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

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2 ABSTRACT

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1 INTRODUCTION

6 Consumer foraging behaviors are dynamic, 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 describing 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.

29   Deriving the within-individual isotopic niche width

30   There are many ways to statistically summarize the integration of prey by a consumer species, however
31   in order to establish a mechanistic link between foraging and the consumer's isotopic composition, we
32   follow 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
43   our probabilistic determination of the consumer's isotopic composition. We focus our attention on the
44   variability of the consumer isotopic distribution, which is equivalent to its isotopic niche width - a statistic
45   of certain interest 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 ψ_i,
47   which determines the number of encounters $M_i(t) = m_i$ between time 0 and time t,

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

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 $\Psi_i = \psi_i$ as a random variable with a Gamma density

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

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

55 derivation described by Ainsworth (REF), if we define the proportional contribution of prey to a consumer's
56 diet to scale with the encounter rate, such that

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

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

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

73   If the isotopic distributions for the set of potential prey follow independent Gaussian distributions, and
74 the dietary behavior of the consumer has a Dirichlet density, the resultant density that describes the isotopic
75 distribution of a consumer's diet $f_Z(Z = z)$ is a mixed Gaussian distribution, with weights given by $\boldsymbol{p}$
76 drawn from the Dirichlet distribution. This density can be written as

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

77 with the expectation

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

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

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

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

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

87   The isotopic variance of the consumer's diet $\text{Var}\{Z\}$ can be simplified by considering a specific set
88 of dietary behaviors. Here we examine how $\text{Var}\{Z\}$ is influenced by generalist vs. specialist consumer
89 diets, as well as the role of general mixing space geometries, in determining consumer isotopic niche
90 width. If a generalist consumer alters its diet to include more of a certain prey k relative to the others, the
91 Dirichlet distribution that defines its dietary behavior goes from $a_i = 1$ for all $i = 1, ..., n$ to $a_{i\neq k} = 1$
92 for $i = 1, ..., n$, with $a_k > 1$. As specialization increases, the Dirichlet parameter corresponding to the
93 targeted prey k, increases to a value much higher than one (pure specialization is obtained only at the limit
94 $a_k \to \infty$). 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
95 specialization on prey k, ranging from $1/n$ (generalization) to 1 (specialization). We can thus substitute
96 $a_0 = (n-1)/(1-s_k)$ 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
97 rewrite Eq. 8 as

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

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

102   The peak $\hat{s}_k$, that describes the maximum isotopic variance of the consumer may or may not fall between
103 $s_k = 1/n$ and $s = 1$, and is only of ecological interest if it does. The peak variance can be solved
104 analytically by setting the derivative of Eq. 9 with respect to s_k equal to zero, and solving for s_k, which
105 results in

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

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

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

The Dynamics of Isotopic Incorporation

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

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

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

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

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

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

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

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

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

158   where $\mathrm{E}\{Z\}$ and $\mathrm{Var}\{Z\}$ are as defined in Eqns. 7 and 8. One can observe that as t increases,
159   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
160   $\mathrm{Var}\{X_c(t)\} \rightarrow \lambda\mathrm{Var}\{Z\}/2$. In other words, the expectation of the consumer's isotopic distribution
161   will equilibrate to that of its diet, while its variance will always be less than the variance of its diet by a
162   factor of $\lambda/2$. Variance decreases as the rate of incorporation decreases due to the consumer averaging its
163   isotopic value over more prey (because the tissue is turning over more slowly), and this serves to average
164   out fluctuations in the consumer's diet.

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

174   As the consumer's diet changes over time, the random variable of interest is now $Z(t)$, which is the
175   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

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

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

Temporally variable diets

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

200   If the consumer's diet is itself variable over time, we do not expect its isotopic composition to equilibrate
201 as it would in a controlled feeding study. For example, the consumer might adopt one diet during the wet
202 season, and another during the dry season, such that it oscillates between the two throughout the year.
203 We consider a composite diet with an isotopic distribution $\mathbb{Z}$ $f_{\mathbb{Z}}$ that dynamically oscillates between two
204 subdiets, which we will refer to as 'seasonal diets'. The seasonal diets have random variables Z_1 and Z_2,
205 distributed according to Eq. 6, where each has a different underlying Dirichlet – encoding which prey
206 the consumer targets during each season with frequency distributions $f_{\boldsymbol{P}_1}$ and $f_{\boldsymbol{P}_2}$ – while the isotopic
207 distributions of prey are assumed to be constant through time. We can thus describe the composite diet as a
208 mix of the seasonal diets, where the mix is characterized by weights that oscillate over time, $\mathcal{U}(t)$, and this
209 determines the contribution of each seasonal dietary strategy to the whole. The frequency distribution for
210 the composite diet is thus

