

¹ Exploring the isotopic niche: isotopic variance,
² physiological incorporation, and the temporal
³ dynamics of foraging

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⁶ **abstract**

⁷ Consumer foraging behaviors are dynamic, changing in response to prey availability,
⁸ seasonality, competition, and even the physiological states of the consumers.
⁹ The isotopic composition of a consumer is a product of these factors as well
¹⁰ as the isotopic ‘landscape’ of its prey, i.e. the isotopic mixing space. Stable
¹¹ isotope mixing models are used to back-calculate the most likely proportional
¹² contribution of a set of prey to a consumer’s diet based on their respective
¹³ isotopic distributions, however they are disconnected from ecological process.
¹⁴ Here we build a mechanistic framework that links the ecological and physiological
¹⁵ processes of an individual consumer to the isotopic distribution that describes its
¹⁶ diet, and ultimately to the isotopic composition of its own tissues, defined as its
¹⁷ ‘isotopic niche’. By coupling these processes, we systematically investigate under
¹⁸ what conditions the isotopic niche of a consumer changes as a function of both
¹⁹ the geometric properties of its mixing space and foraging strategies that may be
²⁰ static or dynamic over time. Results of our analytical derivations reveal general
²¹ insight into the conditions that impact isotopic niche width as a function of
²² consumer specialization on prey, as well as its ability to transition between diets
²³ over time. We show analytically that moderate specialization on isotopically
²⁴ unique prey can serve to maximize a consumer’s isotopic niche width, while
²⁵ temporally dynamic diets will tend to result in peak isotopic variance during
²⁶ dietary transitions. We demonstrate the relevance of our theoretical findings by
²⁷ examining a marine system composed of nine invertebrate species commonly

²⁸ consumed by sea otters. In general, our analytical framework highlights the
²⁹ complex interplay of mixing space geometry and consumer dietary behavior in
³⁰ driving expansion and contraction of the isotopic niche. Because this approach is
³¹ established on ecological mechanism, it is well-suited for enhancing the ecological
³² interpretation, and uncovering the root causes, of observed isotopic data.

³³ 1 Introduction

³⁴ Consumer foraging behaviors are dynamic, often resulting in variable diets that
³⁵ change over time and space as a function of environmental conditions, the
³⁶ densities of consumers and available resources, and even the physiological states
³⁷ of individual foragers, to name a few. Understanding how diets change, and
³⁸ to what extent different conditions promote or inhibit specific changes, is both
³⁹ a challenging theoretical and empirical problem in ecology, but is essential for
⁴⁰ elucidating the adaptive nature of complex ecological systems.

⁴¹ The comparison of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values
⁴² of a consumer with respect to its potential prey is a commonly utilized approach
⁴³ to quantify diet composition. The carbon and nitrogen isotopic composition of a
⁴⁴ consumer represents that of the food it eats, but is offset by predictable amounts,
⁴⁵ often called trophic discrimination factors, that are mediated by consumer
⁴⁶ physiology[?] [?] [?] [?]. The isotopic composition of a consumer thus reflects 1) the
⁴⁷ proportional contribution of different prey to the consumer's diet[?] [?], and 2) the
⁴⁸ isotopic composition of its prey, collectively described as the isotopic, or prey,
⁴⁹ mixing space[?] [?] [?].

⁵⁰ The isotopic niche of a consumer is a low-dimensional specification of the
⁵¹ 'Hutchinsonian niche'[?], an n-dimensional hypervolume that defines all biotic
⁵² and abiotic requirements needed for a species to exist. The isotopic niche is also
⁵³ generally derived from both biotic and abiotic processes, but in contrast to the
⁵⁴ large and ultimately immeasurable construct of the n-dimensional hypervolume,
⁵⁵ isotopic niches are defined exactly as a consumer's isotopic variance with a
⁵⁶ dimension determined by the number of isotope systems employed[?] [?] [?] [?] [?]. It
⁵⁷ is the width, or spread of this distribution that correlates to the breadth of the
⁵⁸ isotopic niche. Although the isotopic niche can be the result of many ecological
⁵⁹ and environmental factors that influence the flow of elements through biological
⁶⁰ systems[?], when it is primarily driven by consumer-resource interactions, the
⁶¹ isotopic niche is synonymous with the trophic niche as defined by ?. Changes

62 in the size of the isotopic niche have been shown to relate to ecosystem frag-
63 mentation[?], evolutionary diversification[?], changes in food availability[?], and
64 even individual responses to seasonal environments[?], however a systematic
65 understanding of how different sources of variability influence the isotopic niche
66 is lacking.

67 Both the consumer's dietary strategy as well as the isotopic mixing space
68 contribute different sources of variability that are reflected in the isotopic compo-
69 sition of the consumer. For example, a consumer could be an obligate specialist
70 on a single prey, such that its dietary variability is extremely low, in which case
71 the isotopic mean and variability of the consumer's tissues will reflect that of its
72 targeted prey. In contrast, the consumer could be a generalist, or intermediate
73 specialist on certain prey such that the variability in its diet as well as the isotopic
74 variability of its prey contributes to its own isotopic composition. Thus, the
75 isotopic composition of a consumer is not only a reflection of what the consumer
76 eats, but is also determined by the mixing space over which it integrates isotope
77 values, and the amount of time over which a particular tissue integrates dietary
78 inputs.

79 The isotopic niche is generally defined with respect to the isotopic variance of
80 a population[?][?][?], however population-level variance is itself an artifact of the
81 individual-level distributions from which the population is composed[?][?]. An
82 important step in understanding how the isotopic niche changes in response to
83 different consumer foraging strategies is to examine how individual-level variation
84 contributions to observed isotopic variability. Individual-level variability, in
85 particular that variability resulting from temporal changes in diet, has large
86 implications for the population[?][?][?]. For example, populations with greater
87 individual-level variability have been shown to exhibit greater stability[?], and in
88 certain cases can increase the likelihood of species coexistence[?]. Changes in
89 individual diet through time is frequently measured via stable isotope analysis of
90 metabolically inert, temporally-integrating tissues such as hair, whiskers, claws,
91 or even growth layers in teeth[?][?][?][?][?][?][?].

92 Once physiologically-mediated isotopic discrimination between a consumer
93 and its food has been accounted for, the isotopic niche is a direct reflection of
94 the proportional contribution of different prey resources to the consumer's diet.
95 Isotope mixing models, which originally used a bootstrapping framework[?][?] and
96 now employ Bayesian methods[?][?][?][?], are used to reconstruct the probability
97 distribution that describes the contribution of different prey; mixing models can
98 only be solved exactly if the number of potential prey resources are less than or

⁹⁹ equal to the number of isotope systems used plus one. These tools are forensic
¹⁰⁰ in nature, and can be used to back-calculate consumer diets across a range
¹⁰¹ of isotopically distinct prey with differing stoichiometries[?], to quantify intra-
¹⁰² and inter-population niche variability[?], to reconstruct diets of extinct taxa[?],
¹⁰³ and even combined with process-based models that are designed to constrain
¹⁰⁴ contribution-to-diet estimates based on known mechanistic relationships between
¹⁰⁵ species[?].

¹⁰⁶ A conceptually divergent, yet parallel, strategy is to consider the inter-related
¹⁰⁷ effects of ecological interactions and the concomitant integration of stable isotope
¹⁰⁸ values, and how these factors combine to result in the isotopic composition of
¹⁰⁹ a consumer. In this way, the consumer's isotopic distribution can be forward-
¹¹⁰ integrated through time based on the mechanistic linkages between its foraging
¹¹¹ strategy, its ability to find and acquire prey, and the isotopic landscape (mixing
¹¹² space) over which its diet is composed. This general perspective has been applied
¹¹³ to investigate properties of the isotopic niche for cases of fixed (non-varying)
¹¹⁴ diets[?]?, and with respect to experimental systems where consumers are forced
¹¹⁵ to switch between unique prey[?]. However, such a process-based framework has
¹¹⁶ not been directly linked to consumer foraging behaviors, prey availability, or
¹¹⁷ other ecological considerations such that the combined impacts of ecologically-
¹¹⁸ mediated dietary variation and mixing space geometry on the isotopic niche can
¹¹⁹ be assessed.

