23)	5.06 (3.37-10.68)	**33.03 (20-85.13)**
Ancient murrelet	7.62 (4.47-13.7)	20.24 (13.49-48.7)	5.72 (3.57-16.27)	1.37 (0.8-5.16)
Pelagic cormorant	5.21 (3.85-7.23)	27.81 (20.78-43.77)	19.68 (13.74-33.77)	137.11 (86.72-269.57)
Rhinoceros auklet	5.39 (3.55-8.52)	31.24 (21.64-59.73)	54.38 (34.78-117.28)	298.45 (170.84-771.4)
Double-crested cormorant	5.29 (3.83-7.47)	41.36 (30.09-66.11)	120.35 (81.87-211.32)	689.04 (425.32-1408.16)

Niche overlap among species

High overlap (greater than 50%) between species pairs (in lower dimensions, 1D, with one exception, and 2D) is consistently reduced with an increase in dimensions (Figure 5.8, 5.Figure 5.9). The effect was not solely due to dimensionality, as the pattern changed with each incorporated dimension. Less significant overlap in some species pairs varied with dimensional approaches; some pairs of species increased overlap from 2D to 3D, but then decreased greatly in 5D (e.g. murrelets overlapping with double-crested cormorant) (Table 5.S7 and Figure 5.8), whereas in other species, the decrease was minimal (murrelets on pelagic cormorant). In general, 5D overlap was significantly reduced as expected, but especially in those species with smallest niches. Double-crested and pelagic cormorants showed the greatest overlap among all pairs of species consistently in all dimensional approaches (Figure 5.8).

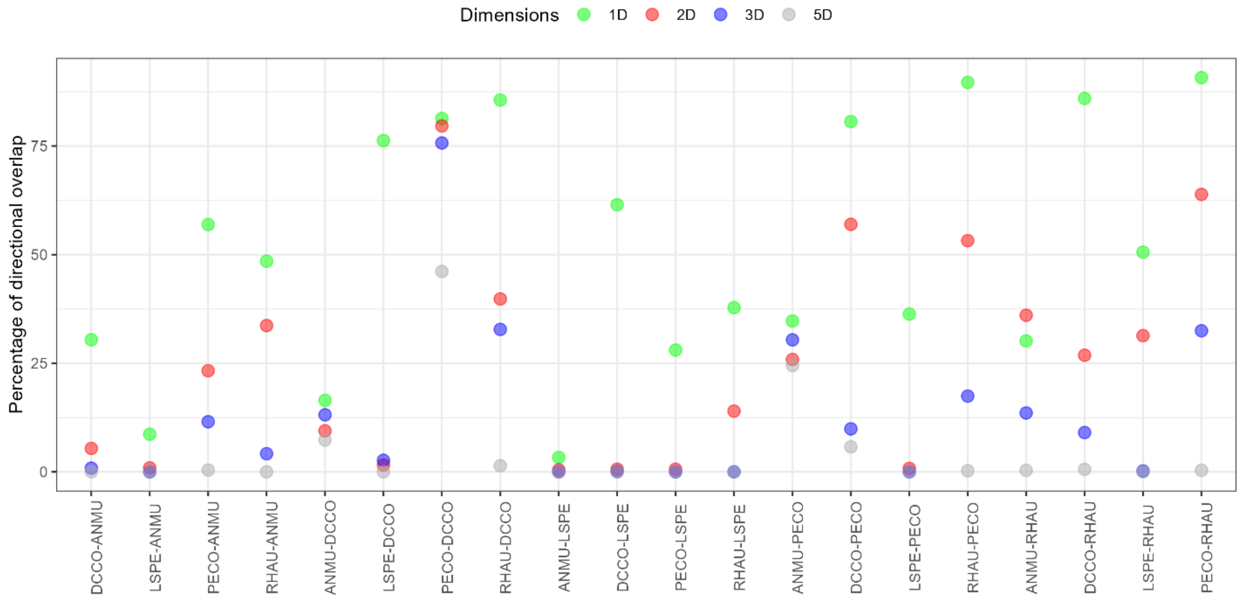

Figure 5.8. Graphical representation of the percentage of directional niche overlap between all pairs of species. Percentage of overlap represents first species overlapping on second species. See Figure 1 caption for species abbreviations.

Dispersion metrics in 2D, 3D, 5D

Species spread (Centroid Distance, CD) for all 5 seabird species showed a small increasing trend from lower to higher dimensions (10% or less) (Table 5.10). On the other hand, an increasing trend observed for NND values and the standard deviation of NND is higher in magnitude, reflecting a variation in density and evenness of species packing, respectively. Independent dimension ranges varied mainly for carbon PC1 (6.7 [4.83-7.95]) and nitrogen PC1 (6.5 [3.35-8.75]), whereas the rest of the dimensions ranged in less than 3 units (Table 5.S12).

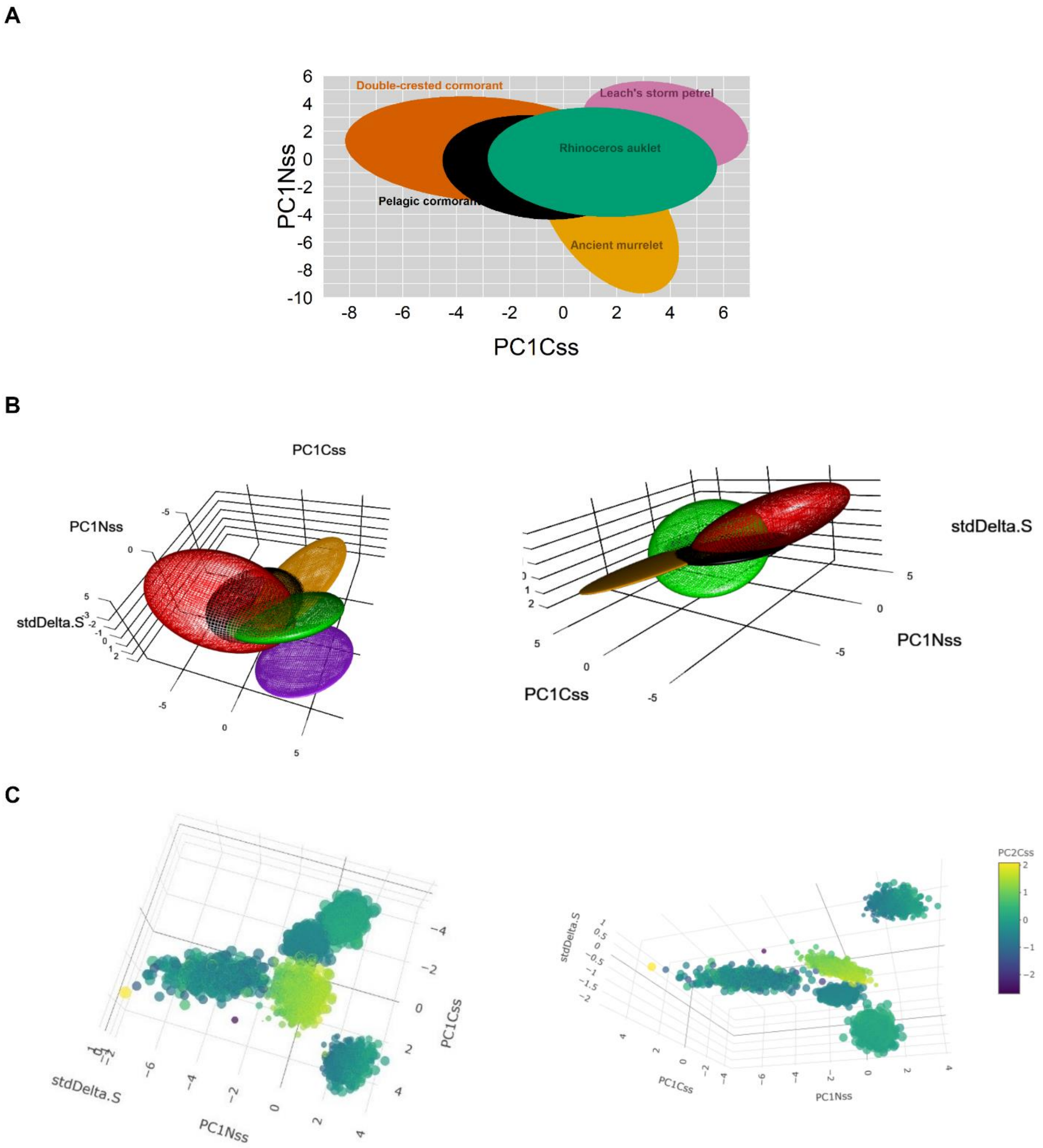

Figure 5.9. Graphical representation of niche sizes in A) 2D (covariance ellipses), B) 3D (covariance ellipsoids) [yellow = ancient murrelet, red = double-crested cormorant, purple = Leach’s storm-petrel, black = pelagic cormorant, green = rhinoceros auklet], and C) 5D (simple five-dimensional plotting of 1k random points) for five species of seabirds in the British Columbia coast, where colour is the 4th dimension (PC2Css), and circle size the 5th dimension (PC2Nss).

Table 5.10. Centroid distance (CD), nearest-neighbor distance (NND), and standard deviation of the NND (SDNND) for all five species of seabirds in 1D, 2D, 3D, and 5D. Mean and quantiles (2. 5% and 97.5%) of the posterior distribution from 100 000 samples.

	CD	NND	SDNND
1D	1.63 (0.03-4.53)	0.003 (0-0.013)	0.004(0.001-0.01)
2D	2.87 (0.5-4.85)	0.012 (0.002-0.042)	0.01(0-0.032)
3D	2.95 (0.61-4.94)	0.055 (0.018-0.148)	0.03(0.01-0.08)
5D	3.27 (1.43-5.05)	0.00002 (0-0.00006)	0.00004(0-0.00011)

Temporal change and overlap in isotopic niches of cormorants: 2D, 3D, 5D

Niche sizes for both cormorant species decreased between the 1970-1989 and the 1990-2006 periods (Table 5.11). Pelagic cormorants decrease in niche size through time when more dimensions were incorporated into the model, whereas double-crested do not (Table 5.11). Double-crested cormorants showed shifts in most independent isotopic dimensions for all 5 axes, whereas pelagic cormorants had no important changes in any dimension (Figure 5.21, Table 5.S8). Double-crested cormorants showed a trend of niche change (distance between centroids of two time periods ≤ 2.4) in all three approaches, although the probability was low (≤ 0.6, Table 5.S9), whereas pelagic cormorants showed a larger change (distance ≤ 0.87 and probability of ≤ 0.2). Conversely, both species showed little difference in overall centroid location (position in the iso-space) for their niches in different periods with double-crested cormorants having significant differences (above 50%) and a higher distance between periods, compared with pelagic cormorants (Table 5.12).

