

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

Justin D. Yeakel<sup>1,2,†,\*</sup>, Uttam Bhat<sup>1,†</sup>, Emma E. Smith<sup>3</sup>, and Seth D.

Newsome<sup>3</sup>

<sup>1</sup> Santa Fe Institute, Santa Fe, New Mexico, USA

<sup>2</sup> School of Natural Sciences, University of California, Merced, Merced, California, USA

<sup>3</sup> Department of Biological Sciences, University of New Mexico, Albuquerque, New Mexico, USA

<sup>†</sup> Contributed equally

Correspondence\*:

Justin D. Yeakel

Santa Fe Institute, Santa Fe, New Mexico, 87505, USA, [jdyeakel@gmail.com](mailto:jdyeakel@gmail.com)

## 2 ABSTRACT

3 For full guidelines regarding your manuscript please refer to Author Guidelines  
4 or **Table ??** for a summary according to article type.

5 **Keywords:** Text Text Text Text Text Text Text Text

## 1 INTRODUCTION

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

10 Analysis of carbon and nitrogen stable isotopes of a consumer with respect to a suite of potential prey is a  
11 commonly used tool for determining diet. As a consumer incorporates the isotopic values of its consumed  
12 resources into its tissues, it becomes a unique ‘blend’ of its prey. Determining the most likely proportional  
13 contribution of prey that determines a given consumer’s diet has thus been the focus of intense interest  
14 (REFS).

15 Of additional interest are the factors that control the consumer’s isotopic niche width, which is defined by  
16 the isotopic variance of the consumer at either the individual or population level. A consumer’s isotopic  
17 niche width, by definition, is a function of the isotopic values of its potential prey (the prey mixing space),  
18 as well as its dietary predilections. For a given mixing space, a consumer with a large isotopic niche width  
19 may be incorporating many isotopically distinct prey into its diet, while a consumer with a small isotopic  
20 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 that describes 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 distribution, 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 description of the consumer dietary strategy, and 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  $\lambda_i$ , which determines the number of encounters  $M_i(t) = m$  between time 0 and time  $t$ ,

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

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  $\Lambda_i = \lambda_i$  as a random variable with a Gamma density

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

Here,  $a_i$  is the dispersion parameter, and  $c$  scales with the time between encounters. If we integrate across all possible values of  $\lambda_i$ , 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

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

then the random variable  $P_i \in \mathbf{P} = p_i \in \mathbf{p}$ , where  $\sum_i p_i = 1$ , has a Dirichlet distribution with density

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

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

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

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  $E\{p_i\} = a_i/a_0$  for prey  $i = 1, \dots, n$ . This density can be written as

$$f_Z(z | \mathbf{a}, \boldsymbol{\mu}, \boldsymbol{\sigma}) = \sum_{i=1}^n \frac{a_i}{a_0} \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{-\frac{(z-\mu_i)^2}{2\sigma_i^2}}, \quad (6)$$

with the expectation

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

76 where  $\mu_i$  is the mean isotopic value for prey  $i$ . This is simply the weighted average of the isotopic values  
 77 for the prey community, where weights are determined by the mean proportional contribution of prey to  
 78 the consumer's diet.

79 Of more interest to us here is the variance of  $f_Z(z)$ , which will allow us to analytically determine the  
 80 isotopic niche width of the consumer as a function of its dietary behavior and the isotopic distributions (or  
 81 mixing space) of its prey. We find that

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

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

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

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

95 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  
 96 isotopic variance of the consumer's diet will always be a concave parabolic function over  $s_k$ . With respect  
 97 to the size of the consumer's isotopic niche width, this means that there can be a peak variance for a value  
 98 of  $s_k$  intermediate to pure generalization ( $s_k = 1/n$ ) and pure specialization ( $s_k = 1$ ).

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

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

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

104 Determination of the inflection point for consumer isotopic variance allows us to predict where the  
 105 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 sheet 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 specializing. 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 later on. Due to 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, shown in Eq. 8.

As the consumer incorporates prey into its diet, the dietary isotopic distribution 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 (blood plasma), and on the slow end occur over years (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 statistical fit with experimental data, the physiological processes that drive incorporation of isotope ratios from one compartment to the other are not well understood, and such fits are only marginally better than a single-compartment approach.

