**Individual Specialization in a Generalist Apex Predator: The Leopard Seal**

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**Abstract**

1. Apex predators are typically considered dietary generalists; often masking individual variability. However, individual specialization—consistent differences in diet and foraging strategies among individuals— is common in apex predators. In some species, only a few specialized individuals can significantly impact prey populations.
2. Leopard seals (*Hydrurga leptonyx*) are apex predators important to the structure and function of the Southern Ocean ecosystem. Leopard seals are broadly described as generalists, but little is known about their trophic ecology at the population or individual level.
3. We analyzed δ13C and δ15N profiles in whiskers (n=46) from 34 leopard seals from an important aggregation in the Western Antarctic Peninsula to assess population and individual trophic variation. We also evaluated individual consistency across years using repeat samples from 7 seals collected over 2-10 years. We compared population and individual isotopic niche space and explored drivers of intraspecific variation in leopard seal trophic ecology.
4. We find that leopard seals have a broad trophic niche (range: 6.96-15.21‰) and are generalists at the population level. However, most individuals are specialists (59% for δ15N and δ13C), with only a few generalists (13% for δ15N, 6% for δ13C). Furthermore, individual seals specialize at different trophic levels, resulting in niche partitioning. Most variation in trophic ecology is driven by individual specialization, but sex and mass also contribute. We also find that some seals specialize over time, consistently foraging at the same trophic level, while others switch trophic levels within and between years.
5. Long-term specialization by only a few leopard seals has likely contributed to the decline of a significant local mesopredator colony; the Antarctic fur seal. Our findings show the importance of examining individual specialization in leopard seals across their range to understand their impact on other prey populations. More broadly, this approach should be applied to other apex predator populations, as a few specialists can significantly impact ecosystems.

**Keywords:** foraging strategies, generalist, individual variation, intraspecific competition, niche variation, specialist

**Introduction**

Classifying species as foraging specialists or generalists can mask individual variability, as individuals within a species, or even within populations, are often not ecologically equivalent (Bolnick et al., 2002; Bearhop et al., 2004; Woo et al., 2008; McPeek and Siepielski, 2019). Specialist species have a narrow niche, where individuals consume the same resources with little intraspecific variation (Figure 1A). In contrast, generalist species have a broad niche, consuming a wide range of resources. Generalist populations may consist of: (1) individual specialists that use different resources with little within-individual but high between-individual variation (Figure 1B), (2) individual generalists that consume a wide variety of resources with high within-individual variation (Figure 1C), or (3) a mix of individual specialists and generalists (Figure 1D; Bolnick et al., 2003; Araújo et al., 2011; Hückstädt et al., 2012).

Life history and ecological factors influence intraspecific variation in foraging patterns (Estes et al., 2003; Tinker et al., 2008; Rosenblatt et al., 2015; Jory et al., 2021). For example, foraging patterns vary with sex (Lewis et al., 2006; Elorriaga-Verplancken et al., 2013; Kernaléguen et al., 2015; Balme et al., 2020), age class (Polis, 1984; Thiemann et al., 2007; Balme et al., 2020), location (Staniland et al., 2010; Corman et al., 2016), and/or morphology (Thiemann et al., 2011; Balme et al., 2020; Lewis et al., 2022). Animals can also show ‘individual specialization’, which refers to individuals that show consistent differences in diet and foraging strategies independent of their life history and morphology (Bolnick et al., 2003; Toscano et al., 2016). High intraspecific variation reduces competition and enhances population stability during resource fluctuations (Bearhop et al., 2004; Svanbäck and Bolnick, 2007; Toscano et al., 2016). Therefore, identifying specialization patterns at both the population and individual level is crucial for evaluating local and species-wide patterns of resource use and ecological adaptability.

Many apex predators are considered generalists due to their broad dietary niches at the population level (Matich et al., 2011; Kim et al., 2012; Vejřík et al., 2023). However, these apex predator populations are often composed of a mix of both specialists and generalists, as documented in sharks (Matich et al., 2011), orcas (Baird et al., 1992; Williams et al., 2004), leopards (Voigt et al., 2018; Balme et al., 2020), wolves (Darimont et al., 2009), cheetahs (Voigt et al., 2014), and polar bears (Thiemann et al., 2011; Sciullo et al., 2017; King, 2024). Individual specialization among apex predators, known for their high energetic demands and foraging efficiency, can significantly impact prey populations, especially when these predators consistently target specific prey species (Williams et al., 2004; Krause et al., 2022). Even a small number of specialist individuals can lead to prey population declines (Williams et al., 2004; Pagano et al., 2018; Krause et al., 2022).

Leopard seals (*Hydrurga leptonyx*) are important apex predators in the Southern Ocean. They are described as generalists because of their diverse diet that includes endothermic mesopredators (e.g., penguins, other seal species) and ectothermic prey (e.g., Antarctic fish, krill, and cephalopods; Krause et al., 2015, 2020). They are also known to exert top-down pressure on prey populations, including Antarctic fur seals (AFS; *Arctocephalus gazella*; Boveng et al., 1998; Schwarz et al., 2013; Krause et al., 2022) and various penguin species (Ainley et al., 2005; Forcada et al., 2009; Krause et al., 2020).

Cape Shirreff on Livingston Island off the Western Antarctic Peninsula (WAP) is a key feeding ground for leopard seals; it’s home to several penguin colonies and the southernmost and regionally-largest AFS breeding colony (Hucke-Gaete et al., 2004). At Cape Shirreff, leopard seals have driven a rapid decline of the AFS population, with an annual average predation rate of ~70% for AFS pups during this study (Vera et al., 2005; Krause et al., 2022). These leopard seals us a variety of specialized prey-hunting tactics, including stalking, ambushing, and kleptoparasitism (Hiruki et al., 1999; Krause et al., 2015). Despite having access to the same prey resources at Cape Shirreff, single-point analysis of scat and stable isotope signatures of blood show that these leopard seals show intraspecific variation in diet (Krause et al., 2020; Sperou et al., 2023). Recent work also shows that leopard seal diets vary with sex and body size, with larger females targeting AFS pups and foraging at higher trophic-levels than males (Krause et al., 2015, 2020; Sperou et al., 2023). This size advantage may allow large females to specialize and target higher trophic level prey compared to conspecifics (Thiemann et al., 2007; Kernaléguen et al., 2015). Therefore, we predict that leopard seals at Cape Shirreff are generalists at the population level but exhibit individual specialization at different trophic levels.

