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

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2 **ABSTRACT**

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5 **Keywords: 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

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

Deriving the within-individual isotopic niche width

30   There are many ways to statistically summarize the integration of prey by a consumer species, however in
31 order to establish a mechanistic link between foraging and the consumer's isotopic distribution, we follow
32 the proceeding heuristic foraging mechanic.

33   We assume that a consumer encounters and consumes resources in proportion to the encounter rate of
34 each prey; prey that are encountered more frequently are assumed to be consumed more frequently. An
35 alternative approach could incorporate preferences (REFS) or even state-dependence (REFS), and we will
36 briefly address these considerations in the Discussion. As prey are encountered and consumed, the prey's
37 isotope values are incorporated into the consumer's tissues weighted by the prey-specific proportional
38 contribution to diet. The resulting distribution that descibes the dietary input of multiple prey (each with an
39 independent Gaussian density that describes the distribution of their isotopic values) is a mixed Gaussian
40 distribution with weights determined by the prey's proportional contribution to diet. This proportional
41 contribution is itself a random variable drawn from a Dirichlet density (a multivariate Beta distribution)
42 that serves as a probabilistic description of the consumer's dietary input. The following section details our
43 probabilistic description of the consumer dietary strategy, and focus our attention on the variability of the
44 consumer isotopic distribution, which is equivalent to its isotopic niche width - a statistic of certain interest
45 to ecologists using stable isotopes as a tool to understand diet.

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

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

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

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

52 Here, a_i is the dispersion parameter, and c scales with the time between encounters. If we integrate across
53 all possible values of λ_i, we obtain the Negative Binomial density with mean encounter rate a_i/c and
54 coefficient of variation $1/\sqrt{a_i}$ (REF Mangel). Following the derivation described by Ainsworth (REF), if

55   we define the proportional contribution of prey to a consumer's diet to scale with the encounter rate, such
56   that

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

57   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

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

58   where $\Gamma(\cdot)$ is the gamma function (REF Mangel). We note that bold-face fonts denote vectors of variables.
59   As such, the expected proportional contribution of a prey i to the consumer's diet has the expectation
60    $\mathrm{E}\{p_i\} = a_i/a_0$ where $a_0 = \sum_i a_i$, and variance

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

61   Describing the dietary behavior of a consumer as a Dirichlet distribution provides a flexible and powerful
62   framework to investigate how different foraging strategies influence a consumer's isotopic niche. For
63   example, a pure generalist consumer would have a Dirchlet distribution with parameters $a_i = 1$ for all
64   prey $i = 1, ..., n$, such that the marginal distribution for $P_i = p_i$ is close to uniform with expectation
65    $\mathrm{E}\{p_i\} = 1/n$. Because we have assumed that the proportional contribution of a prey to the consumer's diet
66   scales with the prey's encounter rate, this would be analogous to a system where a consumer is equally
67   likely to encounter the same number of any prey. In contrast, an obligate specialist would have a Dirichlet
68   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
69   of a Dirichlet distribution is also at the heart of Bayesian isotope mixing models (REFS), which assume a
70   Dirichlet prior and enable the input of alternative dietary information to inform isotopic data.

71   If the isotopic distributions for the set of potential prey follow independent Gaussian distributions, and
72   the dietary behavior of the consumer has a Dirichlet density, the resultant density that describes the isotopic
73   distribution of a consumer's diet $f_Z(Z = z)$ is a mixed Gaussian distribution, with weights given by
74    $\mathrm{E}\{p_i\} = a_i/a_0$ for prey $i = 1, ..., n$. This density can be written as

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

75   with the expectation

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

76   where μ_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

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

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 $i = 1, ..., n$ to $a_{i \neq k} = 1$ for $i = 1, ..., n$, 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 $a_k \to \infty$). 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