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

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

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

213   where the mean isotopic value of the composite diet is averaged over both seasonal diets, weighted by the
214   proportional inclusion of each. In the wet/dry season example, the consumer could either shift gradually
215   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.
216   An example of the latter scenario would be a grizzly bear consumer system, where its diet shift abruptly
217   with the arrival of salmon during spawning season (REF).

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

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

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

225   We gain two key insights from the solution for the variance of the composite diet. 1) The time-averaged
226   variance (denoted by $\langle \cdot \rangle_t$) is simply $\langle \mathrm{Var}\{\mathbb{Z}(t)\}\rangle_t = \alpha_{\mathrm{V}}$, which is only impacted by the average variance
227   between the seasonal diets and the difference in the mean isotope values between the seasonal diets (Fig.
228   5), and 2) the oscillating component shows that the composite dietary variance has twice the frequency of
229   the diet shift $\mathcal{U}(t)$, as well as a $\pi/2$ offset, meaning that the maximal variance of the consumer's composite
230   diet will occur during the transition from one diet to the other (Fig. 4B). Together, these results reveal
231   that if the consumer's diet is varying continuously over time between two seasonal diets, both the mean
232   variance, as well as the difference in the mean isotope values of the seasonal diets – directly reflecting the
233   heterogeneity of prey mixing space geometry – will serve to increase the time-averaged variance of the
234   consumer's diet, and by extention the isotopic variance of the consumer itself.

235   Less intuitively, we observe that the consumer's peak variance, or niche width, as measured by the
236   variance of its composite diet, occurs not during the exclusive adoption of its wet/dry season diets, but

237   during the transition between the two, and this peak variance is driven exclusively by the difference in
238   means between seasonal diets. As the seasonal diets become more heterogeneous in isotopic space, the
239   greater the consumer's peak variance during the transtion, and this occurs because it is sampling between
240   two dietary strategies that are isotopically distinct. We can directly observe this by considering a transition
241   between two diets with a) different means and the same variances, and b) the same means and different
242   variances. In the former case, the peak variance of the composite diet occurs during the transition (Fig
243   4B); in the latter case, because the diets have the same mean isotope value, the peak occurs not during the
244   transition, but when the consumer adopts the diet with the greater variance, which in our example would
245   occur at the height of the season (Fig 4C).

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

$$
\begin{aligned}
\mathrm{Var}\{X_c(t \to \infty)\} = & \alpha_{\mathrm{V}} \frac{\lambda}{2} + \beta_{\mathrm{V}} \frac{\lambda^2}{\sqrt{(2\lambda)^2 + \omega^2}} \sin\left(\omega t - \theta_1\right) \\
& + \gamma_{\mathrm{V}} \frac{\lambda^2}{2\sqrt{\lambda^2 + \omega^2}} \sin\left(2\omega t + \theta_2\right).
\end{aligned}
\tag{18}
$$

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

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

4   DISCUSSION

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

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

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

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

4.1 The isotopic niche over specialization

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

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

Although the specific nature of $\hat{s}$ will depend strongly on mixing space geometry, we can elucidate certain key attributes that will determine the general nature of where this value falls. For mixing space geometries where the targeted prey has higher than average variance, $\hat{s}$ will tend to lie towards prey specialization ($s > 0.5$), however the offset of the mean value of the targeted prey from the mixing space centroid will quickly push $\hat{s}$ to $s \to 0.5$ (Fig. 2A,B). In contrast, if the targeted prey has lower than average variance, $\hat{s}$ will tend to lie towards prey generalization ($s < 0.5$; Fig. 2B,C). As before, if the offset of the targeted prey's mean value increases, $\hat{s} \to 0.5$. 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 marine system composed of twelve species commonly consumed by sea otters (*Enhydra lutris*). In this system, all potential prey resources have unique isotopic means and variances (Fig. XX), including multiple species of sea urchins and crab, worms, clams, abalone, mussels, sea stars, and snails. By altering the underlaying Dirichlet distribution for the sea otter consumer, we can investigate how alternatively targeting each prey species alters its the isotopic variance of its diet across different degrees of specialization (Fig. 3A). We determined the existence of strong nonlinear effects in the isotopic variance of the consumer's diet for 5 out of the 12 potential prey, due to both the relative magnitudes of each prey's means and variances relative to that of the mixing space (Fig. 3B). For targeted prey that resulted in nonlinear variance (including mussels, snails, purple sea urchins, kelp crabs, and sea stars), the maximum isotopic variance was found in the region $s \leq 0.5$.

