REVIEW

Testing the niche variation hypothesis in pinnipeds

Valentina FRANCO-TRECU* Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Igua 4225, 11400 Montevideo, Uruguay. Email: vfranco-trecu@fcien.edu.uy Silvina BOTTA Laboratório de Ecologia e Conservação da Megafauna Marinha – EcoMega, Instituto de Oceanografia, Universidade Federal do Rio Grande – FURG, Avenida Italia km8 s/n, Rio Grande, RS 96203900, Brazil. Email: silbotta@gmail.com

Renan C. DE LIMA Laboratório de Ecologia e Conservação da Megafauna Marinha – EcoMega, Instituto de Oceanografia, Universidade Federal do Rio Grande – FURG, Avenida Italia km8 s/n, Rio Grande, RS 96203900, Brazil. Email: renancdl@gmail.com

Javier NEGRETE Departamento de Biología de Predadores Tope, Instituto Antártico Argentino, Av. 25 de Mayo 1143(B1650HMK), San Martin, Buenos Aires, Argentina and Facultad de Ciencias Naturales, Universidad Nacional de La Plata, Av. 122 y 60 S/N (1900), La Plata, Buenos Aires, Argentina. Email: negretejavi@gmail.com

Daniel E. NAYA Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Igua 4225, 11400 Montevideo, Uruguay. Email: dnaya@fcien.edu.uy

Keywords

global, individual trophic specialisation, pinnipeds, stable isotope analysis, total niche width, vibrissae, whiskers

ABSTRACT

- 1. Individual trophic specialisation (ITS) has many important consequences for ecological and evolutionary processes. An old hypothesis highlighting the relevance of ITS is the niche variation hypothesis (NVH), which proposes that populations composed of trophically specialised individuals have a wider population niche than populations composed of more generalist individuals. Pinnipeds are a good model to test the NVH because they are mostly generalist species, living in dense colonies, and exhibiting variation in trophic niche width among populations.
- 2. We tested the NVH in pinnipeds using longitudinal isotopic data: published δ^{13} C and δ^{15} N data obtained from sequential sections of whiskers (vibrissae) from individuals belonging to 14 populations. To the best of our knowledge, this is the first study evaluating the NVH by using longitudinal isotopic data.
- **3**. We compiled studies that published raw data on δ^{13} C and δ^{15} N for pinniped whisker segments to estimate the within-individual and the between-individuals components of variance, the total niche width (TNW), and ITS. One-dimensional (i.e. δ^{13} C or δ^{15} N) and multi-dimensional (i.e. δ^{13} C and δ^{15} N) analyses were used. Also, we tested whether an evolutionary component would affect the degree of ITS among pinniped species with different levels of shared ancestry.
- **4**. Our results indicate that, in line with the NVH, pinniped populations composed of more specialised individuals tend to show wider trophic niches. When analysing each sex separately, the hypothesis is supported for females but not for males.
- **5**. We believe that physiological and behavioural differences between sexes may explain this result. In females, high TNW is mainly related to greater differentiation among individuals, while in males, it is mainly related to high diversity of resources consumed by all individuals.

Palabras clave

amplitud de nicho poblacional, análisis de isótopos estables, bigotes, especialización trófica individual, global, pinnipedos, vibrisas

RESUMEN EN ESPAÑOL

- 1. La especialización trófica individual (ITS) tiene importantes consecuencias en procesos ecológicos y evolutivos. Una antigua hipótesis que destaca la relevancia de ITS es la hipótesis de variación de nicho (HVN), que propone que las poblaciones compuestas por individuos especializados a nivel trófico tienen un nicho poblacional más amplio que aquellas compuestas por individuos generalistas. Los pinnípedos son un buen modelo para probar el HVN ya que, en su mayoría, son especies generalistas que viven en densas colonias y presentan variaciones en la amplitud del nicho trófico entre poblaciones.
- 2. Pusimos a prueba la HVN en pinnípedos por medio de datos isotópicos longitudinales: datos publicados de δ^{13} C y δ^{15} N obtenidos de secciones secuenciales de bigotes (vibrisas) de individuos pertenecientes a 14 poblaciones. Hasta donde sabemos, este es el primer estudio que evalúa la HVN utilizando datos isotópicos longitudinales.
- 3. Recopilamos estudios que publicaron datos de δ^{13} C y δ^{15} N para segmentos de vibrisas en pinnípedos, para estimar los componentes de varianza intra- e inter-individual, el nicho total poblacional (TNW) e ITS. Se utilizaron análisis unidimensionales (cada isótopo por separado, δ^{13} C o δ^{15} N) y multidimensionales (ambos isótopos juntos). También evaluamos si los diferentes niveles de ascendencia entre las especies de pinnípedos afectaron el grado de ITS.
- 4. Nuestros resultados indican que, en línea con la HVN, las poblaciones de pinnípedos compuestas por individuos más especializados tienden a mostrar nichos tróficos poblacionales más amplios. Al analizar cada sexo por separado, la hipótesis es sustentada para hembras pero no para los machos.
- 5. Las diferencias fisiológicas y de comportamiento entre ambos sexos explicarían estos resultados. En las hembras, un amplio TNW se relacionaría principalmente con una mayor diferenciación entre los individuos, mientras que en los machos se relacionaría principalmente con una gran diversidad de recursos consumidos por todos los individuos.

