Individual and population variation in isotopic niche between two sympatric cormorant species (#120584)

First submission

Guidance from your Editor

Please submit by **20 Aug 2025** for the benefit of the authors (and your token reward) .

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for guidance.

❗ **Custom checks**
Make sure you include the custom checks shown below, in your review.

▦ **Raw data check**
Review the raw data.

🖼 **Image check**
Check that figures and images have not been inappropriately manipulated.

Files

Download and review all files from the materials page.

3 Figure file(s)
2 Table file(s)
1 Other file(s)

❗ Custom checks

Vertebrate animal usage checks

❗ Have you checked the authors ethical approval statement?
❗ Were the experiments necessary and ethical?
❗ Have you checked our animal research policies?

Field study

❗ Have you checked the authors field study permits?
❗ Are the field study permits appropriate?

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

- 1. Basic Reporting
- 2. Study design
- 3. Validity of the findings
- 4. General Comments
- 5. Confidential notes to the editor

- You can also annotate the review pdf and upload it as part of your review (optional).

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

Article types: Research and AI Application

BASIC REPORTING

Include the appropriate criteria template based on the type variable
Clear and unambiguous, professional English used throughout.

The article must be written in English and must use clear, unambiguous, technically correct text. The article must conform to professional standards of courtesy and expression.

Literature references, sufficient field background/context provided.

The article should include sufficient introduction and background to demonstrate how the work fits into the broader field of knowledge. Relevant prior literature should be appropriately referenced.

Professional article structure, figures, tables. Raw data shared.

The structure of the article should conform to an acceptable format of ‘standard sections’ (see our Instructions for Authors for our suggested format). Significant departures in structure should be made only if they significantly improve clarity or conform to a discipline-specific custom.

Figures should be relevant to the content of the article, of sufficient resolution, and appropriately described and labeled.

All appropriate raw data have been made available in accordance with our Data Sharing policy.

Self-contained with relevant results to hypotheses.

The submission should be ‘self-contained,’ should represent an appropriate ‘unit of publication’, and should include all results relevant to the hypothesis.

Coherent bodies of work should not be inappropriately subdivided merely to increase publication count.

EXPERIMENTAL DESIGN

Original primary research within Aims and Scope of the journal.
Research question well defined, relevant & meaningful. It is stated how research fills an identified knowledge gap.

The submission should clearly define the research question, which must be relevant and meaningful. The knowledge gap being investigated should be identified, and statements should be made as to how the study contributes to filling that gap.

Rigorous investigation performed to a high technical & ethical standard.

The investigation must have been conducted rigorously and to a high technical standard. The research must have been conducted in conformity with the prevailing ethical standards in the field.

Methods described with sufficient detail & information to replicate.

Methods should be described with sufficient information to be reproducible by another investigator.

VALIDITY OF THE FINDINGS

Impact and novelty not assessed. Meaningful replication encouraged where rationale & benefit to literature is clearly stated.

Decisions are not made based on any subjective determination of impact, degree of advance, novelty or being of interest to only a niche audience. We will also consider studies with null findings. Replication studies will be considered provided the rationale for the replication, and how it adds value to the literature, is clearly described. Please note that studies that are redundant or derivative of existing work will not be considered. Examples of "acceptable" replication may include software validation and verification, i.e. comparisons of performance, efficiency, accuracy or computational resource usage.

All underlying data have been provided; they are robust, statistically sound, & controlled.

The data on which the conclusions are based must be provided or made available in an acceptable discipline-specific repository. The data should be robust, statistically sound, and controlled.

Conclusions are well stated, linked to original research question & limited to supporting results.

The conclusions should be appropriately stated, should be connected to the original question investigated, and should be limited to those supported by the results. In particular, claims of a causative relationship should be supported by a well-controlled experimental intervention. Correlation is not causation.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Individual and population variation in isotopic niche between two sympatric cormorant species

Gabriela Piriz Corresp., [1] , **Edwin J Niklitschek** [2] , **Valentina Mansilla Gamín** [2] , **Karin Maldonado** [3]

[1] Programa de Doctorado en Ciencias mención Conservación y Manejo de Recursos Naturales, Universidad de Los Lagos, Puerto Montt, Los Lagos, Chile
[2] Centro i~mar, Universidad de Los Lagos, Puerto Montt, Los Lagos, Chile
[3] Departamento de Ciencias, Facultad de Artes Liberales, Universidad Adolfo Ibáñez, Santiago, Chile

Corresponding Author: Gabriela Piriz
Email address: gabriela.pirizm@gmail.com

Background. Coexistence among sympatric, functionally similar species often hinges on niche differentiation, especially as resource competition intensifies during the breeding season. Individual specialisation (IS) can promote coexistence by narrowing individual niches or increasing divergence among individuals. In colonial seabirds, aggregation at limited breeding sites and central-place foraging amplify both intra- and interspecific competition. Here, we assess seasonal shifts in individual and population isotopic niche widths in two sympatric cormorant species to elucidate the mechanisms underlying their coexistence.

Methods. We analysed isotopic composition (δ^{13}C and δ^{15}N) in four tissue types from 111 individuals of *Poikilocarbo gaimardi* and *Leucocarbo atriceps* captured at Pirén Islet (Los Lagos, Chile) during breeding and non-breeding periods. Multivariate generalised linear mixed models estimated isotopic niche components: total niche width (TNW), within-individual component (WIC), and between-individual component (BIC).

Results. *L. atriceps* exhibited 2.2-fold greater TNW than *P. gaimardi* during non-breeding and 2-fold greater during breeding. IS differed markedly between species: *L. atriceps* showed a higher IS during non-breeding (0.541 vs 0.213 in *P. gaimardi*), but decreased by 79.3% during breeding, whereas *P. gaimardi* increased IS by 52.1%. Niche overlap was asymmetric and seasonally variable: *P. gaimardi* exhibited high overlap with *L. atriceps* (95.7% non-breeding, 89.6% breeding), whilst *L. atriceps* showed lower overlap (48.3% non-breeding, 43.7% breeding). Competition indices increased substantially during breeding in both species (307.2% in *L. atriceps*, 233.3% in *P. gaimardi*).

Discussion. Results suggest that coexistence relies on multiple mechanisms, including subtle population niche differentiation, contrasting IS between species, and divergent resource-use strategies. The high niche overlap and narrower niche of *P. gaimardi* suggest greater competitive vulnerability for this Near Threatened species. Conservation of

foraging habitat heterogeneity and prey availability is crucial for maintaining ecological opportunities that sustain these coexistence mechanisms.

Individual and population variation in isotopic niche between two sympatric cormorant species

Gabriela Piriz[1], Edwin J. Niklitschek[2], Valentina Mansilla-Gamín[2], Karin Maldonado[3]

1. Universidad de Los Lagos, Programa de Doctorado en Ciencias, mención Conservación y Manejo de Recursos Naturales, Chinquihue km. 6, Puerto Montt, Chile.

2. Universidad de Los Lagos, Centro i~mar, Chinquihue km. 6, Puerto Montt, Chile.

3. Universidad Adolfo Ibañez, Departamento de Ciencias, Facultad de Artes Liberales, Diagonal Las Torres 2640, Santiago, Chile.

Corresponding Author:

Gabriela Piriz[1]

Camino a Chinquihue km 6 ,Puerto Montt, Los Lagos, 5480000, Chile

Email address: gabriela.pirizm@gmail.com

Individual and population variation in isotopic niche between two sympatric cormorant species

Gabriela Piriz[1], Edwin J. Niklitschek[2], Valentina Mansilla-Gamín[2], Karin Maldonado[3]

1. Universidad de Los Lagos, Programa de Doctorado en Ciencias, mención Conservación y Manejo de Recursos Naturales, Chinquihue km. 6, Puerto Montt, Chile.

2. Universidad de Los Lagos, Centro i~mar, Chinquihue km. 6, Puerto Montt, Chile.

3. Universidad Adolfo Ibañez, Departamento de Ciencias, Facultad de Artes Liberales, Diagonal Las Torres 2640, Santiago, Chile.

Corresponding Author:

Gabriela Piriz[1]

Camino a Chinquihue km 6 ,Puerto Montt, Los Lagos, 5480000, Chile

Email address: gabriela.pirizm@gmail.com

Abstract

Background. Coexistence among sympatric, functionally similar species often hinges on niche differentiation, especially as resource competition intensifies during the breeding season. Individual specialisation (IS) can promote coexistence by narrowing individual niches or increasing divergence among individuals. In colonial seabirds, aggregation at limited breeding sites and central-place foraging amplify both intra- and interspecific competition. Here, we assess seasonal shifts in individual and population isotopic niche widths in two sympatric cormorant species to elucidate the mechanisms underlying their coexistence.

Methods. We analysed isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) in four tissue types from 111 individuals of *Poikilocarbo gaimardi* and *Leucocarbo atriceps* captured at Pirén Islet (Los Lagos, Chile) during breeding and non-breeding periods. Multivariate generalised linear mixed models estimated isotopic niche components: total niche width (TNW), within-individual component (WIC), and between-individual component (BIC).

Results. *L. atriceps* exhibited 2.2-fold greater TNW than *P. gaimardi* during non-breeding and 2-fold greater during breeding. IS differed markedly between species: *L. atriceps* showed a higher IS during non-breeding (0.541 vs 0.213 in *P. gaimardi*), but decreased by 79.3% during breeding, whereas *P. gaimardi* increased IS by 52.1%. Niche overlap was asymmetric and seasonally variable: *P. gaimardi* exhibited high overlap with *L. atriceps* (95.7% non-breeding, 89.6% breeding), whilst *L. atriceps* showed lower overlap (48.3% non-breeding, 43.7% breeding). Competition indices increased substantially during breeding in both species (307.2% in *L. atriceps*, 233.3% in *P. gaimardi*).