Here, we used stable isotope signatures to investigate population and individual niche width and assess individual specialization in leopard seals. Nitrogen and carbon isotope analyses (ẟ15N and ẟ13C) are commonly used to assess a species’ trophic ecology. ẟ13C reflects the source of primary production (e.g., marine vs. terrestrial, pelagic vs. benthic), whereas ẟ15N reflects the trophic level at which individuals forage (Gannes et al., 1998; Tykot, 2004). Obtaining individual-level data on niche width requires the use of accretionary tissues that grow through time (e.g., whiskers, claws, bone, teeth; Bearhop et al., 2004; Elorriaga-Verplancken et al., 2013; Newsome et al., 2015; Eisenmann et al., 2016; Rogers et al., 2020; Lewis et al., 2022; Charapata and Trumble, 2023). We used leopard seal whiskers to generate time series data from the same individual, representing diet signatures over periods ranging from months to a year. We then compared isotopic signatures between and within individuals to identify the degree of individual specialization and determine the population and individual niche width (Voigt et al., 2018; Johnson et al., 2022). Using the largest long-term dataset of isotopic data on leopard seal to date, we asked the following questions: (1) What patterns of trophic specialization do leopard seals show at the population and individual level? (2) How do phenotypic attributes (e.g., sex, mass) influence trophic foraging patterns? (3) Do leopard seals exhibit consistent specialization patterns over time?

**Methods**

*Sample Collection*

Leopard seals were sampled between January and May from 2013 to 2023 at the U.S. Antarctic Marine Living Resources (AMLR) Program ecological monitoring site at Cape Shirreff, Livingston Island in the WAP. Leopard seals were sedated (Pussini and Goebel, 2015; Krause et al., 2016) to allow for the collection of morphometric data (standard length [cm], girths, and mass [kg]), life history traits (sex, age class), and whiskers. Whiskers were collected from 34 leopard seals (28 females, 6 males). Seven females were opportunistically resampled without a full capture (i.e., morphometric data were not collected) 1-3 times after their first handling, resulting in 12 additional whisker samples. In total, we analyzed 46 whiskers (40 females, 6 males). A subset of these whiskers (n=18 from field seasons 2018 and 2019) were previously analyzed by (Charapata et al., 2023).

*Stable Isotope Analysis (SIA)*

Whiskers were wiped with 1:1 ethanol:methanol solvent, sonicated for 30 mins in distilled water, and air dried. Whiskers were measured and sectioned into 0.5-3 mm increments (from root to tip) for a targeted weight of ~0.3 mg (Charapata et al., 2023). Carbon and nitrogen stable isotope analysis was performed at Baylor University using an Elemental Analyzer 4010 Elemental Combustion System paired with a Conflow IV interphase (Thermo Scientific) and Thermo Delta V Advantage continuous flow Isotope Ratio Mass Spectrometer. Whisker nitrogen (ẟ15N) and carbon (ẟ13C) isotope values are expressed in delta notation (ẟ) in units of per mil (‰). Additionally, isotope values are reported as the ratio of the heavy to light isotope relative to international standards--atmospheric nitrogen and Vienna Peedee Belemnite, respectively--using the following equation:

ẟX = [(Rsample/Rstandard) – 1]\*1000

where X is the 13C or 15N and R is the corresponding ratio of 13C/12C or 15N/14N. A two-point calibration curve for calculating ẟ15N and ẟ13C values of samples was established using USGS-40 and USGS-41A international standards. The accuracy and precision of isotopic measurements were calculated based on the long-term mean and standard deviation (SD) of 244 replicates of an internal lab standard (Acetanilide, reported ẟ13C =−29.53±0.01‰, ẟ15N=1.18±0.02‰) measured during each analytical run (n=3 replicates/run). The replicate grand averages obtained were very close to (ẟ13C=−29.42±0.08‰) or within the range (ẟ15N=1.30±0.17‰) of analytical uncertainty of reported values. We measured the atomic C:N ratio for every whisker segment with acceptable atomic ratios ranging from 3.0-4.0 (Newsome et al., 2009; Kernaléguen et al., 2012; Charapata et al., 2023). Nearly all whisker segments had acceptable atomic C:N ratios (3.53±0.14, range: 2.9-4.0). Twelve whisker segments were excluded for having ratios outside this range.

*Time Stamping*

Leopard seals molt and shed their whiskers annually; therefore, whiskers represent growth over a few months and up to one year (Rogers et al., 2016). We timestamped whisker segments based on leopard seal whisker growth characteristics using the Von Bertalanffy growth model (von Bertalanffy, 1938; Rogers et al., 2016) following the approach outlined by (Charapata et al., 2023).

*Data Analysis*

All data were tested for normality and homogeneity of variance before analysis. Results are reported as mean ± standard deviation (SD) unless otherwise stated. We performed all analyses using R (R Core Team, 2022) with RStudio (Team, 2021) and JMP (SAS).

*Population-Level*

Population-level analyses included a total of 46 leopard seal whiskers. Each whisker was treated separately based on preliminary data showing inter-annual isotopic variability. We calculated the population-level mean, SD, and range of δ15N and δ13C values. We used variance component analysis (VCA) to calculate between- and within-individual population variation. Total variance in stable isotopes (“between individuals” variation) indicates variation among individuals in a population, while variance in stable isotopes along the whisker (“within-individual” variation) indicates variation of an individual (Bearhop et al., 2004; Newsome et al., 2009; Hückstädt et al., 2012). We applied the Stable Isotope Bayesian Ellipses in R *SIBER* package (Jackson et al., 2011) to determine population isotopic niche width. We used the standard ellipse area corrected for small sample sizes (SEAc) for individual whisker(s) as the metric for calculating the population isotopic niche area. We also calculated a population-level SEAc and total area (TA) using the pooled δ15N and δ13C values from all whisker segments (n = 46 whiskers; 2,198 segments) to compare our results with a previous study on leopard seals (Botta et al., 2018).