INTRODUCTION

Historically, individuals from the same population have been considered ecologically equivalent (Colwell & Futuyma 1971, Abrams 1980). However, it has become increasingly clear that individuals of many populations cannot be assumed to be homogeneous (Bolnick et al. 2003, Bolnick et al. 2010, Ingram et al. 2018). In an ecological context, diversification among individuals related to their use of different trophic resources is commonly referred to as individual trophic specialisation (ITS). ITS implies that individuals of a single population consume a narrower subset of the resources used by the population as a whole, once the variation related to age, sex, or distinct morphology is removed (Bolnick et al. 2003).

Among-individual variation in ecological attributes (e.g. prey preferences) could have deep consequences for individual fitness (e.g. Cucherousset et al. 2011, Kernaléguen et al. 2016, Costa-Pereira et al. 2019) and can affect population and community dynamics (Bolnick et al. 2003, Quevedo et al. 2009, Araújo et al. 2011, Cloyed & Eason 2016) through several mechanisms (Bolnick et al. 2011). In this sense, trophic specialisation can change the strengths of interspecific interactions and food-web structure, and has many important consequences for ecological and evolutionary processes. These community changes, in turn, can alter the stability, abundance, and extinction risk of populations, as well as the potential for coexistence among species (Araújo et al. 2011, Hart et al. 2016, Costa-Pereira et al. 2018). Moreover, it has been proposed that ITS could affect the ability of a population to cope with environmental disturbances (Okuyama 2008, Vindenes et al. 2008, Araújo et al. 2011), which could be of paramount importance in the current context of global environmental change. Thus, studying trophic variation among individuals can help us understand the ecology and evolution of populations (Bolnick et al. 2003, Bolnick et al. 2011).

An old hypothesis highlighting the relevance of ITS is the niche variation hypothesis (NVH), which proposes that a population's niche expansion is achieved by an increase in resource use variation among individuals (i.e. higher ITS; reflecting a population composed of more specialist individuals, see below; Van Valen 1965. Roughgarden 1972). One potential mechanism to explain the NVH is intra-specific competition; an increase in population abundance leads to top-ranked resources becoming scarce under high competition, making individuals expand their diets towards different and, sometimes, less profitable resources. The emerging pattern is a low dietary overlap among individuals (Svanbäck & Bolnick 2005, Bolnick et al. 2007, Araújo et al. 2011). Decades ago, studies analysing individual specialisation were conducted at the morphological level (Schoener 1986). However, correlation between morphology and diet is often weak or absent, so this approach to testing NVH is not ideal (Werner & Sherry 1987). New techniques to study feeding habits have been used to test the NVH from estimations of resource use variation among individuals, providing contrasting results (Bolnick et al. 2007, Costa et al. 2008, Bison et al. 2015, Cachera et al. 2017, Maldonado et al. 2017). Thus, testing the NVH properly should include a direct estimation of diet diversity at the individual level in relation to population total niche width (TNW; Bolnick et al. 2007).

From an operational perspective, ITS is usually estimated by decomposing the overall variance in the diet of a population (TNW) into two components of variance, the within-individual component (WIC) and the betweenindividuals component (BIC). The ITS is calculated as the ratio between BIC and TNW, which tends to be 1 for populations largely composed of specialist individuals and close to 0 for populations mostly composed of generalist individuals (Roughgarden 1972, 1974, Bolnick et al. 2002).

In the last decades, stable isotope analysis, mainly of carbon (δ^{13} C) and nitrogen (δ^{15} N), has emerged as a key method to investigate trophic habits in wild populations (Forero & Hobson 2003, Perga & Gerdeaux 2005, Crawford et al. 2008). Carbon and nitrogen isotopes are used to estimate the feeding sources and the trophic position, respectively, at different temporal scales, depending on the moment of production and the turnover rate of the tissue analysed (DeNiro & Epstein 1978, 1981, Post 2002, Bearhop et al. 2004). Nutrient source, composition, and characteristics of primary producers, and regional oceanographic phenomena (e.g. occurrence of upwellings) shape isotopic landscapes (Graham et al. 2010) and are propagated up the food web. In the South Atlantic Ocean, for instance, there is an opposite latitudinal trend of $\delta^{13}C$ and $\delta^{15}N$, where Polar and Temperate environments are ¹⁵N-enriched and ¹³C-depleted compared to the Tropics and Subtropics (Graham et al. 2010). Furthermore, a

general and well-known isotopic gradient exists between the ¹³C-enriched coastal/benthic environment, where primary production is based on macrophytes and macroalgae, and the ¹³C-depleted oceanic region, where phytoplankton predominates (Cherel & Hobson 2007).

Considering this, isotopic data from metabolically inert tissues with continuous growth (e.g. tooth dentin or whiskers) represent sequential archives that allow the inference of foraging tactics at the individual level over long periods of time (i.e. Franco-Trecu et al. 2014, Kernalaguen et al. 2015b). Carbon and nitrogen isotopic values obtained from sequentially sampled tissues (i.e. tissues that produce chronologically ordered data) from different individuals belonging to a single population allow the characterisation of the contribution of each individual to the population TNW (Bolnick et al. 2003). In other words, stable isotope analysis of sequential samples of a given tissue permits the estimation of both ITS and TNW (Bolnick et al. 2002, Araújo et al. 2007, Newsome et al. 2007) and, hence, allows the main prediction of the NVH to be tested (i.e. a positive correlation between ITS and TNW). Previous studies testing the NVH through isotope-based metrics used one-dimensional approaches (i.e. evaluated one isotope, Maldonado et al. 2017). However, a multi-dimensional approach was recently proposed (Ingram et al. 2018), which has the advantage of capturing the multi-dimensional nature of the trophic niche (Costa-Pereira et al. 2019, Service et al. 2021).