Discussion. Results suggest that coexistence relies on multiple mechanisms, including subtle population niche differentiation, contrasting IS between species, and divergent resource-use strategies. The high niche overlap and narrower niche of *P. gaimardi* suggest greater competitive vulnerability for this Near Threatened species. Conservation of foraging habitat heterogeneity and prey availability is crucial for maintaining ecological opportunities that sustain these coexistence mechanisms.

1. **Introduction**

Classical ecological theory posits that the coexistence of similar species depends on niche differentiation when resources are scarce, with differences in diet, temporal activity, and spatial distribution facilitating coexistence (Gause, Nastukova & Alpatov, 1934; Schoener, 1974; Phillips et al., 2017). However, this perspective often overlooks the fact that individual niches may occupy rather small fractions of the population niche, leading to highly divergent resource use patterns among individuals across taxa and niche axes (Bolnick et al., 2003). Such individual-level niche partitioning can alleviate intraspecific competition, thereby facilitating species coexistence even in the absence of strict interspecific niche differentiation (Bolnick et al., 2003, 2011; Araújo, Bolnick & Layman, 2011). This phenomenon is associated with individual specialisation, which is driven by inherent traits unique to each individual, rather than by collective factors such as sex, size, or age, and has been shown to have profound implications for population dynamics, species interactions, and community structure (Bolnick et al., 2011; Violle et al., 2012; Barabás & D'Andrea, 2016).

Competition is a central force shaping both inter- and intraspecific niche segregation, fundamentally driven by the limitation of resources such as food, space, or nesting sites. This pressure is particularly acute among specialist species whose ecological requirements and diets overlap, often resulting in intense competitive interactions (Pianka, 1974; Connell, 1980; Letten, Ke & Fukami, 2017). Such competition not only influences individual foraging strategies and population structure (Ward, Webster & Hart, 2006), but also drives evolutionary adaptations (Grant & Grant, 2006; Pfennig & Pfennig, 2012). Moreover, while much research has focused on competition between distantly related species occupying different ecological roles, examining competitive dynamics between closely related species is particularly valuable because these species share similar ecological demands, making competitive interactions more nuanced (Webb et al., 2002; Violle et al., 2011). For example, studies of closely related species, such as Darwin's finches (Grant & Grant, 2006) and sympatric anurans (Cloyed & Eason, 2017), reveal that even subtle differences can promote coexistence despite substantial niche overlap. Ultimately, understanding these fine-scale niche partitioning mechanisms is essential for unravelling the processes that maintain species diversity and stability within ecological communities (Costa-Pereira et al., 2019).

Colonial nesting seabirds, concentrated in dense aggregations on scarce oceanic breeding sites, face intensified intra- and interspecific competition that fundamentally shapes their foraging ecology (Ashmole, 1963; Wittenberger & Hunt, 1985). This spatial limitation amplifies competition for prey in adjacent waters and creates potential "halo effects" around colonies, whilst central-place foraging constraints during breeding force frequent returns to nests for chick provisioning (Birt et al., 1987; Gaston et al., 2007). Marine bird spatial strategies can be classified into three distinct categories: resident species that remain at breeding sites year-round, dispersive species that undertake irregular movements within regional areas, and migratory species that follow predictable seasonal movements between distinct grounds (Newton, 2008; Bunnefeld et al., 2011; Amélineau et al., 2021). Whilst these strategies appear similar during breeding when all species face central-place constraints, they diverge markedly during non-breeding periods, creating distinct ecological opportunities defined by the diversity of accessible resources and habitats.

Fundamentally different spatial strategies generate distinct patterns of individual specialisation across seasons. Resident species, constrained to exploit local marine environments year-round, develop pronounced individual specialisation during breeding when central-place foraging intensifies competition, as exemplified by Kerguelen shags (*Phalacrocorax verrucosus*) and gentoo penguins (*Pygoscelis papua*) that maintain consistent individual preferences in foraging behaviour and dietary selection (Camprasse et al., 2017; Herman et al., 2017). Conversely, dispersive species show reduced individual specialisation during breeding but develop marked individual differences during non-breeding periods when accessing diverse marine environments, as demonstrated by Cory's shearwaters (*Calonectris borealis*) and brown skuas (*Catharacta antarctica lonnbergi*) that exhibit strong individual consistency in migration strategies and habitat use across multiple years (Krietsch et al., 2017; Zango et al., 2019). This fundamental difference in year-round resource accessibility creates dual sources of ecological variation that ultimately shape community structure and competitive dynamics.

The cormorant family (Phalacrocoracidae) provides an excellent model for investigating coexistence mechanisms, as its members share highly similar morphological and functional traits whilst exhibiting significant ecological overlap (Frere, Quintana & Gandini, 2005; Grémillet et al., 2005; Frere et al., 2008). These generalist divers primarily feed on benthic and pelagic fish at high trophic levels, with several species coexisting in shared coastal breeding habitats and restricted foraging areas (Humphries, Hyndes, & Potter, 1992; Sapoznikow & Quintana, 2003; Forero et al., 2004). Despite substantial potential for niche overlap, the mechanisms that prevent competitive exclusion remain unclear, particularly given the ongoing environmental changes (Losos, 2008). Individual specialisation may buffer the effects of interspecific competition, as demonstrated in other taxa (Durell, 2007; Araújo, Bolnick, & Layman, 2011; Costa-Pereira et al., 2019).

We focus on two sympatric cormorants: the Imperial Shag (*Leucocarbo atriceps*), which disperses extensively during non-breeding periods (Yorio et al., 2020), and the Red-legged Cormorant (*Poikilocarbo gaimardi*), which remains resident year-round (Frere et al., 2004). Using stable isotope analysis, we quantified isotopic niche widths to assess seasonal variations in individual specialisation and niche overlap between species at a major colony in southern Chile. Stable isotopes provide insights into both bionomic (resource-use) and scenopoetic (environmental) niche axes, with $\delta^{15}N$ reflecting trophic levels and $\delta^{13}C$ indicating carbon sources (Bearhop et al., 2004; Cherel & Hobson, 2007; Newsome et al., 2007). Different tissue turnover rates reveal dietary information across annual stages, enhancing understanding of niche breadth in mobile marine organisms (Bearhop et al., 2006; Newsome et al., 2007; Jackson et al., 2011).

In the present work, we seek evidence supporting the hypothesis that the coexistence of *P. gaimardi* and *L. atriceps* on Pirén Islet is explained by one or more of the following mechanisms: *Segregation of population niches* (M1), either through the contraction or shift in niche position to enhance partitioning of resources between species; *Enhanced individual specialisation* (M2) through either a reduction of individual niche widths (↓WIC) and/or an increase in distance between individual niche positions (↑BIC) to enhance partitioning of resources between individuals; *Expansion of the total population niche* (M3) towards a greater range of less profitable but relatively more abundant prey resources, which become exploited by different relatively specialised individuals; and *Expansion of the individual niche* (M4) toward a greater range of less profitable but relatively more abundant prey resources, which becomes exploited similarly by all population members. While the first two mechanisms are inspired by the competitive exclusion theory (Gause 1934; Hardin, 1960), the last two mechanisms are inspired by the Optimal Foraging Theory (MacArthur & Pianka, 1966; Stephens & Krebs, 1986).

2. Methods

2.1. Study site

Pirén Islet (41°42’S; 72°41’O) covers an approximate area of 3.15 hectares and is an important breeding site for numerous seabirds and marine mammals in the Reloncaví Sound, known for its high species richness and abundance (Cursach et al., 2022). The islet features a land substrate at its centre covered with shrub vegetation and some trees, providing a resting and breeding ground for at least eight species of seabirds, including four cormorant species: *L. atriceps, P. gaimardi, Nannopterum brasilianus,* and *L. magellanicus* (Pérez-Santos et al., 2022). Recently, the reproduction of a fifth cormorant species, *L. bougainvillii*, has been recorded, making this site the only location where all five cormorant species have been reported to breed along the SE Pacific coast. The Reloncaví Sound is characterised by abundant freshwater, organic matter, and nutrient contributions from Andean rivers such as the Puelo, Petrohué, and Cochamó, which flow into it. These inputs enhance primary and secondary productivity, including that of zooplankton and small pelagic fish, and sustain a rich and diverse marine ecosystem (Iriarte, Pantoja & Daneri, 2014).

The main factors that likely determine the seasonal variability of prey available for seabirds on Pirén islet are artisanal fishing, aquaculture production cycles (Jiménez et al., 2013), other anthropogenic activities in the coastal area (e.g., agricultural runoff introducing nutrients and pollutants into nearshore waters) (Iriarte, González & Nahuelhual, 2010), climatic and oceanographic variability, and the seasonal migrations of prey species (Toledo et al., 2020; Heredia-Azuaje, Niklitschek & Sepúlveda, 2022). Additionally, the intense fishing activity in the surrounding waters has led to the overexploitation of small pelagic species (Subpesca, 2023), directly impacting piscivorous bird species.

2.2. Capture and sample collection.

Adult individuals of *L. atriceps* and *P. gaimardi* at the study site were sampled during the non-breeding season, defined as three months before the start of nesting activity (July-September) of 2022 (five sampling events) and the breeding season (chick-rearing, January-February) of 2022 and 2023 (six and two sampling events, respectively). Sampling was abruptly suspended in 2023 due to the highly pathogenic avian influenza epidemic that affected the SE Pacific coast (Azat et al., 2024). The study was conducted in accordance with the general principles of non-lethal sampling (Waugh & Monamy, 2016) and animal welfare (Zemanova, 2020). Necessary sampling permissions were obtained (Res. N° 7850/2021, Servicio Agrícola y Ganadero, Chile), and the University of Los Lagos Scientific Ethics Committee approved sampling protocols (CEC-Ulagos

ORD. 72/2021).

