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

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ABSTRACT

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1 INTRODUCTION

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

Analysis of carbon and nitrogen stable isotopes of a consumer with respect to a suite of potential prey is a commonly used tool for determining diet. As a consumer incorporates the isotopic values of its consumed resources into its tissues, it becomes a unique 'blend' of its prey. 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 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 descibes 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 ψ_i, which determines the number of encounters $M_i(t) = m$ between time 0 and time t,

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

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

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

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

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

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

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

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 $\mathrm{E}\{p_i\} = a_i/a_0$ where $a_0 = \sum_i a_i$, and variance

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

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 Dirchlet distribution with parameters $a_i = 1$ for all prey $i = 1, ..., n$, such that the marginal distribution for $P_i = p_i$ is close to uniform with expectation $\mathrm{E}\{p_i\} = 1/n$. 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 $\boldsymbol{p}$ drawn from the Dirichlet distribution. This density can be written as

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

with the expectation

$$\mathrm{E}\{Z\} = \sum_{i=1}^{n} \frac{a_i}{a_0} \mu_i, \tag{7}$$

where μ_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

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

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 $\mathrm{Var}\{Z\}$ can be simplified by considering a specific set of dietary behaviors. Here we examine how $\mathrm{Var}\{Z\}$ 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 $i = 1, ..., n$ to $a_{i \neq k} = 1$ for $i = 1, ..., n$, 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 $a_k \to \infty$). 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

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

and note that, independent of the prey mixing space (a function of μ_i and σ_i^2 for prey $i = 1, ..., n$), 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 $s = 1$, 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

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

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

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 occuring at different rates. Though an assumption of multi-compartmental incorporation often does provide better statistical fit with experimental data (REFS), the physiological processes that drive incorporation of isotope ratios from one compartment to the other are not well understood (REF), and such fits are only marginally better than a single-compartment approach.

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 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 the consumer diet, the isotopic distribution of its prey (or mixing space), and λ. In a completely deterministic framework, the isotopic composition of the consumer can be written as an ordinary differential equation

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

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 isotopic value of prey i, respectively.

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

$$\mathrm{d}X_c = (1-\lambda)X_c\mathrm{dt} + \lambda\left(\mathrm{E}\{Z\}\mathrm{dt} + \sqrt{\mathrm{Var}\{Z\}}\mathrm{dW}\right) - X_c\mathrm{dt}. \tag{12}$$

where dW is the increment of Brownian motion (REF MANGEL). This stochastic differential equation describes a process known as an Orstein-Uhlenbeck process, which describes a stochastic process that has a steady state variance around the mean. Because the time interval dt is infinitely short at the continuous limit, the consumer's isotopic distribution will have a Gaussian density (REF). 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

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

where $\mathrm{E}\{Z\}$ and $\mathrm{Var}\{Z\}$ are as defined in Eqns. 7 and 8. One can observe that as t increases, the exponential part of $\mathrm{E}\{X_c(t)\}$ and $\mathrm{Var}\{X_c(t)\}$ go to zero, such that $\mathrm{E}\{X_c(t)\} \rightarrow \mathrm{E}\{Z\}$, and $\mathrm{Var}\{X_c(t)\} \rightarrow \lambda\mathrm{Var}\{Z\}/2$. 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.

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 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

$$\mathrm{E}\{X(t)\} = X(0)\mathrm{e}^{-\lambda t} + \lambda \mathrm{e}^{-\lambda t}\int_{s=0}^{t} \mathrm{e}^{\lambda s}\mathrm{E}\{Z(s)\}\mathrm{d}s,$$
$$\mathrm{Var}\{X(t)\} = \lambda^2 \mathrm{e}^{-2\lambda t}\int_{s=0}^{t} \mathrm{e}^{2\lambda s}\mathrm{Var}\{Z(s)\}\mathrm{d}s. \tag{14}$$