¹²⁰ Here we build a mechanistic framework that links the ecological and phys-
¹²¹ iological processes of an individual consumer to the isotopic distribution that
¹²² describes its diet, and ultimately to the isotopic composition of its own tissues.
¹²³ By coupling these processes, we are able to systematically investigate under
¹²⁴ what conditions the isotopic niche of a consumer changes as a function of both
¹²⁵ geometric properties of its mixing space, and alternative foraging strategies.
¹²⁶ We show that the isotopic variance of a consumer's diet (and by extension the
¹²⁷ width of its isotopic niche) is expected to be a concave parabolic function with
¹²⁸ respect to prey specialization, such that it possesses a peak variance, though the
¹²⁹ appearance of this peak is contingent on mixing space geometry. We demon-
¹³⁰ strate the potential importance of these findings by examining a prey mixing
¹³¹ space for sea otters (*Enhydra lutris*), which are known to possess high dietary
¹³² individuality[?]???.

¹³³ We then extend our framework to explore how a consumer's isotopic niche
¹³⁴ responds to temporally dynamic diets. We examine an example of a switch
¹³⁵ between two probabilistic diets that oscillates between, for example, seasons,

¹³⁶ and show analytically that the maximum expected isotopic niche width occurs
¹³⁷ during the transitions between diets. Determining how different sources of
¹³⁸ variability emerge from ecological, behavioral, and geometric drivers is important
¹³⁹ for interpreting the meaning of concepts such as the isotopic niche. Moreover,
¹⁴⁰ integrating these different sources of variation into a statistical process-based
¹⁴¹ framework lends itself particularly well to hypothesis-testing aimed at uncovering
¹⁴² the root causes of observed isotopic data. We hope that our approach is a
¹⁴³ step towards assessing how the isotopic niche may change due to more complex
¹⁴⁴ foraging behaviors and even population dynamics, and we expand on these ideas
¹⁴⁵ in the Discussion.

¹⁴⁶ 2 Methods & Analysis

¹⁴⁷ We begin by establishing a forward-integration approach for modeling the incor-
¹⁴⁸ poration of stable isotopes from multiple resources into a consumer's tissues. This
¹⁴⁹ new methodology provides an analytical link between the mechanistic drivers of
¹⁵⁰ foraging and the distribution of stable isotope values describing a consumer's tis-
¹⁵¹ sues over time. Using this framework, we aim to 1) examine how certain dietary
¹⁵² behaviors, such as prey specialization and different modes of dietary variation,
¹⁵³ impact the isotopic variance of consumer tissues, and 2) show how these methods
¹⁵⁴ can be expanded to include foraging behaviors that themselves are temporally
¹⁵⁵ dynamic, changing over seasons or years. Accordingly, our general goal is to
¹⁵⁶ reveal how both ecological and geometric factors can influence the expansion
¹⁵⁷ and contraction of isotopic variability, thus aiding ecological interpretation of
¹⁵⁸ the 'isotopic niche'.

¹⁵⁹ Deriving the within-individual isotopic niche width

¹⁶⁰ There are many ways to statistically summarize the integration of prey by a con-
¹⁶¹ sumer species, however in order to establish a mechanistic link between foraging
¹⁶² and the consumer's isotopic composition, we follow the proceeding heuristic for-
¹⁶³ aging mechanic. We assume that a consumer encounters and consumes resources
¹⁶⁴ in proportion to the encounter rate of each prey; prey that are encountered
¹⁶⁵ more frequently are assumed to be consumed more frequently. An alternative
¹⁶⁶ approach could incorporate preferences? or even state-dependence? ?, and
¹⁶⁷ we will briefly address these considerations in the Discussion. As prey are en-
¹⁶⁸ countered and consumed, the prey's isotope values are incorporated into the

169 consumer's tissues weighted by the prey-specific proportional contribution to
 170 diet. The resulting distribution that describes the dietary input of multiple prey
 171 (each with isotope values that are independently and Normally distributed) is a
 172 mixed Normal distribution with weights determined by the prey's proportional
 173 contribution to diet. This proportional contribution is itself a random variable
 174 drawn from a Dirichlet density (a multivariate Beta distribution) that serves
 175 as a probabilistic description of the consumer's dietary input[?]. The following
 176 section details our probabilistic determination of the consumer's isotopic com-
 177 position. We focus our attention on the variability of the isotopic distribution
 178 describing the consumer's diet, which scales directly with the consumer's own
 179 isotopic distribution, which is itself equivalent to the isotopic niche^{??}. Here
 180 and henceforth, we assume that the isotope ratios under consideration follow
 181 dietary pathways such that the isotopic niche is synonymous with the trophic
 182 niche[?].

183 A consumer encounters each prey at a frequency determined by a Poisson
 184 process with parameter ψ_i , which determines the number of encounters $M_i = m_i$
 185 between time 0 and time t , with the frequency distribution

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

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

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

192 Here, a_i is the dispersion parameter, which is proportional to the encounter
 193 rate, and c scales with the time between encounters^{???}. If we integrate across
 194 all possible values of ψ_i , we obtain the Negative Binomial density with mean
 195 encounter rate a_i/c and coefficient of variation $1/\sqrt{a_i}$ [?]. Following the derivation
 196 described by ?, if we define the proportional contribution of prey to a consumer's
 197 diet to scale with the encounter rate, such that

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

198 then the random variable $P_i = p_i$ where $P_i \in \mathbf{P}$ and $p_i \in \mathbf{p}$, and $\sum_i p_i = 1$, and
 199 note that we allow boldface type to denote vectors of variables. From Eq. 3,
 200 it follows that the vector describing the proportional contributions to diet \mathbf{P}
 201 follows a Dirichlet distribution⁷ with density

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

202 where $\Gamma(\cdot)$ is the gamma function cf.⁷. As such, the expected proportional
 203 contribution of a prey i to the consumer's diet has the expectation $E\{P_i\} = a_i/a_0$
 204 where $a_0 = \sum_i a_i$, and variance

$$V\{P_i\} = \frac{a_i(a_0 - a_i)}{a_0^2(a_0 + 1)}. \quad (5)$$

205 In this paper we consider the case where resources are plentiful and feeding is
 206 regular, and we draw a single prey i with probability p_i for inclusion to the
 207 consumer's diet.

208 Describing the dietary behavior of a consumer as a Dirichlet distribution
 209 provides a flexible and powerful framework to investigate how different foraging
 210 strategies influence a consumer's isotopic niche. For example, a pure generalist
 211 consumer would have a Dirichlet distribution with parameters $a_i = 1$ for all
 212 prey $i = 1, \dots, n$, such that the marginal distribution for P_i is close to uniform
 213 with expectation $E\{P_i\} = 1/n$. Because we have assumed that the proportional
 214 contribution of a prey to the consumer's diet scales with the prey's encounter
 215 rate, this would be analogous to a system where a consumer is equally likely
 216 to encounter the same number of any prey. In contrast, an obligate specialist
 217 would have a Dirichlet density that is spiked for a given prey k , such that the
 218 single parameter $a_k \gg 1$, while $a_{i \neq k} = 1$. The use of a Dirichlet distribution
 219 is also at the heart of Bayesian isotope mixing models^{7 8 9 10}, which assume a
 220 Dirichlet prior and enable the input of alternative dietary information to inform
 221 isotopic data.

