

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

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## 2 ABSTRACT

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## 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  
12 is a commonly used tool to explore and quantify diet. As a consumer incorporates the isotopic values of its  
13 resources into its tissues, it becomes a blend of these resources. The isotopic composition of a consumer  
14 thus reflects 1) the proportional contribution of different prey to the consumer's diet, and 2) the isotopic  
15 composition of its prey, which we will call the prey mixing space (REF). Both the consumer's dietary  
16 strategy as well as the prey mixing space contribute different sources of variability that are reflected in the  
17 isotopic composition of the consumer. For example, a consumer could be an obligate specialist on a single  
18 prey, such that its dietary variability is extremely low, in which case the isotopic mean and variability of the  
19 consumer's tissues will reflect that of its targeted prey. In contrast, the consumer could be a generalist, or  
20 intermediate specialist on certain prey such that the variability in its diet as well as the isotopic variability  
21 of the different prey in its diet contributes to its own isotopic composition. It is the isotopic variability of

a consumer, with respect to the mixing space of its prey, that ecologists have termed ‘the isotopic niche’ (REFS).

Determining the most likely proportional contribution of prey that determines a given consumer’s diet has thus been the focus of intense interest (REFS).

Of additional interest are the factors that control the consumer’s isotopic niche width, which is defined by the isotopic variance of the consumer at either the individual or population level. A consumer’s isotopic niche width, by definition, is a function of the isotopic values of its potential prey (the prey mixing space), as well as its dietary predilections. For a given mixing space, a consumer with a large isotopic niche width may be incorporating many isotopically distinct prey into its diet, while a consumer with a small isotopic niche width may be specializing on a single resource.

## 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 (REFS) or even state-dependence (REFS), and we will briefly address these considerations in the Discussion. As prey are encountered and consumed, the prey’s isotope values are incorporated into the consumer’s tissues weighted by the prey-specific proportional contribution to diet. The resulting distribution that describes the dietary input of multiple prey (each with an independent Gaussian density that describes the distribution of their isotopic values) is a mixed Gaussian distribution with weights determined by the prey’s proportional contribution to diet. This proportional contribution is itself a random variable drawn from a Dirichlet density (a multivariate Beta distribution) that serves as a probabilistic description of the consumer’s dietary input. The following section details our probabilistic determination of the consumer’s isotopic composition. We focus our attention on the variability of the consumer isotopic distribution, which is equivalent to its isotopic niche width - a statistic of certain interest to ecologists using stable isotopes as a tool to understand diet.

A consumer encounters each prey at a frequency determined by a Poisson process with parameter  $\psi_i$ , which determines the number of encounters  $M_i(t) = m_i$  between time 0 and time  $t$ ,

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

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

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

Here,  $a_i$  is the dispersion parameter, which is proportional to the encounter rate, and  $c$  scales with the time between encounters. If we integrate across all possible values of  $\psi_i$ , we obtain the Negative Binomial density with mean encounter rate  $a_i/c$  and coefficient of variation  $1/\sqrt{a_i}$  (REF Mangel). Following the derivation described by Ainsworth (REF), if we define the proportional contribution of prey to a consumer's diet to scale with the encounter rate, such that

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

then the random variable  $P_i \in \mathbf{P} = \mathbf{p}$ , where  $\sum_i p_i = 1$ , has a Dirichlet distribution 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 (REF Mangel). We note that bold-face fonts denote vectors of variables. 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  $P_i = p_i$  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 (REFS), which assume a Dirichlet prior and enable the input of alternative dietary information to inform isotopic data.

