

The application of Bayesian hierarchical models to quantify individual diet specialization

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Abstract. Intraspecific variation in ecologically relevant traits is widespread. In generalist predators in particular, individual diet specialization is likely to have important consequences for food webs. Understanding individual diet specialization empirically requires the ability to quantify individual diet preferences accurately. Here we compare the currently used frequentist maximum likelihood approach, which infers individual preferences using the observed prey proportions to Bayesian hierarchical models that instead estimate these proportions. Using simulated and empirical data, we find that the approach of using observed prey proportions consistently overestimates diet specialization relative to the Bayesian hierarchical approach when the number of prey observations per individual is low or the number of prey observations vary among individuals, two common features of empirical data. Furthermore, the Bayesian hierarchical approach permits the estimation of point estimates for both prey proportions and their variability within and among levels of organization (i.e., individuals, experimental treatments, populations), while also characterizing the uncertainty of these estimates in ways inaccessible to frequentist methods. The Bayesian hierarchical approach provides a useful framework for improving the quantification and understanding of intraspecific variation in diet specialization studies.

Key words: American alligator; categorical data; diet analysis; Dirichlet model; intertidal whelks; predator–prey interactions.

INTRODUCTION

Individuals within populations often differ from one another in ways that influence their function in ecological systems (Bolnick et al. 2011, Violle et al. 2012). One manifestation of this intraspecific variation that is expected to have important community- and population-level consequences is individual diet specialization (Bolnick et al. 2003, 2011, Araújo et al. 2011). Theory suggests that individual diet specialization can alter mean interaction strengths between predators and prey, change the perceived topology and consequent dynamics of ecological networks, and drive eco-evolutionary feedbacks when prey preferences are heritable (Bolnick et al. 2011, Schreiber et al. 2011, Gibert and Brassil 2014). Since the seminal paper on measuring diet specialization by Bolnick et al. (2002), empirical studies have further provided insight into the role of competition (e.g., Bolnick et al. 2007, Svänback and Bolnick 2007) and ecological opportunity (e.g., Semmens et al. 2009, Rosenblatt et al. 2015) in promoting diet specialization, and its structure within populations (e.g., Araújo et al. 2008, Tinker et al. 2012). The ability to quantify the prey preferences of individual predators accurately is a

critical prerequisite for testing and developing such theory and empirical insights.

Individual diet specialization has been quantified by comparing each individual's diet preferences to either the preferences of each other individual or to the overall preferences of the aggregate population. Under the assumption that all sampled individuals had equal opportunity to feed on the population's potential prey and exhibit equal handling times, the observed proportions of prey items in an individual's diet have often been equated directly to prey preference. For example, among the most commonly used indices for quantifying a given individual's diet specialization is the proportional similarity index, $PS_i = 1 - 0.5 \sum_j |p_{ij} - v_j|$, where p_{ij} is the observed proportion of prey j in the diet of individual i , and v_j is the average observed proportion of prey j among individuals in the population (Schoener 1968, Feinsinger et al. 1981). PS_i varies from a value of v_j if the individual is a specialist on prey j to a value of 1 if the individual's diet proportions are the same as its population's. Similarly, the Individual Specialization (IS) and E indices have been commonly used to quantify diet specialization among individuals in a population or some other grouping such as location, sex, or experimental treatment (Appendix S1). IS is calculated by averaging over the PS_i values for individuals within the population (Bolnick et al. 2002). The E index is calculated by averaging across all individual-to-individual pairwise proportional similarities (Araújo et al. 2008).