222 If the stable isotope ratios for each of the potential prey follow independent
 223 Normal distributions, and the dietary behavior of the consumer has a Dirichlet
 224 density, the resultant density that describes the isotopic distribution of a con-
 225 sumer's diet $f_Z(Z = z)$ is a mixed Normal distribution, with weights given by \mathbf{p}
 226 drawn from the Dirichlet. Given that the isotopic means and variances for prey

²²⁷ i are denoted by μ_i and σ_i^2 , respectively, this density can be written as

$$f_Z(z|\mathbf{a}, \boldsymbol{\mu}, \boldsymbol{\sigma}) = \left(\sum_{i=1}^n p_i \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{-\frac{(z-\mu_i)^2}{2\sigma_i^2}} \right) f_{\mathbf{P}}(\mathbf{p}|\mathbf{a}), \quad (6)$$

²²⁸ with the expectation

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

²²⁹ Accordingly, the isotopic mean of the consumer's diet is a weighted average of
²³⁰ the isotopic means of its potential prey, where weights are determined by the
²³¹ outcome of the Dirichlet random variable.

²³² Of more interest to us here is the variance of Z , which will allow us to
²³³ analytically determine the isotopic niche width of the consumer as a function of
²³⁴ its dietary behavior and the mixing space of its prey. We find that

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

²³⁵ Although the form of Eq. 8 is not intuitive, we emphasize that - over different
²³⁶ dietary behaviors that shape the Dirichlet distribution and for different isotopic
²³⁷ mixing spaces - it is this equation that governs the expansion or contraction of
²³⁸ the consumer's isotopic niche width, and therefore of chief ecological interest.

²³⁹ The isotopic variance of the consumer's diet $\text{V}\{Z\}$ can be simplified by
²⁴⁰ considering a specific set of dietary behaviors. Here we examine how $\text{V}\{Z\}$
²⁴¹ is influenced by generalist vs. specialist consumer diets, as well as the role of
²⁴² general mixing space geometries, in determining consumer isotopic niche width.
²⁴³ It is important to note that specialism, as discussed here defines the degree to
²⁴⁴ which a consumer's diet is dependent on a single prey resource, ranging from
²⁴⁵ $s = 1/n$ (obligate generalization) to $s = 1$ (obligate specialization). It is thus
²⁴⁶ conceptually different than 'individual specialization' defined as the proportional
²⁴⁷ variance of an individual relative to that of its population Within-Individual
²⁴⁸ Component / Total Niche Width, or WIC/TNW; [?] , and often the variable of
²⁴⁹ interest in other studies examining properties of the isotopic niche [?] [?] [?] [?] .

²⁵⁰ If a generalist consumer alters its diet to include more of a certain prey k
²⁵¹ relative to the others, the Dirichlet distribution that defines its dietary behavior
²⁵² goes from $a_i = 1$ for all $i = 1, \dots, n$ to $a_{i \neq k} = 1$ for $i = 1, \dots, n$, with $a_k > 1$. As
²⁵³ specialization increases, the Dirichlet parameter corresponding to the targeted

254 prey k increases to a value much higher than one (pure specialization is obtained
 255 only at the limit $a_k \rightarrow \infty$). Thus, we can assume that $a_i = 1$ for all $i \neq k$, and
 256 $a_k = (n - 1)s_k/(1 - s_k)$, where s_k denotes specialization on prey k . We can thus
 257 substitute $a_0 = (n - 1)/(1 - s_k)$ and $p_i = a_i/a_0 = (1 - s_k)/(n - 1)$ for all $i \neq k$,
 258 and $a_k/a_0 = s_k$. We can then rewrite Eq. 8 as

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

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

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

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

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

271 Determination of the peak variance allows us to predict where the consumer's
 272 isotopic niche is expected to be maximized as a function of specialization on
 273 different prey. Although here we have focused on the special case where a
 274 consumer targets a single prey, one can rewrite the equation for the consumer's
 275 isotopic niche width with respect to increasing specialization on any number
 276 or combination of prey in the mixing space. For example, in the case where a
 277 consumer specializes on two prey (e.g. two species of crab), one would rewrite Eq.
 278 8 in terms of both s_k (specialization on prey k) and s_l (specialization on prey
 279 l), resulting in a concave parabolic plane in dimensions s_k and s_l . Determining
 280 the maximum variance would then entail taking the derivative of Eq. 8 with
 281 respect to both s_k and s_l . In dimensions higher than 2, the process would be
 282 the same, with the goal of finding the maximum variance over a hyperplane

283 with a number of dimensions determined by the number of prey on which the
284 consumer is preferentially targeting. Because specializing on multiple prey does
285 not introduce anything conceptually unique, we consider only the case of a
286 single-prey specialist.

287 The Dynamics of Isotopic Incorporation

288 We have established a framework for analytically calculating the distribution
289 of isotope values that characterizes a consumer's diet, composed of multiple,
290 isotopically distinct prey. The dietary behavior of the consumer is a function
291 of a single Dirichlet distribution, which is assumed not to change over time,
292 although we will relax this assumption in the next section. Over long timescales
293 the dietary distribution of the consumer is static, with a fixed mean and variance.
294 Over short timescales, the consumer's diet varies as Eq. 5, while its final isotopic
295 distribution has a variability emerging from the combined effects of the Dirichlet
296 and the mixed Normal distribution describing the prey mixing space (Eq. 8).

297 As the consumer acquires and consumes its prey, the isotopic composition
298 of its diet is incorporated into its tissues. The timescale of physiological incor-
299 poration is based on the turnover rate of consumer tissues, which on the fast
300 end can occur within days to weeks (e.g. blood plasma), and on the slow end
301 occur over years (e.g. bone)[?], and can be estimated via controlled feeding
302 studies^{???}. Although the physiological details are not well understood, iso-
303topic incorporation can be modeled using either single- or multi-compartmental
304 approaches^{??}. In a single compartment framework, isotope ratios are ingested
305 with food, and directly incorporated into consumer tissues at a tissue-specific
306 rate. In multiple compartment frameworks, it is assumed that incorporation
307 occurs over multiple body pools, the turnover of each potentially occurring at
308 different rates. Though an assumption of multi-compartmental incorporation
309 can provide better statistical fit with experimental data^{???}, the physiological
310 processes that drive incorporation of isotope ratios from one compartment to
311 the other are not well understood[?], and for many tissues single-compartment
312 models fit as well or better than multi-compartment models[?].

313 In this next section, we assume that the ingested isotope ratios are incorpo-
314 rated into consumer body tissues directly, moderated by the rate of incorporation
315 λ , which is treated as a free parameter. Here we consider only a single compart-
316 ment model, such that isotope ratios are directly shuttled to consumer tissues at
317 rate λ ; we note, however, that functions for multi-compartment models could

318 be used instead, though we do not expect large qualitative differences in results
 319 cf. Fig. 1 in [?]. For simplicity, we assume that time is scaled such that a single
 320 time step corresponds to a single foraging bout. Moreover, we assume that the
 321 consumer is incorporating prey of smaller size than itself, such that $0 < \lambda < 1$.
 322 Thus, we aim to determine the isotopic composition of the consumer X_c as a
 323 function of its diet, the isotopic mixing space, and λ . We note 1) that the isotopic
 324 composition of the consumer could represent its carbon ($\delta^{13}\text{C}$) or nitrogen ($\delta^{15}\text{N}$)
 325 isotope value, and our proceeding derivations work equivalently for both, and 2)
 326 that all trophic discrimination factors are assumed to have been accounted for,
 327 such that X_c directly reflects the consumer's diet. In a completely deterministic
 328 framework, the isotopic composition of the consumer over time t can be written
 329 as an ordinary differential equation, where

$$\frac{d}{dt}X_c(t) = \lambda \sum_{i=1}^N p_i \mu_i - \lambda X_c(t). \quad (11)$$

330 However, we must also take into account the stochastic effects described
 331 in the previous section, including the variation associated with the consumer's
 332 diet and the isotopic variation associated with each prey. We account for these
 333 stochastic effects by describing changes in the consumer's isotopic distribution
 334 with the stochastic differential equation

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

335 where dW is the increment of Brownian motion. This stochastic differential
 336 equation describes an Ornstein-Uhlenbeck process, which is a stochastic process
 337 that has a steady state variance around the mean [?]. Because the time interval
 338 dt is infinitesimal at the continuous limit, the consumer's isotopic distribution
 339 will have a Normal distribution. In this case, if the initial isotopic values of the
 340 consumer at time $t = 0$ is $X_c(0)$, the expectation and variability of X_c at time t
 341 are

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

342 where $E\{Z\}$ and $V\{Z\}$ are as defined in Eqns. 7 and 8. One can observe that as
 343 t increases, the exponential part of $E\{X_c(t)\}$ and $V\{X_c(t)\}$ go to zero, such that

344 $E\{X_c(t)\} \rightarrow E\{Z\}$, and $V\{X_c(t)\} \rightarrow \lambda V\{Z\}/2$. In other words, the expectation
 345 of the consumer's isotopic distribution will equilibrate to that of its diet, while
 346 its variance will always be less than the variance of its diet by a factor of $\lambda/2$.
 347 Variance decreases as the rate of incorporation decreases due to the consumer
 348 averaging its isotopic value over more prey (because the tissue is turning over
 349 more slowly), and this serves to average out fluctuations in the consumer's diet.