*Individual Specialization*

We used two approaches to evaluate the isotopic variation at the individual level. First, we calculated individual isotopic niche with SEAc and TA estimates for each individual’s whisker(s) using the δ15N and δ13C values of the whisker segments; this allowed us to visualize and assess each individual’s range of trophic levels and foraging locations collectively. Next, we calculated δ15N and δ13C specialization indices for each whisker to describe the variance in δ15N and δ13C and calculate the degree of individual specialization (Bolnick et al., 2002; Lewis et al., 2022); this allowed us to separately assess the variation in δ15N and δ13C. The degree of specialization was calculated using the equation:

SI = INW/ (INW + BINW)

Where SI is the specialization index, INW is the individual niche width, and BINW is the between-individual niche width. Individuals that occupied over 50% of the total isotopic niche width (TNW = INW + BINW; (Roughgarden, 1972) were classified as generalists (SI>0.5). Individuals that occupied less than 30% of the total niche width were classified as specialists (SI<0.3; Bolnick et al., 2003; Hückstädt et al., 2012; Newsome et al., 2015; Lewis et al., 2022). Individuals that occupied between 30-50% of the total niche width (0.3<SI<0.5) were classified as intermediates (Lewis et al., 2022).

### Within the δ15N specialist category, some individuals consistently exhibited high δ15N values, while others consistently had medium to low values. Therefore, we performed agglomerative hierarchical clustering to determine whether there were subgroups within our δ15N specialist isotope data using the ‘agnes’ function in the R package *cluster* (Kaufman and Rousseeuw, 2009). To determine the optimal number of clusters, we used the Dunn index, which differentiates between sets of clusters that are compact and well separated (Supplementary Figure 1A). We found two distinct clusters (Supplementary Figure 1B): high trophic level specialists (H-Specialist) and medium to low trophic level specialists (ML-Specialist).

*Trophic Variation & Overlap*

We examined variation and niche overlap in isotopic signatures as a function of sex, body mass, and degree of individual specialization. We focused these analyses solely on δ15N because (1) we were interested in trophic level variability, and (2) leopard seals from Cape Shirreff tend to remain in the near-shore habitat and are primarily coastal foragers (Krause et al., 2015; Kienle et al., 2022b). To investigate variation in δ15N, we ran a linear mixed-effects model (LMM; (Pinheiro and Bates, 2000) using the ‘lmer’ function from the *lme4* package (Bates et al., 2014). This model treated the average δ15N values as response variables with sex, mass, the interaction of sex and mass, and δ15N specialization category (H-Specialist; ML-Specialist; Intermediate; Generalist) as fixed effects and individual as a random effect. Model selection was performed using the R package *MuMIn* (Barton and Barton, 2015) based on the smallest Akaike information criterion corrected for sample size (AICc). The model with the lowest AICc had the highest support, and models with ΔAICc < 2 were considered to have substantial support (Anderson and Burnham, 2002; Franklin et al., 2002). Goodness-of-fit for each model was estimated using marginal (R² LMM(m)) and conditional (R² LMM(c)) coefficients of determination, indicating variance explained by fixed effects alone and by both fixed and random effects, respectively (Nakagawa and Schielzeth, 2013). We examined the contribution of each fixed effect of our top models by looking at the estimated coefficients and p-values and then used ANOVAs on each of our top models. Pairwise comparisons were performed using the ‘emmeans’function from the *emmeans* package with Tukey adjustment for multiple testing δ15N and δ13C (Lenth and Others, 2022). We also used Spearmen’s correlation to assess the relationship between our continuous variables (average δ15N, mass) and the relationship between mass and individual niche width (SEAc). We assessed niche differences and overlap between δ15N specialization categories and sexes using the proportion of paired SEAc shared; this was calculated with the ‘maxLikOverlap*’* function from the *SIBER* package (Jackson et al., 2011).

*Between-Year Variability*

To evaluate between-year variability among repeat individuals (n=7), we used *SIBER* to visualize data and quantify percent overlap between isotopic niches, assessing the similarity/dissimilarity in isotopic composition between years for each individual. We also used a quadratic discriminant analysis (QDA) to simultaneously evaluate δ13C and δ15N (Koehler et al., 2019; Smith et al., 2021). QDA is appropriate for analyzing data that are unequally sampled across years and have unequal variance; this allowed us to effectively assign isotope signatures to specific years for each seal. We considered QDA to be unsuccessful in assigning individual isotope data to their respective years if the results were ≤ 70% (Koehler et al., 2019; Smith et al., 2021), suggesting that the data was too similar to accurately assign it to specific years.

*Temporal Changes*

To investigate yearly and monthly trends in δ15N data, we used generalized additive models (GAMs) with isotopic signatures of whisker segments as the response variable. Year and month from timestamped whiskers were used as temporal predictors, with individual as a random effect, using the formula: δ15N ~ s(Months, k = 10, bs = "cc") + s(Year, k = 10, bs = "tp") + s(Individual.ID, bs = "re"). The “s” represents the smooth functions and “k” represents the number of basis functions used in the smoothing function. For month we used a cyclic spline (bs = 'cc') and for year a thin plate regression spline (bs='tr'; (Wood, 2003). GAMs and corresponding model estimates were conducted using the *mgcv* and *modelbased* R packages (Wood, 2017; Makowski et al., 2020). We evaluated isotopic linear temporal fluctuations in significant variables by using a grid approximation, accompanied by CI 95% (Makowski et al., 2020). Because our dataset is overrepresented in some years/months and underrepresented in others, we created a customized prediction grid based on GAM models fitted on the observed data. The conditional expectations generated by the simulated homogeneous dataset (i.e. simulated data for all years and months for all Individual.ID) allowed parameter estimation using the fitted model. The predicted values were used to calculate the first derivative of the response variable and estimate the linear slope of the isotopic signatures to identify the temporal windows where significant linear increase or decrease of isotopic values occurred in time.

**Results**

We sectioned 46 whiskers and analyzed 2,198 segments for δ13C and δ15N (Table 1). The average number of segments per whisker was 48.5±17.6 (range: 6-90 segments). Timestamped whiskers represented 99.5±52 days (range: 19-286 days), which is consistent with previous estimates (max ~1 year) of leopard seal whisker growth (Rogers et al., 2016; Charapata et al., 2023).

*Population-Level*

Leopard seals were classified as a generalist population, with a large population-level SEAc of 3.35‰² and TA of 39.82‰². Mean δ13C whisker isotopic signature was -21.93±0.8‰ (range: -24.76 to -18.71‰), and mean δ15N was 11.46±1.53‰ (range: 6.49 to 15.21‰). Between-individual variability was higher than within-individual variability in both δ13C (53% vs. 47%, respectively) and δ15N (58% vs. 42%, respectively).