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Using observed diet proportions as estimators of true diet proportions can be viewed as a maximum likelihood estimate at the individual level. Hereafter, we refer to this as the observed proportions method. Although such maximum likelihood estimates are asymptotically unbiased, they can be severely biased for small sample sizes (Bolker 2008). Small sample sizes (the number of prey items per predator individual) are a common feature of predator diet data to which inferences of diet specialization can be particularly sensitive, either because indices rely on the comparison of diet proportions that are observed with error (e.g., individual-to-individual comparisons), or because they rely on the comparison of diet proportions associated with vastly different sample sizes (individual-to-population comparisons). Because the direct use of the observed diet proportions has formed the basis of all previous diet specialization indices, including the commonly used Within Individual Component divided by Total Niche Width (WIC/TNW) index (Appendix S2) and also those seeking to account for incomplete sampling (Novak and Tinker 2015), methods to assess and address this sensitivity are needed.

Here we compare the use of the observed proportions approach to the use of Bayesian hierarchical models for quantifying diet specialization. Bayesian methods are increasingly used in ecology (Ellison 2004, Clark 2005) and have been key to the development of methods for quantifying predator-prey interactions at the species level (e.g., Moore and Semmens 2008, Wolf et al. 2015). When formulated hierarchically (Fordyce et al. 2011), Bayesian models can avoid the aforementioned limitations of the observed proportions approach by providing estimates for each individual that are increasingly pulled towards the population's (group's) mean value the lower an individual's sample size (Gelman et al. 2013). In the context of quantifying diet specialization, this gives lower weight to the diet proportions of individuals having fewer prey observations, potentially reducing the bias of low sample sizes expected for the observed proportions approach. In addition, the Bayesian hierarchical approach permits the variability of diet proportion point estimates to be quantified, both within and among groups, while also characterizing the uncertainty of these estimates in ways inaccessible to currently implemented frequentist methods. Using simulated data where the true diet proportions are known, we examine the accuracy of diet specialization inferences across varying numbers of prey observations per individual, and in populations with heterogeneity in the number of prey observations among individuals. We also examine the correspondence of common indices of diet specialization in the context of the Bayesian framework. Lastly, we reanalyze two published empirical data sets of individual diets to highlight the differences in inferences that the observed proportions and Bayesian hierarchical approaches provide. The data, R code, and technical details for repeating all simulations and empirical analyses are provided in the Supplementary Material.

MATERIALS AND METHODS

We first describe our use of Bayesian hierarchical models in a generic sense before describing the details of our simulations and empirical analyses.

A two-level Bayesian hierarchical model for the diet of a sampled population of individuals may be written as

$$\bar{\mathbf{y}}_i \sim \text{Multinomial}(\bar{\mathbf{p}}_i, n_i) \quad (1)$$

$$\bar{\mathbf{p}}_i \sim \text{Dirichlet}(\bar{\mathbf{q}} \times w) \quad (2)$$

(Fordyce et al. 2011), where $\bar{\mathbf{y}}_i$ is a vector containing the number of each prey type observed in the diet of the i th predator individual, n_i is the total number of prey items observed for the individual, $\bar{\mathbf{p}}_i$ is a vector of the individual's diet proportions (to be estimated), $\bar{\mathbf{q}}$ is a vector of the population's diet proportions (to be estimated), and w is the so-called concentration parameter (to be estimated) of the Dirichlet distribution that characterizes the clustering of the individual diets around the population's mean diet proportions (Fig. 1). The concentration parameter thereby reflects the degree of diet specialization that exists within the population. When no previous knowledge exists on the $\bar{\mathbf{q}}$ and w parameters, uniform priors, such as

$$\bar{\mathbf{q}} \sim \text{Dirichlet}(\bar{\mathbf{1}}) \quad (3)$$

$$w \sim \text{Uniform}(0, c) \quad (4)$$

may be used. Here $\bar{\mathbf{1}}$ is a vector of ones the same length as the total number of prey types observed for the population (Laplace's prior; a uniform Dirichlet distribution) and c is the maximum value that the concentration parameter w may be presumed to achieve.

For our empirical reanalyses we expanded upon this model to include more grouping levels by including additional equations like Eqs. 2–4 with group-specific parameters. We denote these group-specific parameters with subscripts. For example, the concentration parameter describing the clustering of sites within an aggregate population is denoted as w_{sites} , but that of individuals within sites (i.e., individual specialization per se) simply as w .