350 Our static model is defined by a consumer's diet that varies instantaneously
 351 over a given parameterization of $f_Z(z)$. This is relevant for organisms that have
 352 a consistently varying diet over time, however most organisms have diets that
 353 undergo large, qualitative changes over longer periods time. In such cases, the
 354 Dirichlet distribution that characterizes diet during one small temporal interval
 355 will be different than the Dirichlet distribution characterizing diet during another
 356 interval far apart in time. Such a shift might be due to seasonal, ontogenetic, or
 357 demographic changes in the consumer or its prey base over the course of months,
 358 or years, depending on the timescale of interest. In the following section, we will
 359 relax the assumption that diet is characterized by a single Dirichlet distribution,
 360 thus generalizing our formulation of consumer isotopic dynamics as a function of
 361 time.

362 The random variable of interest is now $Z(t)$, which is the trajectory defining
 363 the isotopic distribution of the consumer's diet over time. Solving for $X(t)$, we
 364 find

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

365 By defining the temporal dynamics of diet $Z(t)$ and the incorporation rate λ , we
 366 can thus analytically determine the isotopic mean and variance of the consumer's
 367 tissues.

368 3 Results

369 We have provided an analytical solution for the mean and variance of the
 370 consumer's isotope distribution as a function of its diet and the prey mixing
 371 space. By formulating these solutions in terms of consumer generalization and
 372 specialization (Eq. 9), we make three observations: 1) the variance of the isotopic

³⁷³ distribution of the consumer's diet, $V\{Z\}$, which scales to its isotopic niche width,
³⁷⁴ is concave parabolic (Fig. 1); 2) whether and to what extent $V\{Z\}$ demonstrates
³⁷⁵ measurable nonlinearity depends in part on the geometry of the mixing space;
³⁷⁶ 3) the peak variance over the generalization-specialization continuum is the
³⁷⁷ consumer's maximum isotopic niche width. This point may or may not exist at
³⁷⁸ a value intermediate to an obligate generalist and obligate specialist.

³⁷⁹ The nonlinear nature of the consumer's isotopic niche width as a function
³⁸⁰ of its specialization on certain prey (or combinations of prey) is driven almost
³⁸¹ entirely by the geometry of the prey mixing space. One can gain some intuitive
³⁸² understanding of this nonlinearity by considering the following example, illus-
³⁸³ trated in Fig. 1. In a three-prey system, where all prey have equal isotopic means
³⁸⁴ and variances, a consumer that ranges from generalization on all three prey to
³⁸⁵ specialization on a single prey will likewise have isotopically equivalent diets. As
³⁸⁶ the mean isotope value of the targeted prey is moved away from the others, such
³⁸⁷ that its offset from the mixing space centroid the center of the mixing space;?
³⁸⁸ is increased, the variance function displays increasing nonlinearity. For a skewed
³⁸⁹ mixing space, where one prey source has a very different isotope composition
³⁹⁰ than the rest e.g. a mixing space consisting of terrestrial foods vs. a marine
³⁹¹ subsidy;?
³⁹² , if the consumer incorporates isotopes from all three sources in equal
³⁹³ proportions (a generalist), it will have relatively higher isotopic variance than
³⁹⁴ if its prey exhibited a less skewed mixing space geometry. The skewness of the
³⁹⁵ mixing space increases with the offset of the targeted prey from the mixing space
³⁹⁶ centroid as shown in Fig. 1. As the consumer integrates this isotopically unique
³⁹⁷ prey in greater proportions, the heterogeneity of incorporated isotope values will
³⁹⁸ increase, serving to increase the consumer's isotopic variability. The isotopic
³⁹⁹ variability will then decline as the consumer begins specializing on the atypical
⁴⁰⁰ prey, and if it is consuming this prey exclusively, the isotopic variability of its
⁴⁰¹ diet will reflect the isotopic variability of its prey exactly. The concave parabolic
⁴⁰² nature of the isotopic variability of the consumer's diet can thus be explained
⁴⁰³ by heterogeneous incorporation of isotope ratios over an skewed, or asymmetric,
mixing space.

⁴⁰⁴ Understanding what dietary strategy or mixing space geometry can maximize
⁴⁰⁵ the isotopic niche width of the consumer's diet will serve to help ecologists
⁴⁰⁶ determine what mechanisms - ecological or statistical - may be driving patterns
⁴⁰⁷ in isotope data, or whether these mechanisms can be decoupled at all. Our
⁴⁰⁸ analytical solution for peak variance over dietary specialization on prey k ,
⁴⁰⁹ \hat{s}_k , reveals that maximum isotopic niche width can, but doesn't always, fall in

410 $s_k \in [1/n, 1]$, with bounds denoting exclusive prey generalization or specialization,
411 respectively. If the peak lies outside of this region, changes in isotopic variance
412 as specialization on a targeted prey is increased will appear monotonic or even
413 linear.

414 Although the specific nature of \hat{s}_k will depend strongly on mixing space
415 geometry, we can elucidate certain key attributes that will determine the general
416 nature of where this value falls. For mixing space geometries where the targeted
417 prey has higher than average variance, \hat{s}_k will tend to lie towards prey special-
418 ization ($s_k > 0.5$), however the offset of the mean value of the targeted prey
419 from the mixing space centroid will quickly push \hat{s}_k to $s_k \rightarrow 0.5$ (Fig. 2A,B). In
420 contrast, if the targeted prey has lower than average variance, \hat{s}_k will tend to
421 lie towards prey generalization ($s_k < 0.5$; Fig. 2B,C). As before, if the offset of
422 the targeted prey's mean value increases, $\hat{s}_k \rightarrow 0.5$. In both cases, if the mean
423 value for the targeted prey is close to the mixing space centroid, the maximum
424 isotopic variance for the consumer could lie in any region.

425 Temporally variable diets

426 The equilibrial solution to our stochastic differential equation (Eq. 13) reveals
427 that the isotopic variability of the consumer scales to diet as a factor of $\lambda/2$.
428 As the incorporation rate decreases, such that the turnover time is longer, the
429 isotopic variability of the consumer declines. This is due to the consumer
430 averaging its tissues over a greater number of foraging bouts. Moreover, we
431 observe that as the consumer transitions from some initial isotopic state $X_c(0)$
432 to diet, the variance of the consumer's isotopic values equilibrate twice as fast
433 as the mean value.

