

Exploring the isotopic niche: isotopic variance, physiological incorporation, and the temporal dynamics of foraging

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2 ABSTRACT

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5 **Keywords:** Isotopic niche; Trophic niche width; Mixing space; Dietary variation; Specialization; Dirichlet distribution

1 INTRODUCTION

6 Consumer foraging behaviors are dynamic, often resulting in variable diets that change over time as a
7 function of environmental conditions, the densities of consumer and resource populations, and even the
8 physiological states of individual foragers. Understanding how diets change, and to what extent different
9 conditions promote or inhibit specific changes, is both a challenging theoretical and empirical problem in
10 ecology.

11 The analysis of carbon and nitrogen stable isotope ratios of a consumer with respect to its potential prey is
12 a commonly used approach towards exploring and quantifying diet. As a consumer incorporates the isotopic
13 values of its resources into its tissues, it becomes a blend of these resources. The isotopic composition of a
14 consumer thus reflects 1) the proportional contribution of different prey to the consumer's diet (Moore and
15 Semmens, 2008; Parnell et al., 2010), and 2) the isotopic composition of its prey, collectively described as
16 the isotopic, or prey, mixing space (Phillips, 2001; Phillips and Koch, 2002; Newsome et al., 2007).

17 Both the consumer's dietary strategy as well as the isotopic mixing space contribute different sources of
18 variability that are reflected in the isotopic composition of the consumer. For example, a consumer could
19 be an obligate specialist on a single prey, such that its dietary variability is extremely low, in which case
20 the isotopic mean and variability of the consumer's tissues will reflect that of its targeted prey. In contrast,
21 the consumer could be a generalist, or intermediate specialist on certain prey such that the variability

in its diet as well as the isotopic variability of its prey contributes to its own isotopic composition. The isotopic variability of a consumer thus contains important information regarding the foraging ecology of the consumer, but is also determined by the mixing space over which it integrates isotope ratios. It is this variability that ecologists have coined ‘the isotopic niche’ (Bearhop et al., 2004; Newsome et al., 2007, 2012; Jackson et al., 2011; Martínez del Rio et al., 2009).

The isotopic niche of a consumer is a low-dimensional specification of the ‘Hutchinsonian niche’ (Hutchinson, 1957), an n -dimensional hypervolume that consists of all biotic and abiotic requirements needed for a species to function. In contrast to this large and ultimately immeasurable construct, the isotopic niche is also generally derived from both biotic and abiotic processes, yet can be defined exactly as a consumer’s isotopic variance with a dimension determined by the number of isotope systems employed (Newsome et al., 2007). It is the width, or spread of this distribution that correlates to the breadth of the isotopic niche. Although the isotopic niche can be the result of many ecological and environmental factors that influence the flow of stable isotope ratios through biological systems (Araújo et al., 2007), when it is primarily a function of flow through consumer-resource interactions, the isotopic niche is synonymous with the trophic niche as defined by Bearhop et al. (2004). Changes in the size of the isotopic niche have been shown to relate to ecosystem fragmentation (Layman et al., 2007), changes in food availability (Lehmann et al., 2015), and even individual responses to seasonal environments (Martínez del Rio et al., 2009), however a systematic understanding of how different sources of variability influence the isotopic niche is lacking.

The isotopic niche is generally defined with respect to the isotopic variance of a population (Araújo et al., 2007, 2009; Fink et al., 2012), however population-level variance is itself an artifact of the individual-level distributions from which the population is composed (Bolnick et al., 2007; Araújo et al., 2011). An important step in understanding how the isotopic niche changes in response to different consumer foraging strategies is to examine how individual-level variation contributes to observed isotopic variability. Individual-level variability - in particular that variability resulting from temporal changes in diet - has large implications for the population (Bolnick et al., 2011), and is frequently measured with ratios of stable isotopes via analysis of temporally-integrating tissues such as hair, whiskers, claws, or even laminar teeth (Koch et al., 1995; Matthews and Mazumder, 2004; Sponheimer et al., 2006; Post, 2008; Newsome et al., 2009; Yeakel et al., 2009; Hopkins and Kurle, 2015).

Once physiological fractionations in stable isotope ratios have been accounted for, the isotopic niche is a direct reflection of the proportional contribution of different prey resources to the consumer’s diet. Isotope mixing models, which originally used a bootstrapping framework (Phillips and Gregg, 2003; Phillips et al., 2005) and now employ Bayesian methods (Moore and Semmens, 2008; Parnell et al., 2010; Hopkins and Ferguson, 2012; Parnell et al., 2012), are used to reconstruct the probability distribution that describes the contribution of different prey; mixing models can only be solved exactly if the number of potential prey resources are less than or equal to the number of isotope systems used plus one. These tools are forensic in nature, and have been used to back-calculate consumer diets across ranges of stoichiometrically unique prey (Hopkins and Kurle, 2015), for hierarchically organized populations across complex landscapes (Semmens et al., 2009), for reconstructing diets of extinct taxa (Yeakel et al., 2013), and even combined with process-based models that function to constrain estimates based on known mechanistic relationships between higher-order parameters (Ogle et al., 2014).

A conceptually divergent, yet parallel, strategy is to consider the inter-related effects of ecological interactions and the concomitant integration of stable isotope ratios, and how these factors combine to result in the isotopic composition of a consumer. In this way, the consumer’s isotopic distribution can

be forward-integrated through time based on the mechanistic linkages between its foraging strategy, its ability to find and acquire prey, and the isotopic landscape over which its diet is composed. This general perspective has been applied to investigate properties of the isotopic niche for cases of fixed (non-varying) diets (Araújo et al., 2007, 2009), and with respect to experimental systems with switching between unique prey (Fink et al., 2012). However, such a process-based framework has not been directly linked to consumer foraging behaviors, prey availability, or other ecological considerations such that the combined impacts of ecologically-mediated dietary variation and mixing space geometry on the isotopic niche can be assessed.

Here we build a mechanistic framework that links the ecological processes of an individual consumer to the isotopic distribution that describes its diet, and ultimately to the isotopic composition of its own body tissues. By coupling these processes, we are able to systematically investigate under what conditions the isotopic niche of a consumer changes as a function of both geometric properties of its mixing space, and alternative foraging strategies. We show that the isotopic variance of a consumer's diet (and by extension the width of its isotopic niche) is expected to be a concave parabolic function with respect to prey specialization, such that it possesses a peak variance, though the appearance of measurable nonlinearity is contingent on mixing space geometry. We demonstrate the potential importance of these findings by examining a prey mixing space for sea otter consumers, which are known to possess high dietary individuality (Tinker et al., 2008; Newsome et al., 2015).

We then extend our framework to explore how a consumer's isotopic niche responds to temporally dynamic diets. We examine an example of a switch between two probabilistic diets that oscillates between, for example, wet and dry seasons, and show analytically that the maximum expected isotopic niche width occurs during the transitions between diets. Determining how different sources of variability emerge from ecological, behavioral, and geometric drivers is important for interpreting the meaning of concepts such as the isotopic niche. Moreover, integrating these different sources of variation into a statistical process-based framework lends itself particularly well to hypothesis-testing aimed at uncovering the root causes of observed isotopic data. We hope that our approach is a step towards assessing how the isotopic niche may change due to more complex foraging behaviors and even population dynamics, and we expand on these ideas in the Discussion.

2 METHODS & ANALYSIS

We begin by establishing a forward-integration approach for modeling the incorporation of stable isotopes from multiple resources into a consumer's tissues. This new methodology provides an analytical link between the mechanistic drivers of foraging and the distribution of stable isotope values describing a consumer's tissues over time. Using this framework, we aim to 1) examine how certain dietary behaviors, such as prey specialization and different modes of dietary variation, impact the isotopic variance of consumer tissues thus aiding ecological interpretation of the 'isotopic niche', and 2) show how these methods can be expanded to include foraging behaviors that themselves are temporally dynamic, changing over seasons or years.