Diet specialization at the individual level

We used data simulated under several scenarios to compare the congruence of the observed proportions and Bayesian hierarchical methods in quantifying the diet specialization of individuals using the proportional similarity index, PS_i . First, we simulated multinomial data for 500 populations consisting of 100 individuals that were each observed feeding on either 5, 10, 25, or 50 prey items of up to four different prey types. Second, because in studies of individual predator diets the number of prey items observed per individual varies considerably among

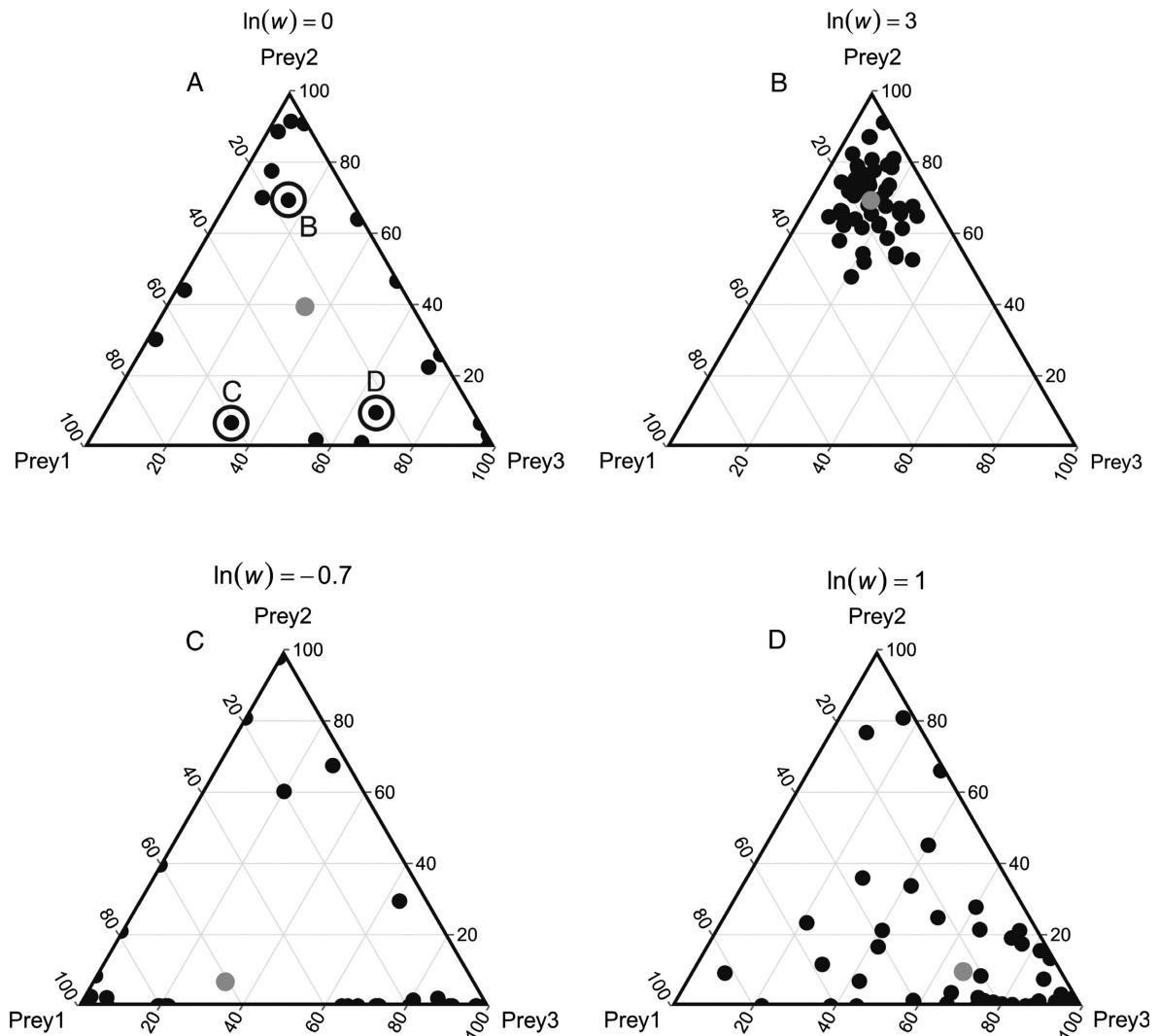


FIG. 1. Hypothetical data illustrate the hierarchical nature of the Bayesian models and the properties of the Dirichlet distribution. In panel A, the black points represent the mean diet proportions of population sub-groups (e.g., sites or treatments) and the gray point denotes the population mean over all sub-groups. The labeled points in panel A represent the mean diet proportions of the sub-groups illustrated in panels B–D. In panels B–D, the black points represent the estimated diet proportions of the individuals within the sub-group, whereas the gray point represents the mean diet of the sub-group. All data were generated from Dirichlet distributions. Each Dirichlet distribution has a vector describing the mean diet proportions of the population or sub-group (the gray points in panels A–D) and a concentration parameter w that describes the extent to which sub-groups (A) or individuals (B–D) are clustered around the population mean (A) or sub-group mean (B–D). A w value of 1 ($\ln(w) = 0$) represents a uniform distribution around the mean (as illustrated in panel A); values >1 ($\ln(w) > 0$) represent a more concentrated distribution (as illustrated in panels B and D); values <1 ($\ln(w) < 0$) represent a more dispersed distribution (as illustrated in panel C).

individuals, we also simulated multinomial data for 500 populations in which 100 different predator individuals per population were observed feeding on a range of prey item counts. The number of observations per individual was stochastically drawn from a beta distribution representing one of three possible scenarios: a uniform distribution of observations per individual, $\text{Beta}(\alpha = 1, \beta = 1)$; a skewed distribution of observations per individual whereby most individuals were observed with few prey items, $\text{Beta}(0.5, 1)$; or a skewed distribution of observations per individual whereby most individuals were