434 If the consumer's diet is itself variable over time, we do not expect its isotopic
435 composition to equilibrate as it would in a controlled feeding study (Eq. 14). For
436 example, the consumer might adopt one diet during the wet season, and another
437 during the dry season, such that it oscillates between the two throughout the
438 year. We consider a composite diet with an isotopic distribution $Z(t) \sim f_Z(t)$
439 that dynamically oscillates between two subdiets, which we will refer to as
440 'seasonal diets' with frequency ω . We note that $1/\omega$ in this context corresponds
441 to the 'dietary correlation time' of ?. Seasonal diets have random variables
442 Z_1 and Z_2 , each distributed according to Eq. 6, though they have different
443 underlying Dirichlet distributions – encoding which prey the consumer targets
444 during each season with frequency distributions f_{P_1} and f_{P_2} – while the isotopic

445 distributions of prey are assumed to be constant over time. We can thus describe
 446 the composite diet as a mix of the seasonal diets characterized by weights that
 447 oscillate over time, and this determines the contribution of each seasonal dietary
 448 strategy to the whole. We define $\mathcal{U}(t)$ to be the proportional contribution of
 449 Z_1 to the composite diet $\mathbb{Z}(t)$ over time, such that it can vary between zero
 450 (no incorporation of Z_1) to unity (complete reliance on Z_1). The frequency
 451 distribution for the composite diet is thus

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

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

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

455 where the isotopic mean of the composite diet is averaged over both seasonal
 456 diets, weighted by the proportional inclusion of each. In the wet/dry season
 457 example, the consumer could either shift gradually from its wet season diet to
 458 its dry season diet if $\mathcal{U}(t)$ is smooth, or shift abruptly if $\mathcal{U}(t)$ is discontinuous.

459 Dietary transitions between seasons tend to be gradual, even if the start/end
 460 of a given season is abrupt??. To understand how a temporally oscillating
 461 diet affects the isotopic variance of the composite diet, we consider the smooth
 462 oscillation $\mathcal{U}(t) = 1/2 + 1/2 \sin(\omega t)$, such that the proportional contribution of
 463 Z_1 oscillates with frequency ω (Fig. 3A). Substituting $\mathcal{U}(t)$ into Eq. 16 provides
 464 the solution to a sinusoidally varying diet, with expectation and variance

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

465 where we have combined the non-oscillating components of the variance into
 466 three parameters α_V , β_V , and γ_V for notational efficiency.

467 We gain three key insights from the solution for the expectation and vari-
 468 ance of the composite diet. 1) As would be expected, the central tendency of
 469 the composite diet is the average of the mean values for each subdiet, while
 470 the amplitude of oscillations is driven entirely by the difference in the mean
 471 values of each subdiet; 2) the time-averaged variance (denoted by $\langle \cdot \rangle_t$) is simply
 472 $\langle V\{\mathbb{Z}(t)\} \rangle_t = \alpha_V$, which is only impacted by the average variance between the
 473 seasonal diets and the difference in the mean isotope values between the seasonal
 474 diets (Fig. 4); 3) the oscillating component shows that the composite dietary
 475 variance has a modified frequency, as well as an offset, meaning that the maximal
 476 variance of the consumer's composite diet generally occurs during the transition
 477 from one diet to the other (Fig. 3B). Together, these results reveal that if the
 478 consumer's diet is varying continuously over time between two seasonal diets,
 479 both the averaged variance, as well as the difference in the mean isotope values
 480 of the seasonal diets – directly reflecting the heterogeneity of prey mixing space
 481 geometry – will serve to increase the time-averaged variance of the consumer's
 482 diet, and by extension the isotopic variance of the consumer itself.

483 Less intuitively, we observe that the consumer's peak variance, or niche width,
 484 as measured by the variance of its composite diet, occurs not during the exclusive
 485 adoption of its subdiets, but during the transition between the two, and this peak
 486 variance is driven exclusively by the difference in means between seasonal diets.
 487 As the seasonal diets become more heterogeneous in isotopic space, the greater
 488 the consumer's peak variance during the transition, and this occurs because it
 489 is sampling between two dietary strategies that are isotopically distinct. We
 490 can directly observe this by considering a transition between two diets with a)

491 different means and the same variances, and b) the same means and different
 492 variances. In the former case, the peak variance of the composite diet occurs
 493 during the transition (Fig 3B); in the latter case, because the diets have the
 494 same mean isotope value, the peak occurs not during the transition, but when
 495 the consumer adopts the diet with the greater variance, which in our example
 496 would occur at the height of the season (Fig 3C).

497 The isotopic composition of a consumer $X_c(t)$ during a single dietary shift is
 498 governed by a single timescale of physiological origin: the rate of incorporation
 499 λ (Eq. 13). However, a seasonally shifting diet that is driven by oscillating
 500 foraging strategies introduces an additional ecological timescale that will affect
 501 $X_c(t)$, determined by the frequency of diet switching ω (Fig. 5A). Depending
 502 on the turnover rate of the tissue of interest and how often the consumer shifts
 503 its diet, the ratio of these timescales ω/λ will impact how the isotopic mean
 504 and variance of the consumer changes over time. For the case of a sinusoidally
 505 varying diet, we can solve for $X_c(t)$ directly, such that

$$\begin{aligned}
 V\{X_c(t \gg 0)\} = & \alpha_V \frac{\lambda}{2} + \beta_V \frac{\lambda^2}{\sqrt{(2\lambda)^2 + \omega^2}} \sin(\omega t - \theta_1) \\
 & + \gamma_V \frac{\lambda^2}{2\sqrt{\lambda^2 + \omega^2}} \sin(2\omega t + \theta_2).
 \end{aligned} \tag{18}$$

506 where the offsets θ_1 and θ_2 are $\tan^{-1}(\omega/2\lambda)$ and $\tan^{-1}(\lambda/\omega)$, respectively. As
 507 in the case of a single diet Z , the time-averaged variance is scaled by the
 508 incorporation rate as $\alpha_V \lambda / 2$. Moreover, we observe that the consumer's isotopic
 509 composition lags behind changes in diet, such that an isotopic shift in the
 510 consumer's tissues is observed after the actual foraging shift. This lag involves
 511 both θ_1 and θ_2 , however these offsets play different roles in contributing to
 512 the lag for different mixing space geometries. When the isotopic means of the
 513 seasonal diets are similar, the lag is mostly due to θ_1 ; when the means are
 514 different and the variances are similar, the lag is mostly due to θ_2 ; when both the
 515 isotopic means and variances of the seasonal diets are different, both contribute
 516 significantly to the lag.

517 As shown in Fig. 5, we observe that 1) the lag between the transition and
 518 the peak variance of the consumer increases with decreasing λ (i.e. increasing
 519 timescale of incorporation), and 2) the amplitude of the variance of $X_c(t)$
 520 decreases with increasing ω (i.e. decreasing timescale of ecological switching).
 521 The first result is not surprising, as it mirrors the role of λ in the static diet

522 example. The second result is less intuitive: in words, as the consumer shifts
523 its diet more frequently, there is still a peak variance during dietary transitions,
524 though with diminishing amplitude, and this would make it more difficult to
525 measure (Fig 5B). This is due to the consumer slowly integrating isotopes into
526 its tissues from both diets, thus averaging across diet-switching events, thus
527 dampening fluctuations. Accordingly, the decrease in the amplitude of isotopic
528 variance of the consumer's tissue is an averaging effect, where the timescale of
529 incorporation is much larger than the timescale of dietary switching.

530 4 Discussion

531 We have established a forward-integration approach towards understanding how
532 the isotopic distribution of an individual consumer evolves due to ecological,
533 physiological, and geometric factors. Our framework introduces mechanistic
534 links between the ecological foraging dynamics of a consumer, the physiological
535 constraints that dictate incorporation, and the more abstract effects of mixing
536 space geometry. We focus our efforts on building an analytical framework
537 to understand how the isotopic variance of an individual – its isotopic niche
538 width – changes as a function of different foraging strategies that are both
539 probabilistic and dynamic over time. We consider two foraging scenarios: 1)
540 *static strategy*: probabilistic consumption of multiple prey, the proportions of
541 which are on average constant over time, and 2) *dynamic strategy*: probabilistic
542 consumption of multiple prey whose relative contribution to consumer's diet
543 varies over time. The former example is most relevant for consumers inhabiting
544 environments where resource availability is stable (reliable), whereas the latter
545 is more appropriate for consumers that prey switch between two qualitatively
546 different subdiets.