Captures were conducted at night, employing two distinct methodologies based on light-attraction techniques. In some cases, researchers approached the island at night in a boat and attracted the cormorants using high-intensity lights (10,000–20,000 lumens), which exhibit positive phototaxis and dive toward the light source, landing in the water near the boat (King et al., 1994). These birds were then captured using nets and modified fishing rods (Morgenthaler, 2019; Alfaro & Aldabe, 2020). Alternatively, researchers landed on the island at night and employed spotlights to dazzle individual cormorants at close range. The intense illumination temporarily immobilises the birds through disorientation, allowing for direct capture with hand-held nets. Following capture, all birds were temporarily housed in cages (0.15-2 hours) before being measured and sampled on the boat. After being measured and sampled, all individuals were banded before release to allow identification of recaptures and prevent repeated measurements. A calliper was used to measure the length of the beak, head, tarsus, and wing, and a spring scale was used to determine body mass. Blood samples (0.5–1.5 ml) were obtained from the brachial or tarsal vein using heparinised syringes with 23–25 gauge needles, and were subsequently refrigerated and centrifuged (4-8 hours after extraction) for 20 minutes at 3,500 rpm. The plasma and red blood cells were dried (48 h at 60 °C) and stored for later isotopic analysis (Cherel et al., 2013). Feather samples from the body and wings (primaries) were collected to obtain isotopic signatures from different periods, as these reflect the individual's diet during the moulting period. Body feathers were used for the non-breeding period, and primary feathers were used for breeding. These samples were cleaned with alcohol and distilled water, dried (48 hours at 60°C), and cut before conducting isotopic analyses.

2.3. Niche analysis

The red blood cells, plasma, and feather samples were ground until a homogeneous consistency was achieved. Approximately 1 mg of each sample was encapsulated in tin capsules to determine its isotopic signature. The stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were conducted at the Centre for Stable Isotopes of the University of New Mexico, United States, using an elemental analyser coupled to an isotopic ratio mass spectrometer with a continuous-flow interface. The stable isotopes were expressed according to the following equation in δ (delta) notation (Coplen, 2011) in units per thousand (‰):

$$\delta X = \left(\frac{Rsample}{Rstandar} - 1 \right) * 1000\,‰$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio of ^{13}C:^{12}C or ^{15}N:^{14}N. The standard value of R is based on Vienna Pee Dee Belemnite (VPDB) for ^{13}C, and atmospheric nitrogen (N_2) for ^{15}N.

We utilised stable isotope data to model the within- and between-individual components (WIC and BIC, respectively) of multidimensional population niches as variance-covariance matrices (Ingram, Costa-Pereira & Araújo, 2018). WIC reflects the average individual resource breadth, represented by the variation in $\delta^{13}C$ and $\delta^{15}N$ of their resources. At the same time, BIC quantifies the average degree of variation in resource use among individuals within a population (Roughgarden, 1972). Thus, the population total niche width (TNW) was calculated as the sum of both components (TNW = WIC + BIC; Roughgarden, 1972). Although individual specialisation (IS) is traditionally defined as WIC/TNW, this relationship is counterintuitive: lower values correspond to greater specialisation (Bolnick et al., 2002). To resolve this, we adopted the complementary metric IS = BIC/TNW (Rosenblatt et al., 2015), which ensures that values directly reflect the intensity of specialisation. Thus, the degree of IS increases when individual niches are narrower (low WIC) and/or more segregated (high BIC).

We estimated the parameters of the niche component matrices (BIC and WIC) using multivariate generalised linear mixed models (MGLMM) through the R package 'MCMCglmm' (Hadfield, 2010), which implements a Monte Carlo Markov chain (MCMC) analysis. We first standardised the data by sample type (e.g., plasma, red blood cells, and feathers) to ensure the niche component matrices would be readily interpretable (Ingram, Costa-Pereira & Araújo, 2018). Individual identity was modelled as a random effect for each population and period to obtain the variances and covariances between individuals (BIC) in δ^{13}C and δ^{15}N dimensions (the 'G-structure'). Thus, the residual variances and covariances (the 'R-structure') represented the average within-individual variation (WIC). The posterior means of each variance-covariance matrix (BIC and WIC) were then summed up to calculate the total niche width (TNW). In this context, the average index of individual specialisation across multiple dimensions within a population was calculated as the ratio between the size (i.e., the sum of the eigenvalues) of the BIC matrix and the size of the TNW matrix (Ingram, Costa-Pereira & Araújo, 2018; Costa-Pereira et al., 2019). Each MCMC run comprised 100,000 iterations (thinning interval = 10, burn-in = 5,000). Convergence was assessed using the Gelman-Rubin diagnostic based on five independent runs.

2.4. Indicators of ecological opportunity

Although it was not possible to directly measure the magnitude of the main ecological factors believed to affect individual specialisation, we employed two indirect indicators previously proposed to evaluate ecological opportunity, defined as the diversity of exploitable resources accessible to a population (Ingram, Costa-Pereira & Araújo, 2018). Seasonal variation in ecological opportunity was indirectly assessed by analysing prey (fish otoliths, cephalopod jaws, polychaete remains, and crustacean exoskeletons) found in pellets collected on the island, which were likely produced by cormorants and other seabirds (Morgenthaler, 2019). Sixty pellets were collected during the non-breeding season (June and September) and 70 during the breeding season (November and December) of the years 2020 and 2022. Pellets were wrapped in aluminium foil and kept frozen until thawed at 60 °C for 20 minutes before dissection. Distilled water was used to detach and separate the remains under a magnifying glass, which were then stored in Eppendorf tubes with 70% alcohol, except for the otoliths, which were stored dry. Each structure was photographed using magnifications of 0.5X and 6.3X. Identification was made using taxonomic keys from García-Godos (2001) and Xavier & Cherel (2021) and assistance from experts (P. Toledo, B. Pacheco, and H. Heredia-Azuje, Centro i~mar, Universidad de Los Lagos). Nominal richness and the reciprocal Simpson index (Magurran, 2004) were used to characterise seasonal trends in prey richness and diversity.

2.5. Indicators of competition

To quantify the intensity of competitive interactions in our study system, we estimated potential competition using the effective abundance of hetero and conspecifics (Nz; Costa-Pereira et al., 2018), a metric that integrates both the local abundance of competing species and their phylogenetic relatedness as a proxy for ecological similarity. This approach is grounded in the principle that competition intensity should be stronger between closely related species due to their shared evolutionary history and similar ecological requirements.

Competition indices were determined for each species during both periods based on the presence of species from the orders Suliformes, Pelecaniformes, Charadriiformes, and Sphenisciformes, which constitute the primary marine bird taxa exploiting similar prey resources, particularly fish and cephalopods (Cherel & Klages, 1998; Furness et al., 2012). These taxonomic groups represent the main seabird competitors in marine ecosystems, sharing overlapping trophic niches and foraging habitats despite differences in foraging strategies and morphological adaptations (Forero et al., 2004; Dehnhard et al., 2020). Census data were collected between May-August for the non-breeding period and October-January for the breeding period, derived from comprehensive surveys conducted between 2020 and 2024 using standardised visual counting techniques combining aerial observations with DJI Mavic Pro drone platforms and systematic direct counts using 10x42 binoculars, conducted during optimal weather conditions by trained observers following established protocols for colonial seabird monitoring (Bibby et al., 2000).

The effective abundance metric is based on the quantitative genetic competition model proposed by Doebeli (1996), which models competitive interactions as a function of phenotypic similarity between species. The index is calculated as:

$$Nz = \sum N(z')\alpha(z, z')$$

Where N(z') represents the observed absolute abundance of hetero and conspecifics, unlike Costa-Pereira et al. (2018), who employed relative abundance measures, we utilised absolute abundance values to avoid potential scaling artifacts. This distinction is important because relative abundance indices can produce identical values regardless of actual population sizes, potentially masking true differences in the intensity of competitive pressure.

The competitive impact α(z,z') represents the per capita reduction in population growth of focal species z caused by each individual of competitor species z', and is modelled using a Gaussian decay function (Doebeli, 1996; Costa-Pereira et al., 2018):

$$\alpha(z, z') = \exp\left(\frac{-(z - z')^2}{2\sigma_\alpha^2}\right)$$

Where the phenotypic difference (z,z') corresponds to the phylogenetic distance between species pairs, calculated from a time-calibrated phylogenetic cladogram constructed using the R package "picante" (Kembel et al., 2010). Within the order Suliformes, interspecific distances were obtained from values reported by Kennedy & Spencer (2014). At the same time, for other potential competitor groups (Charadriiformes, Sphenisciformes, Pelecaniformes), we used average phylogenetic distances between each order and Suliformes as reported by Claramunt & Cracraft (2015). The parameter $\sigma^2 = 0.05$ defines the rate at which competitive intensity declines with increasing phylogenetic divergence, following Costa-Pereira et al. (2018) to approximate the competitive function as a Gaussian curve.

2.6. Statistical analysis

All statistical analyses were performed using R version 4.4.3 (R Core Team, 2023). Generalised linear models (GLM, McCullagh & Nelder, 1989) were used to assess differences in morphometric traits—including mass, beak length and width, leg length, and total length—between species, with the species as the explanatory variable. Gaussian and gamma distributions were compared, and the most informative one was selected using the second-order Akaike’s Information Criterion (AICc) and its relative weight (AICw) as recommended by Burnham & Anderson (2004). Data for most measurements were observed to fit the gamma distribution better.

Fitting GLM models also analysed ecological opportunity data for response indices (Magurran, 2004): i) nominal richness, and ii) inverse Simpson diversity index, assuming Poisson and normal distributions, respectively.

Distribution assumptions for morphometric and ecological opportunity data were tested using Hartig's (2022) simulated and rescaled residuals method and the Kolmogorov-Smirnov uniformity test. Homoscedasticity was assessed using Breusch and Pagan’s test (1979). Overall, we found no evidence against these two main assumptions. Lack of independence among data from the same sampling event (collection day) was addressed through a mixed models approach (Searle, 1987), which allowed for including these events as a random factor.