*Individual Specialization*

Our two approaches to assess specialization (i.e., individual isotopic widths and specialization index) showed that most individuals were specialists (Table 1; Figure 2-3). The mean individual SEAc was 1.12±0.65‰² (range: 0.23-3.28‰²). The mean TA was 4.16±2.13‰² (range: 0.26-9.93‰²). The results of our specialization index and individual isotopic width analysis were consistent: individuals with SEAc values >2 were identified as δ15N or δ13C generalists, while those with SEAc values <1 were classified as δ15N or δ13C specialists.

Based on the δ15N specialization index, 59% of leopard seals (n=27) were specialists, 28% (n=13) were intermediates, and 13% (n=6) were generalists (Figure 2A), with specialists showing little δ15N isotopic variation and generalists exhibiting high δ15N isotopic variation (Figure 2B). Within the δ15N specialists, there were two separate clusters: H-Specialists and ML-Specialists. 13 seals were H-Specialists (mean δ15N=12.90±0.42‰; range: 10.26-15.21‰). 14 seals were ML-Specialists (mean δ15N=11.19±0.54‰; range: 8.39-13.41‰). The δ15N intermediates had a mean δ15N of 10.95±1.10‰ (range: 6.95-14.28‰), and δ15N generalists had a mean δ15N of 10.74±1.15‰ (range: 6.49-14.04‰). A similar pattern was observed for δ13C: 54% (n=25) were specialists, 37% (n=17) were intermediates, and 6% (n=3) were generalists.

The isotopic niche spaces for all individuals, classified by their respective δ15N specialization categories, are shown in Figure 3.

*Trophic Variation & Overlap*

Our top models showed that δ15N varied by sex, mass, δ15N specialization category, and individual (Supplementary Table 1-2). Our top model had an R² (c) of 0.58 and an R² (m) of 0.92, indicating that individual accounted for a significant portion of the model variation. The results of our top models and overlap analysis are detailed below:

1. *δ15N Specialization*. Mean δ15N differed between specialization categories (F3,17.37=23.01, p<0.001). H-Specialists had a higher δ15N (12.90±0.4‰; p<0.001) compared to other groups. ML-Specialists had the next highest δ15N (11.19±0.56‰), followed by intermediates (10.95±1.0‰) and generalists (10.74±1.15‰). Isotopic niche areas, SEAc, and TA values, were the smallest for H-Specialists (SEAc=0.49; TA=1.05‰²) and largest for generalists (SEAc=2.55‰²; TA=2.80‰²; Figure 2A, Figure 3). There was no niche overlap between H-Specialists and other groups. However, ML-Specialists, intermediates, and generalists showed 27-95% overlap (Figure 2A).
2. *Sex differences.* Mean δ15N varied with sex (F1,30.66=11.84; p=0.001). Females had higher δ15N values (11.71±1.39‰) than males (9.92 ± 1.46‰; F1,2197 = 423.3, p < 0.001). The TA was larger in females (6.24‰²) than males (1.69‰²) and driven primarily by δ15N (Supplementary Figure 2A). Females had a slightly smaller SEAc (1.44‰²) compared to males (1.91‰²). Females showed greater inter-individual variation in isotopic niche (individual δ15N means from 9.4 to 13.63‰; δ13C means from -23.26 to -20.74‰) compared to males (individual δ15N means from 8.37 to 10.99‰, δ13C means from -22.74 to -21.51‰). Isotopic niche overlap between males and females was small (range: 7.5-10.0%; Supplementary Figure 2A).
3. *Body Mass.* Mean δ15N varied with mass (F1,5.04=8.84; p=0.03). Larger seals had higher δ15N values than smaller seals (R²=0.28, p<0.05; Supplementary Figure 2B). We found a positive association between δ15N and mass for females (Spearman's ρ=0.40, S=4259.2, p=0.01) and males (Spearman's ρ=0.829, S=6, p=0.05). Lastly, we found a negative relationship between mass and SEAc, with larger individuals having smaller SEAc values than smaller individuals (F1,39=10.3, p=0.002; Supplementary Figure 2C).

*Between-Year Variability*

Between-year variability exhibited two distinct patterns (Figure 4; Supplementary Figure 3). Some seals had consistent foraging patterns. These seals had high overlap in isotopic niche space between years, making assigning isotopic values by year challenging. For example, seal 397 had high isotopic niche overlap over a 10-year period (54%, [23%-91%]; Figure 4) and QDA was unsuccessful (<70%) at assigning isotopic values to different years (45%, [28-60%], Supplementary Table 3-4). Conversely, other seals showed considerable variability in foraging patterns between years. These seals showed little to no overlap in isotopic niche space; this allowed us to successfully assign their isotopic values to different years. For example, seal 12 showed no overlap between years, and QDA was successful at assigning isotopic values to the correct year (96%, [92-100%], Figure 4, Supplementary Table 3-4).

*Temporal Trends*

Temporal variation in δ15N was non-linear. There was a significant non-linear δ15N variation explained by year (F6.95, 7.81 = 7.03, p < 0.001) but not by months (Supplementary Table 4). Year explained some model variance (0.42 [95% CI: 0.31-1.37]). However, most of the model variance (1.30 [95% CI: 0.91-1.4]) was from the random effect (F42.34, 45 = 51.43, p < 0.001), representing intraspecific variability. Analytic estimation of the first derivative calculated from the grid approximation showed temporal windows of significant linear decrease and increase in δ15N throughout the years (Figure 5). From these significant temporal windows, we highlight the decline of δ15N from early 2015 to mid-2017 calculated by our estimation (linear slope = -0.8, CI95% [-1.15-0.44]).

**Discussion**

Individual specialization in apex predators can shape ecosystems by impacting prey populations and resource use. Leopard seals at Cape Shirreff are a generalist population predominantly composed of individual specialists. They show clear niche partitioning between specialization categories (i.e., specialists, intermediates, generalists) and consistent overlap among individuals within those categories. Individual differences are the primary driver of intraspecific variation in leopard seal trophic ecology, but life history traits (i.e., sex, mass) also affect trophic variability. Additionally, some leopard seals consistently specialize across years, while others switch between specialization patterns across years. This is the first study to evaluate individual foraging patterns in leopard seals over extended periods (days to years) using the largest time-series dataset available for this apex predator. As such, our results advance our understanding of apex predators’ trophic ecology at both the population and individual levels, contributing to broader insights into their ecological role. Our findings emphasize the importance of individual diet assessments for apex predators, as only a few individuals disproportionately impact specific prey.