If the isotopic distributions for the set of potential prey follow independent Gaussian 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 Gaussian distribution, with weights given by  $\mathbf{p}$  drawn from the Dirichlet distribution. 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  $\mu_i$  is the mean isotopic value for prey  $i$ . This is simply the weighted average of the isotopic 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 isotopic distributions (or mixing space) of its prey. We find that

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

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

The isotopic variance of the consumer's diet  $\text{Var}\{Z\}$  can be simplified by considering a specific set of dietary behaviors. Here we examine how  $\text{Var}\{Z\}$  is influenced by generalist vs. specialist consumer diets, as well as the role of general mixing space geometries, in determining consumer isotopic niche width. If a generalist consumer alters its diet to include more of a certain prey  $k$  relative to the others, the Dirichlet distribution that defines its dietary behavior goes from  $a_i = 1$  for all  $i = 1, \dots, n$  to  $a_{i \neq k} = 1$  for  $i = 1, \dots, n$ , with  $a_k > 1$ . As specialization increases, the Dirichlet parameter corresponding to the targeted prey  $k$ , increases to a value much higher than one (pure specialization is obtained only at the limit  $a_k \rightarrow \infty$ ). 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 specialization on prey  $k$ , ranging from  $1/n$  (generalization) to 1 (specialization). We can thus substitute  $a_0 = (n-1)/(1-s_k)$  and  $p_i = a_i/a_0 = (1-s_k)/(n-1)$  for all  $i \neq k$ , and  $a_k/a_0 = s_k$ . We can then rewrite Eq. 8 as

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

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

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

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

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  $D = \mu_k$ .

Determination of the peak variance allows us to predict where the consumer's isotopic niche is expected to be maximized as a function of specialization on different prey. Although here we have focused on the special case where a consumer targets a single prey, one can rewrite the equation for the consumer's isotopic niche width with respect to increasing specialization on any number or combination of prey in the mixing space. For example, in the case where a consumer specializes on two prey (i.e. two species of 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.

### The Dynamics of Isotopic Incorporation

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 values vary by the combined effects of the Dirichlet and the mixed Gaussian framework, described by Eq. 8.

As the consumer incorporates prey into its diet, the isotopic distribution 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). Incorporation rates are well known to isotope ecologists and have been observed in both controlled feeding studies (REFS), 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 (REFS). 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 occurring at different rates. Though an assumption of multi-compartmental incorporation often does provide better

148 statistical fit with experimental data (REFS), the physiological processes that drive incorporation of isotope  
 149 ratios from one compartment to the other are not well understood (REF), and such fits are only marginally  
 150 better than a single-compartment approach.

151 In this next section, we assume that the ingested isotope ratios are incorporated into consumer body  
 152 tissues directly, moderated by the rate of incorporation  $\lambda$ , which is treated as a free parameter. For simplicity,  
 153 we assume that time is scaled such that a single time step corresponds to a single foraging bout. Moreover,  
 154 we assume that the consumer is incorporating prey of smaller size than itself, such that  $0 < \lambda < 1$ . Thus,  
 155 we aim to determine the isotopic composition of the consumer  $X_c$  as a function of the consumer diet, the  
 156 isotopic distribution of its prey (or mixing space), and  $\lambda$ . In a completely deterministic framework, the  
 157 isotopic composition of the consumer can be written as an ordinary differential equation

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

158 where the overdot denotes the derivative with respect to time  $t$ , and  $p_i$  and  $\mu_i$  are the proportional  
 159 contribution of prey  $i$  to the diet of the consumer, and the mean isotopic value of prey  $i$ , respectively.

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

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

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

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

169 where  $E\{Z\}$  and  $\text{Var}\{Z\}$  are as defined in Eqns. 7 and 8. One can observe that as  $t$  increases,  
 170 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  
 171  $\text{Var}\{X_c(t)\} \rightarrow \lambda \text{Var}\{Z\}/2$ . In other words, the expectation of the consumer's isotopic distribution  
 172 will equilibrate to that of its diet, while its variance will always be less than the variance of its diet by a  
 173 factor of  $\lambda/2$ . Variance decreases as the rate of incorporation decreases due to the consumer averaging its  
 174 isotopic value over more prey (because the tissue is turning over more slowly), and this serves to average  
 175 out fluctuations in the consumer's diet.

176 An implicit assumption of the static model is that the consumer's diet varies instantaneously over a given  
 177 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

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

### 3 RESULTS

As a consumer samples from multiple prey with stable isotopes values following independent Gaussian 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 equilibrium 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.