547 Our primary findings concern whether and to what extent the peak isotopic
548 variance of the consumer, or maximum isotopic niche width, is realized under
549 different, but definable, conditions with respect to static and dynamic foraging
550 scenarios. When the consumer exhibits a static foraging strategy, the isotopic
551 variance of its diet is tied directly to its prey specialization and the skewness
552 of the isotopic mixing space. We show that as the mixing space becomes more
553 skewed, there is an increasing likelihood that the peak variance will occur at
554 intermediate specialization (where a single prey accounts for ca. 50% of the
555 consumer's diet; Figs. 1,2). When the consumer exhibits a dynamic, yet smoothly

556 varying foraging strategy, we show that the peak variance occurs during the
557 transition from one diet to another, and is offset by a lag that is a function
558 of both its incorporation rate and the timescale over which it shifts between
559 diets (Fig. 3). Below we show that these findings are relevant beyond theory
560 by examining an empirical sea otter mixing space, and discuss areas where
561 additional realism can be incorporated to gain further ecological insight into the
562 isotopic niche.

563 The isotopic niche: generalization vs. specialization

564 To demonstrate the empirical relevance of the nonlinear nature of $V\{Z\}$, we
565 examine a prey-rich marine system near San Simeon and Monterey Bay, Califor-
566 nia, composed of nine invertebrate species commonly consumed by sea otters⁷.
567 In this system, all potential prey resources have unique isotopic means and
568 variances (Fig. 6), including multiple species of sea urchins and crab, clams,
569 abalone, mussels, and snails. We can investigate how alternatively targeting
570 each prey species alters the isotopic variance of a sea otter's diet across different
571 degrees of specialization by modifying the underlying Dirichlet distribution (i.e.
572 by increasing a_k for each species individually, while holding $a_{i \neq k} = 1$; Fig. 7A).
573 We determined the existence of strong nonlinearity in the isotopic variance of
574 diet for 44% of prey species (Fig. 7B). For targeted prey exhibiting nonlinear
575 variance (including mussels, snails, purple sea urchins, and kelp crabs), the
576 maximum isotopic variance was found in the region $s \leq 0.5$.

577 The message that we take from the sea otter example is relatively straight-
578 forward: for a given prey mixing space, a consumer's dietary variability – where
579 the consumer's tissues scale in proportion to its diet by a factor of $\lambda/2$ – will
580 be a function of both mixing space geometry, as well as its dietary strategy,
581 and these effects can be confounding. Despite this, we are able to establish
582 certain predictions for the consumer's isotopic niche width as a function of
583 diet: as the consumer incorporates moderate amounts of isotopically unique
584 prey into its diet, its variance will be expected to increase. Knowledge of the
585 interplay between mixing space geometry and a consumer's dietary strategy, and
586 its consequent effect on the isotopic variance of diet, is particularly important for
587 characterizing consumers based exclusively on isotopic variance. For example,
588 without knowledge of these relationships, a highly variable consumer might be
589 interpreted as a dietary generalist, whereas it might be able to achieve a similarly
590 high or higher variance by moderately focusing its foraging activities on a single

591 prey species with an isotopic distribution far from the mixing space centroid.

592 **The isotopic niche over time**

593 We gain additional insight into the factors influencing consumer isotopic variabil-
594 ity by considering dynamic diets, where the consumer oscillates between different
595 foraging strategies over time. We considered a simple sinusoidal oscillation for
596 $\mathcal{U}(t)$, the proportional contribution of diet 1 to the composite diet over time
597 $\mathbb{Z}(t)$. The subdiets from which the composite diet is composed can be thought
598 of as ‘seasonal diets’. Our analytical results showed that the peak variance
599 of the composite diet occurred during the transition between seasonal diets.
600 Importantly, this is not due to any particular mixing space geometry, but a
601 general result that will always occur, as long as the diets are isotopically distinct
602 (each with a unique mean and variance), and the transition is smooth such that
603 a consumer gradually shifts between different diets, as opposed to an abrupt,
604 discontinuous diet switch.

605 Although the peak variance of $\mathbb{Z}(t)$ is entirely due to ecological diet shifts
606 rather than mixing space geometry, the latter does play a role in determining the
607 mean value (time average) of $V\{\mathbb{Z}(t)\}$. The effect of mixing space geometry on
608 the time-averaged variance of the composite diet is determined by α_V , which is
609 a function of 1) the average variance of the subdiets from which \mathbb{Z} is composed,
610 and 2) the mean difference between the two subdiets (see Eq. 18). As either
611 of these factors increase, the average variance of the composite diet increases,
612 setting the baseline from which the peak dietary variance fluctuates (Fig. 4).
613 We also observed that as the frequency of dietary transitions increased relative
614 to the rate at which the consumer integrates dietary isotopes into its tissues, the
615 consumer’s isotopic variance exhibited lower amplitude as it fluctuated between
616 the different variances of its diet (Fig. 5). This occurs because the greater
617 transition frequencies serve to average variance of the two diets within its tissues.
618 ? found a similar dynamic when they derived an analytical solution for the
619 variance of a consumer population transitioning between two prey.

620 An interesting observation that we gain from exploring a sinusoidal dietary
621 shift is that the variance peak observed during dietary transitions is dependent
622 on the smoothness of the transition. In fact, it is the transition mid-point,
623 at $\mathcal{U}(t) = 0.5$, where the composite diet is pulled equally from each seasonal
624 diet, and this serves to maximize the isotopic heterogeneity of the mixture
625 (the consumer). Thus, when foraging strategies are dynamic, it is the point of

626 maximum isotopic heterogeneity that results in peak isotopic variance of the diet.
627 This is analogous to the cause of peak dietary variance in the static example,
628 where specialization on prey resources with greater isotopic offsets from the
629 mixing space centroid maximizes isotopic heterogeneity, resulting in a variance
630 peak.

631 An extreme alternative to a smooth dietary transition would be one that is
632 discontinuous, as depicted by a step-function, or square wave (Fig. 8A). Such an
633 instantaneous dietary shift is not ecologically unrealistic; e.g. both brown bears
634 and gray wolves abruptly shift their diet to salmon during salmon runs^{???}, as
635 do predators on other prey populations exhibiting localized boom-bust dynamics
636 such as locusts, krill, jellyfish, and sardines^{??}. Because there is no point during
637 a sharp, discontinuous transition that serves to mix subdiets, the variance of
638 the composite diet does not peak in response. Instead, both the expectation
639 and the variance of the composite diet incorporates this step function behavior,
640 transitioning to reflect the shifts between different diets. Because the isotope
641 ratios associated with diet are incorporated gradually into the consumer's tissues,
642 both the mean and the variance of the consumer will adopt a sawtooth-like
643 dynamic (Fig. 8A,B), where they begin to asymptote to the expectation and
644 variance of the subdiets, but are reverted abruptly at the dietary switch. We note
645 that, as in the static example, the isotopic variance of the consumer approaches
646 the variance of its diet twice as fast as its expectation (cf. Eq. 13).

647 Population dynamics and state-dependent foraging

648 We presented a simple dynamic-switching framework, where a consumer oscillates
649 between two different diets over time to explore its effect on its isotopic niche.
650 In reality, a consumer's dietary strategy might be shifting constantly over time,
651 in response to a constantly changing environment. One potentially important
652 extension of our framework could incorporate a population dynamic underlying
653 the availability of potential resources (and by extension the consumer's diet)
654 in a continuous, more complex, and ecologically justified manner. Our original
655 formulation of the Dirichlet distribution that describes the consumer's diet
656 was established on the relationship between the random variables describing
657 the proportional contribution of prey to diet ($P_i = p_i$) and its encounter rate
658 ($\Psi_i = \psi_i$), where $p_i = \psi_i / \sum_j \psi_j$, and this was assumed to have a static
659 distribution over time. However, if the prey are fluctuating in accordance to
660 an underlying population dynamic (for example, determined by a system of

661 differential equations), the encounter rate of each prey would itself be a function
662 of time. By relating the expectation and/or variance of Ψ_i to the density of
663 prey, the parameterization of the Dirichlet can be directly coupled to changes in
664 population densities, thus mechanistically incorporating population dynamics
665 into predictions of a consumer's isotopic composition.