*Population and Individual-Level*

Leopard seals are described as generalist predators due to their diverse diet (Hall-Aspland and Rogers, 2004; Botta et al., 2018; Krause et al., 2020). Our population-level results at Cape Shirreff show leopard seals occupy a broad isotopic niche, primarily driven by their wide range in δ15N values. This finding complements dietary studies showing that leopard seals at Cape Shirreff consume diverse prey, including AFS, penguins, fish, cephalopods, and krill (Krause et al., 2020).

However, like many other apex predators, leopard seals exhibit a high degree of individual specialization. At Cape Shirreff, most (87%) of leopard seals are δ15N specialists or intermediates, while only a few are true δ15N generalists (13%). Consequently, individual leopard seals have relatively narrow niche widths, despite the population having a large overall niche width. Furthermore, among the δ15N specialists, leopard seals show resource partitioning; some specialize on high trophic-level prey, while others specialize on medium-to-low trophic-level prey. The high trophic-level specialists are likely foraging on AFS pups and/or large notothen fish, while the medium-to-low specialists are likely foraging on penguins, cephalopods, fish, or krill (Botta et al., 2018; Krause et al., 2020). This partitioning likely reduces direct competition among individuals and enhances individual foraging efficiency. As we hypothesized, leopard seals at Cape Shirreff collectively have a large population isotopic niche, but exhibit a high degree of individual specialization, leading to relatively narrow and overlapping niches with distinct partitioning between trophic groups.

*Drivers of Individual Specialization*

Resource diversity and competition are known to influence the development of individual-based specialized foraging strategies in many predators (Estes et al., 2003; Layman et al., 2007; Darimont et al., 2009; Weise et al., 2010; Manlick et al., 2021). For example, some Asian predators (e.g., dholes, leopards, tigers) exhibit specialization in prey-rich areas but prey shift in areas with limited resources (Steinmetz et al., 2021). Similarly, we find that individual specialization explains most of the intraspecific variation in leopard seal trophic ecology. We suggest that specialization by leopard seals at Cape Shirreff is driven by the combination of a prey-rich environment and intraspecific competition for high trophic-level prey.

During the study period (2011-2020), Cape Shirreff was home to ~20 seasonal-resident leopard seals (range: 11-41), primarily adult females, with peak numbers in the austral summer (Krause et al., 2022). Despite the variety of prey available around Cape Shirreff, leopard seals appear to preferentially target energy-rich, endothermic prey, such as AFS pups and fledging penguins (Spitz et al., 2014; Krause et al., 2015; Raga et al., 2015; Hinke et al., 2019; Lu et al., 2021). These prey are easily available during the mesopredators' breeding season, driving resource competition among leopard seals and the adoption of individual foraging strategies. To capture prey, leopard seals employ a variety of specialized hunting tactics (Hiruki et al., 1999; Krause et al., 2015) and large adult females often outcompete smaller individuals and even steal prey from conspecifics (Krause et al., 2015, 2020; Sperou et al., 2023). For instance, seal 397, a large adult female, has the highest observed capture rate of AFS pups using an intertidal ambush technique, while other leopard seals simultaneously employed different tactics to target other prey (Krause et al., 2015). Intraspecific competition for these energy-rich resources likely facilitates individual specialization and widens the leopard seals’ trophic niche.

In many apex predators larger individuals (often males) have more varied diets and consume higher trophic-level prey than smaller individuals (Thiemann et al., 2007, 2011; Kernaléguen et al., 2015; Voigt et al., 2018; de Lima et al., 2019; Balme et al., 2020). Similar patterns have been described in leopard seals, where the larger sex (females) outcompete smaller individuals of both sexes, especially in competition for large endothermic prey (Krause et al., 2015, 2020; Sperou et al., 2023). At Cape Shirreff, all larger seals are females, resulting in sex-based differences in trophic level and minimal overlap between sexes. Females occupy a broader isotopic space, forage on higher trophic-level prey, and are more often specialists compared to males. Moreover, all high trophic-level specialists in this study were female. Therefore, larger body sizes seem to provide access to a wider array of higher quality prey (Svanbäck and Bolnick, 2007; Araújo et al., 2011; Balme et al., 2020; Kienle et al., 2022a; Lewis et al., 2022; this study).

Further south in the WAP, Botta et al. (2018) examined leopard seals’ isotopic niche at Danco Coast. Similar to this study, the authors showed that leopard seals had a broad population-level isotopic niche width and that some individual seals consistently had high or low δ15N values along their whiskers (Botta et al., 2018). However, Danco Coast leopard seals occupied lower trophic-levels (mean δ15N = 8.9‰, range: 6.6-12.0‰) compared to Cape Shirreff seals (11.46‰, range: 6.4-15.2‰). This is likely due to prey differences. At Danco Coast, leopard seals are primarily consuming low trophic-level prey (e.g., krill, cephalopods, small fish; Casaux et al., 2009; Botta et al., 2018). In comparison, Cape Shirreff offers greater prey diversity and abundance of higher trophic-level prey (Krause et al., 2020). Additionally, our study included mostly females, while Botta et al. (2018) mostly included male. Therefore, in addition to prey availability, the trophic-level differences between leopard seals at Cape Shirreff and Danco Coast may also be due to sex (and size) differences between the two aggregations.

*Long-Term Specialization*

Some leopard seals are extremely consistent in their foraging patterns, while others are highly flexible. For example, adult female seal 397 remained a high trophic-level specialist over a 10-year period (this study), and primarily targeted AFS pups (Krause et al., 2015). Conversely, adult female seal 12 switched from a high trophic-level specialist to a medium-to-low trophic-level specialist to a generalist over a 5-year period. Similar patterns have been documented in other marine predators (McHuron et al., 2018). For instance, southern rockhopper penguins (*Eudyptes chrysocome*) change diets seasonally, acting as specialists during pre-breeding and generalists during pre-molt (Dehnhard et al., 2016). In other species, individual specialization persists over longer periods. For example, southern elephant seals (*Mirounga leonina*), show consistent foraging patterns within and between years (Hückstädt et al., 2012). Alternatively, some species show a lot of variability. In California sea lions (Zalophus californianus), individuals remain consistent in their diet while others switch diets annually due to ecological shifts (McHuron et al., 2018). Overall, marine predators can range from consistent specialists to flexible generalists.