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

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

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

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

104 Determination of the inflexion 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.

106 Although here we have focused on the special case where a consumer targets a single prey, one can rewrite
107 the equation for the consumer's isotopic niche width with respect to increasing specialization on any
108 number or combination of prey in the mixing space. For example, in the case where a consumer specializes
109 on two prey (i.e. two species of crab), one would rewrite Eq. 8 in terms of both s_k (specialization on
110 prey k) and s_l (specialization on prey l), resulting in a concave parabolic sheet in dimensions s_k and s_l.
111 Determining the maximum variance would then entail taking the derivative of Eq. 8 with respect to both s_k
112 and s_l. In dimensions higher than 2, the process would be the same, with the goal of finding the maximum
113 variance over a hyperplane with a number of dimensions determined by the number of prey on which the
114 consumer is specializing. Because specializing on multiple prey does not introduce anything conceptually
115 unique, we consider only the case of a single-prey specialist.

The Dynamics of Isotopic Incorporation

117 We have established a framework for analytically calculating the distribution of isotope values that
118 characterizes a consumer's diet, composed of multiple, isotopically distinct prey. The dietary behavior of
119 the consumer is a function of a single Dirichlet distribution, which is assumed not to change over time,
120 although we will relax this assumption later on. Due to the central limit theorem, over long timescales
121 the dietary distribution of the consumer is static, with a fixed mean and variance. However, over short
122 timescales, the diet of the consumer varies as Eq. 5, while its isotopic values vary by the combined effects
123 of the Dirichlet and the mixed Gaussian framework, shown in Eq. 8.

124 As the consumer incorporates prey into its diet, the dietary isotopic distribution is incorporated into its
125 tissues. The timescale of physiological isotopic incorporation is based on the turnover rate of consumer
126 tissues, which on the fast end can occur within days to weeks (blood plasma), and on the slow end occur
127 over years (bone). Incorporation rates are well known to isotope ecologists and have been observed in both
128 controlled feeding studies (REFS), and occasionally in the wild (REFS?). Although the physiological details
129 are not well understood, isotopic incorporation can be modeled using either single- or multi-compartmental
130 approaches (REFS). In a single compartment framework, isotope ratios are ingested with food, and directly
131 incorporated into consumer tissues at a tissue-specific rate. In multiple compartment frameworks, it is
132 assumed that incorporation occurs over multiple body pools, the turnover of each occuring at different
133 rates. Though an assumption of multi-compartmental incorporation often does provide better statistical
134 fit with experimental data, the physiological processes that drive incorporation of isotope ratios from
135 one compartment to the other are not well understood, and such fits are only marginally better than a
136 single-compartment approach.

137 In this next section, we assume the ingested isotope ratios are incorporated into consumer body tissues
138 directly, moderated by the rate of incorporation λ, which is treated as a free parameter. Thus, we aim to
139 determine the isotopic compostion of the consumer X_c as a function of the consumer diet, the isotopic
140 distribution of its prey (or mixing space), and λ. In a completely deterministic framework, the isotopic
141 composition of the consumer can be written as an ordinary differential equation

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

142 where the overdot denotes the derivative with respect to time t, and p_i and μ_i are the proportional
143 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 indepedent sources of variation. First, each potential resource i is composed of
146 individuals with isotopic values varying according to independent Gaussian distributions with expecation
147 $E\{X_i\} = \mu_i$, and variance $Var\{X_i\} = \sigma_i^2$. 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

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

151 where dW is the increment of Brownian motion (REF MANGEL). This stochastic differential equation is
152 generally known as an Orstein-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

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

156 where $E\{Z\}$ and $Var\{Z\}$ 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 $Var\{X_c(t)\}$ go to zero, such that $E\{X_c(t)\} \to E\{Z\}$, and
158 $Var\{X_c(t)\} \to \lambda Var\{Z\}/2$. 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 $\boldsymbol{p}$) 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 ($Var\{Z\}$), which is equivalent to its isotopic niche width, is concave