Deriving the within-individual isotopic niche width

There are many ways to statistically summarize the integration of prey by a consumer species, however in order to establish a mechanistic link between foraging and the consumer's isotopic composition, we follow the proceeding heuristic foraging mechanic. We assume that a consumer encounters and consumes resources in proportion to the encounter rate of each prey; prey that are encountered more frequently are assumed to be consumed more frequently. An alternative approach could incorporate preferences (Chesson,

107 1983) or even state-dependence (Mangel and Clark, 1988; Clark and Mangel, 2000; Mangel, 2014), and we
 108 will briefly address these considerations in the Discussion. As prey are encountered and consumed, the
 109 prey's isotope values are incorporated into the consumer's tissues weighted by the prey-specific proportional
 110 contribution to diet. The resulting distribution that describes the dietary input of multiple prey (each with
 111 an independent Normal density that describes the distribution of their isotopic values) is a mixed Normal
 112 distribution with weights determined by the prey's proportional contribution to diet. This proportional
 113 contribution is itself a random variable drawn from a Dirichlet density (a multivariate Beta distribution)
 114 that serves as a probabilistic description of the consumer's dietary input (Ainsworth et al., 2010). The
 115 following section details our probabilistic determination of the consumer's isotopic composition. We focus
 116 our attention on the variability of the consumer isotopic distribution, which is equivalent to its isotopic
 117 niche width (Newsome et al., 2007), and because we assume that the isotope ratios under consideration
 118 follow dietary pathways, is synonymous with the trophic niche width (Bearhop et al., 2004).

119 A consumer encounters each prey at a frequency determined by a Poisson process with parameter ψ_i ,
 120 which determines the number of encounters $M_i = m_i$ between time 0 and time t , with the frequency
 121 distribution

$$f_{M_i}(m_i|\psi_i) = e^{-\psi_i t} \frac{(\psi_i t)^{m_i}}{m_i!}. \quad (1)$$

122 Here and henceforth, we use the general function $f(\cdot)$ to denote different frequency distributions, as well
 123 as uppercase notation to describe stochastic variables, and lowercase notation to describe specific values of
 124 stochastic variables. If we assume that encounter rates are variable, such that some prey are more patchily
 125 distributed than others, we can treat $\Psi_i = \psi_i$ as a random variable with a Gamma density

$$f_{\Psi_i}(\psi_i|c, a_i) = \frac{c^{a_i}}{\Gamma(a_i)} e^{-c\psi_i} \psi_i^{a_i-1}. \quad (2)$$

126 Here, a_i is the dispersion parameter, which is proportional to the encounter rate, and c scales with the
 127 time between encounters (Mangel, 2006; Ainsworth et al., 2010; Yeakel et al., 2014). If we integrate
 128 across all possible values of ψ_i , we obtain the Negative Binomial density with mean encounter rate a_i/c
 129 and coefficient of variation $1/\sqrt{a_i}$ (Hilborn and Mangel, 1997). Following the derivation described by
 130 Ainsworth et al. (2010), if we define the proportional contribution of prey to a consumer's diet to scale
 131 with the encounter rate, such that

$$p_i = \frac{\psi_i}{\sum_{j=1}^n \psi_j}, \quad (3)$$

132 then the random variable $P_i = p_i$ where $P_i \in \mathbf{P}$ and $p_i \in \mathbf{p}$ (we allow boldface type to denote vectors of
 133 variables), and $\sum_i p_i = 1$. From Eq. 3, it follows that vector of proportional contributions \mathbf{P} follows a
 134 Dirichlet distribution (Johnson, 1960) with density

$$f_{\mathbf{P}}(p_1, \dots, p_n|a_1, \dots, a_n) = \frac{\Gamma(\sum_{i=1}^n a_i)}{\prod_{i=1}^n \Gamma(a_i)} \prod_{i=1}^n p_i^{a_i-1}, \quad (4)$$

where $\Gamma(\cdot)$ is the gamma function (cf. Mangel, 2006). As such, the expected proportional contribution of a prey i to the consumer's diet has the expectation $E\{P_i\} = a_i/a_0$ where $a_0 = \sum_i a_i$, and variance

$$\text{Var}\{P_i\} = \frac{a_i(a_0 - a_i)}{a_0^2(a_0 + 1)}. \quad (5)$$

Accordingly, we assume each time interval represents a single foraging bout, where we draw a single prey i with probability p_i for inclusion to the consumer's diet.

Describing the dietary behavior of a consumer as a Dirichlet distribution provides a flexible and powerful framework to investigate how different foraging strategies influence a consumer's isotopic niche. For example, a pure generalist consumer would have a Dirichlet distribution with parameters $a_i = 1$ for all prey $i = 1, \dots, n$, such that the marginal distribution for P_i is close to uniform with expectation $E\{P_i\} = 1/n$. Because we have assumed that the proportional contribution of a prey to the consumer's diet scales with the prey's encounter rate, this would be analogous to a system where a consumer is equally likely to encounter the same number of any prey. In contrast, an obligate specialist would have a Dirichlet density that is spiked for a given prey k , such that the single parameter $a_k \gg 1$, while $a_{i \neq k} = 1$. The use of a Dirichlet distribution is also at the heart of Bayesian isotope mixing models (Moore and Semmens, 2008; Parnell et al., 2010; Hopkins and Ferguson, 2012; Parnell et al., 2012), which assume a Dirichlet prior and enable the input of alternative dietary information to inform isotopic data.

If the stable isotope ratios for each of the potential prey follow independent Normal distributions, and the dietary behavior of the consumer has a Dirichlet density, the resultant density that describes the isotopic distribution of a consumer's diet $f_Z(Z = z)$ is a mixed Normal distribution, with weights given by \mathbf{p} drawn from the Dirichlet. This density can be written as

$$f_Z(z|\mathbf{p}, \boldsymbol{\mu}, \boldsymbol{\sigma}) = \sum_{i=1}^n p_i \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{-\frac{(z-\mu_i)^2}{2\sigma_i^2}}, \quad (6)$$

with the expectation

$$E\{Z\} = \sum_{i=1}^n \frac{a_i}{a_0} \mu_i, \quad (7)$$

where μ_i is the mean isotope value for prey i . This is simply the weighted average of the isotope values for the prey community, where weights are determined by the mean proportional contribution of prey to the consumer's diet.

Of more interest to us here is the variance of Z , which will allow us to analytically determine the isotopic niche width of the consumer as a function of its dietary behavior and the mixing space of its prey. We find that

$$\text{Var}\{Z\} = \sum_{i=1}^n \frac{a_i}{a_0} (\sigma_i^2 + \mu_i^2) - \frac{a_i^2 \mu_i^2}{a_0^2} - \sum_{i \neq j} \frac{a_i a_j \mu_i \mu_j}{a_0^2}. \quad (8)$$

161 Although the form of Eq. 8 is not intuitive, we emphasize that - over different dietary behaviors that shape
 162 the Dirichlet distribution and for different isotopic mixing spaces - it is this equation that governs the
 163 expansion or contraction of the consumer's isotopic niche width, and therefore of chief ecological interest.

164 The isotopic variance of the consumer's diet $\text{Var}\{Z\}$ can be simplified by considering a specific set of
 165 dietary behaviors. Here we examine how $\text{Var}\{Z\}$ is influenced by generalist vs. specialist consumer diets,
 166 as well as the role of general mixing space geometries, in determining consumer isotopic niche width. It
 167 is important to note that specialism, as discussed here defines the degree to which a consumer's diet is
 168 dependent on a single prey resource, ranging from $s = 1/n$ (obligate generalization) to $s = 1$ (obligate
 169 specialization). It is thus conceptually different than 'individual specialization' defined as the proportional
 170 variance of an individual relative to that of its population (Within-Individual Component / Total Niche
 171 Width, or WIC/TNW; Roughgarden, 1979), and often the variable of interest in other studies examining
 172 properties of the isotopic niche (Araújo et al., 2007, 2009, 2011; Layman et al., 2011).