211 If the consumer's diet is itself variable over time, we do not expect its isotopic composition to equilibrate  
 212 as it would in a controlled feeding study. For example, the consumer might adopt one diet during the wet  
 213 season, and another during the dry season, such that it oscillates between the two throughout the year.  
 214 We consider a composite diet with an isotopic distribution  $\mathbb{Z}$   $f_{\mathbb{Z}}$  that dynamically oscillates between two  
 215 subdiets, which we will refer to as 'seasonal diets'. The seasonal diets have random variables  $Z_1$  and  $Z_2$ ,  
 216 distributed according to Eq. 6, where each has a different underlying Dirichlet – encoding which prey  
 217 the consumer targets during each season with frequency distributions  $f_{P_1}$  and  $f_{P_2}$  – while the isotopic  
 218 distributions of prey are assumed to be constant through time. We can thus describe the composite diet as a  
 219 mix of the seasonal diets, where the mix is characterized by weights that oscillate over time,  $\mathcal{U}(t)$ , and this  
 220 determines the contribution of each seasonal dietary strategy to the whole. The frequency distribution for  
 221 the composite diet is thus

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

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

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

224 where the mean isotopic value of the composite diet is averaged over both seasonal diets, weighted by the  
 225 proportional inclusion of each. In the wet/dry season example, the consumer could either shift gradually  
 226 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.  
 227 An example of the latter scenario would be a grizzly bear consumer system, where its diet shift abruptly  
 228 with the arrival of salmon during spawning season (REF).

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

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

234 where we have combined the non-oscillating components into three parameters  $\alpha_V$ ,  $\beta_V$ , and  $\gamma_V$  for  
 235 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  $\lambda$ . 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  $\omega$ . Depending on the turnover rate of the tissue of interest and how often the consumer shifts its diet, the ratio of these timescales  $\omega/\lambda$  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  $\theta_1$  and  $\theta_2$  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  $\theta_1$  and  $\theta_2$ , 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  $\theta_1$ ; when the means are different and the variances are similar, the lag is mostly due to  $\theta_2$ ; when both the isotopic means and variances of the seasonal diets are different, both contribute significantly to the lag.

Increasing  $\omega/\lambda$ , 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  $\lambda$ , and 2) the amplitude of the variance of  $X_c(t)$  decreases with increasing  $\omega$ . The first result is not surprising, as it mirrors the role of  $\lambda$  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. Accordingly, the decrease in the amplitude of isotopic variance of the consumer's tissue is an averaging effect, where the timescale of incorporation is much larger than the timescale of dietary switching.

## 4 DISCUSSION

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

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

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

Our primary findings concern whether and to what extent the peak isotopic variance of the consumer is realized under different, but definable, conditions with respect to static and dynamic foraging strategies. When the consumer exhibits a static foraging strategy, this peak variance can occur if it is an intermediate

specialist, and whether or not peak variance is realized for intermediate specialization is a product of mixing space geometry, and the isotopic variance of the prey that it is preferentially targeting. When the consumer exhibits a dynamic, yet smoothly varying, foraging strategy, the peak variance occurs during the transition from one diet to another, and is offset by a lag that is a function of its incorporation rate, and therefore dependent on the tissue being analyzed. Below we attempt to gain additional understanding for why variance peaks are expected to occur under different ecological circumstances and mixing space 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 underlaying

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  $\alpha_V$ , 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.

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 know 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 the 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  $\Psi_i$  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  $\psi_i$  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.

## 442 From individuals to populations

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

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

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

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

474 There are many sources of variation that contribute to the consumer isotopic composition. These sources  
475 include the geometry of the prey mixing space, the foraging behaviors of the consumers, as well as temporal  
476 changes in the environment that might alter the ability of the consumer to find, acquire, and consume its  
477 prey. Of recent interest among ecologists using stable isotopes to quantify trophic interactions is the width  
478 of a consumer's isotopic niche, which we have interpreted to be its isotopic variance. By coupling this  
479 variance to mechanistic relationships between a consumer and its diet, as well as the isotopic mixing space  
480 of the system, we have presented a systematic exploration of the factors that cause this isotopic niche to both  
481 expand and contract. Incorporating the effects of population dynamics and/or different foraging strategies  
482 will enable hypothesis testing of different ecological mechanisms to generate the isotopic distributions that  
483 are observed in nature. We hope that such a forward-integrating approach, alongside the use of tools such

484 as mixing models to back-calculate dietary incorporation, will serve to expand and enhance the ecological  
485 interpretation of isotopic data.