Inference for morphometric and ecological opportunity data followed a multi-model inference approach, where model selection was based on AICc and AICw (Burnham & Anderson, 2004). Inference about isotopic niche metrics was, instead, directly based on the posterior distribution of the metrics of interest (Gelman et al., 2014).

Isotopic niche overlap between species was calculated as the proportion of the standard ellipse representing the total niche width (TNW) of one species being overlapped by the TNW standard ellipse of the other species. Ellipse and overlap computations were made using the R package '*sf*' in R (Pebesma & Bivand, 2023). This approach provided a readily interpretable measure of relative niche overlap experienced by each population.

3. Results

1.1. Sampling success

A total of 111 individuals were captured: 25 *P. gaimardi* and 18 *L. atriceps* during the non-breeding season and 31 *P. gaimardi* and 37 *L. atriceps* during the breeding season. On average, the *L. atriceps* species exhibited higher values in mass (1.36 fold), wing length (1.06 fold), beak breadth (1.24 fold), and leg length (1.13 fold) than the *P. gaimardi*. In contrast, beak length was similar between species (Supplemental Table S1).

3.1. Isotopic signature

The isotopic composition analysis revealed clear differences in $\delta^{13}C$ and $\delta^{15}N$ values between both species and tissue types for *P. gaimardi* and *L. atriceps* (Table 1). For $\delta^{13}C$, body feathers exhibited similar values across species, while plasma showed the most depleted values overall, with *L. atriceps* being lower than *P. gaimardi* (Table 1). Red blood cells displayed intermediate δ^{13}C levels, also differing between species, with *L. atriceps* again showing values 2.47% lower than *P. gaimardi*. Regarding δ^{15}N values, interspecific differences were evident only in plasma, where *P. gaimardi* was notably enriched compared to *L. atriceps*. Primary feathers showed the highest δ^{15}N enrichment in both species, whereas red blood cells exhibited the lowest values, particularly in *P. gaimardi* (Table 1).

3.2. Niche components

During the non-breeding period, the *L. atriceps* TNW was substantially (2.2-fold) broader than the *P. gaimardi* TNW (P [$TNW_{L.atriceps}$>$TNW_{P.gaimardi}$]= 0.999; Table 2). This difference was driven by a moderately (24.8%) larger WIC (P[$WIC_{L.atriceps}$>$WIC_{P.gaimardi}$] = 0.707), and by a 5.7-fold larger BIC (P[$BIC_{L.atriceps}$>$BIC_{P.gaimardi}$] = 0.998). Consequently, the *L. atriceps* population displayed a much higher degree of individual specialisation (IS= 0.541), estimated to be 60.1% greater than the *P. gaimardi* one (P[$IS_{L.atriceps}$>$IS_{P.gaimardi}$] = 0.985; Table 2).

In contrast, during the breeding period, although *L. atriceps* maintained a 2-fold greater TNW (P[$TNW_{L.atriceps}$>$TNW_{P.gaimardi}$] = 1) and a 2.6-fold higher WIC (P[$WIC_{L.atriceps}$>$WIC_{P.gaimardi}$] = 1) than *P. gaimardi*, but its BIC was 31.2% lower (P[$BIC_{L.atriceps}$<$BIC_{P.gaimardi}$] = 0.750) than in *P. gaimardi* (Table 2). This shift resulted in opposite changes in individual specialisation, where *P. gaimardi* exhibited an individual specialisation index (IS= 0.324) 31.4% higher than that of *L. atriceps* (IS= 0.112, P[$IS_{P.gaimardi}$>$IS_{L.atriceps}$] = 0.979).

When comparing periods within species, notable differences in TNW and its components are evident. In *P. gaimardi*, TNW decreased by 21.4% from the non-breeding to the breeding period (P[$TNW_{breeding}$<$TNW_{non-breeding}$] = 0.902). This reduction was mainly driven by a 33.0% decline in the WIC ($P[WIC_{breeding}<WIC_{non\text{-}breeding}] = 0.974$) despite a 23.1% increase in the BIC ($P[BIC_{breeding}>BIC_{non\text{-}breeding}] = 0.632$). *L. atriceps* exhibited a similar (28.5%) decrease in TNW over the same period ($P[TNW_{breeding}<TNW_{non\text{-}breeding}] = 0.999$); however, in this species, WIC increased by 43.0% ($P[WIC_{breeding}>WIC_{non\text{-}breeding}] = 0.936$), while BIC decreased sharply by 86.7% ($P[BIC_{breeding}>BIC_{non\text{-}breeding}] = 0.999$) during the breeding period. Along with the overall reduction in TNW, the individual specialisation index (IS) declined by 79.30% in *L. atriceps*, indicating a lower individual specialisation during the breeding period ($P[IS_{breeding}<IS_{non\text{-}breeding}] = 0.999$). In contrast, *P. gaimardi* showed a slight increase of 52.11% in this index ($P[IS_{breeding}<IS_{non\text{-}breeding}] = 0.818$).

3.3. Population niche overlap between species.

During the non-breeding season, *P. gaimardi* exhibited a very high degree of niche overlap (95.7%) with *L. atriceps*. In contrast, only 48.3% of the *L. atriceps'* niche overlapped with that of *P. gaimardi* during this period, consistent with the much broader trophic niche (TNW) of *L. atriceps* (Figure 2). During the breeding season, although the overlap decreased by ~ 5–6% for each species, it remained substantially high (89.6%) for *P. gaimardi*, while 43.7% of the *L. atriceps*'s niche overlapped with that of *P. gaimardi* (Figure 2).

3.4. Ecological opportunity and interspecific competition

Overall, the richness and diversity of taxa found in seabird pellets from Pirén Islet were greater during the non-breeding season than during the breeding season (Figure 3), with species richness increasing by 43% and diversity by 14%. Despite these apparent seasonal shifts, the null model—which assumes no seasonal differences—demonstrated stronger empirical support than seasonal alternatives, suggesting these fluctuations may reflect natural variability rather than systematic seasonal patterns.

The competition index exhibited marked seasonal increases and substantial differences between species (Figure 3). *L. atriceps* showed the greatest seasonal increment, rising 307.2% from the non-breeding to breeding season. In contrast, *P. gaimardi* demonstrated a smaller yet considerable increase of 233.3%. Additionally, interspecific differences intensified between seasons. During the non-breeding season, *L. atriceps* recorded a competition index 63.2% higher than *P. gaimardi*, a disparity that widened to 99.4% during the breeding season. This pattern suggests heightened competitive intensity for *L. atriceps*, particularly during reproductive periods (Figure 3).

4. Discussion

Our results show that two sympatric and closely related seabird species exhibit substantial seasonal variation in the size and overlap of their trophic niches, as well as in their niche components and levels of individual specialisation. This variability suggests that these species respond to seasonal changes in prey availability, breeding constraints, and differing dispersal behaviours. These patterns indicate that coexistence is not maintained by a single mechanism, but rather through a combination and alternation of various niche partitioning mechanisms aimed at reducing competition. In the present work, we sought evidence of the relative importance of four non-exclusive mechanisms facilitating coexistence during the breeding season: *Segregation of population niches* (M1), *enhanced individual specialisation* (M2), *expansion of the total population niche* (M3), and *expansion of the individual niche* (M4).

Following classical ecological theory, M1 posits that population-level niche differentiation would be the primary mechanism enabling coexistence between ecologically similar species (Hardin, 1960; Schoener, 1974). However, our results revealed a considerable overlap in isotopic niches between the two cormorants during both seasons. This unexpected finding aligns with recent evidence showing that high niche overlap does not inherently lead to competitive exclusion, particularly when individual specialisation and plasticity buffer interspecific competition (Schirmer et al., 2020; Johnson et al., 2022; Murray et al., 2023). Nonetheless, a subtle segregation in mean isotopic position (primarily in δ^{13}C) and niche overlap was observed during the breeding season, revealing that some divergences in prey selection and/or foraging habitats had contributed to mitigating direct competition at the time energetic and nest-guarding constraints compel both species to forage near the colony (Cherel et al., 2007; Phillips et al., 2017; Jessopp et al., 2020).

The considerable niche overlap we observed in the Pirén islet notably contrasts with the findings of Morgenthaler et al. (2025), which showed great trophic segregation between Atlantic populations of the same two species. These contrasting results may reflect regional differences in ecological opportunity, such as higher prey abundance leading to reduced interspecific competition in our study site. Oceanographic conditions characterise and differentiate both study sites. The Reloncaví sound exhibits higher, although seasonally variable, productivity related to freshwater inputs (Iriarte, González & Nahuelhual, 2010). In contrast, the Patagonian Shelf is characterised by greater fish diversity associated with the confluence of the warm Brazilian and the cold Malvinas currents (Alemany, Acha & Iribarne, 2009). These geographical disparities underscore the context-dependent nature of coexistence mechanisms, where local abiotic and biotic factors interact with species-specific foraging strategies to shape niche dynamics (Morgenthaler et al., 2025).

While finding marked but contrasting seasonal differences in individual specialisation between the two studied species, our results provided limited support for the notion that individual specialisation (M2) can play a significant role in mitigating the effects of competition. Thus, the more resident species, *P. gaimardi,* exhibited some increase in individual specialisation during the breeding season, which was explained by a moderate reduction in WIC as individuals differentiated their resource use, possibly to reduce intraspecific competition under heightened breeding constraints (Phillips et al., 2017). The magnitude of this response appears, however, to be small, given the eightfold seasonal increase in the abundance of its competitor, *L. atriceps*. The more dispersive *L. atriceps* showed, instead, a decrease in individual specialisation during the breeding season, which was explained by a major reduction in BIC, which cancelled out a minor decrease in WIC. This response was likely related to the drastic reduction in ecological opportunity that faces this population during the breeding season as its foraging range becomes limited by nest-guarding and chick-feeding constraints. This is a pattern commonly reported in dispersive seabirds (Harris et al., 2015; Zango et al., 2019), which are seasonally forced to become central-place foragers (Birt et al., 1987; Dehnhard et al., 2020).

