



Simulating realistic predator signatures in quantitative fatty acid signature analysis



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ABSTRACT

Diet estimation is an important field within quantitative ecology, providing critical insights into many aspects of ecology and community dynamics. Quantitative fatty acid signature analysis (QFASA) is a prominent method of diet estimation, particularly for marine mammal and bird species. Investigators using QFASA commonly use computer simulation to evaluate statistical characteristics of diet estimators for the populations they study. Similar computer simulations have been used to explore and compare the performance of different variations of the original QFASA diet estimator. In both cases, computer simulations involve bootstrap sampling prey signature data to construct pseudo-predator signatures with known properties. However, bootstrap sample sizes have been selected arbitrarily and pseudo-predator signatures therefore may not have realistic properties. I develop an algorithm to objectively establish bootstrap sample sizes that generates pseudo-predator signatures with realistic properties, thereby enhancing the utility of computer simulation for assessing QFASA estimator performance. The algorithm also appears to be computationally efficient, resulting in bootstrap sample sizes that are smaller than those commonly used. I illustrate the algorithm with an example using data from Chukchi Sea polar bears (*Ursus maritimus*) and their marine mammal prey. The concepts underlying the approach may have value in other areas of quantitative ecology in which bootstrap samples are post-processed prior to their use.

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1. Introduction

Knowledge of predator diets provides critical insights into many aspects of their behavior and ecology. Quantitative fatty acid signature analysis (QFASA) is a popular method of estimating diets, particularly for marine species (Bowen and Iverson, 2013). QFASA is based on compositional vectors of fatty acid proportions (termed signatures), with diet estimated as the linear mixture of prey signatures that minimizes a measure of distance between modeled and observed predator signatures (Iverson et al., 2004).

The statistical performance of estimators and other analytical techniques in many fields of quantitative ecology is commonly evaluated using computer simulation (e.g., Aing et al., 2011; Baasch et al., 2010; Brenden and Zhao, 2012; Elphick, 2008; Peñaloza et al., 2014). QFASA is no exception, as several investigators have used computer simulation to evaluate one or more aspects of diet estimator performance for their specific application (e.g., Haynes et al., 2015; Thiemann et al., 2008; Wang et al., 2010). Investigators have also used computer simulation to investigate the performance of QFASA estimators from a methodological perspective (e.g., Bromaghin et al., 2015, in press; Iverson et al., 2004; Neubauer and Jensen, 2015; Stewart and Field, 2011).

Evaluating QFASA estimators with simulation involves comparing the known and estimated diets of “pseudo-predators,” whose signatures are

generated from multiple bootstrap samples of prey signature data (Iverson et al., 2004). Simulating predator signatures is therefore more complicated than some bootstrapping procedures because it involves multiple steps. A diet (fixed prey mixture proportions) is first specified, which determines the expected value of a pseudo-predator signature as a function of diet and the mean signature of each prey type. Given specification of a diet, individual prey signatures are sampled with replacement from the observed signature data of each prey type, independently for each pseudo-predator. The mean signature of each prey type is then computed from each sample and a pseudo-predator signature is computed as the weighted average of the mean prey signatures, with the diet proportions as weights. Conditioned on a specific diet, the variance among pseudo-predator signatures therefore depends upon the variance among the mean prey signatures, which is in turn a function of prey-type sample sizes and the individual prey signatures sampled (or “consumed”) from each prey type for each pseudo-predator.

Objective guidance on the selection of prey bootstrap sample sizes appears absent from the QFASA literature; indeed, investigators do not always specify the sample sizes used (e.g., Haynes et al., 2015; Thiemann et al., 2008; Wang et al., 2010). Iverson et al. (2004) used a subjectively selected modest sample size applied equally to all prey types. Conversely, Bromaghin et al. (2015) used bootstrap sample sizes equal to the sample size of each prey type in the prey signature data, which would tend to be larger. Neither approach is justifiable because bootstrap sample sizes directly influence variability in pseudo-predator signatures, perhaps producing signatures with unrealistic levels

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of variation that may subsequently affect statistical properties of the diet estimator. Bromaghin et al. (2015) seemed at least partially aware of this potential, noting that the relatively large sample sizes they used likely produced pseudo-predator signatures with less variance than might be observed among signature samples from free-ranging predators.

I present an algorithm to objectively establish bootstrap prey sample sizes for simulation investigations of QFASA diet estimator performance. Conditioned on a specific diet, the algorithm determines prey sample sizes that approximate the variation in observed predator signature data due solely to the sampling of individual prey animals from prey types. Although the algorithm is grounded within the context of QFASA, the conceptual approach may have value in assessing diet estimators based on other biomarkers, such as stable isotopes (e.g., Chiaradia et al., 2014), or more generally in other situations requiring post-processing of multiple bootstrap samples prior to their application.

2. Material and methods

The algorithm is based on the conceptualization of predator signature variance being attributable to two sources: variation in diet among predators and variation in the individual prey consumed given a diet. Because pseudo-predator signatures are generated conditioned on a specific diet, the degree of variation in predator signatures attributable only to the prey consumed must be determined. Consequently, the diets of a sample of free-ranging predators are estimated and the variances among the estimated diets and the observed signatures are computed for each possible pair of predators. If d_{it} is the estimated diet proportion for predator i and prey type t , s_{if} is the signature proportion for predator i and fatty acid f , n_t is the number of prey types, and n_f is the number of fatty acids, the variance between the estimated diets of predators i and i' was computed as

$$v_{ii'}^d = \sum_{j=1}^{n_t} 0.5(d_{ij} + d_{i'j})^2 - 2d_{ij}d_{i'j}$$

and the variance between the signatures of predators i and i' was computed as

$$v_{ii'}^s = \sum_{f=1}^{n_f} 0.5(s_{if} + s_{i'f})^2 - 2s_{if}s_{i'f}$$

The quantity within the summation of both equations is algebraically equivalent to the empirical sample variance of a sample of size 2.