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

4.2   The isotopic niche over time

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

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

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

383   An extreme alternative to a smooth dietary transition would be one that is discontinuous, as depicted by
384   a step-function. Such an instantaneous dietary shift is not ecologically unrealistic; such a scenario could
385   be realized by the sudden appearance of an alternative dietary resource. For example, grizzly bears shift
386   their diet abruptly to salmon during salmon runs (REFS), while wolves have been know to show an abrupt
387   dietary switch from elk to bison as elk populations decline (Garrot et al). Because there is no point during a
388   sharp, discontinuous transition that serves to mix sub-diets, the variance of the composite diet does not
389   peak in response. Instead, both the expectation and the variance of the composite diet incorporates this step
390   function behavior, transitioning to reflect the shifts between sub-diets. Because the isotope ratios associated
391   with diet are incorporated gradually into the consumer's tissues, both the mean and the variance of the
392   consumer will adopt a sawtooth-like dynamic (Fig. 7), where they begin to asymptote to the expectation
393   and variance of the sub-diets, but are reverted abruptly with the switch in diet. We note that, as in the

394   static example, the isotopic variance of the consumer approaches the variance of its diet twice as fast as its
395   expectation (cf. Eq. 13).

Future directions and extensions

397   Throughout this report, we have focused entirely on the individual, in particular on how the isotopic
398   variance of an individual consumer changes in response to different ecological and isotopic factors.
399   However, most ecological applications using stable isotope ratios operate at the population, though there
400   has been many recent efforts to understand the sources of isotopic variation - at both the individual
401   and population level. Indeed, one can extrapolate what we have learned about variance at an individual
402   level to that of the population. For example, the variance of a population – which is itself defined as a
403   mixture of individuals, each with their own isotopic distribution – is directly related to the variance of
404   individuals within the population (fig. 8). Thus, our determination of variance peaks at the individual level
405   would certainly be 'echoed' at the population level, though there are added complications, such as the
406   heterogeneity of individual mean isotope values, that we do not explore here.
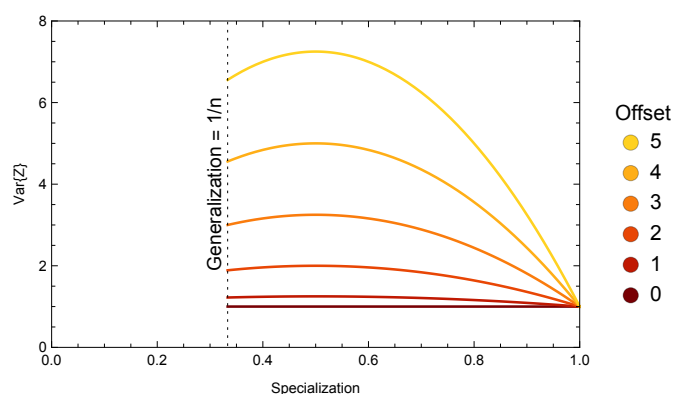