Pinnipeds are a good model in which to test the NVH for several reasons. First, they are considered generalist species with a diverse diet composition (Smout et al. 2014). Second, their ecological opportunity (i.e. diversity of available resources) should differ among populations, and for this reason, they are expected to exhibit variation in TNW. Third, they usually form large breeding colonies and live in sympatry, which may favour a high degree of intraspecific and inter-specific competition (e.g. Páez-Rosas et al. 2014). In addition, there are several studies using stable isotope analysis in sequential segments of pinnipeds' whiskers aimed at answering various questions associated with trophic ecology and/or estimating the degree of ITS (e.g. Franco-Trecu et al. 2014, Kernalaguen et al. 2015a, b, Botta et al. 2018, Lima et al. 2019, Rosas-Hernández et al. 2019).

We tested the NVH in pinnipeds by using published longitudinal δ^{13} C and δ^{15} N data obtained from sequential sections of whiskers from different populations. Since most pinniped species are sexually dimorphic, for populations where both sexes were sampled, we estimated TNW and ITS for each population–sex level, following the strict definition of individual specialisation (sensu Bolnick et al. 2003). We analysed data from pinniped species with different levels of shared ancestry, so we tested the NVH by using both conventional and phylogenetically informed models. Although ITS is mainly driven by ecological conditions and population size, effects of phylogenetic ancestry may influence the predisposition to diversification in trophic habits among species. We combined the one-dimensional approach, which evaluates each isotope separately, with a recently proposed multi-dimensional approach, which, in our case, integrates information from two isotopes in a single analysis (Ingram et al. 2018). To the best of our knowledge, this is the first study evaluating the NVH by using longitudinal isotopic data (i.e. several sequential measurements for each individual). This is important because this method provides no redundant information on resource use by each individual (in contrast to isotopic data from different tissues), and each sample represents the diet over a fairly large period of time (in contrast to gut content or faecal analysis).

METHODS

Database description

We compiled studies that published raw data on δ^{13} C and δ^{15} N for pinnipeds' whisker segments, by entering the searching terms 'isotop* AND whisker' (or 'vibrissae') in the ISI Web of Science, the Dryad database (https:// datadryad.org/), and the SCAR database (https://data.aad. gov.au/trophic/). Also, we included in our database isotopic data from three Antarctic seal populations (Botta et al. 2018), one fur seal, and one sea lion population (Franco-Trecu et al. 2014, Lima et al. 2019), which were published, but not available in public repositories. In total, we were able to retrieve data for 14 pinniped populations, belonging to six otariid and three phocid species (Table 1). All these populations were sampled at communal sites, where co-specific share terrestrial ground for breeding and aquatic areas for foraging (Table 1, see Appendix S1).

Estimation of individual trophic specialisation

Many pinniped species have a strong sexual dimorphism, with males being much larger than females (Ralls & Mesnick 2009), and trophic segregation between sexes is commonly observed in these species (e.g. Steller sea lion *Eumetopias jubatus*, Hobson et al. 1997; Antarctic fur seals *Arctocephalus gazella*, Kernalaguen et al. 2015b; and South American sea lions *Otaria flavescens*, Drago et al. 2015). Because individuals of different age, sex, or morphology groups are expected to have different niches (Bolnick et al. 2003), the within-individual component of variance (WIC) and the between-individuals component of variance (BIC) were estimated for each population and sex

separately, considering only adult animals. From these values, we estimated the overall isotopic variance (TNW=WIC + BIC) and ITS, following the index proposed by Roughgarden (1974) and here called ITS (BIC/TNW). Pinniped families vary in their whisker growth and retention (e.g. McHuron et al. 2016), so inferences made related to ITS and TNW have different temporal resolutions. For phocids, inferences were made at the intra-annual resolution, while for Otariids, inferences included multiple years.

Multi-dimensional and one-dimensional approaches

Both components of variance (WIC and BIC) and the ITS index were estimated in two different ways. First, by a multi-dimensional analysis, using a generalised linear mixed model, with non-informative priors and 23000 iterations, of which 3000 were burned, where δ^{13} C and δ^{15} N were considered as dimensions (Ingram et al. 2018). We used the R-structure posterior means as the WIC, and the G-structure posterior means as the BIC, assuming the random effect of individuals (see Ingram et al. 2018). Second, we estimated separately for δ^{13} C and δ^{15} N, through the decomposition of variances for each population and sex. We assessed differences between sexes in BIC, WIC, TNW and ITS (multi-dimensional and one-dimensional) by using ANOVAs.