173 If a generalist consumer alters its diet to include more of a certain prey k relative to the others, the
 174 Dirichlet distribution that defines its dietary behavior goes from $a_i = 1$ for all $i = 1, \dots, n$ to $a_{i \neq k} = 1$
 175 for $i = 1, \dots, n$, with $a_k > 1$. As specialization increases, the Dirichlet parameter corresponding to the
 176 targeted prey k , increases to a value much higher than one (pure specialization is obtained only at the limit
 177 $a_k \rightarrow \infty$). Thus, we can assume that $a_i = 1$ for all $i \neq k$, and $a_k = (n - 1)s_k/(1 - s_k)$, where s_k denotes
 178 specialization on prey k . We can thus substitute $a_0 = (n - 1)/(1 - s_k)$ and $p_i = a_i/a_0 = (1 - s_k)/(n - 1)$
 179 for all $i \neq k$, and $a_k/a_0 = s_k$. We can then rewrite Eq. 8 as

$$\text{Var}\{Z\} = \frac{1 - s_k}{n - 1} \sum_{i \neq k}^n (\sigma_i^2 + \mu_i^2) + s_k(\sigma_k^2 + \mu_k^2) - \left(\frac{1 - s_k}{n - 1} \sum_{i \neq k}^n \mu_i + s_k \mu_k \right)^2, \quad (9)$$

180 and note that, independent of the prey mixing space (a function of μ_i and σ_i^2 for prey $i = 1, \dots, n$), the
 181 isotopic variance of the consumer's diet will always be a concave parabolic function over s_k . With respect
 182 to the size of the consumer's isotopic niche width, this means that there can be a peak variance for a value
 183 of s_k intermediate to pure generalization ($s_k = 1/n$) and pure specialization ($s_k = 1$).

184 The peak variance \hat{s}_k , which describes the maximum isotopic variance of the consumer, may or may not
 185 fall between $s_k = 1/n$ and $s = 1$, and is only of ecological interest if it does. The peak variance can be
 186 solved analytically by setting the derivative of Eq. 9 with respect to s_k equal to zero, and solving for s_k ,
 187 which results in

$$\hat{s}_k = \frac{A(1 - n) + B(n - 1)^2 + 2C(C - Dn + D)}{2(C - Dn + D)^2}, \quad (10)$$

188 where $A = \sum_{i \neq k}^n (\sigma_i^2 + \mu_i^2)$, $B = (\sigma_k^2 + \mu_k^2)$, $C = \sum_{i \neq k}^n \mu_i$, and $D = \mu_k$.

189 Determination of the peak variance allows us to predict where the consumer's isotopic niche is expected
 190 to be maximized as a function of specialization on different prey. Although here we have focused on
 191 the special case where a consumer targets a single prey, one can rewrite the equation for the consumer's
 192 isotopic niche width with respect to increasing specialization on any number or combination of prey in
 193 the mixing space. For example, in the case where a consumer specializes on two prey (i.e. two species of
 194 crab), one would rewrite Eq. 8 in terms of both s_k (specialization on prey k) and s_l (specialization on prey

l), resulting in a concave parabolic plane in dimensions s_k and s_l . Determining the maximum variance would then entail taking the derivative of Eq. 8 with respect to both s_k and s_l . In dimensions higher than 2, the process would be the same, with the goal of finding the maximum variance over a hyperplane with a number of dimensions determined by the number of prey on which the consumer is preferentially targeting. Because specializing on multiple prey does not introduce anything conceptually unique, we consider only the case of a single-prey specialist.

201 The Dynamics of Isotopic Incorporation

202 We have established a framework for analytically calculating the distribution of isotope values that characterizes a consumer's diet, composed of multiple, isotopically distinct prey. The dietary behavior of the consumer is a function of a single Dirichlet distribution, which is assumed not to change over time, although we will relax this assumption in the next section. By the central limit theorem, over long timescales the dietary distribution of the consumer is static, with a fixed mean and variance. However, over short timescales, the diet of the consumer varies as Eq. 5, while its isotopic distribution has a variability that results from the combined effects of the Dirichlet and the mixed Normal distribution that emerges from the prey mixing space (Eq. 8).

210 As the consumer acquires and consumes prey, the isotopic composition of its diet is incorporated into its tissues. The timescale of physiological isotopic incorporation is based on the turnover rate of consumer tissues, which on the fast end can occur within days to weeks (e.g. blood plasma), and on the slow end occur over years (e.g. bone) (Tieszen et al., 1983). Incorporation rates are well known to isotope ecologists and have been observed in both controlled feeding studies (Kurle, 2009; Kim et al., 2012), and occasionally in the wild (REFS?). Although the physiological details are not well understood, isotopic incorporation can be modeled using either single- or multi-compartmental approaches (Cerling et al., 2006; Martínez del Río and Anderson-Sprecher, 2008). In a single compartment framework, isotope ratios are ingested with food, and directly incorporated into consumer tissues at a tissue-specific rate. In multiple compartment frameworks, it is assumed that incorporation occurs over multiple body pools, the turnover of each potentially occurring at different rates. Though an assumption of multi-compartmental incorporation can provide better statistical fit with experimental data (Cerling et al., 2006; Kurle, 2009; Carleton et al., 2008), the physiological processes that drive incorporation of isotope ratios from one compartment to the other are not well understood (Martínez del Río and Anderson-Sprecher, 2008), and for many tissues single-compartment models fit as well or better than multi-compartment models (Kurle, 2009).

225 In this next section, we assume that the ingested isotope ratios are incorporated into consumer body tissues directly, moderated by the rate of incorporation λ , which is treated as a free parameter. Here we consider only a single compartment model, such that isotope ratios are directly shuttled to consumer tissues at rate λ ; we note, however, that functions for multi-compartment models could be used instead, though we do not expect large qualitative differences in results (cf. Fig. 1 in Martínez del Río and Anderson-Sprecher, 2008). For simplicity, we assume that time is scaled such that a single time step corresponds to a single foraging bout. Moreover, we assume that the consumer is incorporating prey of smaller size than itself, such that $0 < \lambda < 1$. Thus, we aim to determine the isotopic composition of the consumer X_c as a function of its diet, the isotopic mixing space, and λ . In a completely deterministic framework, the isotopic composition of the consumer can be written as an ordinary differential equation

$$\dot{X}_c = (1 - \lambda)X_c + \lambda \sum_{i=1}^N p_i \mu_i - X_c \quad (11)$$

where the overdot denotes the derivative with respect to time t , and p_i and μ_i are the proportional contribution of prey i to the diet of the consumer, and the mean isotope value of prey i , respectively.

However, we must also take into account the stochastic effects described in the previous section, including the variation associated with the consumer's diet and the isotopic variation associated with each prey. We account for these stochastic effects by describing changes in the consumer's isotopic distribution with the stochastic differential equation

$$dX_c = (1 - \lambda)X_c dt + \lambda \left(E\{Z\}dt + \sqrt{\text{Var}\{Z\}}dW \right) - X_c dt. \quad (12)$$

where dW is the increment of Brownian motion. This stochastic differential equation describes a process known as an Ornstein-Uhlenbeck process, which is a stochastic process that has a steady state variance around the mean (Mangel, 2006). Because the time interval dt is infinitely short at the continuous limit, the consumer's isotopic distribution will have a Normal distribution. In this case, if the initial isotopic values of the consumer at time $t = 0$ is $X_c(0)$, the expectation and variability of X_c at time t are

$$\begin{aligned} E\{X_c(t)\} &= E\{Z\} + (X_c(0) - E\{Z\})e^{-\lambda t}, \\ \text{Var}\{X_c(t)\} &= \frac{\lambda \text{Var}\{Z\}}{2} (1 - e^{-2\lambda t}). \end{aligned} \quad (13)$$

where $E\{Z\}$ and $\text{Var}\{Z\}$ are as defined in Eqns. 7 and 8. One can observe that as t increases, the exponential part of $E\{X_c(t)\}$ and $\text{Var}\{X_c(t)\}$ go to zero, such that $E\{X_c(t)\} \rightarrow E\{Z\}$, and $\text{Var}\{X_c(t)\} \rightarrow \lambda \text{Var}\{Z\}/2$. In other words, the expectation of the consumer's isotopic distribution will equilibrate to that of its diet, while its variance will always be less than the variance of its diet by a factor of $\lambda/2$. Variance decreases as the rate of incorporation decreases due to the consumer averaging its isotopic value over more prey (because the tissue is turning over more slowly), and this serves to average out fluctuations in the consumer's diet.