observed with a large number of prey items, $\text{Beta}(1, 0.5)$. Draws from the beta distribution were multiplied by 100 and rounded to the next highest integer, leading to a total range of 1–101 prey items per individual (see Appendix S2 for details, and Data S1, S2 for R code to replicate the simulations).

For each simulation, we implemented the Bayesian hierarchical model (Eqs. 1–4) in OpenBUGS through the R package R2OpenBugs (Lunn et al. 2000, Sturtz et al. 2005), implemented the observed proportions method using the R package RInSp (Zaccarelli et al. 2013), and

compared these to the true PS_i values of all individuals (Data S1, S2). For the Bayesian analysis, we used the mean of the posterior distribution of PS_i as our estimate of PS_i . To quantify differences between the estimates and the true values of PS_i , we calculated the percentage of points falling below the 1:1 line of perfect correspondence (the percentage of negative residuals). A method that equally under- and overestimates PS_i values is expected to have 50% negative residuals. We therefore interpret the percentages of negative residuals for $PS_i > 50\%$ as a measure of a given method's tendency to overestimate diet specialization.

Diet specialization at the population level

Although estimates of diet specialization at the individual level are useful for investigating the relationship between diet specialization and any number of potential continuous traits (e.g., fitness, body size, body shape), researchers have typically been interested in contrasting the relative diet specialization of individuals belonging to different categories, such as experimental treatments, study sites, or sexes. Therefore, we simulated data to compare the two most commonly used indices for estimating relative diet specialization at the population level, IS and WIC/TNW, using the observed proportions method, and the concentration parameter of the Dirichlet distribution (w), which is unique to the Bayesian hierarchical approach. To simplify interpretation, we used the natural log of w , $\ln(w)$ (Fig. 1), to reflect the degree of diet specialization. A positive value of $\ln(w)$ reflects a population of individuals whose diet proportions are concentrated around the mean diet proportion of the population, a value of 0 reflects a population of individuals whose diet proportions are uniformly distributed around the population's mean diet, and a negative value reflects a population of individuals whose diets are dispersed away from the population's mean diet. Therefore, $\ln(w)$ measures a gradient in diet specialization from weak specialization with increasingly large positive values to strong specialization at negative values.