Conventional and phylogenetic analyses

Using multi-dimensional and one-dimensional (δ^{15} N and δ^{13} C) estimations, we assessed the relationship between ITS and TNW via linear models. To evaluate whether phylogenetic relationships between species affected the correlation between ITS and TNW, we also conducted generalised least squares phylogenetic regressions (Grafen 1989). We first built a phylogenetic tree containing the nine species under study based on the phylogenetic tree published by Higdon et al. (2007). Subsequently, we estimated the influence of the phylogeny on ITS by calculating Pagel's λ , optimised using maximum-likelihood transformation. Pagel's λ is a measure of the phylogenetic signal of the residuals of a regression model, which ranges from 0 (no correlation between species) to 1 (correlation between species equal to Brownian expectations; Pagel 1999, Freckleton et al. 2002). Both conventional and phylogenetic analyses were conducted separately for multi-dimensional and one-dimensional estimations ($\delta^{15}N$ and δ^{13} C isotopic values) and were run for three datasets: (1) all sex-population groups, (2) only males, and (3) only females. One population of Arctocephalus gazella (female individuals from Bird Island) that showed an extreme value of TNW was excluded from the analyses to avoid

				Total number of whisker segments (mean±SD per	
Species	Location of population	n Females	n Males	individual)	Source
Arctocephalus pusillus	Kanowna Island, Australia	6	6	722 (60±14)	1
Arctocephalus gazella	Crozet Island, France	10	0	275 (28±6)	2
Arctocephalus gazella	Kerguelen Island, France	10	0	196 (20±5)	2
Arctocephalus gazella	Antarctica	23	0	686 (30±11)	7
Arctocephalus gazella	Marion Island, South Africa	23	0	709 (31±21)	7
Arctocephalus gazella	Bird Island, South Georgia, UK	7	0	105 (13±3)	7
Arctocephalus tropicalis	Crozet Island, France	10	0	312 (32±6)	2
Arctocephalus tropicalis	Amsterdam Island, France	10	0	317 (31±7)	2
Arctocephalus australis	Isla de Lobos, Uruguay	16	13	580 (21±7)	3, 4
Otaria flavescens	Isla de Lobos, Uruguay	5	3	204 (26±10)	3
Zalophus californianus	Isla San Esteban, Mexico	11	0	713 (65±19)	6
Hydrurga leptonyx	Danco Coast, Antarctica	13	20	322 (9±3)	5
Leptonychotes weddellii	Danco Coast, Antarctica	6	8	235 (17±7)	5
Lobodon carcinophaga	Danco Coast, Antarctica	7	4	132 (10±2)	5

Table 1. Numbers of male and female individuals and numbers of whisker segments analysed, for each of 14 pinniped populations, belonging to six otariid and three phocid species. SD, standard deviation

Sources: ¹Kernalaguen et al. (2015a); ²Kernalaguen et al. (2015b); ³Franco-Trecu et al. (2014); ⁴Lima et al. (2019); ⁵Botta et al. (2018); ⁶Rosas-Hernández and Hernández-Camacho (2018); ⁷https://data.aad.gov.au/trophic/ (Scientific Committee on Antarctic Research (2019), Southern Ocean Diet and Energetics Database. doi: 10.26179/5d1aec22f41d5).

model overfitting (see Appendix S2). All the analyses were performed in the free software R (R Core Team 2020), using the packages MCMCglmm 2.32 (Hadfield 2010), phytools 1.0.1 (Revell 2012), caper 1.0.1 (Orme et al. 2018), nlme 3.1.152 (Pinheiro et al. 2022), and phangorn 2.8.1 (Schliep 2011).

Null model construction

Given that a positive relationship between ITS and TNW could emerge due to co-variation effects (since BIC is comprised within TNW and ITS), a null model in which each individual fed randomly from the pool of resources available in its respective population-sex group was generated (Bolnick et al. 2002, 2007). For that purpose, we followed a procedure that decouples the identity of each individual from the columns with its isotopic values, generating a new matrix where $\delta^{15}N$ and $\delta^{13}C$ values of different whisker portions were randomly assigned to each individual. Replicating this procedure 1000 times for each population-sex group (resampling without replacement), we estimated mean values of WIC, BIC, TNW, and ITS (with multi-dimensional and one-dimensional methods). Both conventional and phylogenetic analyses were conducted separately between simulated ITS and observed TNW, to evaluate whether the observed ITS was not greater than expected by chance (Zaccarelli et al. 2013). Then, we assessed the overlap between the slope of the null model and the slope of the observed data based on their 95% confidence intervals.

RESULTS

Considering all the population-sex groups, the range of values estimated by the multi-dimensional method was 0.22–2.06 for TNW and 0.13–0.76 for ITS. As for δ^{15} N, one-dimensional analysis ranges were 0.69-17.29 for TNW and 0.55–0.98 for ITS (see Appendix S3). There were no differences between sexes for the WIC, BIC, TNW, and ITS estimates obtained by multi- and one-dimensional approaches (see Appendices S4-S6). ITS values estimated by the multi-dimensional method increased with TNW at the population-sex level (Fig. 1a). Similar results were found for δ^{15} N in the one-dimensional analysis (Fig. 1b), but not for $\delta^{13}C$ (Tables 2 and 3). Null model slopes did not differ from zero (multi-dimensional analysis: P = 0.67, one-dimensional δ^{15} N: P = 0.82, and onedimensional δ^{13} C: P = 0.09; see Table 2). In addition, observed values of ITS were not included in the 95% confidence interval (Fig. 1a,b), confirming that the positive relationship between observed ITS and TNW was not an artefact.