Table 5.11. Niche sizes for double-crested and pelagic cormorant during the 1970-1989 and 1990-2006 periods in the British Columbia coast. Mode and 5% and 95% quantiles of the posterior distribution from 100 000 samples.

		2d	3d	5d
Double-crested	1970-1989	68.757 (45.269-164.295)	69.467 (41.866-192.405)	93.679 (49.5-316.823)
	1990-2006	8.714 (6.164-16.208)	28.362 (18.259-58.255)	89.93 (53.928-227.88)

Pelagic	1970-1989	31.656 (21.656-53.025)	21.235 (14.26-41.864)	288.338 (172.435-691.15)
	1990-2006	11.331 (7.587-27.397)	3.8 (2.45-11.228)	5.527 (3.002-22.122)

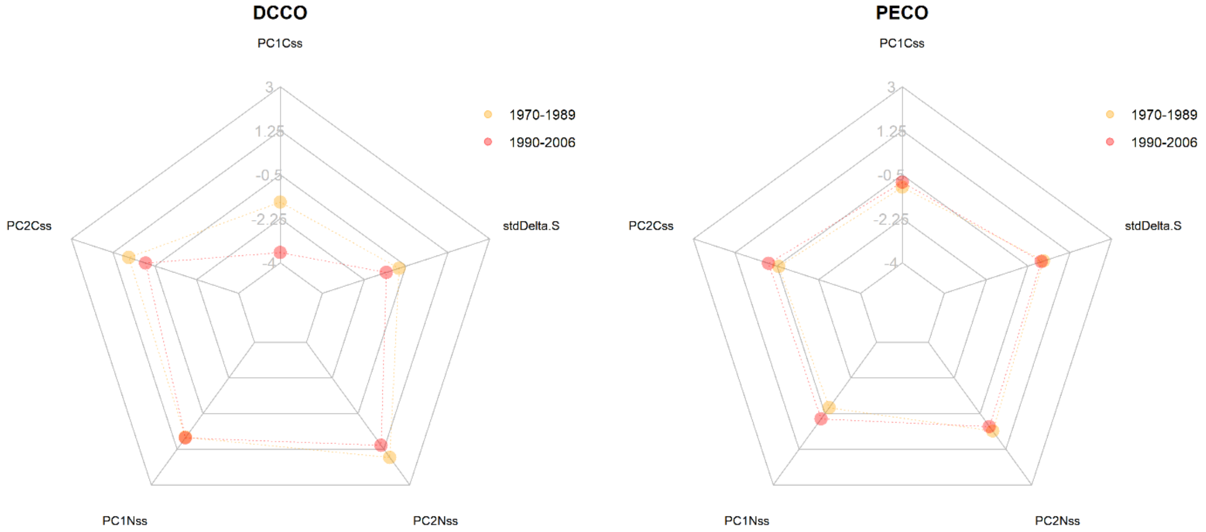

Figure 5.21. Centroid locations for DCCO and PECO in 5 dimensions in two time periods (where PC1Css, PC2Css, PC1Nss, and PC2Nss are the first and second principal components of carbon and nitrogen isotopes of amino acids, respectively. stdDeltaS is the standardized value of δ sulphur

In both species, niche overlap between the two periods was lower in higher dimensions, as expected. As niche volume decreased, the overlap of the late period on the early period overlapped little in double-crested cormorants in all dimensional approaches (see Table 5.6 for directional overlap details). However, the early period niche showed a high overlap with the later period niche in 2D (96.99%) but became minimal toward higher dimensions (11.6% in 5D). In contrast, pelagic cormorants' later period niche overlapped more than 50% on the early period niche throughout all dimensional approaches (Table 5.13). Considering the niche size changes from lower to higher dimensional approaches (Table 5.11) these changes in overlap show differences in niches when incorporating new dimensions.

Table 5.12. Probability of niches for double-crested cormorant and pelagic cormorant in the two time periods having different centroid locations and distance between centroids in 2, 3, and 5 dimensions.

	dim	p	distance
Double-crested	2D	0.6	2.19
	3D	0.558	2.28
	5D	0.571	2.49
Pelagic	2D	0.208	0.875
	3D	0.207	0.881
	5D	0.131	0.543

Table 5.13. Percentage of directional niche overlap between periods for double-crested cormorant and pelagic cormorant (periods in rows overlapping onto periods in columns) for 2D, 3D, and 5D approaches. Bolded are those pairs with high probability values (>50%). Overlap direction is period 1 (row header) with period 2 (column header).

	2d		3d		5d	
Double-crested	1970-1989	1990-2006	1970-1989	1990-2006	1970-1989	1990-2006
1970-1989	NA	19.28	NA	20.27	NA	8.38
1990-2006	**96.99**	NA	47.22	NA	11.6	NA
Pelagic	1970-1989	1990-2006	1970-1989	1990-2006	1970-1989	1990-2006
1970-1989	NA	**53.08**	NA	29.42	NA	2
1990-2006	**91.68**	NA	**88.78**	NA	**56**	NA

Discussion

The use of higher dimensional approaches to assess niche size, overlaps, and community metrics, improved our capacity to detect differences and pattern changes in a community assemblage of seabirds, as suggested by Bowes [40]. Specifically, the isospace produced considering a five-dimension "Hutchinson" hypervolume, made possible via the use of sulphur and amino acid-specific isotopes, improved our understanding of niche space compared to the use of bulk carbon and nitrogen. Moreover, PC1 of nitrogen was associated with baseline $\delta^{15}N$ levels and PC2 was associated with trophic position, illustrating that using bulk $\delta^{15}N$ as a metric of trophic position could lead to incorrect inferences. Polito[80] also found that two species of penguin were differentiated when using essential amino acids of carbon isotope values, which did not occur when using only bulk isotopic values. Ranking of niche size and Layman metrics (centroid distance, nearest neighbour distance, and standard deviation of the nearest neighbour distance) were remarkably similar across dimensions, although absolute values were larger in higher dimensions, as suggested by Mammola[81]. Thus, the overall topology of the guilds' n-dimensional space did not change, but species segregated differently from one another in higher dimensions. As herring stocks decreased over time since the 1950s due to depletion by commercial fisheries[82], a generalist species' (double-crested cormorant) hypervolume remained constant while a specialist species' (pelagic cormorant) hypervolume decreased, illustrating how the topology can change over time.

The increase in dimensionality enlarged the niche size for each species and showed a shift in the trend in size in 5D. We observed a consistent pattern of niche size, with double-crested cormorants having the largest niche of all five species, followed by the rhinoceros auklet, and pelagic cormorant. In 2D and 3D, ancient murrelet and Leach's storm-petrel followed with the smallest niches, the latter showing the smallest niche. But in 5D these two species switched positions, as murrelets were the species with the smallest niche. Thus, Leach's storm-petrel had a small dietary niche along the classic isotopic dimensions (trophic position, offshore/nearshore habitat), but extended that niche through finer scale dimensions revealed by amino acid-specific isotopes, which is consistent with the large habitat size (large foraging range over offshore habitats) and variable diet (myctophid fish and invertebrates) in that species. Niche size calculation in higher dimensions seems to be affected somewhat by the formula incorporated by Swanson[45], and should be interpreted with caution for analyses with more than three dimensions.

Increasing dimensions significantly affected overlap among species (Figure 5.8 and Table 5.S7) from lower to higher dimensional approaches. Although a pattern can be observed of less overlap when using more dimensions compared to fewer dimensions, some species pairs do not follow the expected pattern. Some species-pairs slightly increased in overlap with the increase from 2D to 3D (auklets-murrelets, murrelets-double-crested, murrelets-pelagic, etc.), but then in most cases, overlap between pairs dropped dramatically in 5D. That change in overlap can be associated with the changes in the niche size of each species or group. When increasing dimensions, larger niche species tend to increase niche volume, but that increase moves away from the corresponding species pair, whereas small niche species retained the overlapping section of their niche in the same proportion as to the larger niche species. That result would be consistent with the described difference in the diet of, for example, the two cormorants where both are eating similar fish species, but pelagic cormorants feed at lower trophic levels and have a more restricted diet than double-crested cormorants [36,58].

Conversely, increasing information by incorporating additional dimensions into niche size calculations can produce changes in the rankings of previously observed niche sizes. Specifically, smaller niche species can experience an increase in niche size in higher dimensional approaches, and surpass other species compared to lower dimensional approaches. That was seen in our analyses in storm-petrels vs. murrelets in 5D, presumably associated with their differences in prey [83,84]. In addition, contrary to what would be expected, the overlap of certain species, such as murrelets, at higher dimensions remains somewhat important with the other species, like fish-eating species, pelagic and double-crested cormorants (Table 5.S7).

Layman metrics in a multidimensional space. All Layman dispersion metrics calculated increased, in different magnitudes, from lower to higher dimensional approaches, as expected. Species packing increased only slightly from low to higher dimensions, showing a similar structure of the assemblage in the community. Conversely, the greater increase in density of species packing (NND) and evenness of species packing (SDNND) with higher dimensions demonstrates that the use of new dimensions incorporates new information about all species. That may allow for better comparison and detection of changes that would otherwise be unnoticed with the use of fewer dimensions or only bulk isotopes of carbon and nitrogen as suggested by Bowes[40].

Changes in time for cormorants. Cormorants show a very distinct temporal niche trend, especially in 5D [42]. A lower dimensional approach shows an important difference in niche size change in time for double-crested, and, of lower magnitude, for pelagic cormorant, which becomes switched in higher dimensions (Table 5.11). The information incorporated by the higher resolution of amino acid-specific isotopes shows a significant reduction in the isotopic niche of pelagic cormorants, which does not occur in double-crested cormorants. Although niche sizes change, the overlap of pelagic cormorant niches over time is greater, whereas double-crested niche overlap in time is minimal in higher dimensions. There is some evidence that both double-crested and pelagic cormorant populations in Pacific Canada have declined in recent decades, likely due to several factors, including prey availability [57]. The once enormous herring spawns in the Salish Sea [85], occurring during the pre-laying period for cormorants, are greatly reduced in size and the reduction of this prey may be the reason for the changes. Indeed, the changes over time are largely in carbon axes rather than trophic position (PC2 of $\delta^{15}N$), which is consistent with a change from schooling to benthic prey. The niche size stability in higher dimensions in double-crested cormorants during the last decades may reflect some flexibility in the capacity of changing prey types but retain a similar niche breadth, by switching to benthic or freshwater prey. Contrarily, the niche size reduction seen in pelagic cormorants, but greater overlap in the later period, may reflect changes in fish abundance or diversity near the coast and rocky bottoms, which may mean a lesser capacity to shift prey type.