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 $\boldsymbol{p}$) 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 ($\mathrm{Var}\{Z\}$), which is equivalent to its isotopic niche width, is concave parabolic; 2) whether and to what extent the $\mathrm{Var}\{Z\}$ demonstrates measurable nonlinearity depends in part on the geometry of the mixing space; 3) the inversion point, or the peak, of $\mathrm{Var}\{Z\}$ 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'. 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 $f_{\boldsymbol{P}_1}$ and $f_{\boldsymbol{P}_2}$ – 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

$$f_{\mathbb{Z}(t)} = \left(\mathcal{U}(t) f_{Z_1} + (1 - \mathcal{U}(t)) f_{Z_2}\right) f_{\boldsymbol{P}_1} f_{\boldsymbol{P}_2}. \tag{15}$$

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

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

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 proporitonal 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

$$\begin{aligned} \mathrm{Var}\{\mathbb{Z}(t)\} = &\overbrace{\frac{\mathrm{Var}\{Z_1\} + \mathrm{Var}\{Z_2\}}{2} + \frac{1}{2}\left(\frac{\mathrm{E}\{Z_1\} - \mathrm{E}\{Z_2\}}{2}\right)^2}^{\alpha_{\mathrm{V}}} \\ &+ \overbrace{\frac{\mathrm{Var}\{Z_1\} - \mathrm{Var}\{Z_2\}}{2}}^{\beta_{\mathrm{V}}} \sin(\omega t) + \overbrace{\frac{1}{2}\left(\frac{\mathrm{E}\{Z_1\} - \mathrm{E}\{Z_2\}}{2}\right)^2}^{\gamma_{\mathrm{V}}} \sin\left(2\omega t + \frac{\pi}{2}\right). \end{aligned} \tag{17}$$

where we have combined the non-oscillating components into three parameters α_{V}, β_{V}, and γ_{V} for notational efficiency.

We elucidate three important insights from Eq. 17. 1) The time-averaged variance (denoted by $\langle\cdot\rangle_t$) is simply $\langle \mathrm{Var}\{\mathbb{Z}(t)\}\rangle_t = \alpha_{\mathrm{V}}$, which is 2) 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 3) the oscillating component includes doubling of frequency and a $\pi/2$ offset, meaning that the maximal variance of the consumer's composite diet will occur during the shifts from one diet to the other (Fig. 4B).

4 DISCUSSION

4.1 The isotopic niche from generalization to specialization

One can gain some intuitive understanding of this nonlinearity by considering the following example, illustrated in Fig. 1. In a 3-prey system, where all prey have equal isotope means and variance, a consumer that ranges from generalizing on all three prey to specializing on a single prey will have equivalent dietary isotope distributions. As the mean value for the isotopic distribution of the targeted prey is moved away from the others, such that its offset from the 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 its own 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 consumer isotopic variability 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 will serve to help ecologists determine what mechanisms - ecological or statistical - may be driving isotopic 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 $s \in [1/n, 1]$. 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 ingredients 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 specialization ($s > 0.5$), however the offset of the mean value for the targeted prey from the mixing space centroid will push $\hat{s}$ to $s \to 0.5$ (Fig. 2A,B). In contrast, if the targeted prey has lower than average variance, $\hat{s}$ will tend to lie towards generalization (Fig. 2B,C). As before, if the offset of the targeted prey's mean value increases, $\hat{s} \to 0.5$. 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 $\mathrm{Var}\{Z\}$, we examine a prey-rich sea otter system from xx. In this system, there are 12 potential prey resources with varying isotopic means and variances (FIGURE?), including sea urchins, multiple species of crab, abalone, mussels, and snails. By altering the underlaying Dirichlet distribution for the sea otter consumer, we can investigate how alternatively targeting each prey alters its isotopic variance across different degrees of specialization. We determined the existence of strong nonlinear effects on the isotopic variance of the consumer for 5 out of the 12 potential prey, due to both the relative magnitudes of each prey's means and variance relative to that of the mixing space (Fig. 3). For targeted prey that resulted in nonlinear variance (including mussels, snails, purple sea urchins, kelp crabs, and seastars), the maximum isotopic variance was found in the region $s \leq 0.5$.