Figure 1: Variance of the isotopic distribution of diet with respect to specialization on a single prey, $\mathrm{Var}\{Z(s)\}$. This illustrative example shows a three-prey system with prey means $\{-15, -15+\text{offset}, -15\}$ and equal variances; colors depect specialization on prey 2 with a mean isotopic value that is a function of some offset amount. As the offset of the targeted prey increases, so does the nonlinear nature of $\mathrm{Var}\{Z\}$.
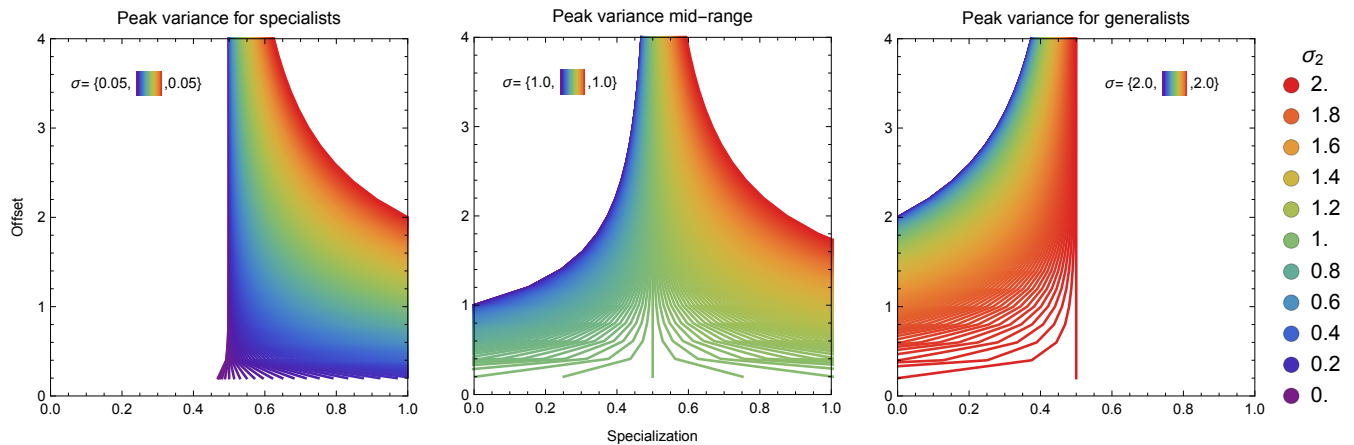
Figure 2: Maximal consumer isotopic varaince (niche width) over the specialization index s as a function of mixing space geometry. A specialization value of $s = 1/n$ denotes obligate generalization, while $s = 1$ denotes obligate specialization. Left, center, and right panel show the effect of different 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.
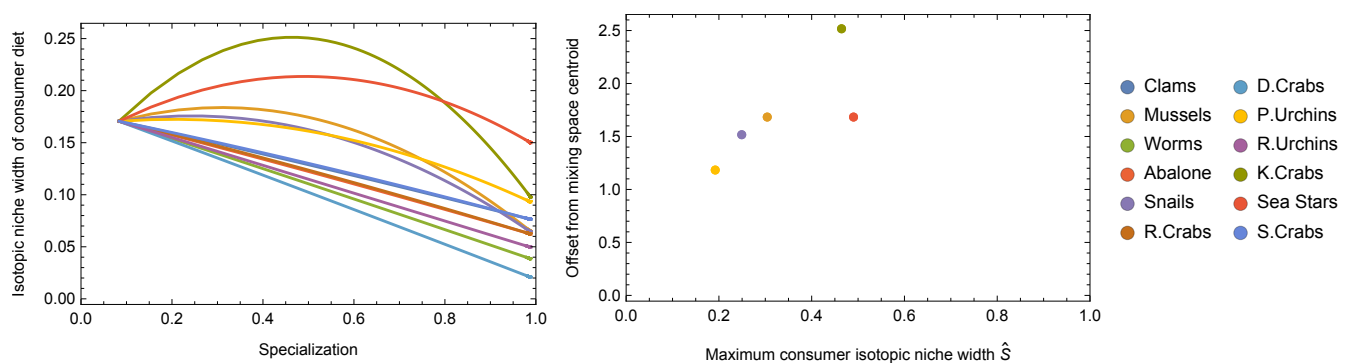
Figure 3: Left panel: Predicted sea otter isotopic niche width over different degrees of specialization on each prey in the system (colors). Right panel: Calculated maximum consumer niche width values as a function of specialization and the offset of the prey mean from the mixing space centroid.
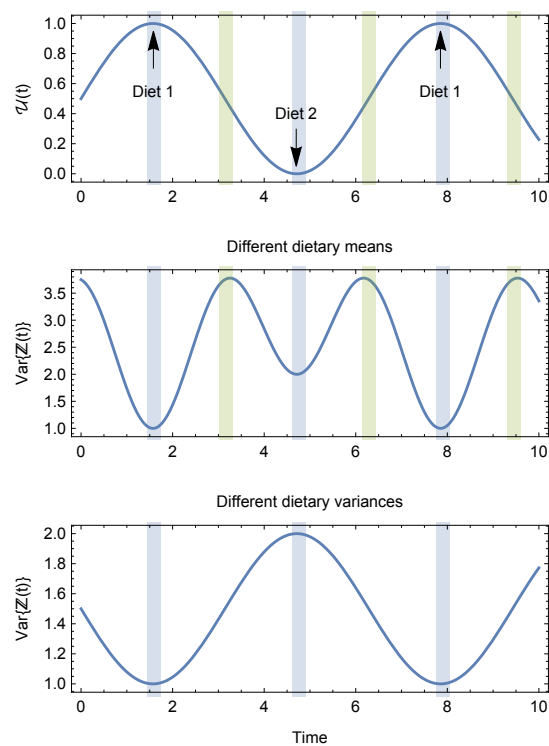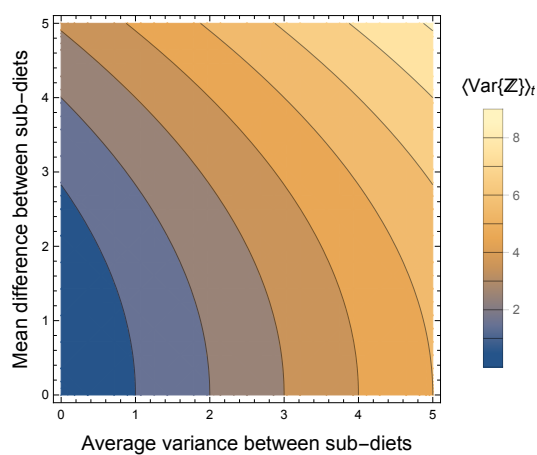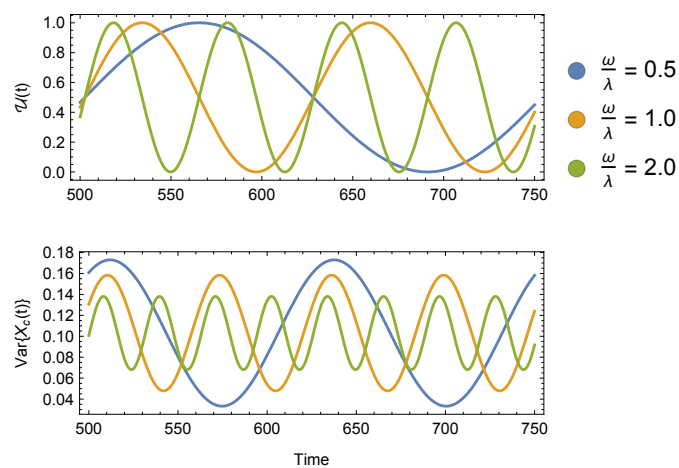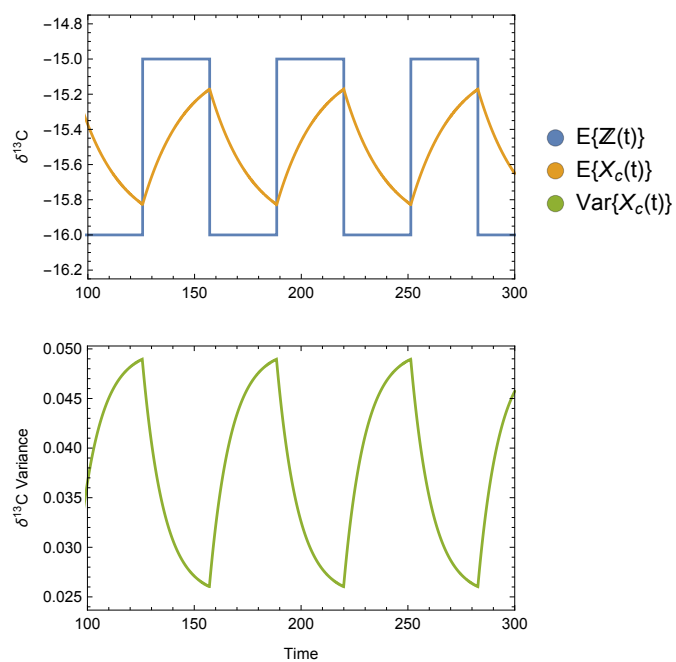
Figure 4

Figure 5

Figure 6

Figure 7

Figure 8