In this next section, we assume the ingested isotope ratios are incorporated into consumer body tissues directly, moderated by the rate of incorporation  $\lambda$ , which is treated as a free parameter. Thus, we aim to determine the isotopic composition of the consumer  $X_c$  as a function of the consumer diet, the isotopic distribution of its prey (or mixing space), and  $\lambda$ . 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  $\mu_i$  are the proportional contribution of prey  $i$  to the diet of the consumer, and the mean isotopic value of prey  $i$ , respectively.

144 However, we must also take into account the stochastic effects described in the previous section, and  
 145 here we consider two independent sources of variation. First, each potential resource  $i$  is composed of  
 146 individuals with isotopic values varying according to independent Gaussian distributions with expectation  
 147  $E\{X_i\} = \mu_i$ , and variance  $\text{Var}\{X_i\} = \sigma_i^2$ . Secondly, in this section we consider a consumer diet is  
 148 variable, yet static (such that it can be described by a time-invariant probability distribution), there is  
 149 variation in the consumption of prey across short periods of time.

150 The consumer's isotopic distribution changes in accordance to the stochastic differential equation

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

151 where  $dW$  is the increment of Brownian motion (REF MANGEL). This stochastic differential equation is  
 152 generally known as an Ornstein-Uhlenbeck process (more?). Because the time interval is infinitely short at  
 153 the continuous time limit, the consumer's isotopic distribution will have a Gaussian density. In this case, if  
 154 the initial isotopic values of the consumer at time  $t = 0$  is  $X_c(0)$ , the expectation and variability of  $X_c$  at  
 155 time  $t$  are

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

156 where  $E\{Z\}$  and  $\text{Var}\{Z\}$  are as defined in Eqns. 7 and 8. One can observe that as  $t$  increases,  
 157 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  
 158  $\text{Var}\{X_c(t)\} \rightarrow \lambda \text{Var}\{Z\}/2$ . In other words, the expectation of the consumer's isotopic distribution  
 159 will equilibrate to that of its diet, while its variance will always be less than the variance of its diet by a  
 160 factor of  $\lambda/2$ . This decrease in variance is due to the fact that the consumer-diet mix has a biased weight  
 161 towards its own body tissues, such that  $\lambda < 1/2$ .

### 3 RESULTS

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

172 We have provided an analytical solution for the mean and variance of the consumer's isotope distribution  
 173 as a function of its diet and the isotope mixing space. By formulating these solutions in terms of consumer  
 174 generalization and specialization, we consider three important observations: 1) the variance of the  
 175 consumer's isotope distribution ( $\text{Var}\{Z\}$ ), which is equivalent to its isotopic niche width, is concave

176 parabolic; 2) whether and to what extent the  $\text{Var}\{Z\}$  demonstrates measurable nonlinearity depends  
177 in part on the geometry of the mixing space; 3) the inversion point, or the peak, of  $\text{Var}\{Z\}$  over the  
178 generalization-specialization continuum is the consumer's maximum isotopic niche width. This point may  
179 or may not exist at a value intermediate to an obligate generalist or obligate specialist.

180 One can gain some intuitive understanding of this nonlinearity by considering the following example,  
181 illustrated in Fig. 1. In a 3-prey system, where all prey have equal isotope means and variance, a consumer  
182 that ranges from generalizing on all three prey to specializing on a single prey will have equivalent  
183 dietary isotope distributions. As the mean value for the isotopic distribution of the targeted prey is moved  
184 away from the others, such that its offset from the centroid is increased, the variance function displays  
185 nonlinearity. This can be understood by considering two prey with the same mean value, and the targeted  
186 prey with a very different mean value. As the consumer incorporates isotopic ratios from all three prey  
187 in equal proportions, it will have increased isotopic variance due to the large spread of the prey. As the  
188 consumer integrates this isotopically atypical prey in greater proportions, the heterogeneity of incorporated  
189 isotope ratios will increase, serving to increase its own isotopic variability. The isotopic variability will  
190 then decline as it begins specializing on the atypical prey, and if it is consuming this prey exclusively, the  
191 isotopic variability of its diet will reflect the isotopic variability of its prey exactly. The concave parabolic  
192 nature of consumer isotopic variability can thus be explained by heterogeneous incorporation of isotope  
193 ratios over an asymmetric mixing space.