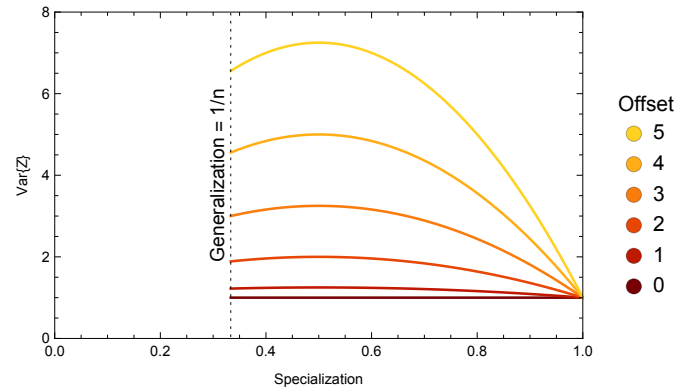


Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey,  $\text{Var}\{Z(s)\}$ . This illustrative example shows a three-prey system with prey means  $\{-15, -15 + \text{offset}, -15\}$  and equal variances; colors depict specialization on prey 2 with a 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  $\text{Var}\{Z\}$ .

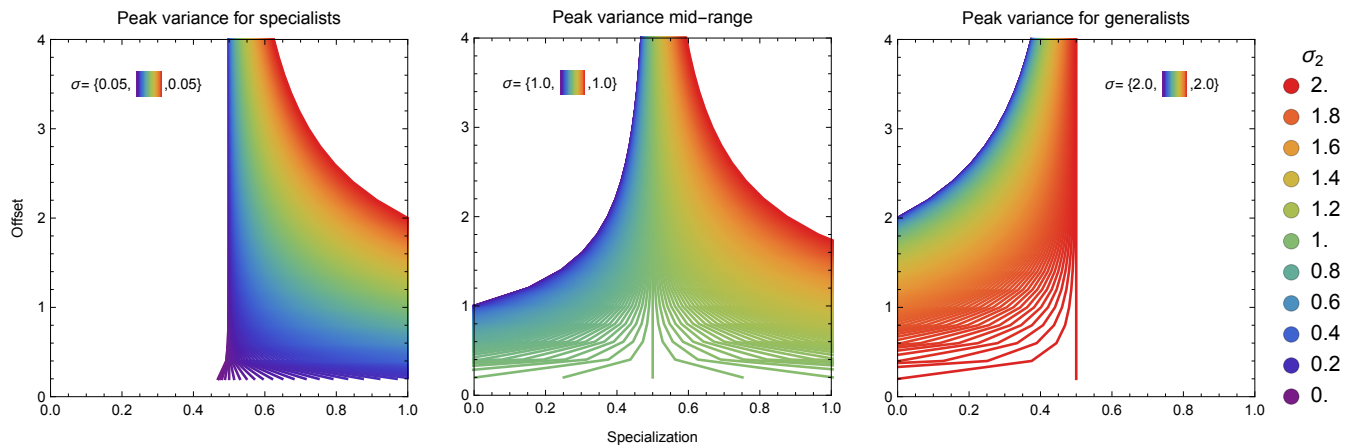


Figure 2: Maximal consumer isotopic variance (niche width) over the specialization index  $s$  as a function of mixing space geometry. A specialization value of  $s = 1/n$  denotes obligate generalization, while  $s = 1$  denotes obligate specialization. Left, center, and right panel show the effect 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.