Our research demonstrates how the use of higher n-dimensional approaches, as suggested by Hutchinson [1], can incorporate greater details and show better segregation patterns in a community, especially with the combinations of compound-specific amino acid isotopes. Those additional isotopes can provide valuable, less biased information on the ecological roles of species within a community, and at the same time overcome the lack of information contained only in two niche proxies. The overall topology of the community remained constant, but patterns of overlap and segregation among species varied significantly with increased dimensions, as well as changes in specific niche hypervolume size. We encourage researchers to incorporate more dimensions (sulphur, amino acids) into isotopic niche models to detect more accurate differences in niche composition.

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Contributions of authors

The concept of this study was developed by K.E. and F.V.O. J.E. provided the long-term isotopic dataset from ECCC-CWRC. A.C. and F.V.O. wrote the additional R code for data processing and analyses. F.V.O. processed the results and wrote the manuscript. E.C. provided guidance in the direction of the analyses and results presentation. All authors designed the study, discussed analysis and results, edited manuscript text, and gave final approval for publication.

Additional Information

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Chapter 6 General discussion

Ecologic ontological motivations

Throughout my academic career I have been puzzled with how living systems work in all their levels of organization. From cellular and biochemical processes, such as producing ATP inside a mitochondrion from a glucose molecule, to large scale ecological patterns worldwide, such as El Niño events changing oceanic circulation and affecting animal behaviour. Such processes at the extremes of the biological hierarchy spectrum, but especially those in between at the individual level—foraging movement, prey, and mate selection—or at a higher level—population dynamics, community assemblages, and predatory interactions—have driven my scientific curiosity. This curiosity is similar to the one that has driven ecological research in the last century, and it still moves researchers to venture into diverse systems under diverse environmental conditions. In ontology, humans try to describe the nature of being, and usually try to put a value to that being. I wanted to begin this discussion by giving a value to the motivations of ecological research and my research in ecological systems. The value of the motivation for ecological research surpasses that of many other sciences, because most other sciences are founded, to a greater or lesser extent, in other motivations than curiosity alone (e.g. pharmaceutical, engineering, energy industries).

Ecological processes in nature are known to be very complex (Pimm, 1984) and although a degree of natural variation among ecosystems may exist, it is a general rule that this high complexity is maintained throughout all ecosystems (Levin, 1998). During my doctoral journey, I am thankful to my supervisor (K. Elliott, but maybe not at the moment) for encouraging me to read two seminal papers in the history of ecology and evolutionary biology, both in reference to saints which was something very much to my liking: Santa Rosalia (Hutchinson, 1959) and San

Marcos (Gould & Lewontin, 1979). Both pieces made history by challenging the classic way of thinking within the scientific community about complex processes. Those processes were: drivers of species diversity and inferences in evolutionary biology. (Hutchinson, 1959) said that "in order to understand the higher intricacies of any ecological system, it is most easy to start from [a] crudely simple point of view". Similarly, (Gould & Lewontin, 1979) stated that "in natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory". They later argue that researchers had minimized the rivaling ideas to a point that their conclusions seem the most likely plausible. These two ideas have resonated in my head since starting my projects in the global South or in aspects of ecology the seem to have been somewhat neglected, which I present in this thesis.

Niche wars in ecology

Here, I have addressed several questions in ecological niche research with a focus on seabirds as my study system, providing important information for conservation and management purposes in aspects of energy balance, foraging movements, and niche segregation. Ecological niches are complex biological concepts that have evolved over time while scientists have incorporated or extracted elements from them (Elton, C.S., 1927; Grinnell, 1917; Hutchinson, 1957; Pocheville, 2015). I have seen frequently that the idea of "niche" in current ecological research, especially in terms of new analytical tools popping out in the literature, revolves around the geographical distribution of species and the environmental variables that may drive that distribution (Brown & Carnaval, 2019; Kearney & Porter, 2009; Sillero et al., 2021). The use of the word "niche" has surely evolved, devolved, or has even been deconstructed so often to the point of being molded to particular approaches and research areas that can difficult to clearly define nowadays

(McInerny & Etienne, 2012). Nonetheless, this only reflects how complex the natural history and ecology of each individual species can be. Terminology issues apart, we can clearly say that this complexity can now be addressed by means of several methods currently used in ecological research, such as biologgers, stable isotopes, doubly labelled water, and point-of-care devices, that allow investigators to obtain data that was very difficult to nearly impossible to obtain a couple of decades ago. By these means I have been able to address ecological niches in different levels of the ecosystem, starting with defining the energetic niche of a seabird, the Peruvian booby *Sula variegata*, off the coast of central Peru (Chapter 3), then to contrasting the foraging and nutritional niche of the two seabirds, the Peruvian booby and the guanay cormorant (*Phalacrocorax bougainvillii*) also off the Peruvian coast (Chapter 4), and finally, to assessing niche segregation as snapshot in time and across five decades in an larger assemblage of seabirds (five species) off the coast of British Columbia (Chapter 5).

Ecological niches have been traditionally evaluated as snapshots in time of usually one species due to the complexity stated above (e.g. difficulty in measuring several variables of ecological interest relevant to the species natural history), and though this posed as a limitation in ecological research it is surely a first step in understanding any ecological system. One key concept of species niches described historically is the identification of variables that contribute to a species fitness, or in other words, variables that define the species optimal operational limits or ranges (Elton, C.S., 1927; Grinnell, 1917; Hutchinson, 1957; Pocheville, 2015).

Nutritional niches: intrinsic drivers of fitness

In Chapters 3 and 4, I have investigated proxies of species fitness by defining ranges of nutritional niches, such as activity-specific energy expenditure and physiological fitness (by means of nutritional metabolites) in Peruvian boobies and guanay cormorants. Energy expenditure in a seabird should be closely correlated to efficiency or rate of energy gain through foraging, as a response to foraging success or energy input when foraging (Wilson et al., 2011). That is, as energy availability diminishes, individuals must expend more energy to obtain diminishing resources (Wilson et al., 2011). Both species, boobies and cormorants, during my data collection, have similar foraging and nutritional niches (activity budgets, foraging range, nutritional status) as other sulids or cormorants. This is expected especially under good conditions when the ecological constraints for the species are not strong and harsh conditions do not hamper the fitness or survival of the populations. Lack of information during harsh years is a significant caveat to address this idea, because due to costs and logistic constraints (difficulty in sampling animals) there are smaller samples sizes of wild animals during harsh year conditions. The potential for lower success may deter researchers from such endeavours.

Physiological or nutritional traits (apart from environmental tolerance, such as thermal parameters) are not commonly used to describe ecological niches in living organism, but there is increasing interest in incorporating such measurements in different disciplines (Kearney & Porter, 2009) from archaebacteria (Bayer et al., 2016), to plants (Higgins et al., 2012), to amphibians (Gouveia et al., 2014), to birds and mammals (Khaliq et al., 2015). One would expect a strong correlation between the activity patterns, energy expenditure, and nutritional state of wild animals, as these three traits and strongly interlinked; energy expenditure is partly dependent on activity patterns and nutritional state is linked to energy expenditure. We have seen in Chapter 3 that Peruvian boobies incur high energetic costs, especially during flight, most likely due to the costs of plunge diving (combining flight and water immersion for this high aspect ratio bird). This elevated cost of flight, and overall maintenance, can only be possible in a highly productive habitat such as that of the upwelling driven nutrient-rich waters of the Humbolt Current System. Understanding the energetic costs of wild free-ranging animals can provide important information in the development of *energyscapes*, or energy maps, which represent available energy and the potential drivers of change of such availability, and how this can alter species distributions (Shepard et al., 2013; Wilson et al., 2012). In the Humboldt Current System, large fluctuations in climate (e.g. El Niño Southern Oscillation) can modify energy availability for large marine predators in the system, dramatically changing overall movement, distribution, and fitness from previous historical levels.

The expected physiological responses in seabirds under harsh conditions or low energy (prey) availability are commonly expected to be clear-cut, but they have proven to be diverse and even opposing in several taxa (Romero & Gormally, 2019). Under regular or normal conditions, vertebrates, seabirds included, are expected to perform optimally, and secure their fitness by providing sufficient energy to themselves and even their offspring (Orians, 1979; Pyke, 2019). Even though Peruvian boobies have a high energetic cost of foraging (Chapter 2), they can perform well under normal conditions, reflected in their foraging behaviour patterns and nutritional condition (metabolite concentrations; Chapter 3). Moreover, Peruvian boobies and guanay cormorants showed a similar pattern of nutritional condition and foraging behaviour during a ‘normal’ year (2019). Conversely, during harsh, El Niño-like conditions (2018), both species shifted their behaviour to compensate for the reduced energy input (low prey availability) and we would expect it to reflect in their fitness (as seen in their nutritional condition via their metabolite concentration). This was impossible to detect during our sampling because of reduced capture rate for guanay cormorants during the harsh conditions (2018). Nonetheless, it is clear that both species show different foraging patterns (Weimerskirch et al., 2010, 2012, also this thesis), occupying different niches in the Humboldt Current System, and this difference also occurs during harsh conditions (Chapter 3) as it would be expected from niche theory.

Arguably, shifts in the behavior or nutritional condition of seabird populations should not always be apparent in short spans of time (two years) as animals use different strategies to compensate with nutritional deficiencies (Holden et al., 2019) or may be blurred with individual differences within a population (Phillips et al., 2017). Nonetheless, investigating these shifts at a population level is necessary to shed light into the natural life histories of poorly and understudied species, such those in the global South. For example, Antarctic petrels showed a varied response in metabolites in relation to foraging habitat and effort (which is expected to correlate with prey availability and energy intake), assuming that shifts in foraging strategies may alter other aspects of the individuals fitness not easily detected by the those methods (Tarroux et al., 2020). Similarly, Peruvian boobies did not show a significant relationship between foraging effort and nutritional condition, which is probably compensated in modifying their reproductive input, as boobies are known to abandon their clutches promptly under negative environmental conditions that result in low prey availability. This evolutionary adaptation seems very interesting considering that most species in family Sulidae show obligate siblicide reducing the pressure over the brooding parents (Drummond et al., 2008). In Peruvian boobies, this absence of siblicide behaviour among chicks may influcen the parents decisions and nutritional state in the long term. For example, glucose is tightly regulated by insulin and glucagon in vertebrates, and increases both during stress (to mobilize resources needed to overcome the stress) and shortly after feeding. The combination of time since feeding (which we cannot measure directly) and individual stress (proximity to abandonment threshold) may have created enough noise that we could not detect a relationship between glucose and foraging parameters.