An implicit assumption of the static model is that the consumer's diet varies instantaneously over a given parameterization of $f_Z(Z)$. This is relevant for organisms that have a consistently varying diet over time, however most organisms have diets that undergo large changes over longer periods time. In such cases, the Dirichlet distribution that characterizes diet during one small temporal interval will be different than the Dirichlet distribution characterizing diet during another interval far apart in time. Such a shift might be due to seasonal, ontogenetic, or demographic changes in the consumer's prey base over the course of months to years. In the following section, we will relax the assumption that diet is characterized by a single Dirichlet distribution over time, thus generalizing our formulation of consumer isotopic dynamics as a function of time.

As the consumer's diet changes over time, the random variable of interest is now $Z(t)$, which is the trajectory defining the isotopic values of the consumer's diet over time. Solving for $X(t)$, we find

$$\begin{aligned}
E\{X(t)\} &= X(0)e^{-\lambda t} + \lambda e^{-\lambda t} \int_{s=0}^t e^{\lambda s} E\{Z(s)\} ds, \\
\text{Var}\{X(t)\} &= \lambda^2 e^{-2\lambda t} \int_{s=0}^t e^{2\lambda s} \text{Var}\{Z(s)\} ds,
\end{aligned} \tag{14}$$

and this is conceptually analogous to the formulation of consumer isotopic variance as derived by Fink et al. (2012).

3 RESULTS

As a consumer samples from multiple prey with stable isotopes values following independent Normal distributions, its tissues become a mixture of these distributions. The weights that control the contributions of each prey to the consumer mix are determined by the dietary behavior of the consumer, which we have shown follows a Dirichlet distribution. The use of the Dirichlet distribution in this context follows previous ecological models by Ref(Ainsworth, others?), and is also used as a prior in Bayesian isotope mixing models. We note that Bayesian mixing models are essentially models that explore the opposite question that we are investigating: they are used to estimate the dietary behavior of the consumer (the posterior probability distribution for the proportional contribution vector \mathbf{p}) given the isotopic distributions of both consumer and prey, whereas we are investigating factors that impact the isotopic distribution of the consumer as a function of different prey mixing spaces and consumer dietary behaviors.

We have provided an analytical solution for the mean and variance of the consumer's isotope distribution as a function of its diet and the isotope mixing space. By formulating these solutions in terms of consumer generalization and specialization, we make three observations: 1) the variance of the consumer's isotope distribution ($\text{Var}\{Z\}$), which is equivalent to its isotopic niche width, is concave parabolic; 2) whether and to what extent the $\text{Var}\{Z\}$ demonstrates measurable nonlinearity depends in part on the geometry of the mixing space; 3) the inversion point, or the peak, of $\text{Var}\{Z\}$ over the generalization-specialization continuum is the consumer's maximum isotopic niche width. This point may or may not exist at a value intermediate to an obligate generalist or obligate specialist.

Temporally variable diets

The equilibrial solution to our stochastic differential equation (Eq. 12) reveals that the isotopic variability of the consumer scales to diet as a factor of $\lambda/2$. As the incorporation rate decreases, such that the turnover time is long, the isotopic variability of the consumer declines. Moreover, we observe that as the consumer transitions from some initial isotopic state $X_c(0)$ to diet, the variance of the consumer's isotopic values equilibrate twice as fast as the mean value, as shown in the exponential component of Eq. 13.

If the consumer's diet is itself variable over time, we do not expect its isotopic composition to equilibrate as it would in a controlled feeding study. For example, the consumer might adopt one diet during the wet season, and another during the dry season, such that it oscillates between the two throughout the year. We consider a composite diet with an isotopic distribution $\mathbb{Z} f_{\mathbb{Z}}$ that dynamically oscillates between two subdiets, which we will refer to as 'seasonal diets' with frequency ω . We note that $1/\omega$ in this context is synonymous with the 'dietary correlation time' of Fink et al. (2012). The seasonal diets have random variables Z_1 and Z_2 , distributed according to Eq. 6, where each has a different underlying Dirichlet – encoding which prey the consumer targets during each season with frequency distributions f_{P_1} and f_{P_2}

– while the isotopic distributions of prey are assumed to be constant through time. We can thus describe the composite diet as a mix of the seasonal diets, where the mix is characterized by weights that oscillate over time, $\mathcal{U}(t)$, and this determines the contribution of each seasonal dietary strategy to the whole. The frequency distribution for the composite diet is thus

$$f_{\mathbb{Z}(t)} = (\mathcal{U}(t)f_{Z_1} + (1 - \mathcal{U}(t))f_{Z_2}) f_{P_1} f_{P_2}. \quad (15)$$

If we do not specify the type of oscillation that drives changes in diet over time, the expectation and variance for the isotopic distribution of the composite diet over time are

$$\begin{aligned} E\{\mathbb{Z}(t)\} &= \mathcal{U}(t)E\{Z_1\} + (1 - \mathcal{U}(t))E\{Z_2\}, \\ \text{Var}\{\mathbb{Z}(t)\} &= \mathcal{U}(t)\text{Var}\{Z_1\} + (1 - \mathcal{U}(t))\text{Var}\{Z_2\} + \mathcal{U}(t)(1 - \mathcal{U}(t)) (E\{Z_1\} - E\{Z_2\})^2, \end{aligned} \quad (16)$$

where the mean isotopic value of the composite diet is averaged over both seasonal diets, weighted by the proportional inclusion of each. In the wet/dry season example, the consumer could either shift gradually from its wet season diet to its dry season diet if $\mathcal{U}(t)$ is smooth, or shift abruptly if $\mathcal{U}(t)$ is a step function. An example of the latter scenario would be a grizzly bear consumer system, where its diet shift abruptly with the arrival of salmon during spawning season (REF).

Most dietary transitions between seasons tend to be gradual, even if the end/start of a given season is abrupt (REF). To understand how a temporally oscillating diet affects the isotopic variance of the composite diet, we consider the smooth oscillation $\mathcal{U}(t) = 1/2 + 1/2 \sin(\omega t)$, which determines the proportional contribution of diet 1. Here, $\mathcal{U}(t)$ varies between 0 and 1, with a frequency ω (Fig. 4A). Substituting $\mathcal{U}(t)$ into Eq. 16 provides the solution to a sinusoidally varying diet, where

$$\begin{aligned} \text{Var}\{\mathbb{Z}(t)\} &= \overbrace{\frac{\text{Var}\{Z_1\} + \text{Var}\{Z_2\}}{2} + \frac{1}{2} \left(\frac{E\{Z_1\} - E\{Z_2\}}{2} \right)^2}^{\alpha_V} \\ &+ \overbrace{\frac{\text{Var}\{Z_1\} - \text{Var}\{Z_2\}}{2}}^{\beta_V} \sin(\omega t) + \overbrace{\frac{1}{2} \left(\frac{E\{Z_1\} - E\{Z_2\}}{2} \right)^2}^{\gamma_V} \sin\left(2\omega t + \frac{\pi}{2}\right). \end{aligned} \quad (17)$$

where we have combined the non-oscillating components into three parameters α_V , β_V , and γ_V for notational efficiency.

We gain two key insights from the solution for the variance of the composite diet. 1) The time-averaged variance (denoted by $\langle \cdot \rangle_t$) is simply $\langle \text{Var}\{\mathbb{Z}(t)\} \rangle_t = \alpha_V$, which is only impacted by the average variance between the seasonal diets and the difference in the mean isotope values between the seasonal diets (Fig. 5), and 2) the oscillating component shows that the composite dietary variance has twice the frequency of the diet shift $\mathcal{U}(t)$, as well as a $\pi/2$ offset, meaning that the maximal variance of the consumer's composite diet will occur during the transition from one diet to the other (Fig. 4B). Together, these results reveal that if the consumer's diet is varying continuously over time between two seasonal diets, both the mean variance, as well as the difference in the mean isotope values of the seasonal diets – directly reflecting the

heterogeneity of prey mixing space geometry – will serve to increase the time-averaged variance of the consumer's diet, and by extension the isotopic variance of the consumer itself.