The empirical relationship between $(v_{ii'}^s, v_{ii'}^d)$ pairs was used to approximate the limit of the variation between signatures as the variation between diets approached 0, denoting nearly identical diets. Although there are numerous ways this could be done, I used a nonparametric loess smoother to approximate the relationship between $(v_{ii'}^s, v_{ii'}^d)$ pairs and identified the predicted value of the variation between signatures for the pair of predators with the minimum observed variation in diets. This predicted value was denoted V_T because it serves as the target level of variation to achieve among bootstrap-generated pseudo-predator signatures.

The bootstrap prey sample size algorithm is based on the empirical sample variance among the signature proportions for each fatty acid within each prey type, i.e., s_{if}^2 , where s^2 is the usual empirical single-sample variance, t denotes prey type, and f denotes fatty acid. Because it is computationally inefficient to bootstrap sample a large number of prey from a type that is not important to the diet, s_{if}^2 is down-weighted by the proportion of each prey type in the diet π_t . In addition, all of the variance within a prey type is essentially acquired if the bootstrap sample size reaches the observed sample size. Consequently, one could cap the bootstrap prey sample size at the observed sample size for each prey type or, as I have done, down-weight the variances s_{if}^2 by the

proportion of the observed prey sample size included in the bootstrap sample. The weighted variance measure on which the algorithm is based is therefore

$$\tilde{s}_{if}^2 = \pi_t \left(1 - \frac{m_t^b}{m_t}\right) s_{if}^2$$

where m_t is the observed sample size of prey type t and m_t^b is the number of that prey type in the bootstrap sample.

Given the preliminary computations of V_T and \tilde{s}_{if}^2 and the specification of a diet π_t , the sample size algorithm consists of the following iterative steps.

- a. Start with a sample of size $m_t^b = 1$ from each prey type and compute \tilde{s}_{if}^2 . If the diet proportions π_t for some prey types were exactly 0, their starting sample size could alternatively be set at 0.
- b. For each of a specified number of pseudo-predators, draw a bootstrap sample of the prey data with the current sample size for each prey type, compute the mean signature for each prey type, and compute the pseudo-predator signature as a weighted average of the mean prey signatures using the diet proportions as weights.
- c. Compute the empirical sample variance among the pseudo-predator signature proportions for each fatty acid and sum the variances across fatty acids, resulting in the variance measure V^* . If $V^* \leq V_T$, stop; the current bootstrap sample sizes produce pseudo-predator signatures with the correct expected value (mean) and a realistic level of variance; otherwise, continue.
- d. Identify the fatty acid among the predator pseudo-signatures with the greatest variance, i.e., contributing most to V^* , say fatty acid k .
- e. Identify the prey type q with the maximum value of \tilde{s}_{iq}^2 , increment the bootstrap sample size of prey type q by 1, update the values of \tilde{s}_{iq}^2 to reflect the increase in the bootstrap sample size, and return to Step b.

3. Results

The sample size selection algorithm is illustrated using a predator data set containing 61 signatures from adult male polar bears (*Ursus maritimus*) of the Chukchi Sea (courtesy U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, Alaska) and a prey data set with signatures of 357 prey from 7 marine mammal species known to be eaten by polar bears or available in the region and potentially eaten by polar bears. The prey data were compiled from sources at Dalhousie University (<http://dx.doi.org/10.15273/10222/57254>) and the U.S. Geological Survey, Alaska Science Center (<http://dx.doi.org/10.5066/F7PR7T2W>). Rode et al. (2014) and Bromaghin et al. (2015) provide additional information about these data. The diets of individual polar bears were estimated using the extended dietary suite of 41 fatty acids (Iverson et al., 2004), the “all mink” calibration coefficients of Thiemann et al. (2008), and the Aitchison distance measure in the predator optimization space (Bromaghin et al., 2015). One hundred pseudo-predator signatures were generated at each step of the algorithm.

For these data, the mean value of $v_{ii'}^s$ increased modestly as the value of $v_{ii'}^d$ increased from 0.0 to approximately 0.05, after which the rate of increase moderated (Fig. 1). The minimum observed value of $v_{ii'}^d$ was 8.087×10^{-6} and the corresponding predicted (mean) value of $v_{ii'}^s$ from the loess smooth was 9.048×10^{-4} , which was taken as the target level of variation V_T . Sample size determination was conditioned on the mean of the estimated diets among adult male polar bears: 47.0% bearded seal (*Erignathus barbatus*), < 0.0% beluga whale (*Delphinapterus leucas*), 13.8% bowhead whale (*Balaena mysticetus*), < 0.0% ribbon seal (*Histiophoca fasciata*), 38.1% ringed seal (*Pusa hispida*), 1.0% spotted seal (*Phoca largha*), and < 0.0% Pacific walrus (*Odobenus rosmarus*). Note that this estimated mean diet differs somewhat from the estimate

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