Seabird assemblage niche segregation

Large assemblages of species coexisting in the same space and time show significant differences in ecological niches (in a diverse range of approaches, e.g. diet, spatial, isotopic; Bolton et al., (2019)). In Chapters 3 and 4 we demonstrate that species do segregate in aspects such as behaviour, physiology, and isotopic indicators (proxies of diet). This segregation may be more or less apparent in certain aspects or measured variables (also considered dimensions of a niche), hence studying only a two species or few (two or three) dimensions of a niche may not show how this ecological segregation is actually occurring. In chapter 4, I have explored and demonstrated how increasing ecological dimensions (in this case stable isotope values) to higher levels, unlike classic two-dimensional biplots, or even three-dimensional approaches, can detect additional differences in segregation patterns that may be otherwise overlooked. Increasing dimensionality in ecological studies poses several constraints, from logistic (larger sample size, greater costs, increased laboratory equipment, longer processing times, greater computational requirements, etc., as described in Caughlan 2001) to mathematical constraints (e.g. dimensionality, as describe in Morowitz (1980)).

Seabirds, within and among species, use a very broad spectrum of foraging strategies, which go hand to hand with the resulting selected prey (species, size, quality, etc.). From clearly defined generalist seabirds, such as large, coastal gull species, to the more specialized Peruvian anchovy exclusive (or almost exclusive) boobies, the diversity of prey and strategies to capture prey is reflected in the ecological niches of seabird assemblages (Barbosa & Moreno, 1999; Ceia &

Ramos, 2015) and even within populations (Shaffer et al., 2017). Such variability in an assemblage of seabirds, may also blur potential detectable differences in ecological niches as they would be expected niche theory. These blurred differences can be explained by the "imperfect generalist" concept that has been applied from bacteria (Barrett et al., 2005), to landbirds (De León et al., 2014), to large scale evolutionary models (Orlando & Hall, 2015). The concept states that "evolution in complex environments will result neither in narrow specialists nor in complete generalists but instead in overlapping imperfect generalists" (sensu Barrett et al., 2005). The results of Chapters 4 and 5 clearly show some level of overlapping niches in the seabird species studied, both in the short-term (one year, Peruvian boobies and guanay cormorants) and in the long-term (decades, 5-seabird assemblage in British Columbia coast). Careful examination of ecological niches should improve understanding of the level of segregation that occur in different ecological systems. Kent & Sherry (2020) re-examined the foundational work in ecology by MacArthur (1958), and found that although prey widely overlaps, behavioural differences in micro-habitat selection do reflect ecological niche differences that allow coexistence. Such micro-habitat differences may be easily overlooked, or nearly impossible to detect with current technological advances, in wide-ranging species such as seabirds. Hence, incorporating several other variables in the description of niches, either by replacing classically used variables, or increasing dimensionality, is something to be observed by researchers. Although seabird research has been increasingly incorporating data to inferences (e.g. biologging, remote sensing) there is still a general trend in the use of variables to assess ecological niche (e.g. isotopes, foraging parameters, environmental/climate variables) and these assessments are mainly descriptive (Tremblay et al., 2009).

Limitations of research: another dimension to consider

The use amino acid specific isotope values, physiological metabolites, energetic budgets, or fine-scale spatial analyses, as proxies to describe ecological niches in seabirds are elements needed to incorporate more accurate information into niche ecology. However, they only provide imperfect estimates of niches. Firstly, what we expected to see as active ecological segregation among competing and coexisting species could be the result of evolutionary processes ("the ghost of competition past") especially under high prey abundance and good climatic conditions. Secondly, this incorporation of additional variables or dimensions brings us to what I call "the lack-of-data challenge" or the fact that to analyze several relationships in ecological research there are certain data thresholds (Walker & Meyers, 2004) that are often difficult to overcome when doing research in wild free-ranging animals under natural conditions. This is especially true for larger vertebrate species such as seabirds, which do not all have the same sensitivity to manipulation and sampling, making research of certain seabird species very difficult, and even more difficult, to obtain a large enough sample size. Such is the case for guanay cormorants, that during harsh year conditions become so sensitive that is nearly impossible to sample a sufficient sample size of individuals, and even more so to retrieve biologging devices (Chapter 3).

Current issues in lack of data for ecological research can be addressed by a suit of strategies, such as resampling methods, collaborative fieldwork (allowing for sampling of populations by different research groups at the same time or through time), data sharing platforms (e.g. DRYAD, Movebank, etc.), among others. Surely the continuous growth of ecological and scientific advances in the last decades has led to a continuous enthusiasm on presenting more complex and more elaborate analysis and theories in ecology, especially in the study of ecological niches. The currently used and evolving field methods and analyses (amino acid specific isotopic analyses, more miniaturized GPS-accelerometers, point of care devices, etc.) discussed above surely prove that ecological data is indeed flowing into the scientific literature constantly. At the same time, so are the statistical tools and methods and means to analyze those data via the increasing number of free and collaborative statistical packages in open-source platforms, such as R. All of these could lead us to believe that complexity is indeed a requirement in niche ecology research.

However, I would bring back some of those thoughts presented by Hutchinson (1959) and Gould & Lewontin (1979) around to fifty years ago: sometimes simple and straightforward approaches in ecology and evolutionary research are necessary to explain or begin to explain some of those highly complex and n-dimensional ecological systems.

Future research

As mentioned above, one of the most limiting factors in ecological studies of wild animals is the lack of data or statistical power. Research on seabirds in the global South is all prey to this devil. Increasing information in energy expenditure and accelerometry of seabirds in the Peruvian Humboldt Current system would greatly improve management of fisheries from an exosystemic approach. Measuring daily energy expenditure in guanay cormorants and Peruvian pelicans can help achieve this goal. In the same sense, validating the use of accelerometry to estimations energy expenditure would greatly facilitate research in marine systems off the Peruvian coast.

Moreover, tracking nutritional state and foraging effort of the three main guano seabird's species is a necessity not addressed yet. Although foraging ecology research of seabirds has increased in Peru many limitations still exist. Tracking foraging effort and nutritional state of guanay cormorants and Peruvian pelican in other colonies is necessary and should a priority of future reseach.

A long-term dataset of foraging effort, nutritional, and isotopic changes are key elements in the future management of any marine ecosystem in the planet and should be also replicated in the global South, including the Peruvian Humboldt Current System.

Chapter 7 Conclusions

Ecological niches are complex multidimensional conceptual spaces that wildlife researchers use to define the life history of a given species or population. My thesis has shown that although this definition is possible, it requires a series of considerations and careful analysis of the most relevant variables (Chapters 3, 4, and 5) and time scales (Chapters 4 and 5).

Seabirds are excellent study systems for testing ecological niche hypotheses such as energetic niche and activity budgeting (Chapter 3), foraging and physiological niche shifts in time of sympatric species (Chapter 4), and niche segregation of coexisting species assemblages (Chapter 5). I found a strong correlation between activity budgets and energy expenditure in plunge-diving seabirds, the Peruvian booby, using a direct method to estimate energy expenditure for the first time. I also described the high energetic costs of flight for this endemic species of the Humboldt Current System. I found differences in the foraging and physiological niches of Peruvian boobies and guanay cormorants and how these niches shift due to extrinsic factors, like harsh-condition years, such as those under strong El Niño influence. Finally, I showed that ecological niches in multispecies assemblages can be defined using an n-dimensional approach, by means of amino acid specific isotope values. I show that it is only by means of adequate incorporation of dimensions into the modeled niche that we can detect patterns such as segregation or overlap, otherwise undetected. Overall, my thesis provides novel information on the study of ecological niches, especially those of seabirds.

The guano islands have been sources of wonder for time immemorial, from the Quechua people (commonly referred to as the Incan civilization) to the opening scene of Netflix's *Our Planet*. Likewise, seabirds were the source of both legend and food for Haida, Nuu-chah-nulth and other First Nations on British Columbia's coast. I believe the ancient Inca administrators of the guano islands —the first example of protected area and wildlife conservation in the historical record— would be intrigued by my thesis. Understanding how seabirds move in the ocean they protected, and how the changes prey availability due to climate change may affect their nutritional state, may explain shifts they had seen centuries ago. In the same sense, seeing how "you are what you eat" by using isotopic indicators and how species can do different things to avoid competition and increase their success (fitness) could show them how the great biodiversity they protected in their ecosystems, is key in the processes and functioning of any region.

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Supplementary information for Chapter 3

Supplementary Tables

Table S3.1. Full AICc rankings for DEE estimation models for male and female Peruvian boobies.

Model Structure *Males*	df	logLik	AICc	delta	weight
Null	2	-0.44	6.88	0.00	0.661605
DBAdaily	3	0.27	10.26	3.37	0.122484
TimeCol + TimeFlyPluRest	3	-0.23	11.26	4.37	0.074393
TimeColRest + TimeFlyPlu	3	-0.30	11.41	4.52	0.068946
TimeColRest + TimeFly + TimePlu	4	3.08	11.84	4.96	0.055436
DBACol + DBAFlyPluRest	4	1.24	15.52	8.64	0.008801
DBAColRest + DBAFlyPlu	4	0.87	16.27	9.38	0.006076
TimeCol + TimeRest + TimeFlyPlu	4	-0.23	18.45	11.57	0.002035
TimeCol + TimeFly + TimePlu + TimeRest	5	3.17	23.65	16.77	0.000151
DBAColRest + DBAFly + DBAPlu	5	1.97	26.05	19.17	0.000046
DBACol + DBARest + DBAFlyPlu	5	1.44	27.13	20.24	0.000027
DBACol + DBAFly + DBAPlu + DBARest	6	3.00	48.01	41.12	0.000000

Females	df	logLik	AICc	delta	weight
TimeColRest + TimeFlyPlu	3	11.64	-13.84	0.00	0.580990
TimeCol + TimeFlyPluRest	3	10.61	-11.79	2.05	0.208334
TimeColRest + TimeFly + TimePlu	4	12.19	-9.71	4.14	0.073472
TimeCol + TimeRest + TimeFlyPlu	4	11.84	-9.02	4.82	0.052182
DBAdaily	3	9.01	-8.58	5.26	0.041884
Null	2	6.48	-7.45	6.39	0.023772
DBAColRest + DBAFlyPlu	4	10.15	-5.64	8.20	0.009613
DBACol + DBAFlyPluRest	4	9.87	-5.07	8.77	0.007235
TimeCol + TimeFly + TimePlu + TimeRest	5	12.21	-2.42	11.43	0.001917
DBACol + DBARest + DBAFlyPlu	5	10.36	1.28	15.12	0.000302
DBAColRest + DBAFly + DBAPlu	5	10.34	1.31	15.15	0.000298
DBACol + DBAFly + DBAPlu + DBARest	6	10.46	12.09	25.93	0.000001

Table S2. Model estimates for best parametrized model estimating mass-specific DEE from AICc rankings for Peruvian Boobies (sexes grouped). Parameters are DBA at the colony and DBA away from the colony.