Regarding differences between sexes, ITS and TNW were unrelated in males in both the multi-dimensional and the one-dimensional analysis (Table 2). By contrast, a significant and positive correlation between ITS and TNW was observed for females in the multi-dimensional analysis and for δ^{15} N in the one-dimensional analysis (explaining 34% and 45% of overall variance, respectively; see Table 2). Phylogenetic analyses were congruent with conventional ones, indicating a positive and significant correlation between ITS and TNW, both in the multi-dimensional analysis and for δ^{15} N in the one-dimensional analysis, for all sex–population groups, and for females (Table 3). A positive and significant correlation between ITS and TNW for δ^{13} C in males was also detected (Table 3).

DISCUSSION

The results presented here provide empirical support for the NVH, showing that pinniped populations with wider trophic niches are composed of more trophically distinct individuals. Specifically, the trophic component of the niche represented by the variance of δ^{15} N values showed a strong positive correlation with the level of ITS, and this was particularly true for females. These results agree with the prediction by Bolnick et al. (2007) that the NVH probably holds for many animal populations.

One-dimensional analyses clearly indicate that, in our case, a positive relationship exists between ITS and TNW for $\delta^{15}N$ values. This, in turn, suggests that individual diversification associated with a larger TNW is driven by variation in trophic level of prey, which is related to the prey species or size of prey consumed. Most pinnipeds are generalists, and the diversity of potential prey means that individuals can diverge in relation to the trophic level of prey they consume, increasing the TNW in this niche axis (Sánchez-Hernández et al. 2021). The diet of otariid species includes prey from different trophic levels, ranging from decapod species (shrimp and lobsters) to predatory fish (e.g. largehead hairtail Trichiurus lepturus; Franco-Trecu et al. 2013, Cárdenas-Alayza et al. 2022); even seabirds have been documented as prey (e.g. Machado et al. 2021). Thus, knowing the origin of variation among

individuals is important for understanding the ecology of populations and communities (Bolnick et al. 2003, Bolnick et al. 2011, Costa-Pereira et al. 2019).

Male and female pinnipeds differ in their reproductive behaviour, which could affect trophic habits in the sexes (i.e. Drago et al. 2015, Lima et al. 2021). Specifically, males do not experience limitations associated with rearing pups, and hence, after a short reproductive period, they are free to use feeding areas that are far from the reproductive colonies. In phocids, lactation is continuous and short (days or weeks), but otariid females perform foraging trips during lactation, which usually lasts between 4 and 12 months (Schulz & Bowen 2005), restricting foraging grounds to areas that are close to the breeding colony (Le Boeuf et al. 2000, Meynier et al. 2008). Lactation and pup care in otariid females tend to result in increased foraging site fidelity because breeding females are only able to visit one or a few food patches during each foraging trip, thus preventing a relationship between TNW and potential diversification in the environments used for feeding. This diversification would be reflected in δ^{13} C values. In addition, the high energetic costs of lactation in pinnipeds (Schulz & Bowen 2005) could raise the need for food consumption in females during a significant part of the year, producing a stronger intra-specific competition among females than among males. In line with these biological differences between sexes, we found that the regression model constructed for females explained more variance than the model that included both sexes (multi-dimensional: 34% for females, 27% for both sexes; $\delta^{15}N$ onedimensional: 45% for females, 31% for both sexes). Conversely, the relationship between ITS and TNW



Fig. 1. Relationship between individual trophic specialisation index (ITS) and total niche width (TNW), estimated by the multi-dimensional method (a), and by the one-dimensional method for δ^{15} N data (b). Estimations based on observed data are shown with a dashed line, whereas estimations based on the null model are shown with a solid line. Females are shown with stars and males with dots.

Table 2. Linear models between indices of individual trophic specialisation (ITS) and total niche width (TNW), obtained in multi-dimensional and onedimensional analyses (δ 13C and δ 15N), for each observed and simulated (null model) dataset. Slope values are presented with associated standard errors in parentheses, *P*-values, and R^2

		Multi-dimensional			One-dimensional $\delta^{15}N$			One-dimensional δ^{13} C		
Dataset	n*	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value	R ²
Observed sex-population group	18	0.17 (0.07)	0.02	0.27	0.01 (0.004)	0.008	0.31	0	0.87	0.06
Null sex-population group	18	0	0.67	0.06	0	0.693	0.05	0	0.12	0.09
Observed females	12	0.21 (0.08)	0.03	0.34	0.01 (0.003)	0.007	0.45	0	0.41	0.03
Null females	12	0	0.07	0.22	0	0.42	0.03	0	0.38	0.01
Observed males	6	0.11 (0.13)	0.46	0.07	0.01 (0.01)	0.34	0.03	0.03 (0.02)	0.14	0.32
Null males	6	0	0.81	0.23	0	0.31	0.01	-0.01 (0.006)	0.21	0.20

*One-dimensional δ^{15} N estimations have a value of n+1 because the data available for Zalophus californianus females were only for δ^{15} N.