666 Furthermore, the relationship between p_i and ψ_i explicitly assumes passive
667 foraging between the consumer and its potential prey, and this holds for our
668 original static (single diet) example, our shifting diet example, and would hold
669 for the example above where the Dirichlet changes in response to an underlying
670 population dynamic. Although this is not a bad starting point, and may be
671 a perfectly reasonable assumption for a filter feeder that consumes resources
672 indiscriminately, it is not a reliable assumption for most organisms that may
673 rank prey based on intrinsic traits (e.g., energetic yield, handling/processing
674 time). Instead, a more complex relationship between p_i and the attributes of
675 the consumer's prey, and perhaps attributes of the consumer itself, could be
676 used to determine the parameterization of the Dirichlet distribution defining the
677 consumer's diet over time.

678 For example, our framework implicitly assumes that there is a steady state
679 influx of prey biomass to match the metabolic expenses of the consumer. In
680 other words, prey are chosen in accordance to the Dirichlet distribution, but
681 it is assumed that each foraging bout contributes equally to the consumer's
682 diet, and that the consumer always finds a meal. In reality, the success of a
683 given foraging bout is not certain, and there is some risk of not finding any
684 prey at all⁷; in such a case, the consumer would resort to metabolizing its own
685 tissues^{7,8}. Such a dynamic would directly impact the rate of incorporation
686 by altering the proportional contribution of newly consumed isotopes to the
687 turnover of the consumer's body tissues. Moreover, the foraging decisions that a
688 consumer makes are often a function of its energetic state^{7,9}, which changes as it
689 successfully or unsuccessfully finds and acquires its prey⁷. Such state-dependent
690 foraging may be difficult to treat analytically, but could be explored numerically,
691 and this approach would be useful for hypothesis testing, particularly when
692 one is interested in comparing the effects of different foraging strategies on the
693 statistical properties of the consumer's isotopic composition.

694 From individuals to populations

695 Finally, the framework that we have presented has focused entirely on the
696 individual, in particular on how the isotopic variance of an individual consumer
697 changes in response to different ecological and physiological factors as well as
698 aspects of the isotope mixing space it utilizes. Most ecological applications using
699 stable isotope analysis operate at the level of the population, although there is a
700 rich literature of efforts that use stable isotope analysis to understand sources of
701 isotopic variation at the level of the individual? ? ? ? ? ? ? .

702 Understanding how variance percolates from prey to the individual consumer
703 is a necessary first step for understanding sources of isotopic variation at popu-
704 lation level. Such considerations quickly become complex, as there are scenarios
705 when the isotopic variance of an individual is or is not closely coupled to the
706 variance of the population. For example, if individuals within a population have
707 similar means and - for simplicity - equal variances, then the variance of the
708 population will scale linearly with the variance of the individuals (Fig. 9A,B).
709 This relationship highlights an important message: when individuality is low, the
710 variance of the population is entirely explained by the variance of the individuals;
711 this means that the results that we have presented for a consumer individual are
712 expected to scale directly to that of the population. However, if the individuals
713 within a population have very different means and relatively small variances,
714 then there will not be a significant relationship between population-level and
715 individual-level variation (Fig. 9C,D).

716 We can imagine different individual-population relationships occurring within
717 a 2-D state-space defined by individuality on one axis and specialization on the
718 other. At the extremes, a population could consist of 1) obligate specialists with
719 low individuality where all individuals specialize on the same resource, 2) obligate
720 specialists with high individuality where all individuals specialize on different
721 resources, and 3) obligate generalists with low individuality where all individuals
722 are generalists; an obligate generalist with high individuality cannot exist in
723 this context. These potential end-members are discussed at length in ? and ?.
724 As we have seen in the above analyses, the variation of individuals is driven
725 by a complex interplay between mixing space geometry, consumer foraging
726 behaviors, and physiological incorporation. How these different population-
727 level end-members might shape both individual and population-level isotopic
728 distributions is an important question, though the answers will likely harbor
729 additional complexities. For example, isotopically similar individuals with low

730 variances imply that all individuals are consuming similar things, in similar
731 quantities, such that individuality is low, though our results show that low
732 isotopic variance need not indicate specialization or generalization *per se* (cf.
733 Figs 1,7). Accounting for individual variation in dietary proclivities over time is
734 bound to complicate interpretation further.

735 Conclusions

736 There are many sources of variation that contribute to a consumer's isotopic
737 composition. These sources include the geometry of the prey mixing space,
738 the foraging behaviors of the consumers, as well as temporal changes in the
739 environment that might alter the ability of the consumer to find, acquire, and
740 consume its prey. Along with physiological incorporation of isotopes into con-
741 sumer tissues, these factors serve to drive the temporal evolution of the isotopic
742 distribution, or isotopic niche, of the consumer. By coupling the isotopic variance
743 of this distribution to mechanistic relationships between the consumer and its
744 diet, as well as the isotopic mixing space of the system, we have presented a
745 systematic exploration of the factors that cause the isotopic niche to both expand
746 and contract. Incorporating the effects of population dynamics and/or more
747 complex foraging strategies will enable hypothesis testing of different ecological
748 mechanisms to generate the isotopic distributions that are observed in nature.
749 We hope that such a forward-integrating approach, alongside the use of tools such
750 as mixing models to back-calculate dietary composition, will serve to expand
751 and enhance the ecological interpretation of isotopic data.

752 Disclosure/Conflict-of-Interest Statement

753 The authors declare that the research was conducted in the absence of any
754 commercial or financial relationships that could be construed as a potential
755 conflict of interest.

756 Author Contributions

757 JDY, UB, EAES, and SDN conceived the idea. JDY and UB designed the
758 statistical framework and conducted the analyses. EAES and SDN contributed
759 empirical data. All authors contributed equally to drafting and writing the
760 manuscript.

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⁷⁶⁷ **References**

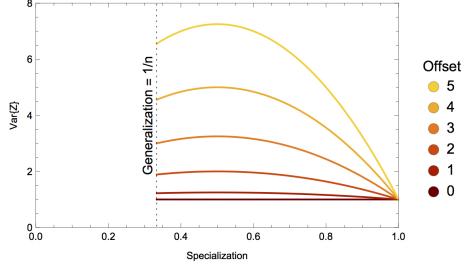


Figure 1. Variance of the isotopic distribution of a consumer's diet, $V\{Z\}$, with respect to specialization on a single prey, s_k . This illustrative example shows a three-prey system with prey means $\{-15, -15 + \text{offset}, -15\}$ and equal variances; colors depict specialization on prey 2 with a mean isotope value that is a function of some offset amount. As the offset of the targeted prey increases, so does the nonlinearity of $V\{Z\}$.

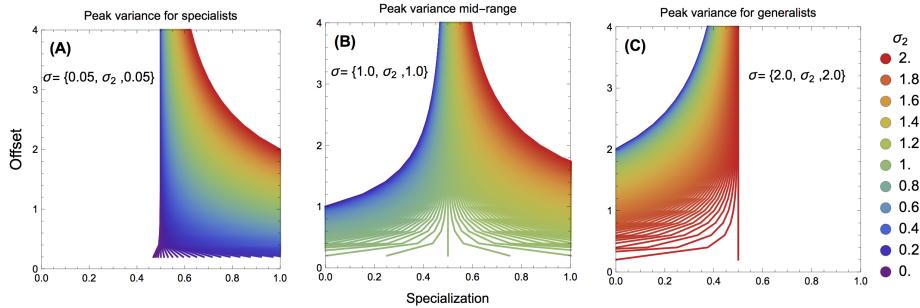


Figure 2. Maximal consumer isotopic variance \hat{s}_k over the specialization index s as a function of mixing space geometry. (A) and (B) If the targeted prey has a higher than average isotopic variance, the maximum consumer niche width will lie towards consumer specialization. (B) and (C) If the targeted prey has a lower than average isotopic variance, the maximum consumer niche width will like towards consumer generalization. (A), (B), and (C) 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 $s = 0.5$.