	Estimate	Std. Error	t	p
(Intercept)	7.67E-01	2.47E-01	3.109	0.0145
DBACol	-7.94E-05	1.92E-04	-0.413	0.6905
DBAFlyPluRest	1.40E-04	5.77E-05	2.428	0.0414

Table S3.3. Activity-specific time budget and DBA values for all Peruvian boobies in Guañape island in 2019.

Activity	Mean proportion	Hours/day	Stdev	Min	Max
Colony	0.81	19.43	0.08	0.54	0.90
Flying	0.16	3.84	0.04	0.08	0.25
Plunging	0.003	0.067	0.001	0.001	0.005
Resting	0.03	0.67	0.05	0.00	0.24

DBA	MeanDBA (*g*)	Stdev	Min	Max
DBAColony	987.92	194.94	685.27	1410.67
DBAFlying	1914.11	637.72	976.06	3056.26
DBAPlunging	40.44	13.08	17.79	55.87
DBAResting	82.96	46.37	16.37	189.94

Supplementary figures

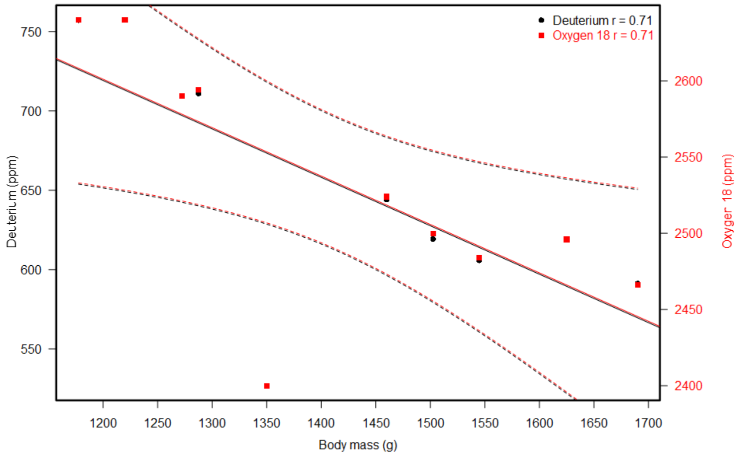


Figure S3.1. Relationship of Oxygen-18 and deuterium ^{2}H with body mass after dilution of doubly labelled water for Peruvian boobies at Guañape Norte Island in 2019. Correlation values were obtained from pearson's coefficient (r).

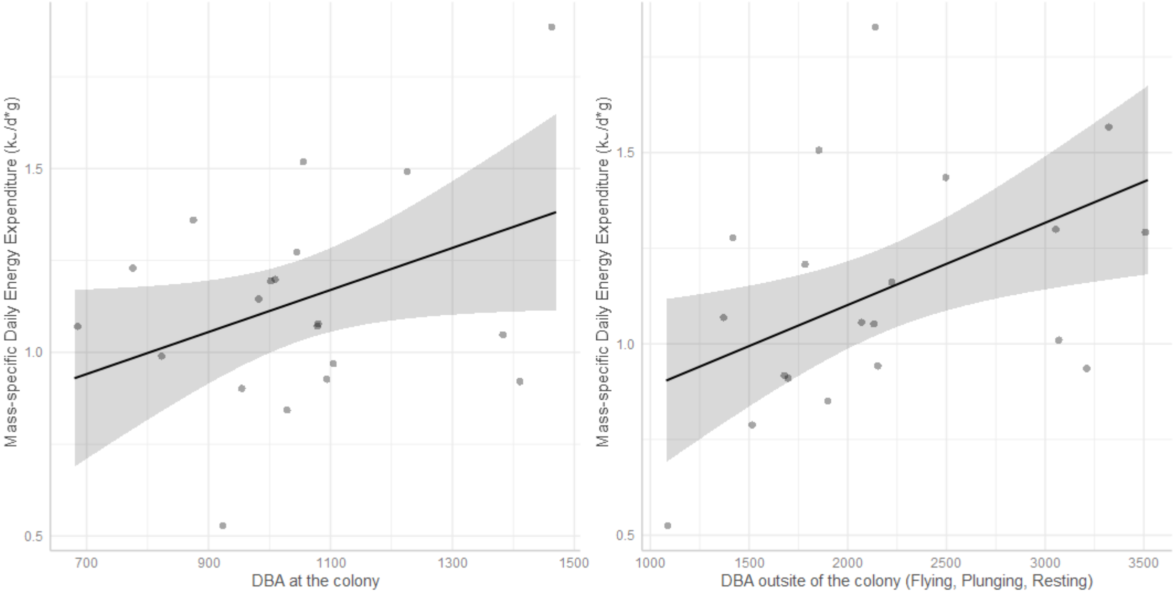
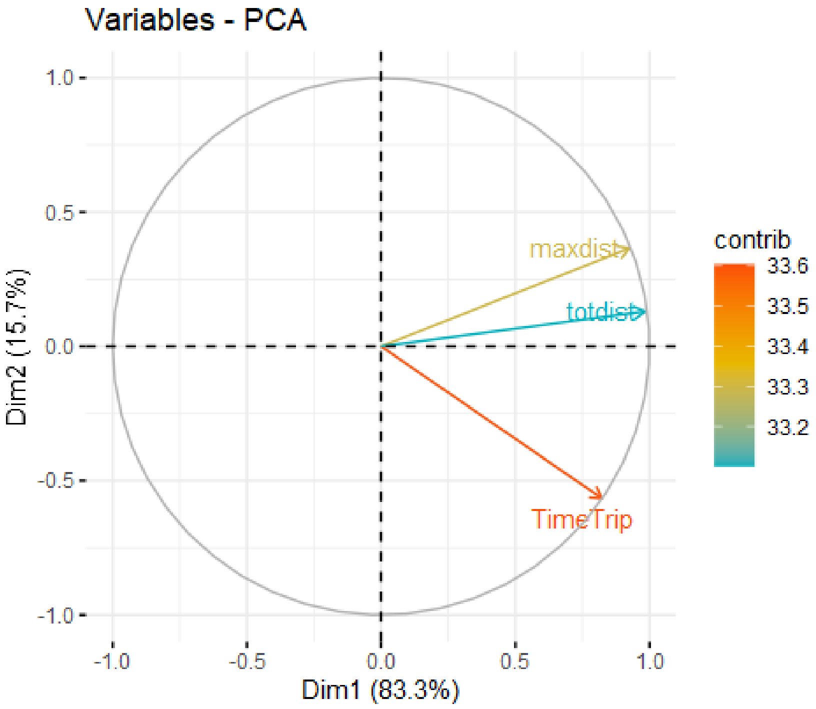


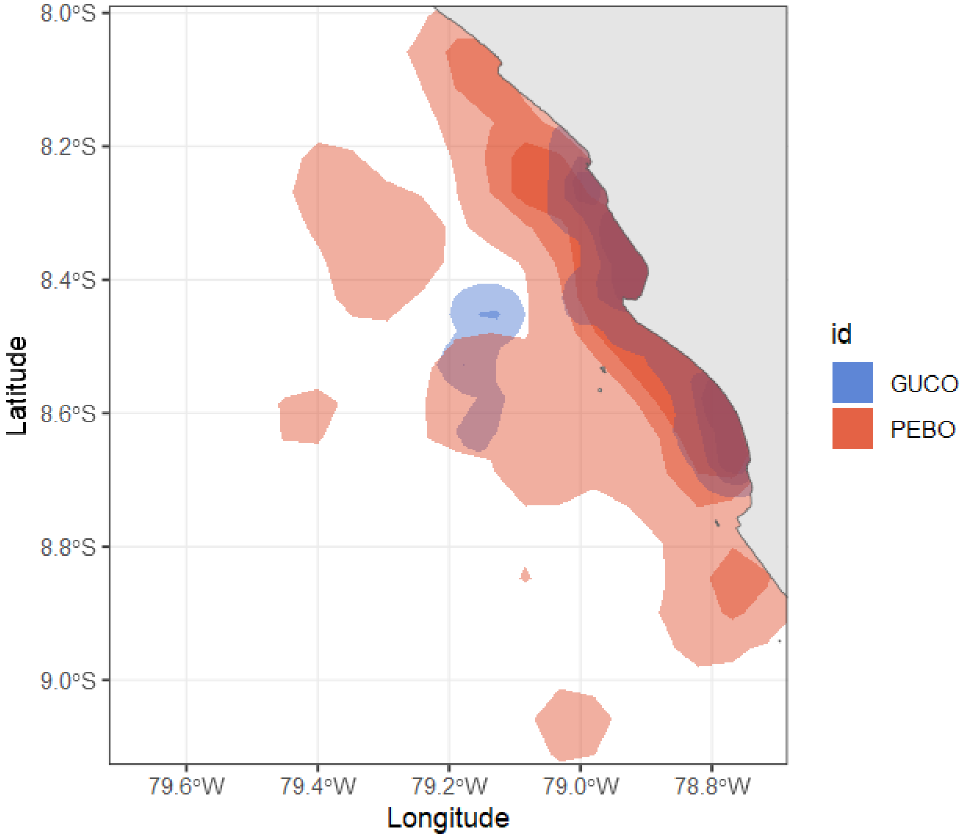
Figure S3.2. Model prediction results (marginal effects) for mass-specific DEE from best parametrized activity-specific model including (mean daily DBA at the colony and DBA away from the colony).