Unlike expectations from M3 and optimal foraging theory, the total population niche width (TNW) did not increase during the breeding season in either of the two studied species. Instead, a decrease in TNW—particularly pronounced in *L. atriceps*—was observed during this period. This suggests that expanding the trophic population niche to include suboptimal prey was not a strategy used to alleviate the seasonal increase in potential competition, at least in this case study. We speculate that population niche expansion was constrained by limited ecological opportunities around breeding sites, given the relatively short foraging ranges reported for cormorants (*L. triceps*, 10-50 km; *P. gaimardi*, 0.1-4.1 km; Gandini et al., 2005; Quintana et al., 2010). During the non-breeding season, a noticeable expansion of TNW occurred in both species, but via different mechanisms. In the dispersive *L. atriceps*, expansion occurred through increased segregation between individual niches (BIC), following the niche variation hypothesis (Van Valen, 1965), which postulates that the release of competitive constraints permits greater individual diversification in resource use. In contrast, in the resident *P. gaimardi*, it occurred through an expansion of WIC, indicating that individuals broadened their respective dietary niches via 'parallel release' (Bolnick et al., 2010), where all individuals simultaneously expand their niche widths in response to increased ecological opportunity. These divergent mechanisms highlight how life-history strategies influence species' responses to ecological opportunities—a crucial consideration for predicting resilience under environmental change.

The WIC of *L. atriceps* increased during the breeding season, as predicted by M4, i.e. by the Optimal Foraging Theory operating at the individual level (Sheppard et al., 2018; Costa-Pereira et al., 2019). The causal relationship between heightened competition and the observed expansion in WIC in *L. atriceps* remains somewhat unclear. While individuals likely expanded their trophic niche to compensate for the diminished availability of optimal or preferred prey (Bolnick et al., 2010), this reduced availability may have resulted from both the seasonally constrained foraging range and increased competition during the breeding season. Regardless, this seasonal expansion of WIC parallels responses observed in other dispersive seabirds facing seasonal spatial constraints, where behavioural plasticity enhances resource exploitation efficiency (Ceia & Ramos, 2015).

Opposing M4 predictions and *L. atriceps'* responses, *P. gaimardi* exhibited a reduction in WIC during the breeding season, which was consistent instead with M2 predictions, i.e. with an individual niche partitioning strategy. These contrasting responses may reflect physiological, anatomical, and behavioural differences between these two species, leading to different levels of individual plasticity —a key trait for withstanding environmental fluctuations and resource depletion (Bolnick et al., 2003; Valladares et al., 2015). The observed patterns may also reflect broader ecological principles: dispersive species, such as *L. atriceps*, leverage plasticity to exploit variable resources (Phillips et al., 2017; Zango et al., 2019), while resident species, like *P. gaimardi*, rely on specialised, consistent foraging tactics (Lewke, 1982; Campana et al., 2022).

While our stable isotope analysis provided valuable insights into the trophic ecology of *L. atriceps* and *P. gaimardi*, several methodological constraints common to this approach warrant further consideration. First, isotopic niche metrics represent an indirect approach to infer about resource use patterns and rely on several key assumptions. Critical to our case is that isotopic baselines and discrimination factors are spatially and temporally stable (Bearhop et al., 2004; Newsome et al., 2007). Second, stable isotope analysis has a limited ability to resolve fine-scale dietary differences, particularly when prey species share similar isotopic signatures (Newsome, Clementz & Koch, 2010; Phillips et al., 2014). Third, quantifying ecological opportunity and competition indices in marine systems remains inherently challenging due to the dynamic nature of prey availability and the difficulty of directly measuring interspecific interactions in pelagic environments (Harris et al., 2015; Phillips et al., 2017). Hence, our reliance on surrogate indicators may have oversimplified the complex interplay between resource partitioning and competition in this case study. Future studies, both here and elsewhere, would benefit from integrating isotopic mixing models (e.g., SIAR, MixSIAR) with direct dietary sampling methods (e.g., regurgitates, GPS tracking) to refine estimates of prey contributions and validate niche partitioning mechanisms (Newsome et al., 2012; Ibarra et al., 2018).

Sampling limitations imposed additional limitations on the current study. The 2023 outbreak of highly pathogenic avian influenza (Azat et al., 2024) abruptly halted our fieldwork, resulting in reduced sample sizes, particularly for *P. gaimardi*, during both the

2023 breeding and non-breeding seasons. Additionally, the logistical difficulties of capturing and handling these birds exceed our expectations, given their sensitivity to disturbance. Furthermore, the roughness of the coastal terrain appears to be higher than previously reported in other colonies of the same two species, particularly for the more elusive *P. gaimardi* (King et al., 1994; Morgenthaler et al., 2025). Larger, multi-year datasets would strengthen the robustness of individual specialisation metrics and improve statistical power to detect subtle seasonal shifts (Bolnick et al., 2003; Ceia & Ramos, 2015).

Despite the ecological and economic relevance of the SE Pacific coastline, few ecological studies have addressed the trophic ecology and niche dynamics of coastal seabirds, such as cormorants. Even fewer have focused on individual specialisation, whose understanding may be critical to enhancing conservation strategies for marine birds, given its role in buffering populations against environmental change (Bolnick et al., 2011; Valladares et al., 2015; Manlick, Maldonado & Newsome, 2021). Our findings demonstrate that the coexistence of sympatric cormorants hinges not on broad population-level segregation but on nuanced individual strategies, underscoring the importance of preserving heterogeneous foraging habitats to sustain ecological opportunity. This consideration may be especially important for *P. gaimardi*, which is currently classified as “Near Threatened” according to the IUCN Red List (BirdLife International, 2018). The species’ narrower individual niches and higher isotopic overlap with *L. atriceps* suggest competitive vulnerability. Protecting prey availability and environmental quality in foraging zones, as well as reducing anthropogenic pressures over breeding sites, are the most urgent tasks here (Furness et al., 2012; Thaxter et al., 2012; Soldatini et al., 2015).

5. Conclusions

Our results indicate that coexistence between dispersive *L. atriceps* and the resident *P. gaimardi* at the Pirén Islet is sustained by a dynamic interplay of niche partitioning and resource-use strategies, which shift according to season and ecological conditions. The dispersive species consistently exhibits a broader population niche than the resident, particularly during the non-breeding season when ecological opportunity is greater and competition is reduced. Despite a high degree of niche overlap between the species, the dispersive cormorant's ability to exploit a wider range of resources, likely due to its mobility, appears to buffer direct interspecific competition.

The evidence for individual specialisation as a mechanism underpinning coexistence between these cormorant species is suggestive but not unequivocal. While patterns of individual specialisation are observed—such as higher specialisation in *L. atriceps* during the non-breeding season and a modest increase in *P. gaimardi* during breeding—these trends are not sufficiently strong or consistent to be considered definitive proof. Instead, the results point to a more nuanced scenario in which individual specialisation may contribute to coexistence, but its role is likely context-dependent and intertwined with other ecological processes.

In summary, the coexistence of these closely related cormorant species cannot be attributed to a single mechanism. Rather, it results from the combined effects of partial niche segregation, varying levels of individual specialisation, and context-dependent responses to competition and ecological opportunity. Crucially, divergent life-history strategies also play a key role, highlighting the need to consider both intra- and interspecific variation when analysing the ecological processes that sustain biodiversity in complex communities.

6. Acknowledgements

We are grateful to all those who assisted us in the field across various campaigns, including Jorge Aguilar; the Captain and his brothers Marcelo and Rodrigo, crew members of the LM *Perlita*; and the following individuals for their valuable support: Nicole Arcaya, Francisca Bustos, Gabriela Contreras, Daniela Díaz, Daniel González, Carla Guerrero, Yethro Henríquez, Heide Heredia, Paula Muñoz, Joaquín Navarro, Fernanda Ojeda, Bárbara Pacheco, César Rehbein, Daniela Salazar, Martín Schönherr, Daniel Terán, and Pamela Toledo. We also thank the Red de observadores de aves y vida silvestre de Chile (ROC) for their valuable support in the field.

7. **References**.

Alemany, D., E. M. Acha, and O. Iribarne. 2009. The relationship between marine fronts and fish diversity in the Patagonian Shelf Large Marine Ecosystem. Journal of Biogeography 36:2111–2124.

Alfaro, M., and J. Aldabe. 2020. Colecta y manejo de aves en el ambiente y métodos alternativos para el estudio en campo. Pages 122–141.

Amélineau, F., B. Merkel, A. Tarroux, S. Descamps, T. Anker-Nilssen, O. Bjørnstad, V. S. Bråthen, O. Chastel, S. Christensen-Dalsgaard, J. Danielsen, F. Daunt, N. Dehnhard, M. Ekker, K. E. Erikstad, A. Ezhov, P. Fauchald, M. Gavrilo, G. T. Hallgrimsson, E. S. Hansen, M. P. Harris, M. Helberg, H. H. Helgason, M. K. Johansen, J. E. Jónsson, Y. Kolbeinsson, Y. Krasnov, M. Langset, S. H. Lorentsen, E. Lorentzen, M. V. Melnikov, B. Moe, M. A. Newell, B. Olsen, T. Reiertsen, G. H. Systad, P. Thompson, T. L. Thórarinsson, E. Tolmacheva, S. Wanless, K. Wojczulanis-Jakubas, J. Åström, and H. Strøm. 2021. Six pelagic seabird species of the North Atlantic engage in a fly-and-forage strategy during their migratory movements. Marine Ecology Progress Series 676:127–144.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948–958.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473.