Less intuitively, we observe that the consumer's peak variance, or niche width, as measured by the variance of its composite diet, occurs not during the exclusive adoption of its wet/dry season diets, but during the transition between the two, and this peak variance is driven exclusively by the difference in means between seasonal diets. As the seasonal diets become more heterogeneous in isotopic space, the greater the consumer's peak variance during the transition, and this occurs because it is sampling between two dietary strategies that are isotopically distinct. We can directly observe this by considering a transition between two diets with a) different means and the same variances, and b) the same means and different variances. In the former case, the peak variance of the composite diet occurs during the transition (Fig 4B); in the latter case, because the diets have the same mean isotope value, the peak occurs not during the transition, but when the consumer adopts the diet with the greater variance, which in our example would occur at the height of the season (Fig 4C).

The isotopic composition of a consumer $X_c(t)$ during a single dietary shift is governed by a single timescale of physiological origin: the rate of incorporation λ . However, a seasonally shifting diet that is driven by oscillating foraging strategies introduces an additional ecological timescale that will affect $X_c(t)$, determined by the frequency of diet switching ω . Depending on the turnover rate of the tissue of interest and how often the consumer shifts its diet, the ratio of these timescales ω/λ will impact how the isotopic mean and variance of the consumer changes over time. For the case of sinusoidally varying diet, we can solve for $X_c(t)$ directly, such that

$$\begin{aligned} \text{Var}\{X_c(t \rightarrow \infty)\} = & \alpha_V \frac{\lambda}{2} + \beta_V \frac{\lambda^2}{\sqrt{(2\lambda)^2 + \omega^2}} \sin(\omega t - \theta_1) \\ & + \gamma_V \frac{\lambda^2}{2\sqrt{\lambda^2 + \omega^2}} \sin(2\omega t + \theta_2). \end{aligned} \quad (18)$$

where the offsets θ_1 and θ_2 are $\tan^{-1}(\omega/2\lambda)$ and $\tan^{-1}(\lambda/\omega)$, respectively. As in the static case (where diet was not varying over long periods of time), the time-averaged variance is $\alpha_V \lambda/2$. Moreover, we observed that the consumer's isotope composition lags behind changes in diet, such that an isotopic shift in the consumer's tissues is observed after the actual foraging shift. This lag involves both θ_1 and θ_2 , however these offsets play different roles in contributing to the lag for different mixing space geometries. When the isotopic means of the seasonal diets are similar, the lag is mostly due to θ_1 ; when the means are different and the variances are similar, the lag is mostly due to θ_2 ; when both the isotopic means and variances of the seasonal diets are different, both contribute significantly to the lag.

Increasing ω/λ , such that the timescale of ecological switching relative to that of isotopic incorporation decreases, we observe that 1) the lag between the transition and the peak variance of the consumer increases with decreasing λ , and 2) the amplitude of the variance of $X_c(t)$ decreases with increasing ω . The first result is not surprising, as it mirrors the role of λ in the static diet example. The second result is less intuitive: in words, as the consumer shifts its diet more frequently, there is still a peak variance during dietary transitions, though with diminishing amplitude, and this would make it more difficult to measure. This is due to the consumer slowly integrating isotope ratios from both diets, thus averaging across diet-switching events.

359 Accordingly, the decrease in the amplitude of isotopic variance of the consumer's tissue is an averaging
360 effect, where the timescale of incorporation is much larger than the timescale of dietary switching.

4 DISCUSSION

361 The use of stable isotope ratios in ecology has increased exponentially in the last twenty years. Recent
362 development of tools designed to increase the utility of using stable isotope ratios to infer diet have focused
363 almost entirely on Bayesian mixing models. Bayesian isotope mixing models are extremely useful for
364 backwards-estimating the probability distribution the described the proportional contribution of each
365 species to the consumer's diet, where both the isotopic composition of the consumer and potential prey
366 are known. However, there are many cases where these tools cannot be used, and this may be due to 1)
367 incomplete knowledge of the mixing space (REFS), 2) an isotopically confounded mixing space (REFS),
368 or 3) under-sampling of the consumer and/or its potential prey.

369 We assert that it is useful to establish a forward-integration approach towards understanding how the
370 isotopic distribution of a consumer individual changes due to both ecological, physiological, and isotopic
371 variables. Our goal is to provide a framework that introduces mechanistic links between the ecological
372 foraging dynamics of a consumer, the physiological constraints that dictates incorporation, and the more
373 abstract effects of mixing space geometry. This approach does not replace the utility of isotope mixing
374 models, but instead offers an opposing framework by which the isotopic composition of a consumer
375 can be understood. Where isotope mixing models are aimed on answering the question: 'what was the
376 most likely dietary behavior that produced the observed isotope ratios of a consumer given some mixing
377 space geometry', we explore how different ecological scenarios can alter the isotopic composition of a
378 consumer individual. We focus our efforts on building an analytical framework to understand how the
379 isotopic variance of an individual (i.e. its isotopic niche width) changes as a function of different foraging
380 strategies that are both probabilistic and dynamic over time.

381 In constructing an analytical approach towards understanding isotopic variance at the individual consumer
382 level, we have found some non-intuitive results (though intuitive in hindsight) that will be important to
383 consider when one is interpreting the isotopic variation of consumers over different timescales. We consider
384 two different general foraging strategies for an individual consumer: 1) *static strategy*: probabilistic
385 consumption of multiple prey, the proportions of which are - on average - constant over time, and 2)
386 *dynamic strategy*: probabilistic consumption of multiple prey that varies over long periods of time. The
387 former example is most relevant for consumers inhabiting relatively constant environments, whereas the
388 latter is more appropriate for consumers with a shifting diet between years, season, or even for shorter
389 timescales.

390 Our primary findings concern whether and to what extent the peak isotopic variance of the consumer is
391 realized under different, but definable, conditions with respect to static and dynamic foraging strategies.
392 When the consumer exhibits a static foraging strategy, this peak variance can occur if it is an intermediate
393 specialist, and whether or not peak variance is realized for intermediate specialization is a product of
394 mixing space geometry, and the isotopic variance of the prey that it is preferentially targeting. When the
395 consumer exhibits a dynamic, yet smoothly varying, foraging strategy, the peak variance occurs during
396 the transition from one diet to another, and is offset by a lag that is a function of its incorporation rate,
397 and therefore dependent on the tissue being analyzed. Below we attempt to gain additional understanding
398 for why variance peaks are expected to occur under different ecological circumstances and mixing space
399 geometries.

4.1 The isotopic niche over specialization

The nonlinear nature of the consumer's isotopic niche width as a function of its specialization on certain prey (or combinations of prey) is driven almost entirely by the geometry of the prey isotope mixing space. One can gain some intuitive understanding of this nonlinearity by considering the following example, illustrated in Fig. 1. In a three-prey system, where all prey have equal isotopic means and variance, a consumer that ranges from generalization on all three prey to specialization on a single prey will have isotopically equivalent diets. As the mean isotopic value of the targeted prey is moved away from the others, such that its offset from the mixing space centroid is increased, the variance function displays nonlinearity. This can be understood by considering two prey with the same mean value, and the targeted prey with a very different mean value. As the consumer incorporates isotopic ratios from all three prey in equal proportions, it will have increased isotopic variance due to the large spread of the prey. As the consumer integrates this isotopically atypical prey in greater proportions, the heterogeneity of incorporated isotope ratios will increase, serving to increase the consumer's isotopic variability. The isotopic variability will then decline as it begins specializing on the atypical prey, and if it is consuming this prey exclusively, the isotopic variability of its diet will reflect the isotopic variability of its prey exactly. The concave parabolic nature of the isotopic variability of the consumer's diet can thus be explained by heterogeneous incorporation of isotope ratios over an asymmetric mixing space.

Understanding what dietary strategy or mixing space geometry can maximize the isotopic niche width of the consumer's diet, $\text{Var}\{Z\}$, will serve to help ecologists determine what mechanisms - ecological or statistical - may be driving isotope data. Our analytical solution for this peak variance over dietary specialization (\hat{s}) reveals that maximum isotopic niche width can, but doesn't always, fall in $s \in [1/n, 1]$, with bounds denoting exclusive prey generalization or specialization, respectively. If the peak lies outside of this region, changes in isotopic variance as specialization on a targeted prey is increased will appear monotonic or even linear.