Table 3. Phylogenetic analyses of the relationship between indexes of individual trophic specialisation (ITS) and total niche width (TNW), obtained by multi- and one-dimensional analyses (δ 13C and δ 15N), for each observed and simulated (null model) dataset. Slope values are presented with associated standard error in parentheses, *P*-values, and Pagel's λ

		Multi-dimensional		One-dimensional $\delta^{15}N$			One-dimensional δ^{13} C			
Dataset	n*	Slope	P-value	λ	slope	P-value	λ	slope	P-value	λ
Observed sex-population group	18	0.18 (0.06)	0.01	0.61	0.01 (0.004)	0.02	0.17	0	0.94	0.07
Null sex-population group	18	0	0.96	0.40	0	0.93	0.26	0	0.06	0.61
Observed females	12	0.14 (0.07)	0.06	0.94	0.01 (0.002)	0.007	0.47	0	0.43	0.32
Null females	12	0	0.16	0.69	0	0.59	0.41	0	0.22	0.43
Observed males	6	0.09 (0.12)	0.52	0.35	0.02 (0.01)	0.09	0.41	0.04 (0.01)	0.05	0.88
Null males	6	0	0.55	1.00	-0.01 (0.005)	0.07	0.62	-0.01 (0.005)	0.09	0.61

*One-dimensional $\delta^{15}N$ estimations have a value of n+1 because only $\delta^{15}N$ data were available for female Zalopus californianus.

assessed only for males was not significant for any isotope. However, the lower number of populations including males (n = 6) than those with females (n = 13) in our dataset, as well as the lower mean sample size for male populations (see Table 1), could affect the output of the statistical tests that were conducted. More studies analysing trophic habits using stable isotopes in whiskers of male pinnipeds are desirable.

Phylogenetically informed analyses were, in general, congruent with conventional ones, which was expected since ITS varies dynamically with environmental conditions (e.g. food availability) as well as with population attributes (e.g. density). However, phylogenetic analyses revealed an important phylogenetic signal in δ^{13} C in males (λ value of 0.88) associated with a positive and significant relationship between ITS and TNW for this isotope and sex. We suspect that, in agreement with the between-sex differences discussed above, if males are less limited in the duration of their foraging trips than females, they can reduce their diet overlap by foraging in different areas. This, in turn, may result in males of a single population consuming prey from different habitats (e.g. offshore, coastal, and estuarine).

Although a bias towards the publication of positive results is likely to exist (so that the occurrence of individual specialisation prevails among published articles), many studies confirm that individuals' niches are often much narrower than population niches (Bolnick et al. 2003, 2010). This is consistent with the hypothesis of Bolnick et al. (2003), which states that individual specialisation is substantial and common in natural populations. In turn, ITS appears to have a large impact on TNW (Bison et al. 2015, Maldonado et al. 2017), as predicted by the NVH and as shown here by using longitudinal isotopic data from various pinniped species and populations. Future work should focus on the identification of the ecological and environmental drivers of the relationship between ITS and TNW (e.g. population size, ecological opportunity, or diet diversity of each population). Understanding these drivers will enhance our understanding of the mechanisms behind this relationship (i.e. intra-specific or inter-specific competition) and, hence, understanding of the role of individual specialisation communities within and ecosystems.

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DATA AVAILABILITY STATEMENT

Data from our study are freely available online as Supporting Information (Appendix S7).

REFERENCES

- Abrams P (1980) Some comments on measuring niche overlap. *Ecology* 6: 44–49.
- Araújo MS, Bolnick DI, Machado G, Giaretta AA, Reis SF (2007) Using δ 13C stable isotopes to quantify individuallevel diet variation. *Oecologia* 152: 643–654.
- Araújo MS, Layman C, Bolnick DI (2011) The ecological causes of individual specialization. *Ecology Letters* 14: 948–958.
- Bearhop S, Adams CE, Waldrons S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007–1012.
- Bison M, Ibanez S, Redjadj C, Boyer F, Coissac E, Miquel C et al. (2015) Upscaling the niche variation hypothesis from the intra- to the inter-specific level. *Oecologia* 179: 835–842.
- Bolnick, DI, Amarasekare, P, Araújo, MS, Bürger, R, Levine, JM, Novak, M, Rudolf, VH, Schreiber, SJ, Urban, MC, Vasseur, D (2011) Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* 26: 183–192.
- Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (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.
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28.
- Bolnick DI, Svänback R, Araújo MS, Persson L (2007) More generalized populations are also more heterogeneous:

comparative support for the niche variation hypothesis. *Proceedings of the National Academy of Sciences* 104: 10075–10079.

- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. *Ecology* 83: 2936–2941.
- Botta S, Secchi ER, Rogers TL, Prado JHF, de Lima RC, Carlini P, Negrete J (2018) Isotopic niche overlap and partition among three Antarctic seals from the Western Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography* 149: 240–249.
- Cachera M, Ernande B, Villanueva MC, Lefebvre S (2017) Individual diet variation in a marine fish assemblage: Optimal Foraging Theory, Niche Variation Hypothesis and functional identity. *Journal of Sea Research* 120: 60–71.
- Cherel Y, Hobson KA (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.
- Cloyed CS, Eason PK (2016) Different ecological conditions support individual specialization in closely related, ecologically similar species. *Evolutionary Ecology* 30: 379–400.
- Colwell RK, Futuyma DJ (1971) On the measurement of niche breath and overlap. *Ecology* 52: 567–576.
- Costa GC, Mesquita DO, Colli GR, Vitt LJ (2008) Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages? *American Naturalist* 172: 868–877.
- Costa-Pereira R, Rudolf VHW, Souza FL, Araújo MS (2018) Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology* 87: 1452–1464.
- Costa-Pereira R, Toscano B, Souza FL, Ingram T, Araújo MS (2019) Individual niche trajectories drive fitness variation. *Functional Ecology* 33: 1–12.
- Crawford K, McDonald RA, Bearhop S (2008) Applications of stable isotope techniques to the ecology of mammals. *Mammal Review* 38: 87–107.
- Cucherousset J, Acou A, Blanchet S, Britton R, Beaumont W, Gozlan R (2011) Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. *Oecologia* 167: 75–84.
- Cárdenas-Alayza S, Torres D, Gutiérrez D, Tremblay Y (2022) Resource partitioning as a mechanism for trophic segregation in sympatric otariids from the productive upwelling Peruvian Humboldt Current System. *Austral Ecology* 47: 775–790.
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506.
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341–351.

- Drago M, Franco-Trecu V, Zenteno L, Szteren D, Crespo EA, Riet Sapriza FG, de Oliveira L, Machado R, Inchausti P (2015) Sexual foraging segregation in South American sea lions increases during the pre-breeding period in the La Plata River. *Marine Ecology Progress Series* 525: 261–272.
- Forero MG, Hobson KA (2003) Using stable isotopes of nitrogen and carbon to study seabird ecology: applications in the Mediterranean seabird community. *Scientia Marina* 67: 23–32.
- Franco-Trecu V, Aurioles-Gamboa D, Inchausti P (2014) Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids. *Marine Biology* 161: 609–618.
- Franco-Trecu V, Drago M, Riet-Sapriza FG, Parnell A, Frau R, Inchasuti P (2013) Bias in diet determination: incorporating traditional methods in Bayesian mixing models. *PLoS One* 8(11): e80019.
- Freckleton RP, Harvey PH, Pagel MA (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160: 712–726. https://doi. org/10.1086/343873
- Grafen A (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society B* 326: 119–157.
- Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles-Gamboa D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes – Understanding Movement, Pattern,* and Process on Earth Through Isotope Mapping, 299–318. Springer, the Netherlands.
- Hadfield JD (2010) MCMC Methods for multi-response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software* 33: 22.
- Hart SP, Schreiber SJ, Levine JM (2016) How variation between individuals affects species coexistence. *Ecology Letters* 19: 825–838.
- Higdon JW, Bininda-Emonds ORP, Beck RMD, Ferguson SH (2007) Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology* 7: 216.
- Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigation trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Marine Mammal Science* 13: 114–132.
- Ingram T, Costa-Pereira R, Araújo MS (2018) The dimensionality of individual niche variation. *Ecology* 99: 536–549.
- Kernalaguen L, Arnould J, Guinet C, Cherel Y (2015a) Determinants of individual foraging specialisation in large marine vertebrates, the Antarctic and Subantarctic fur seals. *Journal of Animal Ecology* 84: 4.
- Kernalaguen L, Cherel Y, Knox T, Baylis A, Arnould J (2015b) Sexual niche segregation and gender-specific

individual specialisation in a highly dimorphic marine mammal. *PLoS One* 10: e0133018.

- Kernaléguen L, Cherel Y, Guinet C, Arnould JPY. (2016) Mating success and body condition not related to foraging specializations in male fur seals. *Royal Society Open Science* 3: 160143.
- Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS (2000) Foraging ecology of northern elephant seals. *Ecological Monography* 70: 353–382.
- Lima R, Franco-Trecu V, Carrasco TS, Inchausti P, Secchi E, Botta S (2021) Segregation of diets by sex and individual in South American fur seals. *Aquatic Ecology* 56: 1–17.
- Lima R, Franco-Trecu V, Vales D, Inchausti P, Secchi E, Botta S (2019) Individual foraging specialization and sexual niche segregation in South American fur seals. *Marine Biology* 166: 32–44.
- Machado R, Perez MS, Arús BA, de Lima R, Botta S, Valiati VH, Oliveira LR, Carlos CJ (2021) Penguin predation by extra-limital sub-Antarctic fur seals *Arctocephalus tropicalis*. *Polar Biology* 44: 2321–2327.
- Maldonado K, Bozinovic F, Newsome SD, Sabat P (2017) Testing the niche variation hypothesis in a community of passerine birds. *Ecology* 98: 903–908.
- McHuron EA, Walcott SM, Zeligs J, Skrovan S, Costa DP, Reichmuth C (2016) Whisker growth dynamics in two North Pacific pinnipeds: implications for determining foraging ecology from stable isotope analysis. *Ecology Progress Series* 554: 213–224.
- Meynier L, Morel PCH, Chilvers BL, Mackenzie DDS, MacGibbon A, Duignan PJ (2008) Temporal and sex differences in the blubber fatty acid profiles of the New Zealand sea lion *Phocarctos hookeri*. *Marine Ecology Progress Series* 366: 271–279.
- Newsome SD, Martinez del Rio C, Bearhop S, Phillip DL (2007) A niche for isotopic ecology. *Frontiers in Ecological Environmental* 5: 429–436.
- Okuyama T (2008) Individual behavioral variation in predator-prey models. *Ecological Research* 23: 665–671.
- Orme D, Freckleton RP, Thomas GH, Petzoldt T, Fritz SA, Isaac N (2018) CAPER: comparative analyses of phylogenetics and evolution in R. *Methods in Ecology and Evolution* 3: 145–151.
- Pagel MC (1999) The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology* 48: 612–622.
- Perga MC, Gerdeaux D (2005) 'Are fish what they eat' all year round? *Oecologia* 144: 598–606.
- Pinheiro J, Bates D, R Core Team. (2022) nlme: Linear and Nonlinear Models. R package version 3.1-157, https:// CRAN.R-project.org/package=nlme
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718. https://doi.org/10.2307/3071875