Supplementary information for Chapter 4

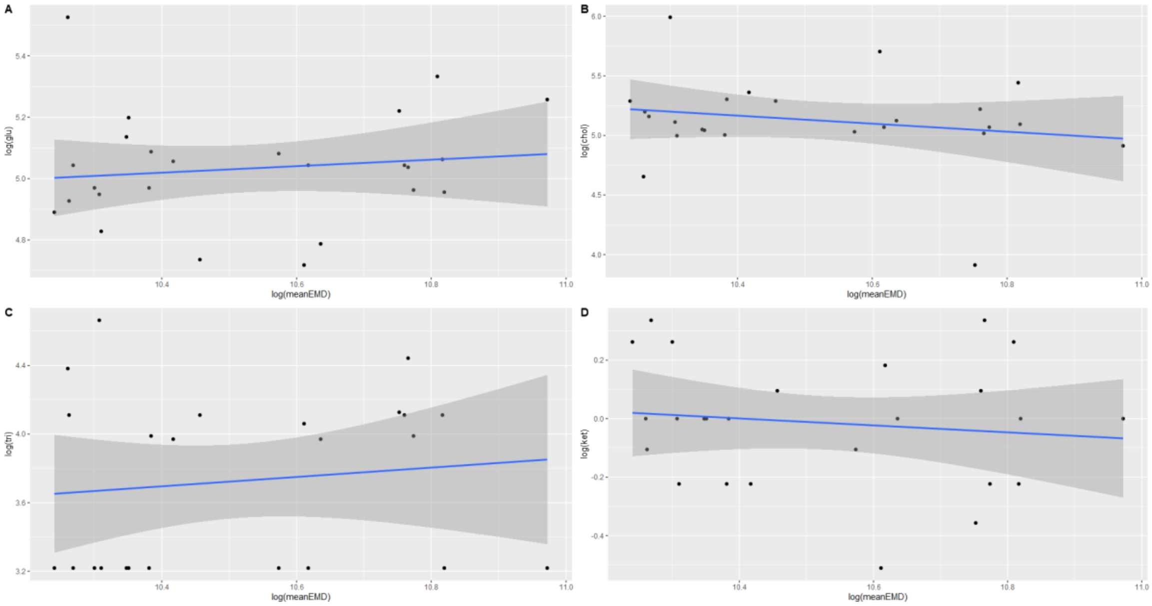
SI Figures 4



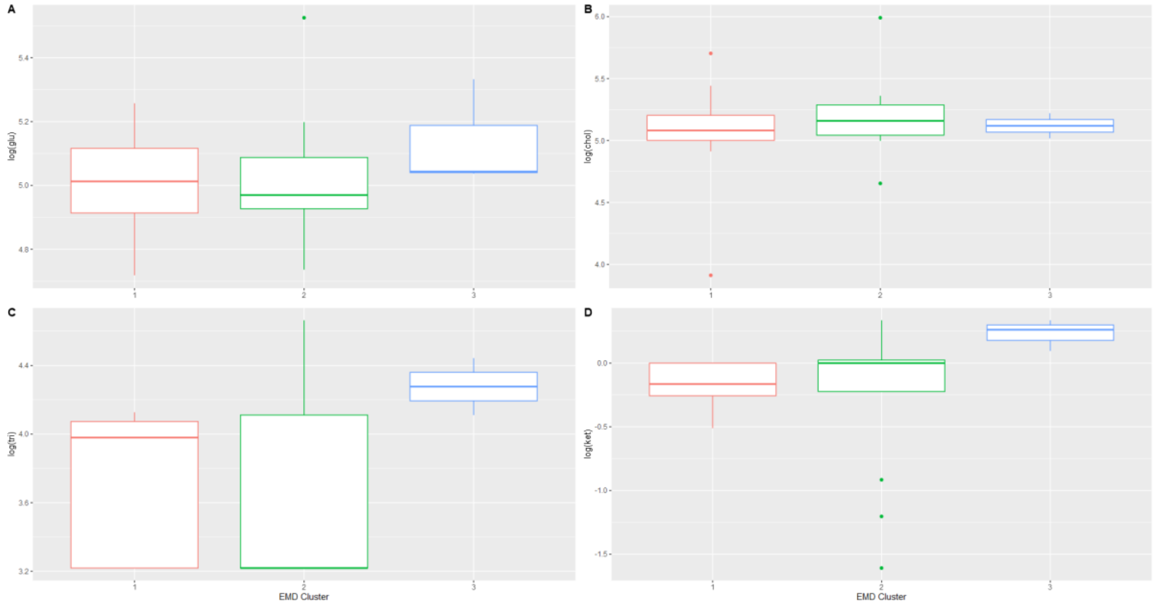
SI Figure 4.1. Principal component analysis for foraging parameters: total trip duration, total distance path distance, maximum distance from the colony.



SI Figure 4.2. Kernel density of diving location of both Peruvian seabird species during 2019.



SI Figure 4.3. Mean EMD similarity value for each last trip for boobies in 2019 in relation to metabolite concentration (log) for 37 last trips of Peruvian boobies and Guanay Cormorants.



SI Figure 4.4. Boxplots representing metabolite concentration (log10) differences among EMD similarity classification clusters for the 37 last trips of Peruvian boobies and Guanay Cormorants. All metabolites are in logarithmic scale: (A) glucose, (B) cholesterol, (C) triglycerides, (D) ketones (letter represent significant differences from post-hoc TukeyHSD test).

SI Tables 4

SI Table 4.1. Linear model structure for AIC for metabolite and foraging effort comparisons.

reg0 <- lm(log(metabolite) ~ 1)
reg1 <- lm(log(metabolite) ~ log(sinousity))
reg2 <- lm(log(glu) ~ PC1)
reg3 <- lm(log(metabolite) ~ PC1 + log(sinuos))
reg4 <- lm(log(metabolite) ~ PC1 *log(sinuos))
reg5 <- lm(log(metabolite) ~ PC1 *latency)
reg6 <- lm(log(metabolite) ~ latency)
reg0 <- lm(log(metabolite) ~ 1)

SI Table 4.2. Foraging effort metrics for significant models assessing differences between boobies and cormorants in 20198 and 2019.

Variable	Cat.	predicted	std.error	conf.low	conf.high	group
Total trip duration	2018	0.9	0.1	0.7	1.0	-
	2019	0.5	0.0	0.5	0.6	-
Total trip path (km)	GUCO	3.8	0.1	3.7	4.0	-
	PEBO	4.1	0.1	4.0	4.2	-
Max. distance from colony	GUCO	3.1	0.1	2.9	3.2	-
	PEBO	3.2	0.0	3.2	3.3	-
Sinuosity	GUCO	-3.2	0.1	-3.5	-2.9	2018
		-4.2	0.1	-4.3	-4.0	2019
	PEBO	-3.4	0.1	-3.6	-3.2	2018
		-3.8	0.0	-3.9	-3.7	2019

SI Table 4.3. Metabolite value differences between boobies and cormorants in 2019. Values are log -transformed as modelled. Asterisks represent significant models.

Species	Metabolite	predicted	std.error	conf.low	conf.high	Model
PEBO	Glucose*	5.05	0.03	4.99	5.11	Mixed
GUCO		4.81	0.05	4.71	4.91	
PEBO	Cholesterol	5.13	0.07	4.99	5.28	Mixed weighted
GUCO		5.28	0.12	5.04	5.51	
GUCO	Triglycerides*	3.36	0.09	3.17	3.55	Mixed weighted
PEBO		3.78	0.12	3.54	4.01	
PEBO	Ketones*	-0.03	0.04	-0.11	0.06	Mixed
GUCO		0.34	0.07	0.20	0.48	

SI Table 4.4. Metabolite value differences in boobies between 2018 and 2019. Values are log -transformed as modelled. Asterisks represent significant models.

Year	Metabolite	predicted	std.error	conf.low	conf.high	Model
2018	Glucose	4.98	0.21	4.56	5.39	
2019		5.05	0.03	4.99	5.12	Mixed weighted
2018	Cholesterol	4.62	0.24	4.13	5.12	
2019		5.13	0.06	5.01	5.26	Mixed weighted
2018	Triglycerides	4.10	0.27	3.55	4.64	
2019		3.78	0.12	3.53	4.02	Mixed
2018	Ketones*	-1.77	0.31	-2.40	-1.14	
2019		-0.03	0.04	-0.12	0.06	Mixed weighted

Supplementary information for Chapter 5

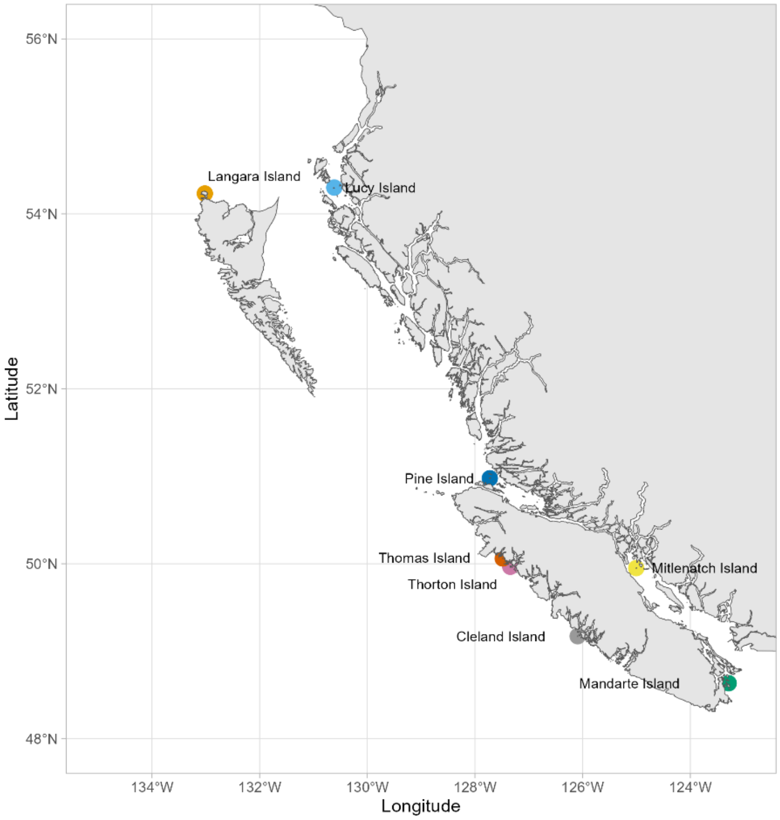


Figure 5.S1. Sampling locations for 6 seabird species along the British Columbia coast. Species per location: ANMU = Langara Is.; DCCO = Mandarte Is., PECO = Mandarte Is., Mitlenatch Is.; LSPE = Cleland Is., Thomas Is., Thorton Is.; RHAU = Lucy Is., Pine Is.)