Azat, C., M. Alvarado-Rybak, J. F. Aguilera, and J. A. Benavides. 2024. Spatio-temporal dynamics and drivers of highly pathogenic avian influenza H5N1 in Chile. Frontiers in Veterinary Science 11.

Barabás, G., and R. D’Andrea. 2016. The effect of intraspecific variation and heritability on community pattern and robustness. Ecology Letters 19:977–986.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007–1012.

Bearhop, S., R. Phillips, R. McGill, Y. Cherel, D. Dawson, and J. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Marine Ecology Progress Series 311:157–164.

Bibby, C. J. 2000. Bird census techniques. Second Edition. Elsevier, London.

BirdLife International. 2018. IUCN Red List of Threatened Species: *Poikilocarbo gaimardi*. IUCN Red List of Threatened Species.

Birt, V., T. Birt, D. Goulet, D. Cairns, and W. Montevecchi. 1987. Ashmole’s halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40:205–208.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Bolnick, D. I., T. Ingram, W. Stutz, L. K. Snowberg, O. Lau, and J. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society B: Biological Sciences 277:1789–1797.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, M. L. Forister, and A. E. M. A. McPeek. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist 161:1–28.

Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanbäck. 2002. Measuring individual-level resource specialization. Ecology 83:2936–2941.

Breusch, T. S., and A. R. Pagan. 1979. A simple test for heteroscedasticity and random coefficient variation. Econometrica: Journal of the Econometric Society:1287–1294.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Burnham, K., and D. Anderson. 2004. Model selection and multi-model inference (Second Edition). Springer, New York (USA).

Campana, J. L. M., A. Raffard, A. S. Chaine, M. Huet, D. Legrand, and S. Jacob. 2022. Dispersal plasticity driven by variation in fitness across species and environmental gradients. Ecology Letters 25:2410–2421.

Camprasse, E. C. M., Y. Cherel, J. P. Y. Arnould, A. J. Hoskins, and C. A. Bost. 2017. Combined bio-logging and stable isotopes reveal individual specialisations in a benthic coastal seabird, the Kerguelen shag. PLOS ONE 12:e0172278.

Ceia, F. R., and J. A. Ramos. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. Marine Biology 162:1923–1938.

Cherel, Y., and K. A. Hobson. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Marine Ecology Progress Series 329:281–287.

Cherel, Y., K. A. Hobson, C. Guinet, and C. Vanpe. 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. Journal of Animal Ecology 76:826–836.

Cherel, Y., A. Jaeger, R. Alderman, S. Jaquemet, P. Richard, R. M. Wanless, R. A. Phillips, and D. R. Thompson. 2013. A comprehensive isotopic investigation of habitat preferences in nonbreeding albatrosses from the Southern Ocean. Ecography 36:277–286.

Cherel, Y., and N. Klages. 1998. A review of the food of albatrosses. Pages 113–136 Albatross biology and conservation. Surrey Beatty & Sons, Chipping Norton, NSW.

Claramunt, S., and J. Cracraft. 2015. A new time tree reveals Earth history's imprint on the evolution of modern birds. Science Advances 1:e1501005.

Cloyed, C. S., and P. K. Eason. 2017. Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. Royal Society Open Science 4:170060.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138.

Coplen, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Communications in Mass Spectrometry 25:2538–2560.

Costa-Pereira, R., M. Araújo, F. Souza, and T. Ingram. 2019. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. Proceedings of the Royal Society B: Biological Sciences 286:20190369.

Costa-Pereira, R., V. Rudolf, F. Souza, and M. Araújo. 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology 87:1452–1464.

Cursach, J., J. Vilugrón, J. Rau, C. Tobar, and C. Oyarzún. 2022. Islas Caicura (41° S): sitio importante para la reproducción de aves y mamíferos marinos del seno de Reloncaví, sur de Chile. Anales del Instituto de la Patagonia 50:1–13.

Dehnhard, N., H. Achurch, J. Clarke, L. N. Michel, C. Southwell, M. D. Sumner, M. Eens, and L. Emmerson. 2020. High inter□ and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: Generalist foraging as an adaptation to a highly variable environment? Journal of Animal Ecology 89:104–119.

Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. Journal of Evolutionary Biology 9:893–909.

Durell, S. E. A. L. V. D. 2007. Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biological Reviews 75:503–518.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology 73:789–801.

Frere, E., P. Gandini, J. Ruiz, and Y. A. Vilina. 2004. Current status and breeding distribution of Red-legged Cormorant *Phalacrocorax gaimardi* along the chilean coast. Bird Conservation International 14:113–121.

Frere, E., F. Quintana, and P. Gandini. 2005. Cormoranes de la costa patagónica: estado poblacional, ecología y conservación. El hornero 20:35–52.

Frere, E., F. Quintana, P. Gandini, and R. P. Wilson. 2008. Foraging behaviour and habitat partitioning of two sympatric cormorants in Patagonia, Argentina: habitat partitioning of two sympatric cormorants. Ibis 150:558–564.

Furness, R. W., H. M. Wade, A. M. C. Robbins, and E. A. Masden. 2012. Assessing the sensitivity of seabird populations to adverse effects from tidal stream turbines and wave energy devices. ICES Journal of Marine Science 69:1466–1479.

Gandini, P., E. Frere, and F. Quintana. 2005. Feeding Performance and Foraging Area of the Red-Legged Cormorant. Waterbirds 28:41–45.

García-Godos, I. 2001. Patrones morfológicos del otolito sagitta de algunos peces óseos del Mar Peruano. Boletín Instituto del Mar del Perú 20:1–83.

Gaston, K. J., R. G. Davies, C. D. L. Orme, V. A. Olson, G. H. Thomas, T.-S. Ding, P. C. Rasmussen, J. J. Lennon, P. M. Bennett, I. P. F. Owens, and T. M. Blackburn. 2007. Spatial turnover in the global avifauna. Proceedings of the Royal Society B: Biological Sciences 274:1567–1574.

Gause, G. F., O. K. Nastukova, and W. W. Alpatov. 1934. The influence of biologically conditioned media on the growth of a mixed population of *Paramecium caudatum* and *P. aureliax*. Journal of Animal Ecology 3:222–230.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2014. Bayesian data analysis. Chapman & Hall/CRC Boca Raton, FL, USA.

Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's Finches. Science 313:224–226.

Grémillet, D., G. Kuntz, A. J. Woakes, C. Gilbert, J.-P. Robin, Y. Le Maho, and P. J. Butler. 2005. Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. Journal of Experimental Biology 208:4231–4241.

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Harris, M. P., M. F. Leopold, J.-K. Jensen, E. H. Meesters, and S. Wanless. 2015. The winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands. Ibis 157:468–479.

Hartig, F. 2022, September 8. DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. Version 0.4.6.

Heredia-Azuaje, H. J., E. J. Niklitschek, and M. Sepúlveda. 2022. Pinnipeds and salmon farming: Threats, conflicts and challenges to co-existence after 50 years of industrial growth and expansion. Reviews in Aquaculture 14:528–546.

Herman, R. W., F. C. L. Valls, T. Hart, M. V. Petry, W. Z. Trivelpiece, and M. J. Polito. 2017. Seasonal consistency and individual variation in foraging strategies differ among and within (*Pygoscelis*) penguin species in the Antarctic Peninsula region. Marine Biology 164:115.

Humphries, P., G. A. Hyndes, and I. C. Potter. 1992. Comparisons between the diets of distant taxa (teleost and cormorant) in an Australian estuary. Estuaries 15:327.

Ibarra, C., C. Marinao, N. Suárez, and P. Yorio. 2018. Differences between colonies and chick-rearing stages in Imperial Cormorant (*Phalacrocorax atriceps*) diet composition: implications for trophic studies and monitoring. The Wilson Journal of Ornithology 130:224–234.

Ingram, T., R. Costa-Pereira, and M. Araújo. 2018. The dimensionality of individual niche variation. Ecology 99:536–549.

Iriarte, J. L., H. E. González, and L. Nahuelhual. 2010. Patagonian fjord ecosystems in Southern Chile as a highly vulnerable region: problems and needs. AMBIO 39:463–466.

Iriarte, J. L., S. Pantoja, and G. Daneri. 2014. Oceanographic processes in Chilean Fjords of Patagonia: from small to large-scale studies. Progress in Oceanography 129:1–7.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Jessopp, M., G. E. Arneill, M. Nykänen, A. Bennison, and E. Rogan. 2020. Central place foraging drives niche partitioning in seabirds. Oikos 129:1704–1713.

Jiménez, J. E., A. M. Arriagada, F. E. Fontúrbel, P. A. Camus, and M. I. Ávila-Thieme. 2013. Effects of exotic fish farms on bird communities in lake and marine ecosystems. Naturwissenschaften 100:779–787.

Johnson, D. L., M. T. Henderson, D. L. Anderson, T. L. Booms, and C. T. Williams. 2022. Isotopic niche partitioning and individual specialization in an Arctic raptor guild. Oecologia 198:1073–1084.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Kennedy, M., and H. G. Spencer. 2014. Classification of the cormorants of the world. Molecular Phylogenetics and Evolution 79:249–257.

King, D., K. J. Andrews, J. O. King, R. D. Flynt, J. F. Glahn, and J. L. Cummings. 1994. A night-lighting technique for capturing cormorants 65:254–257.

Krietsch, J., S. Hahn, M. Kopp, R. A. Phillips, H. U. Peter, and S. Lisovski. 2017. Consistent variation in individual migration strategies of brown skuas. Marine Ecology Progress Series 578:213–225.

Letten, A. D., P. J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and contemporary niche theory. Ecological Monographs 87:161–177.