- Páez-Rosas D, Rodríguez-Pérez M, Riofrío-Lazo M (2014) Competition influence in the segregation of the trophic niche of otariids: a case study using isotopic bayesian mixing models in Galapagos pinnipeds. *Rapid Communications in Mass Spectrometry* 28: 2550–2558.
- Quevedo M, Svanbäck R, Eklov P (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology* 90: 2263–2274. https://doi. org/10.1890/07-1580.1
- R Core Team (2020) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3–900051–07-0
- Ralls K, Mesnick S (2009) Sexual dimorphism. In: Perrin WF, Wuersig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*, 1005–1011. Academic Press, Amsterdam, the Netherlands and Boston, USA.
- Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x
- Rosas-Hernández MP, Aurioles-Gamboa D, Hernández-Camacho CJ (2019) Specialized foraging habits of adult female California sea lions Zalophus californianus. Marine Mammal Science 35: 1463–1488. https://doi.org/10.1111/ mms.12603
- Rosas-Hernández MP, Hernández-Camacho C (2018) Differences in the isotopic niche and trophic position of female California Sea Lions (*Zalophus californianus*) in distinct oceanographic conditions. *Aquatic Mammals* 44: 374–388.
- Roughgarden J (1972) Evolution of niche width. American Naturalist 106: 683–718.
- Roughgarden J (1974) Niche width: biogeographic patterns among Anolis lizard populations. American Naturalist 108: 429–442.
- Sánchez-Hernández J, Hayden B, Harrod C, Kahilainen KK (2021) Population niche breadth and individual trophic specialisation of fish along a climate-productivity gradient. *Reviews in Fish Biology and Fisheries* 31: 1025–1043.
- Schliep KP (2011) phangorn: phylogenetic analysis in R. Bioinformatics 27: 592–593. https://doi.org/10.1093/bioin formatics/btq706
- Schoener TW (1986) A brief history of optimal foraging ecology. In: Kamil AC, Drebs JR, Pulliam HR (eds) *Foraging Behavior*, 5–67. Springer, New York, USA.
- Schulz TM, Bowen DW (2005) The evolution of lactation strategies in pinnipeds: a phylogenetic analysis. *Ecological Monographs* 75: 159–177.
- Scientific Committee on Antarctic Research. (2019) Southern ocean diet and energetics database. https://doi. org/10.26179/5d1aec22f41d5
- Service C, Ingram T, Reimchen T, Darimont C (2021) Intrapopulation foraging niche variation between

phenotypes and genotypes of spirit bear populations. *Ecology and Evolution* 11: 5025–5037.

- Smout S, Rindorf A, Hammond P, Harwood J, Matthiopoulos J (2014) Modelling prey consumption and switching by UKgrey seals. *ICES Journal of Marine Science* 71: 81–89.
- Svanbäck R, Bolnick DI (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research* 7: 993–1012.
- Van Valen L (1965) Morphological variation and width of ecological niche. American Naturalist 99: 377–390.
- Vindenes Y, Engen S, Saether BE (2008) Individual heterogeneity in vital parameters and demographic stochasticity. *American Naturalist* 171: 455–467. https:// doi.org/10.1086/528965
- Werner TK, Sherry TW (1987) Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's Finch" of Cocos Island, Costa Rica. *Proceedings of the National Academy of Sciences* 84: 5506–5510.
- Zaccarelli N, Bolnick DI, Mancinelli G (2013) RInSp: an R package for the analysis of individual specialization in resource use. *Methods in Ecology and Evolution* 4: 1–6.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Map with distribution of pinniped populations' localities used in this study.

Appendix S2. Relationship between individual trophic specialization index (ITS) and total niche width (TNW) estimated by multidimensional methods, including the estimation for the population of *A. gazella* from Bird Island (females).

Appendix S3. Components of niche variance – within individual component (WIC), between individuals component (BIC), and total niche width (TNW = BIC+WIC)

- and trophic specialisation index (ITS = BIC/TNW), obtained by multi- and one-dimensional analyses, for each population and sex group.

Appendix S4. Results of ANOVA between sexes for the different estimates.

Appendix S5. Component of variance (BIC and WIC) related to TNW estimated by multi-dimensional analysis for all sex–group populations.

Appendix S6. Component of variance (BIC and WIC) related to TNW estimated to δ^{15} N by one-dimensional analysis for all sex–group populations.

Appendix S7. Carbon and nitrogen isotopic values of whiskers of South American fur seal (*Arctocephalus australis*) and sea lion (*Otaria flavescens*) from Uruguay, and Antarctic seals (*Hydrurga leptonyx, Leptonychotes weddellii* and *Lobodon carcinophaga*).