Foraging strategy variability may buffer populations against rapid environmental changes. In northern elephant seals (*Mirounga angustirostris*), females with high site fidelity to particular foraging locations had higher foraging success in average climate conditions; however, females with weak fidelity outperformed females with strong fidelity during anomalous climate conditions (Abrahms et al., 2018). This suggests that maintaining multiple strategies within a population, such as individual generalists and specialists, can have population-level benefits (Winemiller, 1989; Codron et al., 2012; Abrahms et al., 2018; McHuron et al., 2018). Specifically, intraspecific variability found in leopard seals at Cape Shirreff may provide resilience to the changing ecosystem of the WAP.

Long-term specialization by an apex predator can lead to sustained impacts on prey populations. At Cape Shirreff, leopard seals specializing on AFS pups have been proposed as the primary driver of the catastrophic decline in the local AFS population (Krause et al., 2022). Our study supports this hypothesis. First, we find that large adult females at Cape Shirreff are primarily high trophic level specialists. Second, some of these females show multi-year patterns of specialization on AFS. Our findings match those described for orcas (*Orcinus orca*). Williams et al. (2004) estimated that a pod of five orcas specializing on sea otters could kill 8,500 otters annually. Their model showed that if only ~4% of the 170 orca individuals around the Aleutian archipelago specialized on sea otters, they could drive the sea otters to extinction within 3-4 months (Williams et al., 2004). Likewise, at Cape Shirreff, only ~20 individual leopard seals are responsible for the population collapse of AFS since 2007 (Krause et al., 2022).

Looking across our study period, we also note that leopard seals at Cape Shirreff experienced a significant population-level decline in δ15N values between 2015 and 2017. This decline in δ15N coincides with a decrease in the AFS population (Krause et al., 2022) and the two penguin species, gentoo (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarcticus*), found breeding at this location (Hinke et al., 2019). Therefore, this decrease in δ15N may have been caused by a decline in nitrogen rich prey. Between 2017-2023, sightings of leopard seals at Cape Shirreff decreased by 76% (Krause et al., 2024; Woodman et al., 2024). This substantial drop in leopard seal numbers may explain the more recent increase in δ15N values (2018-2023), as reduced competition has allowed the few remaining leopard seals (e.g., seal 397) to continue specializing on the remaining high trophic-level prey. Although previous studies have analyzed the isotopic values of available prey at Cape Shirreff (Krause et al., 2020), shifts in δ15N could also be influenced by changes in other ecological factors and variations at the base of the food web (Queirós et al., 2024). Nevertheless, together, these findings highlight the complexity of predator-prey dynamics and emphasize the importance of concurrently monitoring predator and prey populations to understand ecosystem-level processes.

*Conclusions*

Apex predators play a crucial role in shaping ecosystem dynamics, often exerting substantial influence on prey populations and resource distribution through their trophic interactions. The leopard seal population at Cape Shirreff demonstrates this influence, as it is composed mostly of individual specialists, with a few generalists. Long-term patterns of high trophic-level specialization have likely led to the decline of the AFS population at Cape Shirreff. Our study provides a compelling explanation for the dramatic impact a few specialist apex predator individuals can have on prey populations. While we focused on a single location, genetic studies on this aggregation indicate that it may be representative of the species (Bender et al., 2023), for which most populations appear to be genetically connected (Davis et al., 2008). Leopard seals are distributed across the Southern Ocean, including South America, Australia, and New Zealand (Hupman et al., 2020; Borras-Chavez et al., 2024), requiring future research to examine the degree of specialization across the species' range and how this impacts local prey populations. Our findings have far-reaching implications, as many current ecosystem management and conservation strategies assume that most apex predators are generalists and that individuals exert similar effects on prey populations. However, if specialization patterns consistently vary among individuals, uniform conservation and management strategies could lead to unintended consequences in many ecosystems. This research is essential given the uncertain prey abundance for these predators in the face of changing climate conditions.