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

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

208 To demonstrate the empirical relevance of the nonlinear nature of  $\text{Var}\{Z\}$ , we examine a prey-rich sea  
209 otter system from xx. In this system, there are 12 potential prey resources with varying isotopic means  
210 and variances (FIGURE?), including sea urchins, multiple species of crab, abalone, mussels, and snails.  
211 By altering the underlying Dirichlet distribution for the sea otter consumer, we can investigate how  
212 alternatively targeting each prey alters its isotopic variance across different degrees of specialization. We  
213 determined the existence of strong nonlinear effects on the isotopic variance of the consumer for 5 out of  
214 the 12 potential prey, due to both the relative magnitudes of each prey's means and variance relative to  
215 that of the mixing space (Fig. 3). For targeted prey that resulted in nonlinear variance (including mussels,  
216 snails, purple sea urchins, kelp crabs, and seastars), the maximum isotopic variance was found in the region  
217  $s \leq 0.5$ .



The equilibrated 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.

- *Consumer isotopic niche width is concave parabolic*
- *This means that there is a maximum isotopic niche width for the consumer; this maximum value may lie between the consumer being a generalist or a specialist*
- **see figure 2:** *Where the maximum value lies is a function of the mixing space...*
  - *If the targeted prey has a higher than average variance, the maximum variance for the consumer will tend to be on the specialist side of the specialization matrix*
  - *If the targeted prey has a lower than average variance, the maximum variance for the consumer will tend to be on the generalist side of the spectrum*
- *Where the maximum value lies also has to do with how different the targeted prey's mean value is from the rest of the isotope mixing space (the offset).*
  - *If the offset is low (such that the targeted prey's mean is near... but not on... the centroid), the maximum consumer niche width can be very close to the 'generalization' or 'specialization' side of the spectrum.*
  - *If the offset is HIGH (such that the targeted prey's mean is far from the centroid), the maximum consumer niche width becomes very close to  $s = 0.5$ ...*
- **see Figure 3:** *This is not theoretical... we see that the consumer isotopic variance shows these properties for different targeted prey in the sea otter example!*

## 4 DISCUSSION

### 4.1 Temporal dietary dynamics

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

We now assume that diet (but not the isotopic distribution of prey) changes over time, such that the random variable of interest is now  $Z(t)$ . Solving for  $X(t)$ , we find



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

where  $Z(t)$  is the time trajectory of the consumer diet's isotopic values. Because we have assumed that the isotopic distributions of resources are constant, only the dietary strategy of the consumer can change through time. For example, we might assume that if the consumer prefers prey 1 over prey 2 in the first part of the year, and prey 2 over prey 1 in the second part of the year, the expectation of the proportional contribution of prey to the diet of the consumer might oscillate sinusoidally over a year. Because the isotopic values of prey are incorporated into the tissues of the consumer non-instantaneously, we would expect that the isotopic realization of such a dietary shift to be offset in time from the actual shift in prey.

Incorporating different classes of prey-switching dynamics permits an understanding of how the isotopic composition of a consumer reflects changes in its behavior over time as a function of the incorporation rate  $\lambda$ . To gain an intuitive understanding of how ecological dynamics are portrayed by consumer isotope values, we consider two types of prey-switching behavior: *i*) an instantaneous shift from one dietary strategy to another (such as those used in feeding experiments), and *ii*) a sinusoidally varying dietary strategy.

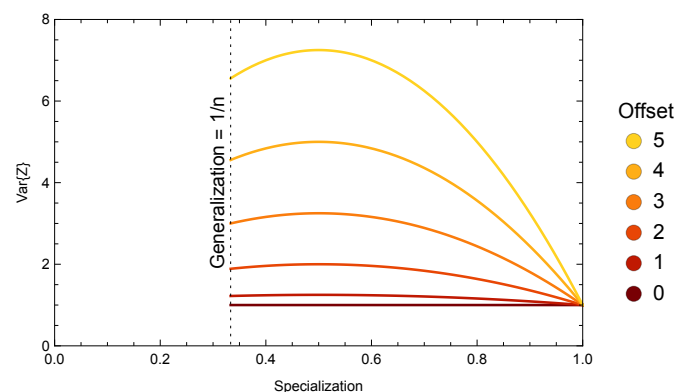


Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey,  $\text{Var}\{Z(s)\}$ . This illustrative example shows a three-prey system with prey means  $\{-15, -15 + \text{offset}, -15\}$  and equal variances; colors depict specialization on prey 2 with a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