Although the specific nature of \hat{s} will depend strongly on mixing space geometry, we can elucidate certain key attributes that will determine the general nature of where this value falls. For mixing space geometries where the targeted prey has higher than average variance, \hat{s} will tend to lie towards prey specialization ($s > 0.5$), however the offset of the mean value of the targeted prey from the mixing space centroid will quickly push \hat{s} to $s \rightarrow 0.5$ (Fig. 2A,B). In contrast, if the targeted prey has lower than average variance, \hat{s} will tend to lie towards prey generalization ($s < 0.5$; Fig. 2B,C). As before, if the offset of the targeted prey's mean value increases, $\hat{s} \rightarrow 0.5$. In both cases, if the mean value for the targeted prey is close to the mixing space centroid, the maximum isotopic variance for the consumer could lie in any region.

To demonstrate the empirical relevance of the nonlinear nature of $\text{Var}\{Z\}$, we examine a prey-rich marine system composed of twelve species commonly consumed by sea otters (*Enhydra lutris*). In this system, all potential prey resources have unique isotopic means and variances (Fig. XX), including multiple species of sea urchins and crab, worms, clams, abalone, mussels, sea stars, and snails. By altering the underlying Dirichlet distribution for the sea otter consumer, we can investigate how alternatively targeting each prey species alters its the isotopic variance of its diet across different degrees of specialization (Fig. 3A). We determined the existence of strong nonlinear effects in the isotopic variance of the consumer's diet for 5 out of the 12 potential prey, due to both the relative magnitudes of each prey's means and variances relative to that of the mixing space (Fig. 3B). For targeted prey that resulted in nonlinear variance (including mussels, snails, purple sea urchins, kelp crabs, and sea stars), the maximum isotopic variance was found in the region $s \leq 0.5$.

The message that we take from the sea otter example is relatively straightforward: for a given prey mixing space, a consumer's dietary variability – where the consumer's tissues scale in proportion to its diet by a factor of $\lambda/2$ – will be a function of both mixing space geometry, as well as its dietary strategy, and these effects can be confounding. Despite this, we are able to establish certain predictions for the consumer's isotopic niche width as a function of diet: as it targets prey with isotopic values farther from the mixing space centroid, the variance will be expected to increase. In a sense, such an application could serve as a null model to explain isotopic variance as opposed to an explanation based purely on consuming a greater variety of prey.

4.2 The isotopic niche over time

We gain additional insights into the factors influencing consumer isotopic variability by considering dynamic diets, where the consumer oscillates between different foraging strategies over time. We considered a simple sinusoidal oscillation, $\mathcal{U}(t)$, that controlled the proportional contribution of two sub-diets, which we referred to as 'seasonal diets' to the composite diet over time $\mathbb{Z}(t)$. Our analytical results showed that the peak variance of the composite diet occurred during the transition between seasonal diets. Importantly, this is not due to any particular mixing space geometry, but a general result that will always occur, as long as the diets are isotopically distinct (each with a unique mean and variance), and the transition is smooth.

Although the peak variance of $\mathbb{Z}(t)$ is entirely due to ecological diet shifts irrespective of that actual isotopic composition of the diets that the consumer is shifting between, the isotope mixing space does play a role in determining the magnitude of $\text{Var}\{\mathbb{Z}(t)\}$, as averaged over time. This effect of mixing space geometry on the time-averaged variance of the composite diet is determined by α_V , which is a function of 1) the average variance of the sub-diets from which \mathbb{Z} is composed, and 2) the mean difference between the two sub-diets. As either of these factors increase, the average variance of the composite diet increases, setting the baseline from which the peak variance fluctuates.

We also observed that as the frequency of dietary transitions increased relative to the rate at which the consumer integrates dietary isotope ratios into its tissues, the consumer's isotopic variance exhibited lower amplitude as it fluctuated between the different variances of its diet. This occurs because the greater transition frequencies serve to average variance of the two diets within its tissues. Fink et al. (2012) found a similar dynamic when they derived an analytical solution for the variance of a consumer population transitioning between two prey. As the frequency of dietary transitions increased, the variance of the consumer population became small, effectively because the individual consumer diets increased the averaging effects of the two prey; as the frequency decreased, the variance of the population approached that of the prey.

An interesting observation that we gain from exploring a sinusoidal dietary shift is that the variance peak observed during the dietary transition is dependent on such a transition being smooth. In fact, it is the mid-point of this transition, at $\mathcal{U}(t) = 0.5$, where the composite diet is pulled equally from each seasonal diet, and this serves to maximize the isotopic heterogeneity of the mix. Thus, when foraging strategies are dynamic, it is the point of maximum isotopic heterogeneity that maximizes dietary variance, and this is analogous to the cause of peak dietary variance in the static example, where specialization on prey resources with greater isotopic offsets from the mixing space centroid maximizes isotopic heterogeneity, thus resulting in a variance peak.

An extreme alternative to a smooth dietary transition would be one that is discontinuous, as depicted by a step-function. Such an instantaneous dietary shift is not ecologically unrealistic; such a scenario could be realized by the sudden appearance of an alternative dietary resource. For example, grizzly bears shift

their diet abruptly to salmon during salmon runs (REFS), while wolves have been known to show an abrupt dietary switch from elk to bison as elk populations decline (Garrot et al). Because there is no point during a sharp, discontinuous transition that serves to mix sub-diets, the variance of the composite diet does not peak in response. Instead, both the expectation and the variance of the composite diet incorporates this step function behavior, transitioning to reflect the shifts between sub-diets. Because the isotope ratios associated with diet are incorporated gradually into the consumer's tissues, both the mean and the variance of the consumer will adopt a sawtooth-like dynamic (Fig. 7), where they begin to asymptote to the expectation and variance of the sub-diets, but are reverted abruptly with the switch in diet. We note that, as in the static example, the isotopic variance of the consumer approaches the variance of its diet twice as fast as its expectation (cf. Eq. 13).

Population dynamics and state-dependent foraging

We presented a simple dynamic-switching framework, where a consumer oscillates between two different diets over time to explore its effect on its isotopic niche. In reality, a consumer's dietary strategy might be shifting constantly over time, in response to a constantly changing environment. One potentially important extension of our framework could incorporate a population dynamic underlying the availability of potential resources (and by extension the consumer's diet) in a continuous, more complex, and ecologically justified manner. Our original formulation of the Dirichlet distribution that describes the consumer's diet was established on the relationship between the random variables describing the proportional contribution of prey to diet ($P_i = p_i$) and its encounter rate ($\Psi_i = \psi_i$), where $p_i = \psi_i / \sum_j \psi_j$, and this was assumed to have a static distribution over time. However, if the prey are fluctuating in accordance to an underlying population dynamic (for example, determined by a system of differential equations), the encounter rate of each prey would itself be a function of time. By relating the expectation and/or variance of Ψ_i to the density of prey, the parameterization of the Dirichlet can be directly coupled to changes in population densities, thus mechanistically incorporating population dynamics into predictions of a consumer's isotopic composition.

Furthermore, the relationship between p_i and ψ_i explicitly assumes passive foraging between the consumer and its potential prey, and this holds for our original static (single diet) example, our shifting diet example, and would hold for the example above where the Dirichlet changes in response to an underlying population dynamic. Although this is not a bad place to start, and may be a perfectly reasonable assumption for a filter feeder that consumes resources indiscriminately, it is not a reliable assumption for most organisms. Instead, a more complex relationship between p_i and the attributes of the consumer's prey, and perhaps attributes of the consumer itself, could be used to determine the parameterization of the Dirichlet distribution defining the consumer's diet over time.

For example, our framework implicitly assumes that there is a steady state influx of prey biomass to match the metabolic expenses of the consumer. In other words, prey are chosen in accordance to the Dirichlet distribution, but it is assumed that each foraging bout contributes equally to the consumer's diet, and that the consumer always finds a meal. In reality, the success of a given foraging bout is not certain, and there is some risk of not finding any prey at all; in such a case, the consumer would resort to metabolizing its own tissues. Such a dynamic would directly impact the rate of incorporation by altering the proportional contribution of newly consumed isotope ratios to the turnover of the consumer's body tissues. Moreover, the foraging decisions that a consumer makes are often a function of its energetic state, which changes as it successfully or unsuccessfully finds and acquires its prey. Such state-dependent foraging may be difficult to treat analytically, but could be explored numerically, and this approach would be useful for hypothesis

testing, particularly when one is interested in comparing the effects of different foraging strategies on the statistical properties of the consumer's isotopic composition.