Lewke, R. E. 1982. A comparison of foraging behavior among permanent, summer, and winter resident bird groups. The Condor: Ornithological Applications 84:84–90.

Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing.

Manlick, P. J., K. Maldonado, and S. D. Newsome. 2021. Competition shapes individual foraging and survival in a desert rodent ensemble. Journal of Animal Ecology 90:2806–2818.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. 2nd edition. Chapman and Hall, London, U.K.

Morgenthaler, A. 2019. El uso de los recursos tróficos de cuatro especies simpátricas de cormoranes (*Phalacrocorax gaimardi*, *P. magellanicus*, *P. brasilianus* y *P. atriceps*) en la Ría Deseado, provincia de Santa Cruz. Universidad Nacional del Comahue. Centro Regional Universitario Bariloche.

Morgenthaler, A., A. Millones, P. Gandini, D. Procopio, and E. Frere. 2025. Sympatric seabirds: exploring multidimensional niche partitioning among four cormorant species. Marine Ecology Progress Series 752:169–186.

Murray, D. L., J. Gobin, A. Scully, and D. H. Thornton. 2023. Conventional niche overlap measurements are not effective for assessing interspecific competition. Frontiers in Ecology and Evolution 11.

Newsome, S. D., M. T. Clementz, and P. L. Koch. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Marine Mammal Science 26:509–572.

Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Newsome, S. D., J. Yeakel, P. Wheatley, and M. Tinker. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. Journal of Mammalogy 93:329–341.

Newton, I. 2008. The migration ecology of birds. First edition. Academic Press.

Pebesma, E., and R. Bivand. 2023. Spatial data science: with applications in R. Chapman and Hall/CRC, New York.

Pérez-Santos, I., P. Diaz, C. Schwerter, F. Barrera, M. Diaz, T. Matamala, P. Toledo, P. Muñoz, A. Sandoval, S. Arenas, and R. Altamirano. 2022. Plan de Monitoreo Ambiental por potencial impacto al medio ambiente marino, generado por mortalidad de salmones al interior de jaulas del centro de cultivo Caicura de Salmones BLUMAR. Etapa III. Page 229. Centro i~mar, Universidad de Los Lagos, Puerto Montt, Chile.

Pfennig, D. W., and K. S. Pfennig. 2012. Development and evolution of character displacement. Annals of the New York Academy of Sciences 1256:89–107.

Phillips, D. L., R. Inger, S. Bearhop, A. L. Jackson, J. W. Moore, A. C. Parnell, B. X. Semmens, and E. J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835.

Phillips, R. A., S. Lewis, J. González-Solís, and F. Daunt. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecology Progress Series 578:117–150.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71:2141–2145.

Quintana, F., R. Wilson, P. Dell’Arciprete, E. Shepard, and A. G. Laich. 2010. Women from Venus, men from Mars: inter□sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. Oikos 120:350–358.

R Core Team. 2023.R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenblatt, A. E., J. C. Nifong, M. R. Heithaus, F. J. Mazzotti, M. S. Cherkiss, B. M. Jeffery, R. M. Elsey, R. A. Decker, B. R. Silliman, L. J. Guillette, R. H. Lowers, and J. C.

Larson. 2015. Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator. Oecologia 178:5–16.

Roughgarden, J. 1972. Evolution of niche width. American Naturalist:683–718.

Sapoznikow, A., and F. Quintana. 2003. Foraging behavior and feeding locations of Imperial Cormorants and Rock Shag breeding sympatrically in Patagonia, Argentina. Waterbirds 26:184.

Schirmer, A., J. Hoffmann, J. A. Eccard, and M. Dammhahn. 2020. My niche: individual spatial niche specialization affects within- and between-species interactions. Proceedings of the Royal Society B: Biological Sciences 287:20192211.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Searle, S. R. 1987. Linear models for unbalanced data. Wiley, New York (USA).

Sheppard, C., R. Inger, R. Mcdonald, S. Barker, A. Jackson, F. Thompson, E. Vitikainen, M. Cant, and H. Marshall. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecology Letters 21.

Soldatini, C., Y. V. Albores-Barajas, M. Tagliavia, B. Massa, L. Fusani, and V. Canoine. 2015. Effects of human disturbance on cave-nesting seabirds: the case of the storm petrel. Conservation Physiology 3:cov041.

Subpesca. 2023. Estado de la situación de las principales pesquerías chilenas, 2022. Page 137. Subsecretaría de Pesca y Acuicultura, Chile.

Thaxter, C. B., B. Lascelles, K. Sugar, A. S. C. P. Cook, S. Roos, M. Bolton, R. H. W. Langston, and N. H. K. Burton. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biological Conservation 156:53–61.

Toledo, P., E. J. Niklitschek, A. M. Darnaude, F. P. Leiva, C. Harrod, S. Lillo, V. Ojeda, S. Klarian, B. E. Molina-Burgos, and P. Gálvez. 2020. The trophic ecology of partial migration: insights from southern hake *Merluccius australis* off NW Patagonia. ICES Journal of Marine Science 77:1927–1940.

Valladares, F., C. C. Bastias, O. Godoy, E. Granda, and A. Escudero. 2015. Species coexistence in a changing world. Frontiers in Plant Science 6:866.

Van Valen, L. 1965. Morphological variation and width of ecological niche. The American Naturalist 99:377–390.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution 27:244–252.

Violle, C., D. R. Nemergut, Z. Pu, and L. Jiang. 2011. Phylogenetic limiting similarity and competitive exclusion. Ecology Letters 14:782–787.

Ward, A. J. W., M. M. Webster, and P. J. B. Hart. 2006. Intraspecific food competition in fishes. Fish and Fisheries 7:231–261.

Waugh, C. A., and V. Monamy. 2016. Opposing lethal wildlife research when nonlethal methods exist: Scientific whaling as a case study. Journal of Fish and Wildlife Management 7:231–236.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology, Evolution, and Systematics 33:475–505.

Wittenberger, J. F., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Pages 1–78 Avian Biology. Elsevier.

Xavier, J. C., and Y. Cherel. 2021. Cephalopod beak guide for the Southern Ocean: An update on taxonomy (revised edition). British Antarctic Survey, Cambridge, UK.

Yorio, P., L. Pozzi, G. Herrera, G. Punta, W. S. Svagelj, and F. Quintana. 2020. Population trends of Imperial Cormorants (*Leucocarbo atriceps*) in northern coastal Argentine Patagonia over 26 years. Emu - Austral Ornithology 120:114–122.

Zango, L., J. M. Reyes-González, T. Militão, Z. Zajková, E. Álvarez-Alonso, R. Ramos, and J. González-Solís. 2019. Year-round individual specialization in the feeding ecology of a long-lived seabird. Scientific Reports 9:11812.

Zemanova, M. A. 2020. Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods. Wildlife Biology 2020.

Table 1(on next page)

Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) for Red-legged cormorant (*Poikilocarbo gaimardi*) and Imperial shag (*Leucocarbo atriceps*) across four tissue types.

Mean (± SD) stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for the Red-legged cormorant (*Poikilocarbo gaimardi*) and Imperial shag (*Leucocarbo atriceps*) across four tissue types (body feathers, primary feathers, plasma, and red blood cells). Different superscript letters denote differences among tissue types within species, and shaded cells indicate differences between species within each tissue, as determined by the most informative model. Absence of superscript letters indicates no model achieved an AICw > 0.67.

	δ^{13}C		δ^{15}N	
Sample type	*P. gaimardi*	*L. atriceps*	*P. gaimardi*	*L. atriceps*
Feather (body)	-14.33 ± 0.245^{a}	-14.124 ± 0.256^{a}	17.426 ± 0.157^{a}	17.426 ± 0.932
Feather (primary)	-14.48 ± 0.239^{a}	-14.280 ± 0.237^{a}	17.683 ± 0.153^{b}	17.667 ± 0.728
Plasma	-16.197 ± 0.227^{b}	-16.714 ± 0.228^{b}	16.993 ± 0.139^{c}	16.682 ± 0.658
Red blood cells	-15.176 ± 0.227^{c}	-15.561 ± 0.228^{c}	16.537± 0.139^{d}	16.575 ± 0.583

Table 2(on next page)

Total niche width, niche components, individual specialisation, and population niche overlap for Red-legged cormorant (*Poikilocarbo gaimardi*) and Imperial shag (*Leucocarbo atriceps*) during breeding and non-breeding periods.

Total niche width (TNW), within-individual component (WIC), between-individual component (BIC), individual specialisation (IS = BIC/TNW), and percentage of population niche overlap (% Overlap) are presented for the Red-legged cormorant (*Poikilocarbo gaimardi*) and the Imperial shag (*Leucocarbo atriceps*) during both breeding and non-breeding periods at Pirén islet (Los Lagos, Chile). Values represent the mean ± SE, calculated from the posterior distributions of the analysed data. Different superscript letters (a, b) indicate differences between periods within each species. The symbols (triangle, circle) denote differences between species during the non-breeding period, while (diamond , plus) indicate differences between species during the breeding period. The mean posterior distribution determined this. Absence of superscript letters indicates that no differences were found at P > 0.67.