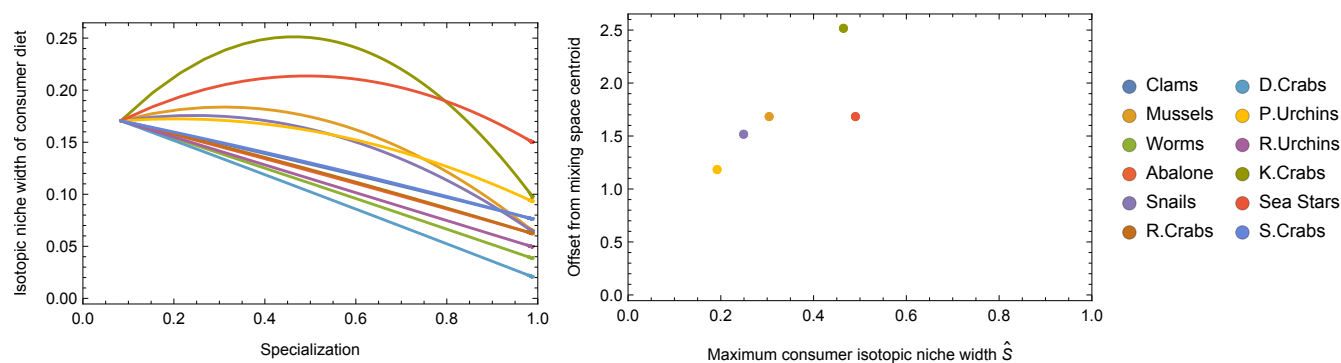


Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.