Table 5.S1. Study species, abbreviation codes, and samples sizes in each sampling period.

Species	Code	1970-1989	1990-2006
Ancient murrelet *Synthliboramphus antiquus*	ANMU	2	4
double-crested cormorant *Phalacrocorax auritus*	DCCO	6	11
Leach's Sstorm-petrel Oceanodrama leucorhoa	LSPE	8	3
pelagic cormorant *Phalacrocorax pelagicus*	PECO	13	6
Rhinoceros auklet *Cerorhinca monocerata*	RHAU	0	10

Table 5.S2. PCA loadings for all amino acids for carbon and nitrogen variables

	PCA.1	PCA.2
dN_Ala	16.07	1.90
dN_Asp	7.70	23.67
dN_Glu	8.45	9.15
dN_Gly	7.20	1.16
dN_Ile	15.76	3.42
dN_Leu	14.96	0.01
dN_Lys	2.56	19.72
dN_Phe	3.63	30.57
dN_Pro	7.36	10.07
dN_Val	16.32	0.33

	PCA.1	PCA.2
dC_Ala	11.90	0.00
dC_Val	11.87	1.61
dC_Gly	9.12	2.85
dC_Ile	8.65	15.04
dC_Leu	11.90	1.50
dC_Pro	6.16	50.18
dC_Asp	7.63	1.58
dC_Phe	12.32	0.60
dC_Glu	9.70	13.23
dC_Lys	10.74	13.42

Table 5.S3. Centroid locations for each dimension of the 5-dimensional model of five species of seabirds on the coast of British Columbia. The first two PCA components represent all amino acid specific carbon and nitrogen isotopes, and standardized bulk sulphur. Mean and quantiles (2.5% and 97.5% in brackets) of the posterior distribution from 100k samples. For species abbreviations see Table 5.S1.

	PC1Css	PC2Css	PC1Nss	PC2Nss	stdDelta.S
ANMU	1.69	-0.47	-4	-0.06	0.2
	(0.92-2.47)	(-1.22-0.28)	(-5.67--2.33)	(-0.54-0.42)	(0.1-0.3)
DCCO	-2.88	0.14	0.68	1.27	-1.14
	(-3.78--1.98)	(-0.13-0.41)	(0.02-1.34)	(0.88-1.65)	(-1.61--0.66)
LSPE	3.82	-0.36	2.41	-1.3	1.19
	(3.15-4.49)	(-0.89-0.18)	(1.71-3.1)	(-2.02--0.58)	(1.14-1.24)
PECO	-0.93	-0.45	-0.62	0.28	0.12
	(-1.51--0.35)	(-0.68--0.21)	(-1.23-0)	(-0.07-0.64)	(0.04-0.2)
RHAU	1.46	1.29	-0.23	-1.22	0.28
	(0.49-2.42)	(0.9-1.67)	(-1.12-0.66)	(-1.99--0.45)	(-0.27-0.82)

Table 5.S4. Bhattacharrya Coefficient for the probability of overlap between posterior distribution of each independent isotopic dimension (first two PCA components for all amino acid specific carbon and nitrogen isotopes and standardized bulk sulphur) for species pairs. Bolded are those with high probability values (>0.8). For species abbreviations see Table 5.S1

PC1Css

	DCCO	LSPE	PECO	RHAU
ANMU	0.001	0.048	0.015	**0.950**
DCCO	1.000	0.000	0.064	0.001
LSPE	0.000	1.000	0.000	0.048
PECO	0.064	0.000	1.000	0.031
RHAU	0.001	0.048	0.031	1.000

PC2Css

	DCCO	LSPE	PECO	RHAU
ANMU	0.424	0.**966**	0.**793**	0.048
DCCO	1.000	0.449	0.093	0.016
LSPE	0.449	1.000	**0.853**	0.016
PECO	0.093	0.853	1.000	0.000
RHAU	0.016	0.016	0.000	1.000

PC1Nss

	DCCO	LSPE	PECO	RHAU
ANMU	0.018	0.002	0.058	0.059
DCCO	1.000	0.068	0.156	0.501
LSPE	0.068	1.000	0.000	0.017
PECO	0.156	0.000	1.000	**0.854**
RHAU	0.501	0.017	**0.854**	1.000

PC2Nss

	DCCO	LSPE	PECO	RHAU
ANMU	0.040	0.172	0.697	0.225
DCCO	1.000	0.005	0.054	0.004
LSPE	0.005	1.000	0.047	**0.993**
PECO	0.054	0.047	1.000	0.067
RHAU	0.004	**0.993**	0.067	1.000

stdDeltaS

	DCCO	LSPE	PECO	RHAU
ANMU	0.005	0.000	**0.662**	**0.631**
DCCO	1.000	0.000	0.006	0.049
LSPE	0.000	1.000	0.000	0.045
PECO	0.006	0.000	1.000	0.509
RHAU	0.049	0.045	0.509	1.000

Table 5.S5. Probability that the two species have different centroid location values in 2, 3, and 5 dimensions (A, B, C respectively) and distance between centroid locations between species pairs in 2, 3, and 5 dimensions (D, E, F respectively). For species abbreviations see Table 5.S1.

A)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	0.998	0.999	0.974	0.929
DCCO	0.998	0	1	0.935	0.995
LSPE	0.999	1	0	1	0.991
PECO	0.974	0.935	1	0	0.925
RHAU	0.929	0.995	0.991	0.925	0

B)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	0.997	0.999	0.972	0.922
DCCO	0.997	0	1	0.96	0.996
LSPE	0.999	1	0	1	0.994
PECO	0.972	0.96	1	0	0.917
RHAU	0.922	0.996	0.994	0.917	0

C)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	0.998	0.998	0.969	0.953
DCCO	0.998	0	1	0.973	0.998
LSPE	0.998	1	0	1	0.994
PECO	0.969	0.973	1	0	0.982
RHAU	0.953	0.998	0.994	0.982	0

D)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	6.58	6.77	4.31	3.82
DCCO	6.58	0	**6.95**	**2.39**	4.47
LSPE	6.77	6.95	0	5.65	3.6
PECO	4.31	2.39	5.65	0	2.47
RHAU	3.82	4.47	3.6	2.47	0

E)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	6.71	6.84	4.3	3.82
DCCO	6.71	0	**7.33**	2.7	4.71
LSPE	6.84	7.33	0	5.76	3.72
PECO	4.3	2.7	5.76	0	**2.49**
RHAU	3.82	4.71	3.72	2.49	0

F)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	0	6.89	6.98	4.35	4.41
DCCO	6.89	0	**7.8**	**2.96**	5.47
LSPE	6.98	7.8	0	5.99	4.11
PECO	4.35	2.96	5.99	0	3.42
RHAU	4.41	5.47	4.11	3.42	0

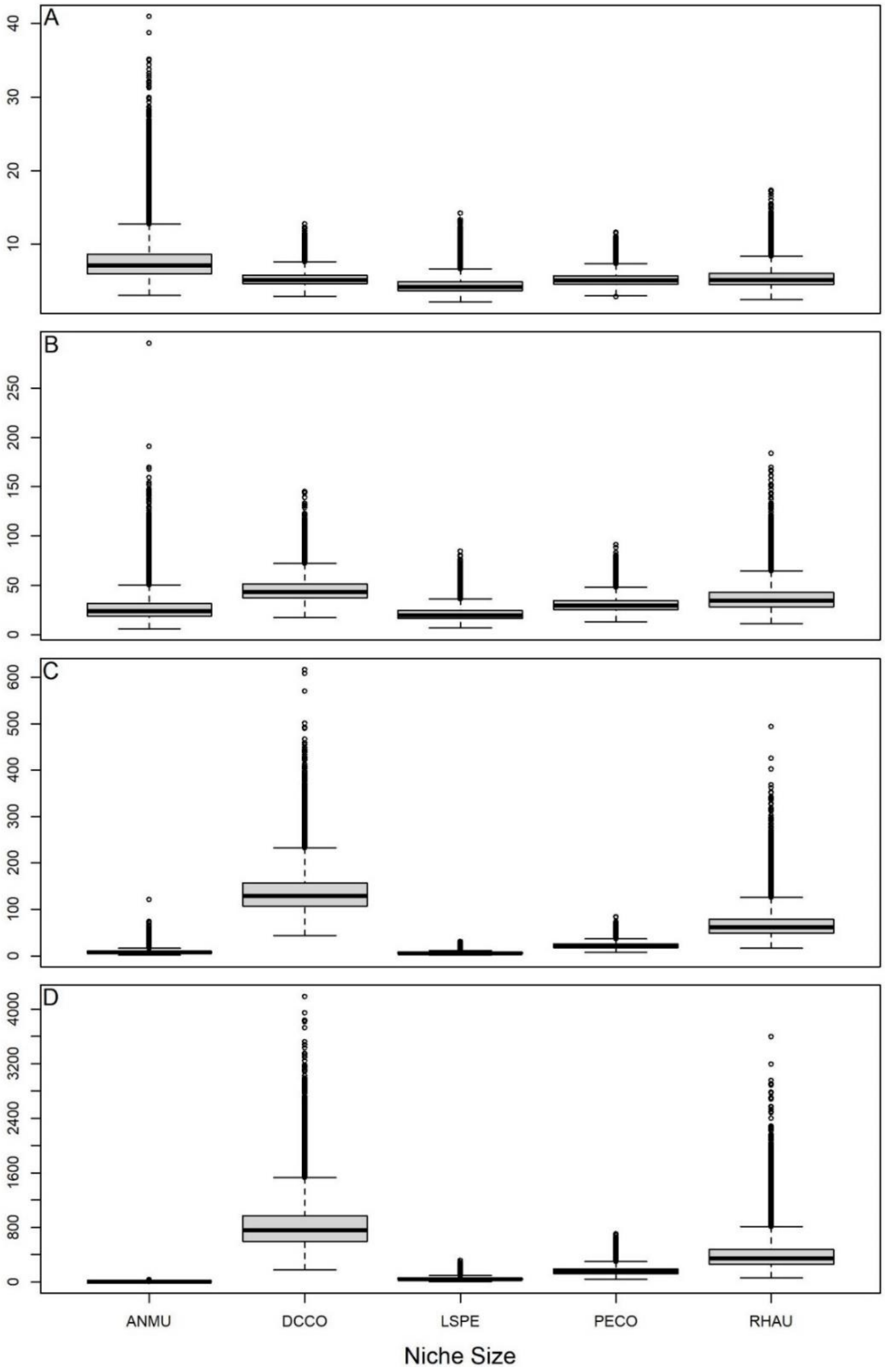


Figure 5.S2 Niche sizes for five species of seabirds on the coast of British Columbia from 100k samples for 2D, 3D, and 5D approaches (A), B) and C) respectively). For species abbreviations see Table 5.S1

Table 5.S6. Bhattacharrya Coefficient for the probability of overlap between posterior distribution of niche sizes for species pairs for each dimensional approach (A = 2D, B = 3D, C = 5D). Bolded are those pairs with high probability values (>0.8). For species abbreviations see Table 5.S1.