From individuals to populations

Finally, the framework that we have presented has focused entirely on the individual, in particular on how the isotopic variance of an individual consumer changes in response to different ecological and isotope-related factors. Most ecological applications using stable isotope ratios operate at the level of the population, though there have been many recent efforts to understand different sources of isotopic variation across multiple ecological scales.

Understanding how variance percolates from prey to the individual consumer is a necessary first step to understand the source of isotopic variation at the level of the population. Such considerations quickly become complex, as there are scenarios when the isotopic variance of an individual is closely coupled to the variance of the population, and scenarios when it is not. For example, if individuals within a population have similar means and - for simplicity - equal variances, then the variance of the population will increase quadratically with the variance of the individuals (Fig. 8A). However, if the individuals within a population have very different means and relatively small variances, then there will not be a significant relationship between population and individual-level variation (Fig. 8B). Accordingly, we expect that our determination of peak variances due to both mixing space and ecological interactions at the individual level to also be true at the population level, as long as the individuals within the population are isotopically similar.

We can imagine different individual-population relationships occurring within a 2-D state-space defined by individuality on one axis and specialization on the other. At the extremes, a population could consist of 1) obligate specialists with low individuality (where all individuals specialize on the same resource), 2) obligate specialists with high individuality (where all individuals specialize on different resources), and 3) obligate generalists with low individuality (where all individuals are generalists; an obligate generalist with high individuality cannot exist in this context). How these different behaviors might shape individual and population-level isotopic distributions is an important question, though the answers will likely be complex. For example, isotopically similar individuals with low variances imply that all individuals are consuming similar things, in similar quantities, such that individuality is low, though our results show that low isotopic variance need not indicate specialization or generalization *per se* (cf. Figs 1,3). See Bearhop et al. (2004) and Fink et al. (2012) for an overview and quantitative analysis of these issues, respectively.

Of greater potential interest, and relevant to the framework that we have presented, is the scenario in which individuals have different diets that are themselves shifting in time (or not). Our approach could be used to hypothesis-test potential ecological/population/behavioral mechanisms that might contribute to the observed isotopic distributions at both the individual and population level, and this would be particularly powerful if one had access to tissues that integrate over time such as hair, whiskers, claws, or even laminar teeth.

There are many sources of variation that contribute to the consumer isotopic composition. These sources include the geometry of the prey mixing space, the foraging behaviors of the consumers, as well as temporal changes in the environment that might alter the ability of the consumer to find, acquire, and consume its prey. Of recent interest among ecologists using stable isotopes to quantify trophic interactions is the width of a consumer's isotopic niche, which we have interpreted to be its isotopic variance. By coupling this variance to mechanistic relationships between a consumer and its diet, as well as the isotopic mixing space of the system, we have presented a systematic exploration of the factors that cause this isotopic niche to both expand and contract. Incorporating the effects of population dynamics and/or different foraging strategies

572 will enable hypothesis testing of different ecological mechanisms to generate the isotopic distributions that
573 are observed in nature. We hope that such a forward-integrating approach, alongside the use of tools such
574 as mixing models to back-calculate dietary incorporation, will serve to expand and enhance the ecological
575 interpretation of isotopic data.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

576 The authors declare that the research was conducted in the absence of any commercial or financial
577 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

578 The statement about the authors and contributors can be up to several sentences long, describing the tasks
579 of individual authors referred to by their initials and should be included at the end of the manuscript before
580 the References section.

ACKNOWLEDGMENTS

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583 Text Text Text Text Text Text Text Text Text Text.
584 *Funding:* Text Text Text Text Text Text Text Text.

SUPPLEMENTAL DATA

585 Supplementary Material should be uploaded separately on submission, if there are Supplementary Figures,
586 please include the caption in the same file as the figure. LaTeX Supplementary Material templates can be
587 found in the Frontiers LaTeX folder

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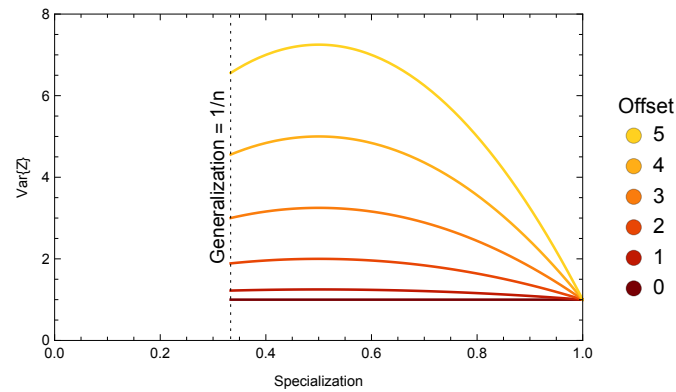


Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey, $\text{Var}\{Z(s)\}$. This illustrative example shows a three-prey system with prey means $\{-15, -15 + \text{offset}, -15\}$ and equal variances; colors depict specialization on prey 2 with a mean isotopic value that is a function of some offset amount. As the offset of the targeted prey increases, so does the nonlinear nature of $\text{Var}\{Z\}$.

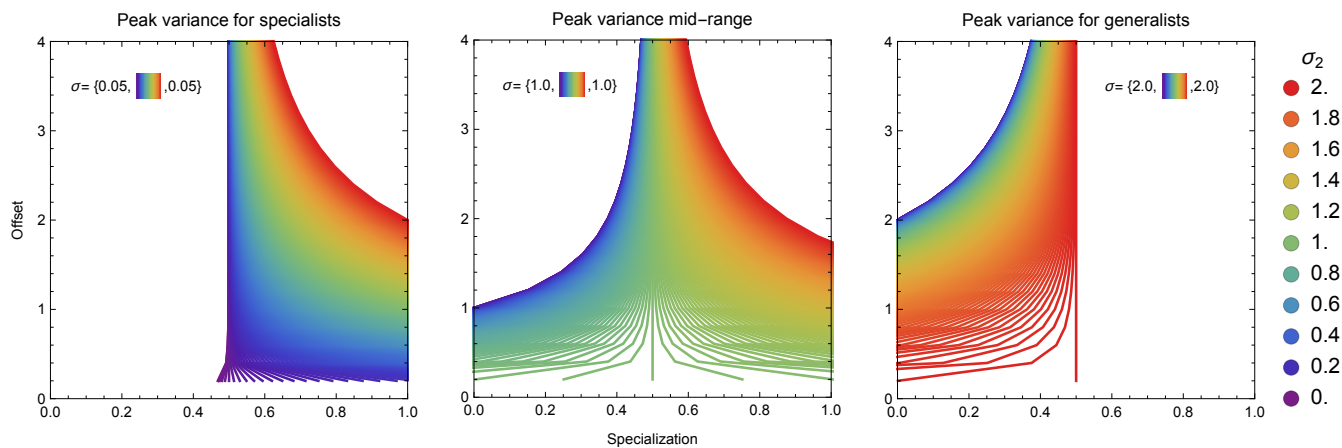


Figure 2: Maximal consumer isotopic variance (niche width) over the specialization index s as a function of mixing space geometry. A specialization value of $s = 1/n$ denotes obligate generalization, while $s = 1$ denotes obligate specialization. Left, center, and right panel show the effect of different mixing space geometries on the location of maximal consumer niche width over s . All panels: as the mean offset of the targeted prey is farther from the centroid of the mixing space, the maximal consumer isotopic niche width tends towards $s = 0.5$. Left and Center panel: If the targeted prey has a higher than average isotopic variance, the maximum consumer niche width will lie towards consumer specialization. Center and Right panel: If the targeted prey has a lower than average isotopic variance, the maximum consumer niche width will like towards consumer generalization.