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**Tables**

**Table 1.** Summary of isotopic values for leopard seals (34 individuals, 46 whiskers) categorized based on the δ15N category: high trophic-level specialist (H-Specialist), medium-to-low trophic-level specialist (ML-Specialist), intermediate, and generalist. '*n*' is the number of whisker segments analyzed. ‘SEAc’ is the standard ellipse area corrected for small sample sizes for each individual’s whisker(s). Seals with an asterisk (\*) were sampled in multiple years.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| ID | Sex | Year | *n* | *δ*15N | SD | Range | *δ*13C | SD | Range | SEAc ‰² |
| H-Specialist | | | | | | | | | | |
| 9 | F | 2014 | 51 | 12.94 | 0.89 | 10.88-14.21 | -21.79 | 0.46 | -22.83 to -20.94 | 1.16 |
| 12\* | F | 2018 | 61 | 13.14 | 0.63 | 10.88-13.87 | -21.41 | 0.19 | -21.98 to -20.92 | 0.29 |
| 57\* | F | 2018 | 45 | 13.13 | 0.83 | 10.92-14.05 | -21.36 | 0.27 | -22.13 to -20.82 | 0.57 |
| F | 2023 | 6 | 13.16 | 0.30 | 12.69-13.63 | -21.67 | 0.23 | -21.87 to -21.26 | 0.23 |
| 84\* | F | 2017 | 26 | 13.23 | 0.28 | 12.64-13.82 | -21.68 | 0.29 | -22.49 to -21.37 | 0.26 |
| 128\* | F | 2014 | 44 | 12.58 | 0.28 | 12.02-13.66 | -20.81 | 0.44 | -22.78 to -20.37 | 0.38 |
| 394 | F | 2013 | 22 | 13.34 | 0.49 | 12.12-13.92 | -21.14 | 0.30 | -21.94 to -20.68 | 0.43 |
| 397\* | F | 2014 | 77 | 12.27 | 0.65 | 11.01-13.97 | -22.11 | 0.54 | -23.30 to -21.30 | 1.00 |
| F | 2018 | 46 | 12.55 | 0.41 | 11.66-13.49 | -21.69 | 0.46 | -23.06 to -20.97 | 0.57 |
| F | 2019 | 62 | 12.47 | 0.31 | 11.02-12.97 | -21.56 | 0.59 | -23.82 to -20.87 | 0.48 |
| F | 2023 | 49 | 12.63 | 0.45 | 11.64-13.62 | -21.60 | 0.50 | -23.03 to -20.89 | 0.73 |
| 406\* | F | 2013 | 71 | 13.63 | 0.57 | 12.35-15.21 | -21.02 | 0.40 | -22.30 to -18.71 | 0.63 |
| 422 | F | 2013 | 59 | 12.26 | 0.76 | 10.26-13.43 | -21.16 | 0.40 | -22.85 to -20.47 | 0.93 |
| ML-Specialist | | | | | | | | | | |
| 12\* | F | 2013 | 47 | 10.98 | 0.93 | 8.60-12.26 | -21.29 | 0.38 | -22.73 to -20.77 | 1.15 |
| 16 | F | 2014 | 36 | 11.67 | 0.85 | 10.22-13.41 | -22.14 | 0.32 | -22.85 to -21.51 | 0.75 |
| 37\* | F | 2019 | 47 | 11.45 | 0.56 | 9.78-12.47 | -21.43 | 0.59 | -22.96 to -20.56 | 1.02 |
| F | 2023 | 35 | 11.67 | 0.73 | 10.17-13.36 | -22.02 | 0.50 | -23.26 to -21.35 | 1.18 |
| 63 | F | 2014 | 52 | 11.08 | 0.73 | 8.51-12.56 | -21.87 | 0.55 | -22.80 to -20.81 | 1.21 |
| 84\* | F | 2014 | 23 | 11.07 | 0.89 | 9.92-12.61 | -22.55 | 0.47 | -23.09 to -21.59 | 0.82 |
| 120 | M | 2017 | 18 | 10.98 | 0.41 | 10.06-11.78 | -21.54 | 0.35 | -22.60 to -21.03 | 0.48 |
| 143 | F | 2018 | 29 | 10.31 | 0.87 | 8.93-12.53 | -22.39 | 0.27 | -23.06 to -21.90 | 0.69 |
| 144 | M | 2018 | 44 | 10.70 | 0.97 | 8.65-12.29 | -21.97 | 0.60 | -23.11 to -20.92 | 0.82 |
| 145 | F | 2018 | 64 | 11.85 | 0.79 | 10.17-13.11 | -22.91 | 0.60 | -23.69 to -21.69 | 1.20 |
| 153 | F | 2019 | 48 | 11.60 | 0.75 | 10.48-13.38 | -21.98 | 0.58 | -22.87 to -20.82 | 0.93 |
| 158 | F | 2019 | 44 | 11.98 | 0.59 | 10.51-12.90 | -21.48 | 0.24 | -22.19 to -20.98 | 0.43 |
| 159 | F | 2019 | 43 | 11.27 | 0.64 | 9.70-12.69 | -22.16 | 0.65 | -23.20 to -21.02 | 1.19 |
| 162 | F | 2019 | 74 | 10.07 | 0.77 | 8.39-11.81 | -23.14 | 0.56 | -24.76 to -21.89 | 1.41 |
| Intermediate | | | | | | | | | | |
| 18 | F | 2014 | 46 | 10.79 | 1.25 | 7.34-12.54 | -22.42 | 0.59 | -23.75 to -21.46 | 1.61 |
| 36 | F | 2013 | 89 | 11.83 | 1.04 | 8.29-13.35 | -21.58 | 0.59 | -23.74 to -20.67 | 1.38 |
| 37\* | F | 2014 | 44 | 11.47 | 1.03 | 9.01-12.73 | -21.95 | 0.72 | -23.99 to -20.97 | 1.72 |
| 71 | F | 2013 | 27 | 12.23 | 1.23 | 9.42-13.95 | -21.30 | 0.57 | -22.43 to -20.52 | 1.03 |
| 128\* | F | 2023 | 47 | 12.03 | 1.12 | 7.82-15.17 | -21.38 | 0.33 | -22.68 to -20.93 | 1.21 |
| 140 | M | 2018 | 56 | 8.36 | 1.07 | 6.95-11.68 | -21.51 | 0.87 | -23.46 to -20.36 | 2.73 |
| 141 | M | 2018 | 60 | 10.20 | 1.38 | 7.74-12.14 | -22.57 | 0.50 | -24.25 to -21.96 | 1.56 |
| 142 | F | 2018 | 44 | 10.83 | 1.23 | 7.61-12.31 | -22.21 | 1.02 | -24.43 to -20.70 | 3.28 |
| 156 | F | 2019 | 77 | 10.79 | 1.19 | 8.28-13.23 | -22.28 | 0.84 | -23.99 to -20.87 | 1.06 |
| 157 | M | 2019 | 71 | 10.59 | 1.02 | 8.02-11.89 | -22.74 | 0.64 | -23.95 to -21.30 | 1.64 |
| 160 | F | 2019 | 73 | 10.15 | 1.16 | 7.93-11.87 | -23.26 | 0.43 | -23.32 to -20.83 | 1.01 |
| 161 | F | 2019 | 69 | 10.56 | 1.22 | 7.96-14.13 | -22.02 | 0.66 | -23.32 to -20.83 | 0.80 |
| 406\* | F | 2014 | 56 | 12.56 | 1.06 | 10.25-14.28 | -21.79 | 0.28 | -22.55 to -21.22 | 0.87 |
| Generalist | | | | | | | | | | |
| 12\* | F | 2017 | 22 | 11.39 | 1.58 | 8.26-14.04 | -22.10 | 0.13 | -22.44 to -21.88 | 0.71 |
| 37\* | F | 2013 | 36 | 11.09 | 1.41 | 7.54-12.87 | -21.65 | 0.66 | -23.07 to -21.04 | 1.85 |
| 62 | F | 2023 | 25 | 12.18 | 1.59 | 9.40-14.38 | -21.56 | 0.38 | -22.41 to -20.93 | 1.58 |
| 111 | M | 2017 | 53 | 9.35 | 1.53 | 6.49-12.51 | -22.07 | 0.37 | -23.05 to -21.52 | 1.60 |
| 138 | F | 2018 | 30 | 11.10 | 1.95 | 6.96-13.80 | -20.74 | 0.48 | -22.50 to -19.83 | 2.90 |
| 171 | F | 2020 | 51 | 9.35 | 1.48 | 7.16-12.82 | -22.86 | 0.53 | -23.77 to -21.70 | 1.60 |