Species	Period	TNW	WIC	BIC	IS=BIC/TNW	% Overlap
P. gaimardi	non-breeding	1.39 ± 0.19$^{a,\blacktriangle}$	1.09 ± 0.16$^{a,\blacktriangle}$	0.30 ± 0.14$^{\blacktriangle}$	0.213 ± 0.08$^{a,\blacktriangle}$	95.7 ± 5.41$^{a,\blacktriangle}$
	breeding	1.09 ± 0.15$^{b,\blacklozenge}$	0.73 ± 0.10$^{b,\blacklozenge}$	0.36 ± 0.14$^{\blacklozenge}$	0.324 ± 0.09$^{b,\blacklozenge}$	89.6 ± 6.97$^{b,\blacklozenge}$
L. atriceps	non-breeding	3.06 ± 0.71$^{a,\bullet}$	1.36 ± 0.29$^{a,\bullet}$	1.70 ± 0.72$^{a,\bullet}$	0.541 ± 0.11$^{a,\bullet}$	48.3 ± 9.39$^{\bullet}$
	breeding	2.19 ± 0.23$^{b,\boldsymbol{+}}$	1.94 ± 0.22$^{b,\boldsymbol{+}}$	0.25 ± 0.11$^{b,\boldsymbol{+}}$	0.112 ± 0.05$^{b,\boldsymbol{+}}$	43.7 ± 5.93$^{\boldsymbol{+}}$

Figure 1

Isotopic niche components of *Poikilocarbo gaimardi* and *Leucocarbo atriceps* during non-breeding and non-breeding periods at Pirén islet, Chile.

Total niche width (TNW), within-individual component (WIC), and between-individual component (BIC) for two species, A) Red-legged cormorant (*Poikilocarbo gaimardi*) and B) Imperial shag (*Leucocarbo atriceps*), during both breeding and non-breeding periods in Pirén islet (Los Lagos, Chile). The figure was constructed using the posterior means of the model parameters; for simplicity, the effects of parameter variability within the posterior distributions are not shown.

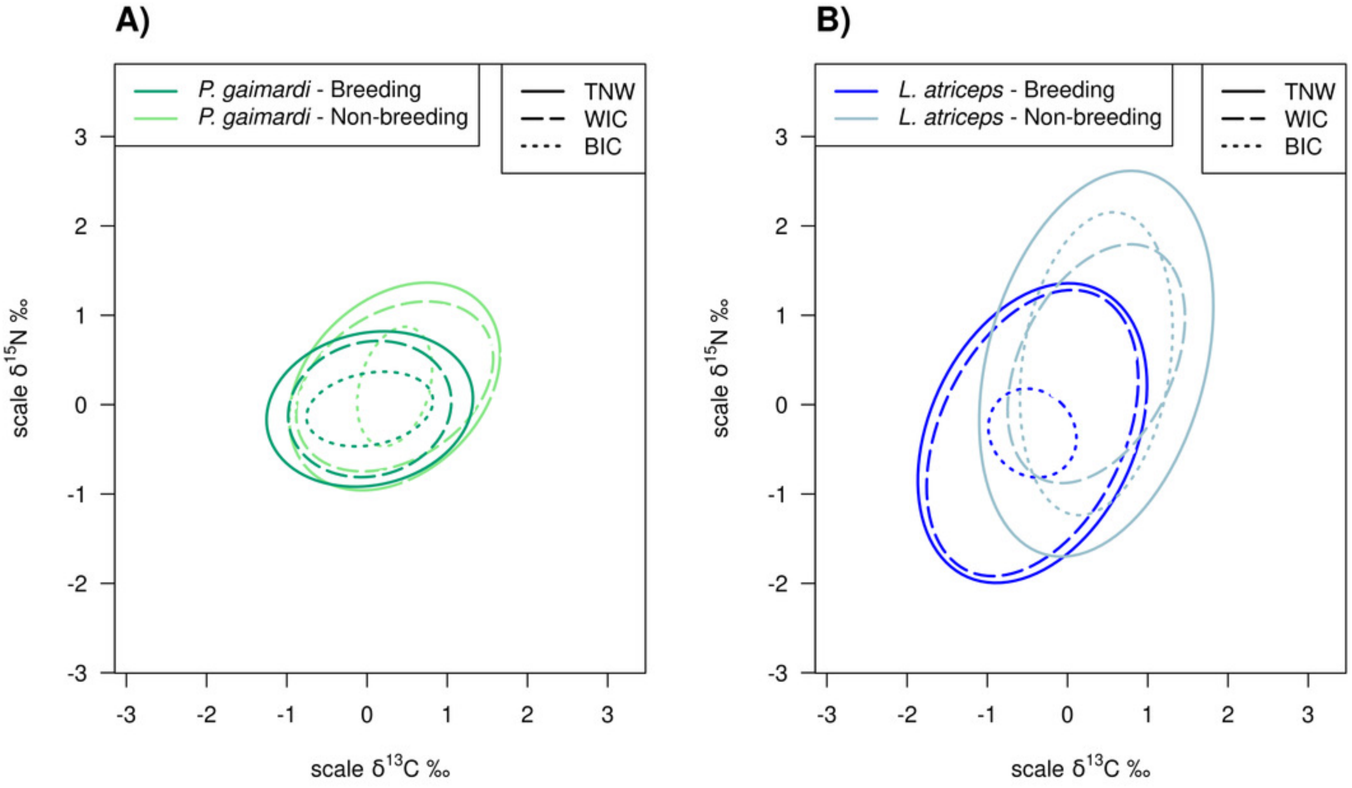

Figure 2

Isotopic niche overlap between *Poikilocarbo gaimardi* and *Leucocarbo atriceps* during breeding and non-breeding periods at Pirén islet, Chile.

Population total niche width (TNW) overlap between Red-legged cormorant (*Poikilocarbo gaimardi*) and Imperial shag (*Leucocarbo atriceps*) during A) breeding and B) non-breeding periods at Pirén islet (Los Lagos, Chile). The figure illustrates the extent of isotopic niche overlap, based on the posterior means of the model parameters; for simplicity, the effects of parameter variability within the posterior distributions are not shown.

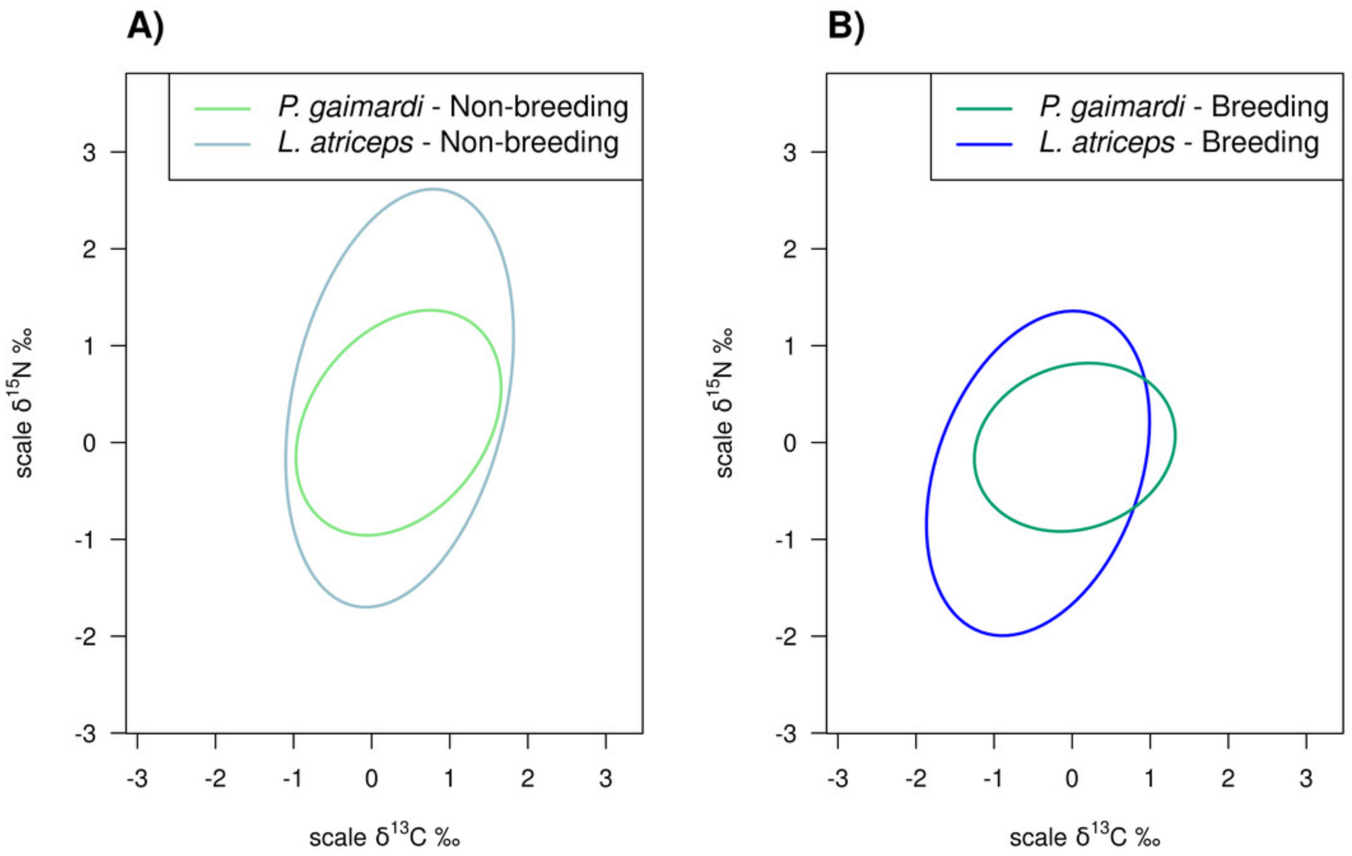

Figure 3

Taxonomic richness, diversity, and competition index of *Poikilocarbo gaimardi* and *Leucocarbo atriceps* during breeding and non-breeding seasons at Pirén islet, Chile.

A) Taxonomic richness (mean ± standard error) and B) diversity (inverse Simpson index, mean ± standard error) of taxa identified in seabird pellets collected at Pirén islet (Los Lagos, Chile) during breeding and non-breeding seasons in 2020 and 2022. C) Mean (± standard deviation) competition index for the Red-legged cormorant (*Poikilocarbo gaimardi*) and D) for the Imperial shag (*Leucocarbo atriceps*) during non-breeding and breeding seasons from 2020 to 2024 at Pirén islet (Los Lagos, Chile).