176   parabolic; 2) whether and to what extent the $\mathrm{Var}\{Z\}$ demonstrates measurable nonlinearity depends
177   in part on the geometry of the mixing space; 3) the inversion point, or the peak, of $\mathrm{Var}\{Z\}$ 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   The width, or variance, of the consumer's isotopic niche is necessarily concave parabolic over the
181   specialization metric s, where $s = 1/n$ refers to an obligate generalist, and $s = 1$ refers to an obligate
182   specialist. This means that there is a peak isotopic variance that lies somewhere along this specialization
183   continuum, however it is only of interest to us of it lies in $s \in [1/n, 1]$.

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

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

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

212

213   • *Consumer isotopic niche width is concave parabolic*

214   • *This means that there is a maximum isotopic niche width for the consumer; this maximum value may*
215   *lie between the consumer being a generalist or a specialist*

216   • **see figure 2:** *Where the maximum value lies is a function of the mixing space...*

217   • *If the targeted prey has a higher than average variance, the maximum variance for the consumer*
218   *will tend to be on the specialist side of the specialization metrix*

219   • *If the targeted prey has a lower than average variance, the maximum variance for the consumer will*
220   *tend to be on the generalist side of the spectrum*

221   • *Where the maximum value lies also has to do with how different the targeted prey's mean value is from*
222   *the rest of the isotope mixing space (the offset).*

223   • *If the offset is low (such that the targeted prey's mean is near... but not on... the centroid), the*
224   *maximum consumer niche width can be very close to the 'generalization' or 'specialization' side of*
225   *the spectrum.*

226   • *If the offset is HIGH (such that the targeted prey's mean is far from the centroid), the maximum*
227   *consumer niche width becomes very close to $s = 0.5$...*

228   • **see Figure 3:** *This is not theoretical... we see that the consumer isotopic variance shows these*
229   *properties for different targeted prey in the sea otter example!*

4 DISCUSSION

4.1 Temporal dietary dynamics

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

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

$$E\{X(t)\} = X(0)e^{-\lambda t} + \lambda e^{-\lambda t} \int_{s=0}^{t} e^{\lambda s} E\{Z(s)\} ds,$$

$$\mathrm{Var}\{X(t)\} = \lambda^2 e^{-2\lambda t} \int_{s=0}^{t} e^{2\lambda s} \mathrm{Var}\{Z(s)\} ds \qquad (14)$$

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

248   Incorporating different classes of prey-switching dynamics permits an understanding of how the isotopic
249   composition of a consumer reflects changes in its behavior over time as a function of the incorporation rate

250 λ. To gain an intuitive understanding of how ecological dynamics are portrayed by consumer isotope values,
251 we consider two types of prey-switching behavior: *i*) an instantaneous shift from one dietary strategy to
252 another (such as those used in feeding experiments), and *ii*) a sinusoidally varying dietary strategy.
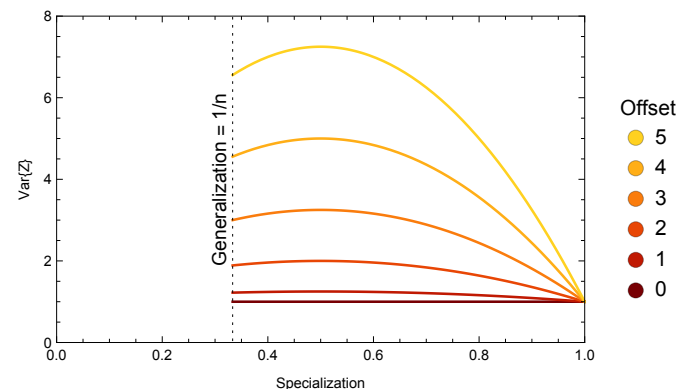

Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey, $\mathrm{Var}\{Z(s)\}$. This illustrative example shows a three-prey system with prey means $\{-15, -15+\text{offset}, -15\}$ and equal variances; colors depect specialization on prey 2 with a mean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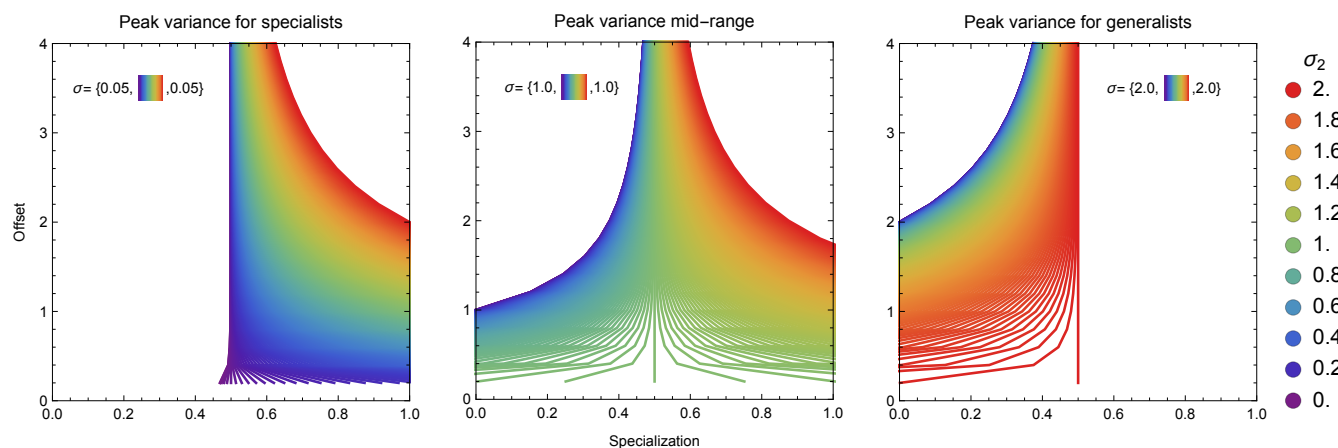

Figure 2: Maximal consumer isotopic varaince (niche width) over the specialization index s as a function of mixing space geometry. A specialization value of $s = 1/n$ denotes obligate generalization, while $s = 1$ denotes obligate specialization. Left, center, and right panel show the effect of different 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.
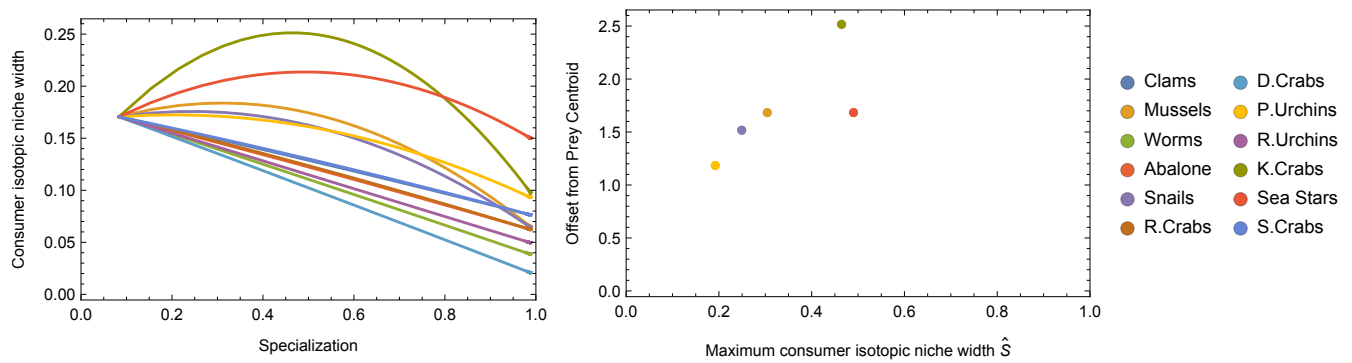
Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.