**Figures**

**Figure 1**. Conceptual model showing four different population-level patterns of dietary specialization based on isotope signatures of individual diets (δ15N) over time adapted from (Vander Zanden et al., 2010). Circles represent individuals and their δ15N value for a layer of inert tissue (e.g., whisker, baleen, claws) reflecting diet. Arrows track changes in individual δ15N values through time. (**A**) A specialist population with a small isotopic niche width composed of four specialist individuals with overlapping δ15N values; (**B**) A generalist population with a large isotopic niche width composed of four different δ15N specialist individuals; (**C**) A generalist population with a large isotopic niche width composed of four generalist individuals; (**D**) A generalist population with a large isotopic niche width composed of two generalist and two specialist individuals.

**Figure 2.** Isotopic analysis of leopard seal whiskers. (**A**) Population-level isotopic space (δ15N and δ13C) for leopard seals color-coded by δ15N specialization category: high trophic-level specialist (H-Specialist; blue), medium-to-low trophic-level specialist (ML-Specialist; green), intermediate (orange), and generalist (yellow). Each point represents the average isotopic value for an individual’s whisker(s). Ellipses show standard isotopic ranges for each δ15N specialization category: dashed for 75% and solid for 50% of data. Pie chart shows the proportion of the population in each δ15N specialization category. (**B**) Representative plots of δ15N signatures for a leopard seal whisker of each δ15N specialization category (HL-Specialist: Seal 84; ML-Specialist: Seal 144; Intermediate: Seal 37; Generalist: Seal 111). Leopard seal art 2024Roger Hall© inkart.net. Leopard Seal photo by Renato Borras-Chavez.

**Figure 3.** Individual-level isotopic space (δ15N and δ13C) for leopard seals color-coded by δ15N specialization category: high trophic-level specialists (H-Specialists; blue variations), medium-to-low trophic-level specialists (ML-Specialists; green and purple variations), intermediates (orange and red variations), and generalists (yellow and pink variations). Ellipses represent the standard isotopic ranges encompassing 75% of the data for each individual’s whisker(s), while points indicate the average isotopic value for each individual's whisker(s). Dotted lines represent the δ15N range for each category. Leopard seal art 2024Roger Hall© inkart.net.

**Figure 4.** Comparison of isotopic consistency between a long-term δ15N specialist (**A**; Seal 397) and a variable specialist (**B**; Seal 12) across different years. Bivariate plots of isotopic space (δ15N and δ13C) for Seal 397 (**C**), showing consistency in δ15N values across the years, and for Seal 12 (**D**), showing variation in δ15N values across the years. Each point represents an individual whisker segment. The dark grey polygon shows the individual’s total isotopic space. The light grey polygon shows the population’s total isotopic space. The colors represent the δ15N specialization category assigned each year: high δ15N specialists (H-Specialists) in blues, medium-to-low specialists (ML-Specialists) in green, and generalists in yellow. Box and whisker plots of δ15N values for Seal 397 (**E**) and Seal 12 (**F**) show examples of consistency (**E**) in δ15N isotope values across different years compared to variability associated with prey switching (**F**). In both plots, horizontal bars represent the mean concentrations for each individual and the ends represent the range. Leopard seal photos by Dan Costa.

**Figure 5.** Yearly trends in δ15N values for leopard seals (2012-2023). Top panel shows the yearly δ15N values with the fitted trend (blue line) and the 95% confidence interval (shaded area). Bottom panel shows the slope of the seasonal rate of change in the predicted δ15N values based on the first derivative of the fitted GAM shown in the upper panel. The bottom panel displays temporal windows where significant linear increase or decrease of isotopic values occurred in time, with the red line representing the fitted trend. Blue and red shaded areas indicate non-significant and significant effects, respectively, at the 95% confidence level.

**Data Accessibility**

The data supporting this study will be made publicly available in the Dryad Digital Repository within the next few months.

**Conflict of Interest**

The authors declare no competing interests.

**Author Contributions**

Emily S. Sperou contributed to conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, visualization, and writing (original draft, reviewing & editing of the manuscript). Douglas J. Krause and Renato Borras-Chavezcontributed to conceptualization, data curation, investigation, methodology, project administration, resources, and writing (reviewing & editing of the manuscript). Patrick Charapata and Kerri J. Smith contributed to methodology, investigation, project administration, resources, and writing (reviewing & editing of the manuscript). Michael E. Goebelcontributed to data curation, investigation, resources, and writing (reviewing & editing of the manuscript). Bradley Thompson, Azana Best, and Jaelyn Andersoncontributed to investigation, methodology, and writing (reviewing & editing of the manuscript). Daniel P. Costa and Daniel E. Crockercontributed to data curation, project administration, and writing (reviewing & editing of the manuscript). Carolina A. Bonin contributed to conceptualization, funding acquisition, project administration, and writing (reviewing & editing of the manuscript). Sarah S. Kienle contributed to conceptualization, data curation, funding acquisition, investigation, project administration and writing (reviewing & editing of the manuscript). All authors contributed to the article and approved the manuscript.

**Acknowledgements**

We thank the US Antarctic Program, the crew of the Lawrence M. Gould, and NOAA Antarctic Marine Living Resources Program and all researchers involved in the field for logistic support during data collection. A special thanks to Dr. R. Zhang at the Baylor Stable Isotope Facility for his expertise and help running samples. All research was approved by the Institutional Animal Care and Use Committees at the University of California, Santa Cruz and NOAA Fisheries, and conducted under federal authorizations for marine mammal research under National Marine Fisheries Service permits #19439, #16472, #20599, #25786 and Antarctic Conservation Act permits #2018-016 and #2012-005, #2013-003, #2017-012, and 2021-002. This work was funded by an NSF 2146068 awarded to SSK and CAB. This work was also supported by the AMNH Lerner Gray Memorial Fund and the American Philosophical Society Lewis and Clark Fund for Exploration and Field Research grant awarded to ESS.