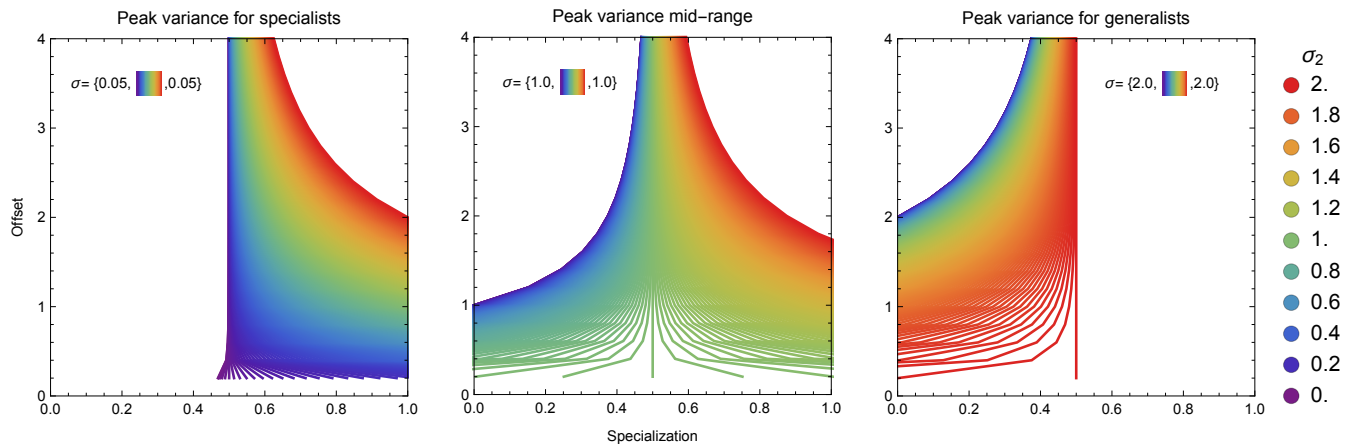


Figure 2: Maximal consumer isotopic variance (niche width) over the specialization index  $s$  as a function of mixing space geometry. A specialization value of  $s = 1/n$  denotes obligate generalization, while  $s = 1$  denotes obligate specialization. Left, center, and right panel show the effect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

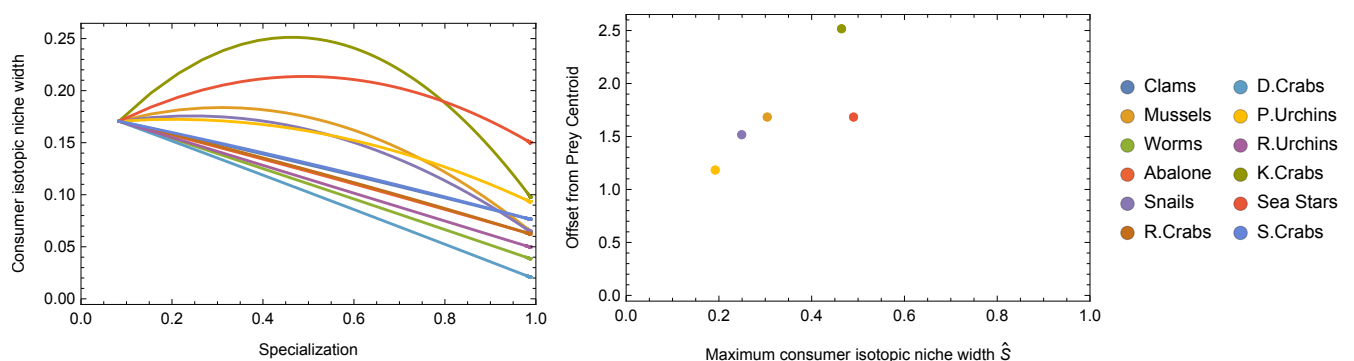


Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.