4.2 The isotopic niche over time

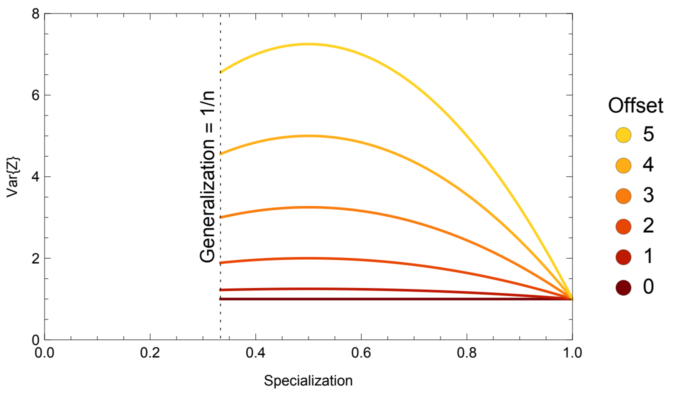

Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey, $\mathrm{Var}\{Z(s)\}$. This illustrative example shows a three-prey system with prey means $\{-15, -15{+}\mathrm{offset}, -15\}$ and equal variances; colors depect specialization on prey 2 with a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

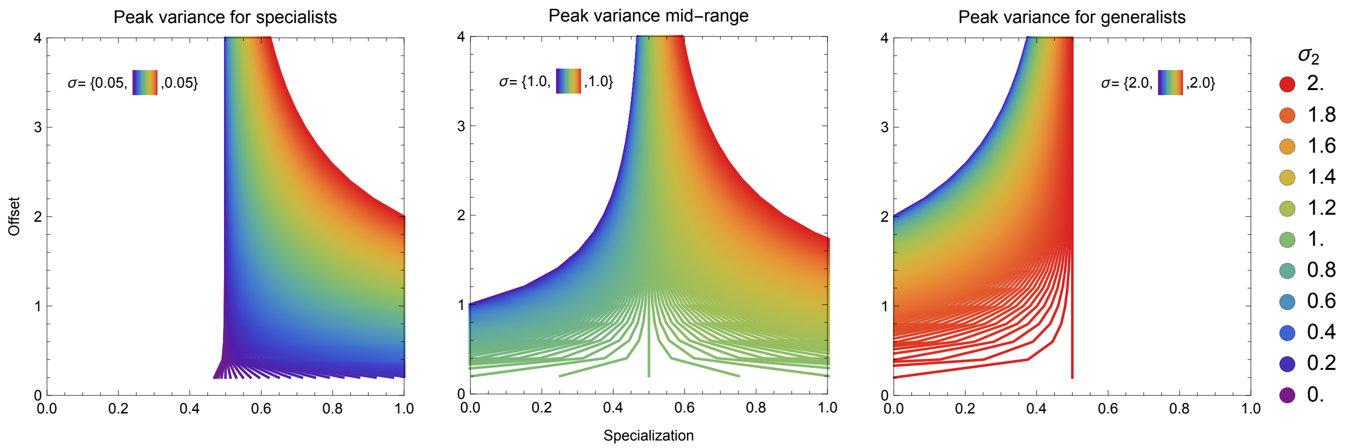

Figure 2: Maximal consumer isotopic varaince (niche width) over the specialization index s as a function of mixing space geometry. A specialization value of $s = 1/n$ denotes obligate generalization, while $s = 1$ denotes obligate specialization. Left, center, and right panel show the effect of different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