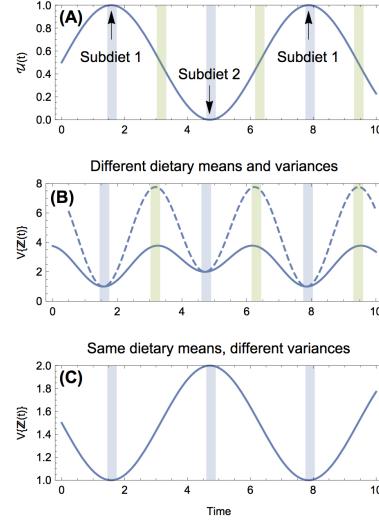


Figure 3. (A) The proportional contribution of Diet 1 to the composite diet Z over time. (B) The isotopic variance of the composite diet $V\{Z(t)\}$ when subdiets 1 and 2 have different means and variances. The peak variance occurs during the dietary transitions (green shading), whereas the troughs reflect the variances of subdiet 1 and 2, respectively (blue shading). (C) The isotopic variance of the composite diet $V\{Z(t)\}$ when subdiets 1 and 2 have the same means but different variances. When the subdiets have the same means, $V\{Z(t)\}$ oscillates to reflect the respective variances of the subdiets, and does not exhibit peak variance during the dietary transition.

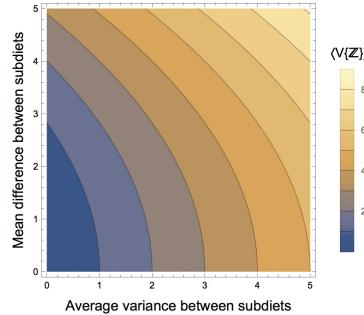


Figure 4. Components of the mixing space that affects the time-averaged variance of the composite diet, $\langle V\{Z\} \rangle_t$. As the average variance between the subdiets increases, the time-averaged variance of the composite diet increases. As the difference in the isotopic means of the subdiets increase, the time-averaged variance of the composite diet increases, though at a slower rate.

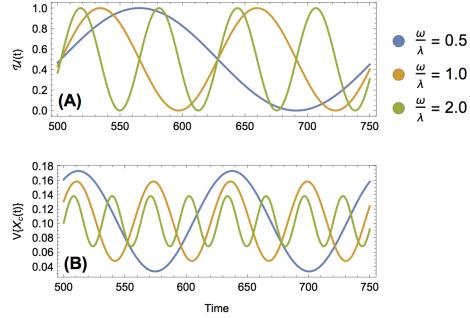


Figure 5. (A) A sinusoidally varying diet, where $U(t) = 1/2 + 1/2 \sin(\omega t)$ for increasing values of ω , or equivalently, decreasing timescales of dietary switching. (B) The isotopic variance of a consumer over time $V\{X_c(t)\}$ across increasing values of ω relative to the consumer's incorporation rate λ . As the timescale of diet switching decreases relative to the timescale of isotopic incorporation, the amplitude of isotopic variance decreases due to increased isotopic averaging over faster shifts in diet.

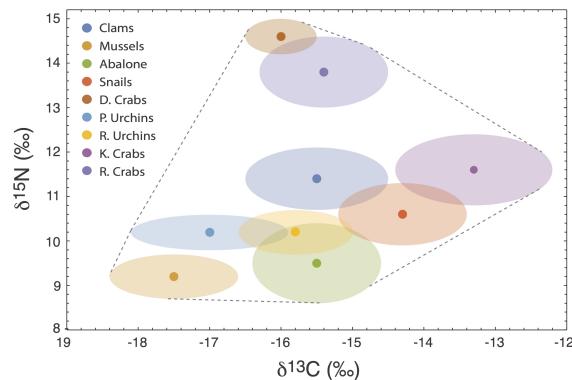


Figure 6. The isotopic mixing space ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) for a sea otter consumer near San Simeon and Monterey Bay, California, composed of nine commonly consumed invertebrate species. Units are per-mil (\textperthousand).

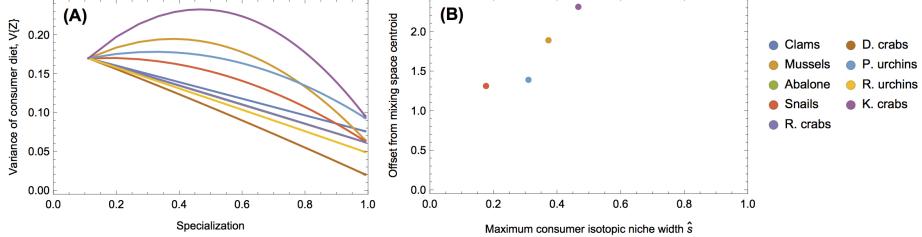


Figure 7. (A) Predicted variance in $\delta^{13}\text{C}$ of sea otter diets over different degrees of specialization on each prey in the system (colors). (B) Calculated maximum consumer niche width values as a function of specialization and the offset of the prey isotopic mean from the mixing space centroid.

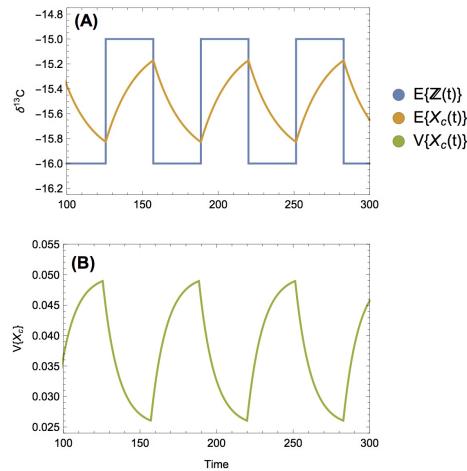


Figure 8. (A) The mean isotopic value of the composite diet over time $E\{\mathbb{Z}(t)\}$ when diet-switching is discontinuous, following a square wave pattern, where subdiets have a mean $\delta^{13}\text{C}$ value of -15 and -16, respectively. The mean isotopic value of the consumer over time $E\{X_c(t)\}$ is observed to abruptly change directions when its diet transitions, asymptotizing towards (but not reaching) the isotopic mean of its current diet. (B) Consumer isotopic variance $V\{X_c(t)\}$ follows a similar trajectory over time, asymptotizing towards (but not reaching) the isotope variance of its current diet. When diets follow a discontinuous switching dynamic, the peak variance does not appear at the transition, as it does when the diet switching is smooth.

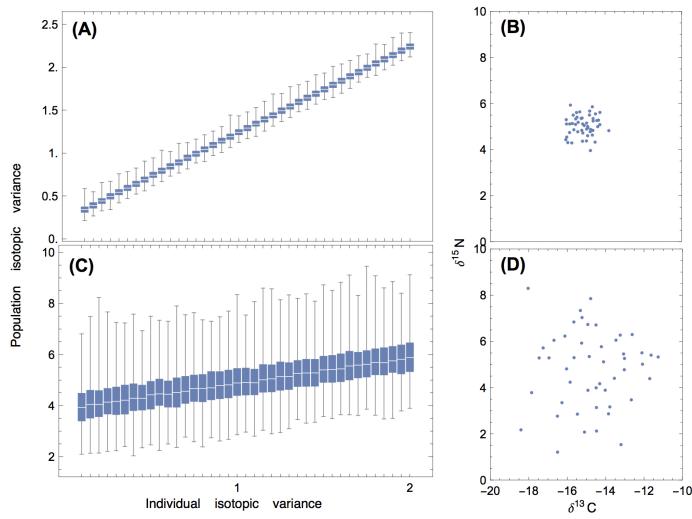


Figure 9. Population isotopic variance vs. individual isotopic variance where mean isotope values of individuals are randomly drawn from a Normal distribution (50 individuals per population; 1000 replicates), and individuals are assumed to have the same variance. (A) and (B) When the mean values of individuals are randomly drawn from a normal distribution with low variance, there is a linear relationship between individual-level and population-level isotopic variance. (C) and (D) When the mean values of individuals are randomly drawn from a normal distribution with high variance, the relationship becomes masked by noise.