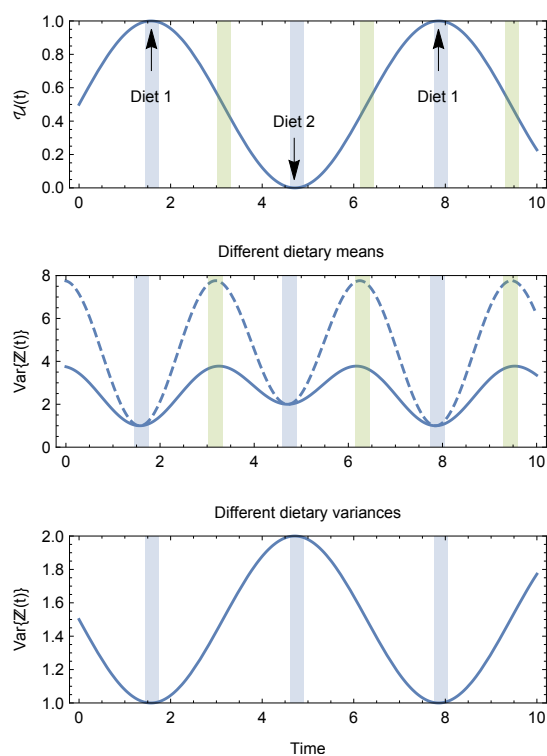


Figure 4

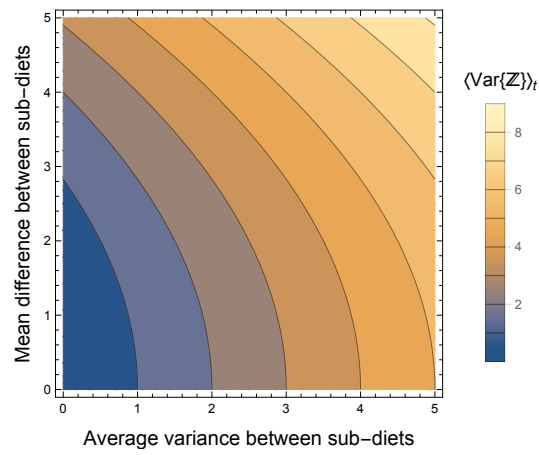


Figure 5

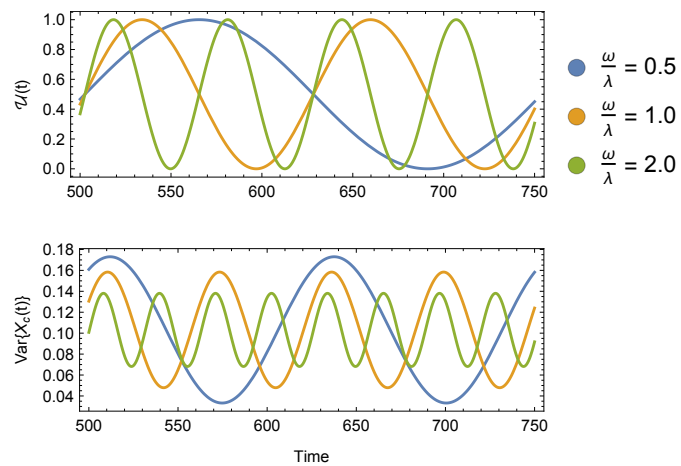


Figure 6

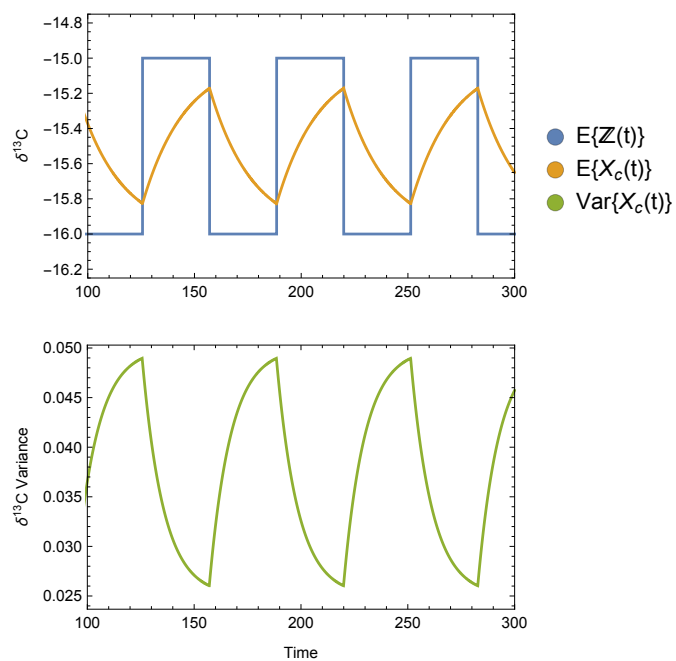


Figure 7

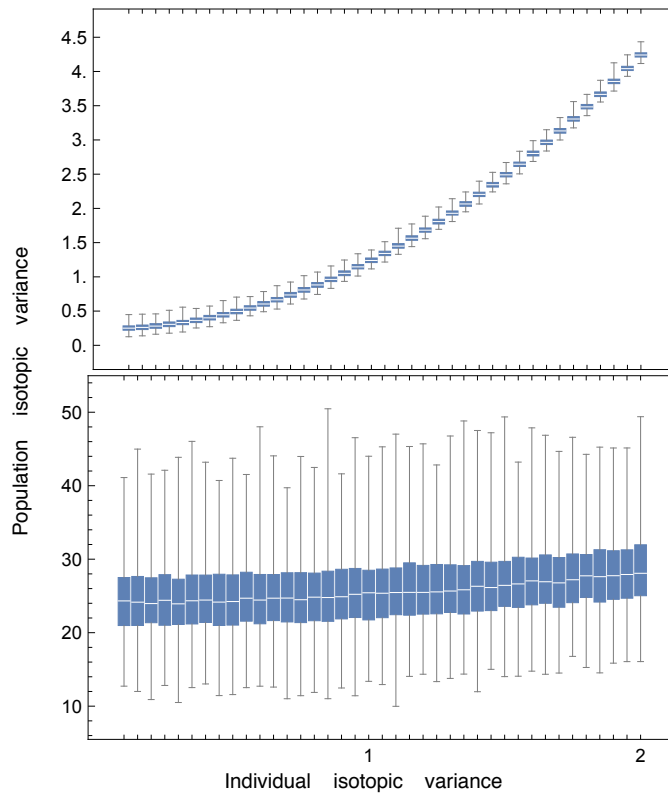


Figure 8