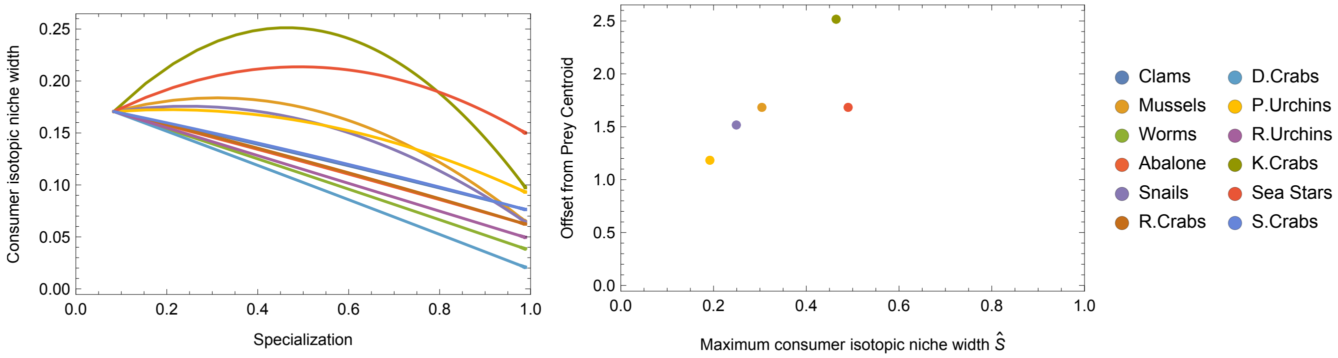

Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.

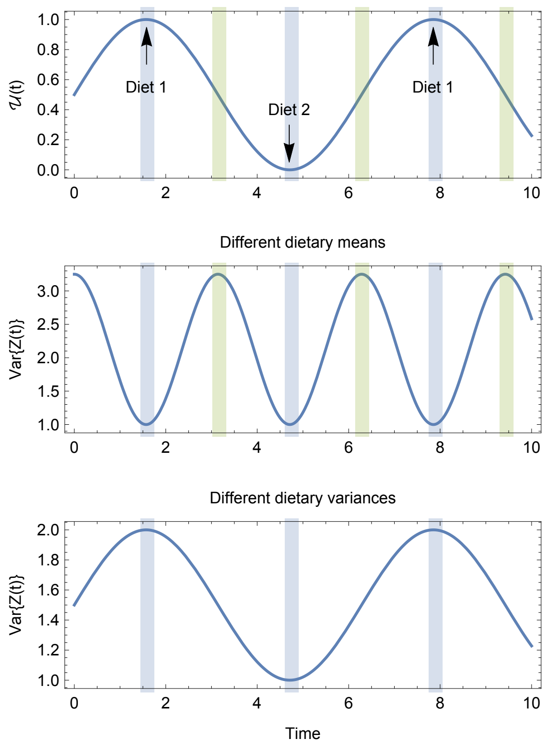

Figure 4

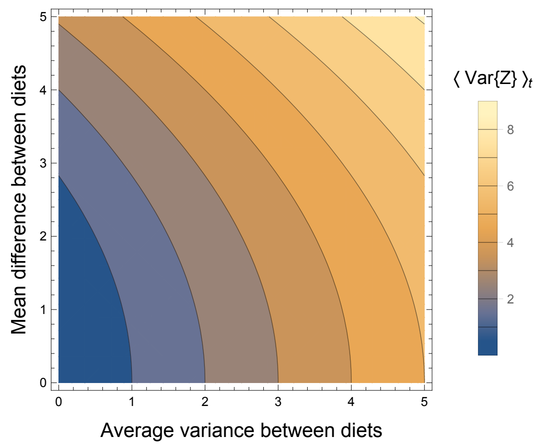

Figure 5

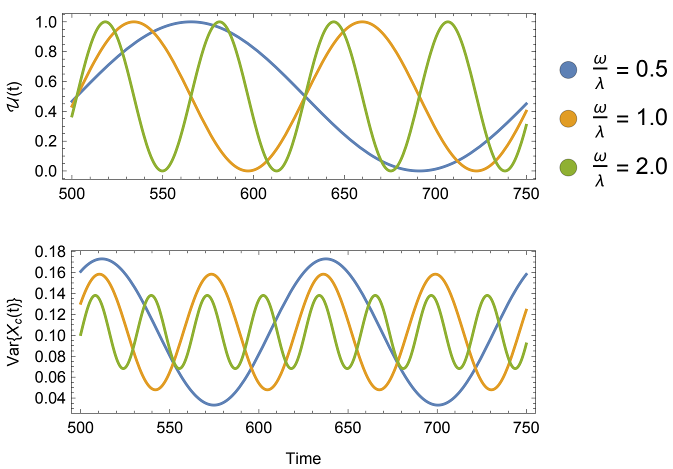

Figure 6