A)	DCCO	LSPE	PECO	RHAU
ANMU	0.60	**0.95**	**0.87**	**0.85**
DCCO	1	0.34	0.70	**0.89**
LSPE	0.34	1	0.73	0.64
PECO	0.70	0.73	1	**0.94**
RHAU	**0.89**	0.64	**0.94**	1

B)	DCCO	LSPE	PECO	RHAU
ANMU	0.00	**0.95**	0.35	0.05
DCCO	1	0.00	0.00	0.53
LSPE	0.00	1	0.13	0.00
PECO	0.00	0.13	1	0.23
RHAU	0.53	0.00	0.23	1

C)	DCCO	LSPE	PECO	RHAU
ANMU	0.00	0.02	0.00	0.00
DCCO	1	0.00	0.08	0.63
LSPE	0.00	1	0.25	0.06
PECO	0.08	0.25	1	0.57
RHAU	0.63	0.06	0.57	1

Table 5.S7. Percentage of niche overlap between all species (Species A rows overlapping onto Species B in columns) for 2D, 3D, and 5D approaches (A), B) and C) respectively). Bolded are those pairs with high probability values (>50%), except in 5D where the highest value is bolded, but below 50%. For species abbreviations see Table 5.S1.

A)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	NA	9.45	0.5	25.78	36.09
DCCO	5.42	NA	0.62	**56.95**	26.84
LSPE	0.96	1.57	NA	0.81	31.32
PECO	23.33	**79.66**	0.63	NA	**63.78**
RHAU	33.87	39.74	14.01	**53.14**	NA

B)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	NA	12.84	0	30	13.39
DCCO	0.83	NA	0.07	9.88	9.07
LSPE	0	2.5	NA	0	0.22
PECO	11.32	**75.51**	0	NA	32.83
RHAU	4.08	32.42	0.02	17.5	NA

C)	ANMU	DCCO	LSPE	PECO	RHAU
ANMU	NA	7.43	0	24.46	0.36
CO	0.02	NA	0	5.71	0.59
LSPE	0	0.03	NA	0	0.02
PECO	0.43	***45.86***	0	NA	0.35
RHAU	0	1.44	0	0.24	NA

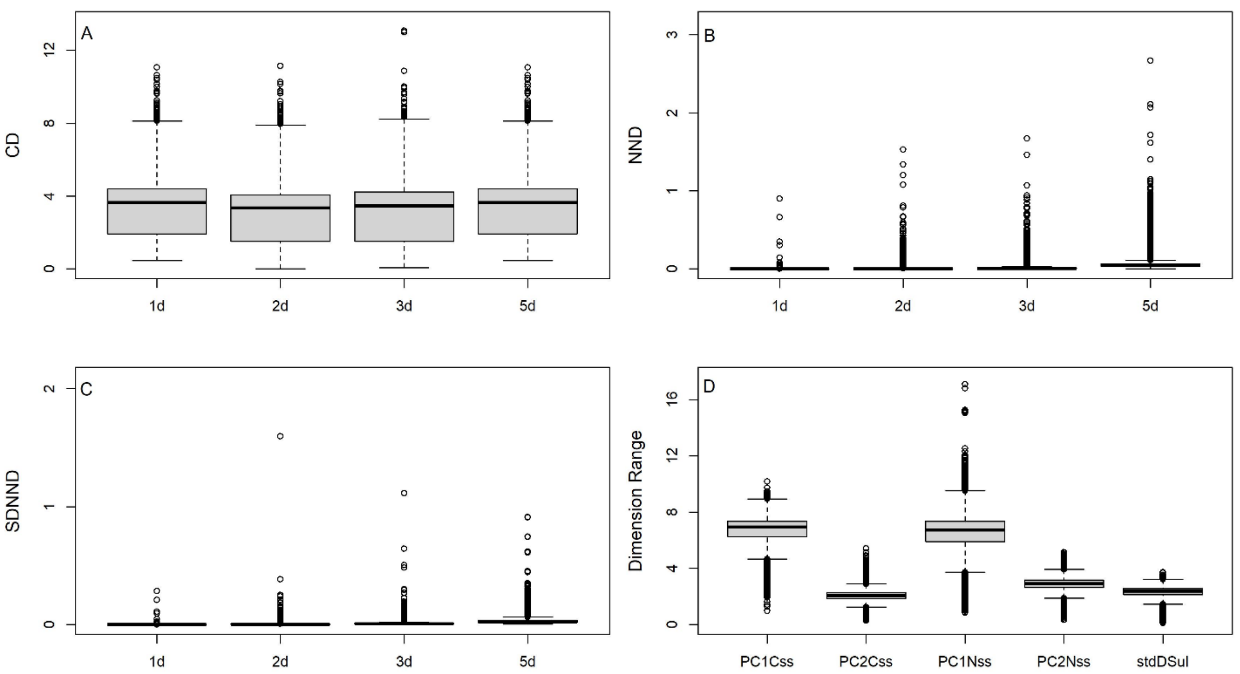


Figure 5.S3. A) Centroid Distance (CD), B) Nearest-Neighbor-Distance (NND), C) Standard deviation of the nearest neighbor distance (SDNND), and D) range of each dimension for all five species of seabirds in 1D, 2D, 3D, and 5D.

Table 5.S8. Centroid locations for each dimension for the 5-dimensional model double-crested cormorant (DCCO) and pelagic cormorant (PECO) in the British Columbia coast. First two PCA components for all amino acid specific carbon and nitrogen isotopes and standardized bulk sulphur. Mean and 2.5% and 97.5% quantiles (in brackets) of the posterior distribution from 100k samples.

DCCO	PC1Css	PC2Css	PC1Nss	PC2Nss	stdDelta.S
1970-1989	-1.59 (-3.98,0.78)	0.59 (0.11,1.08)	0.67 (-1.44,2.77)	1.65 (0.9,2.4)	-0.79 (-1.78,0.2)
1990-2006	-3.59 (-4.2,-2.99)	-0.11 (-0.49,0.27)	0.69 (0.22,1.15)	1.06 (0.5,1.62)	-1.33 (-1.98,-0.68)
PECO	PC1Css	PC2Css	PC1Nss	PC2Nss	stdDelta.S
1970-1989	-0.99 (-1.76,-0.23)	-0.58 (-0.94,-0.22)	-0.79 (-1.69,0.11)	0.35 (-0.17,0.87)	0.15 (-0.05,0.34)
1990-2006	-0.79 (-2.09,0.51)	-0.15 (-0.62,0.31)	-0.24 (-1.09,0.61)	0.14 (-0.57,0.85)	0.06 (-0.37,0.49)

Table 5.S9. Bhattacharrya Coefficient for the probability of overlap between the posterior distribution of each independent isotopic dimension (first two PCA components for all amino acid specific carbon and nitrogen isotopes and standardized bulk sulphur) between time periods for double-crested cormorant (DCCO) and pelagic cormorant (PECO). Bolded are those with high probability values (>0.8)

	PC1Css	PC2Css	PC1Nss	PC2Nss	stdDelta.S
DCCO	0.280671	0.085839	0.690387	0.5351465	*0.7229053*
PECO	**0.937017**	0.568858	**0.8109186**	**0.9207483**	**0.8706205**

Table 5.S10. Bhattacharrya coefficient of niche size distributions of PECO and DCCO in different time intervals

	2d	3d	5d
PECO	0.4093703	0.1654886	0.003084003
DCCO	0.006725132	0.4647408	**0.9800721**

Table 5.S11. Layman metrics for PECO and DCCO

PECO	5D	3D	2D
CD	0.8 (0.3-1.77)	0.59 (0.13-1.38)	0.58 (0.11-1.38)
NND	0.05 (0.02-0.16)	0.01 (0-0.03)	0.01 (0-0.01)
SDNND	0.04 (0.01-0.1)	0.01 (0-0.03)	0 (0-0.01)
Range PC1Css	1.7 (0.79-3.23)	1.48 (0.72-2.71)	1.48 (0.72-2.68)
Range PC2Css	0.9 (0.52-1.41)		
Range PC1Nss	1.59 (0.85-2.66)	1.44 (0.78-2.31)	1.44 (0.78-2.32)
Range PC2Nss	1.03 (0.51-1.86)		
Range stdDelta.S	0.54 (0.24-1.05)	0.21 (0.12-0.35)	

DCCO	5D	3D	2D
CD	1.53 (0.62-3.61)	1.33 (0.4-3.16)	1.26 (0.35-3.04)
NND	0.08 (0.03-0.25)	0.03 (0-0.07)	0.04 (0-0.02)
SDNND	0.06 (0.02-0.16)	0.02 (0-0.06)	0.01 (0-0.03)
Range PC1Css	3.76 (2.08-6.33)	3.52 (2.06-5.59)	3.53 (2.04-5.67)
Range PC2Css	1.18 (0.78-1.73)		
Range PC1Nss	2.41 (0.8-5.07)	2.13 (0.72-4.37)	2.12 (0.71-4.36)
Range PC2Nss	1.34 (0.75-2.18)		
Range stdDelta.S	1.53 (0.79-2.66)	1.36 (0.74-2.23)	

Table 5.S12. Ranges of posterior distributions of all independent isotopic dimensions, with 100000 iterations.

	Ranges
PC1Css	6.7(4.83-7.95)
PC2Css	2.02(0.94-2.65)
PC1Nss	6.5(3.35-8.75)
PC2Nss	2.92(1.67-3.64)
stdDelta.S	2.23(1.12-2.88)