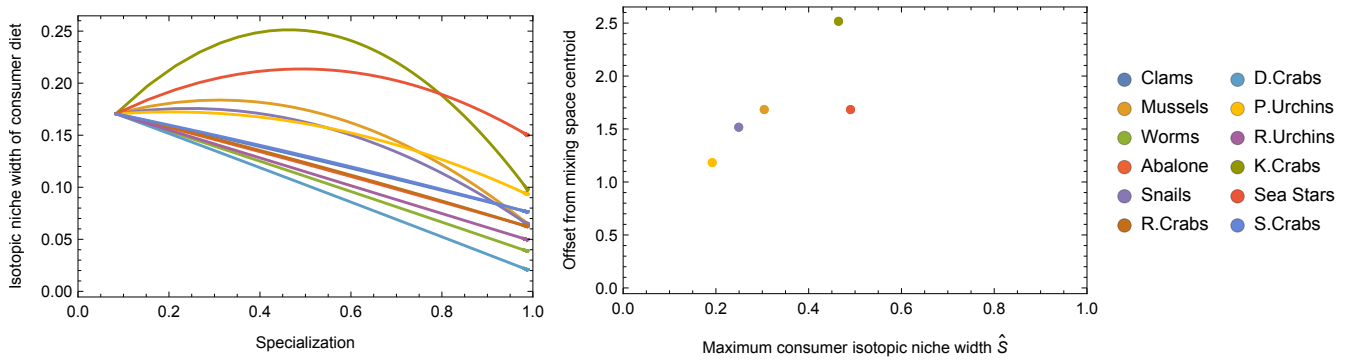


Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.

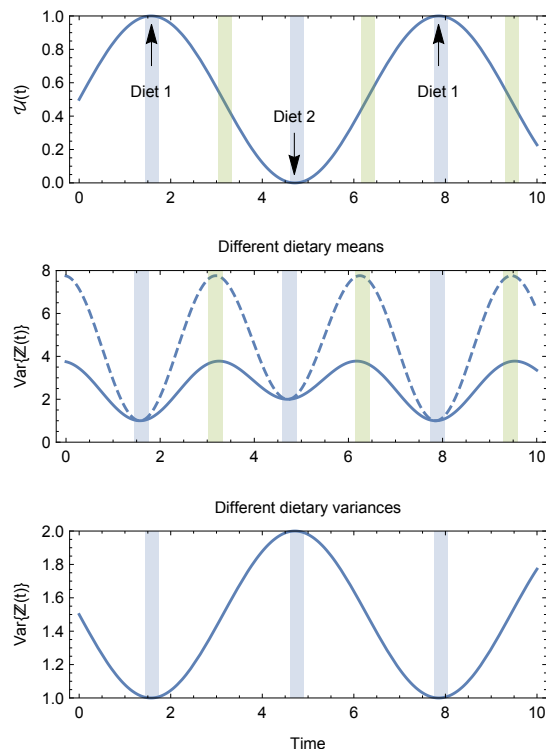


Figure 4

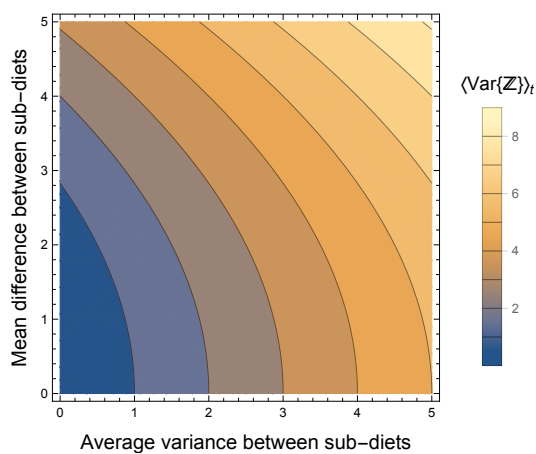


Figure 5

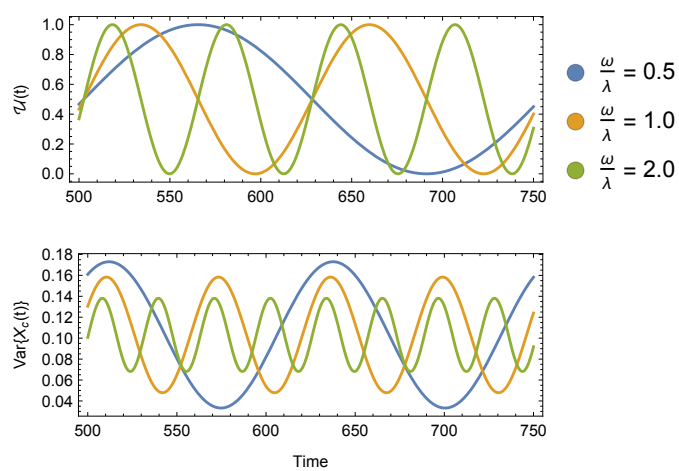


Figure 6

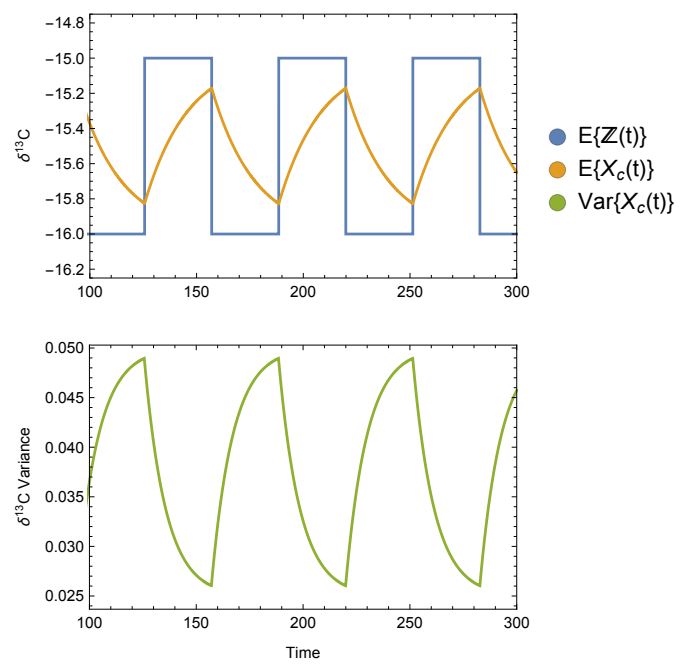


Figure 7

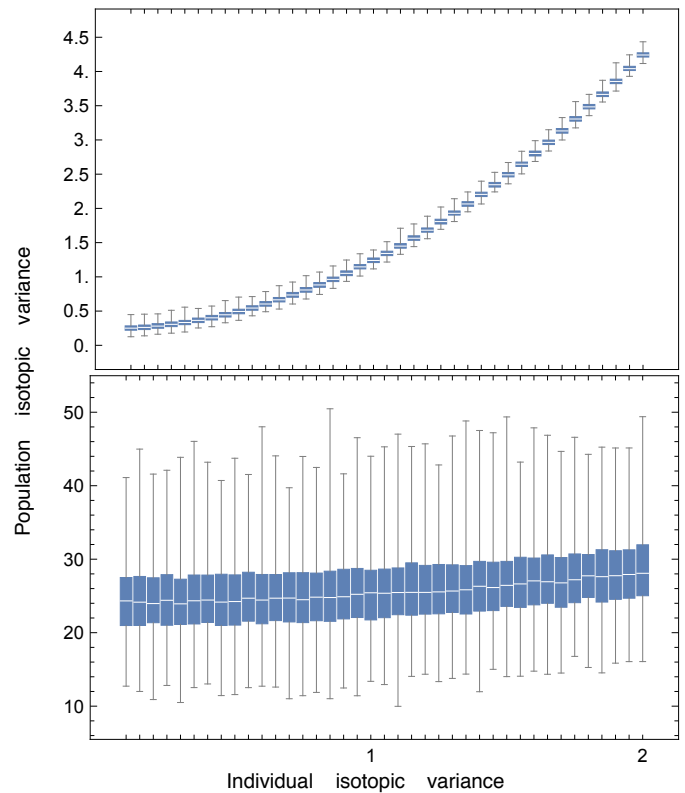


Figure 8