To compare methods, we used Eqs. 1 and 2 to simulate multinomial data for 1,000 populations of 100 individuals, each feeding on up to four prey types with the count of observed prey items per individual drawn from a uniform distribution that ranged from 3 to 50 items, reflective of a typical empirical range for gut content data (for details, see Appendix S2). For each population, we then implemented the Bayesian hierarchical model (Eqs. 1–4), implemented the observed proportions method using RInSp (Data S3), and contrasted the estimates of IS, WIC/TNW, and the concentration parameter $\ln(w)$ by graphing the indices against one another. We also examined the accuracy with which the Bayesian method was able to estimate true $\ln(w)$ values, and the accuracy with which the observed proportions method was able to estimate IS and WIC/TNW, by calculating R^2 values and evaluating the average difference from the true values.

Analysis of empirical data

Simulations are limited in that they reflect only certain aspects of real data. We therefore also reanalyzed two empirical data sets that represent contrasting data-collection methods and predator types: (1) gut contents from American alligators, *Alligator mississippiensis*, containing multiple prey items per gut collected in a one-time snapshot fashion (Fig. 1A; Rosenblatt et al. 2015), and (2) repeated longitudinal observations of intertidal whelks, *Vasula (= Thais) melones*, that feed on only one prey item at a time (Fig. 1B; West 1988).

Alligator data.—These data represent 1,452 American alligators (combined female and male) across 19 sites in the southeastern United States. We grouped the 11–38 families of prey species observed in the diets at each site into nine functional groups: fish, molluscs, crustaceans, aquatic insects, terrestrial insects, amphibians, reptiles, birds, and mammals. Plant material was removed prior to analysis. This reduced the sparseness of the data and reduced the degree to which species-specific variation in prey community composition inflated inferences of between site variation in diet specialization.

We fit three Bayesian hierarchical models to these data: (1) a two-level model with all individuals grouped into a single population (Eqs. 1–4), (2) a three-level model with individuals nested within site, and (3) a four-level model with individuals nested within sex nested within site (see Appendix S3 for details). We fit the three competing models in JAGS using the R package rjags (Plummer 2003, 2016) and calculated the Widely Applicable Information Criterion (also known as the Watanabe-Akaike Information Criterion; WAIC) using the R package loo to select among them (Watanabe 2010, Gelman et al. 2014, Vehtari et al. 2016). WAIC is an information criterion that, like other information criteria, provides a measure of model fit that is penalized by the number of model parameters, but has a sound theoretical foundation in Bayesian statistics (Watanabe 2010, Gelman et al. 2014). We considered models whose WAIC scores were within 1 standard error (SE) of one another to be indistinguishable on the basis of WAIC. In cases where this occurred among the set of top models we chose to analyze the simplest model on the basis of parsimony. To permit the comparison of PS_i , IS, and WIC/TNW estimates, we applied the observed proportions method to the data using RInSp after splitting the data to the lowest level of the selected Bayesian hierarchical model. The code and data used in the analysis can be found in Data S4 and S5.

Whelk data.—These longitudinal data represent 95 whelks from two rocky intertidal sites on the Pacific Coast of Panama (West 1988). Individually tagged and measured whelks were observed every 12 hours over a period of 3 months and, in total, were observed feeding on 19 species of gastropods, bivalves, and polychaetes.

Species were not pooled into functional groups for the analysis of the whelk data. West reported data for individuals with at least five prey observations per individual and categorized the whelks into three size classes.

We fit three Bayesian hierarchical models to these data: (1) a two-level model with all individuals grouped into a single population (Eqs. 1–4), (2) a three-level model with individuals categorized by size class, and (3) a four-level model with individuals categorized by size class nested within site (see Appendix S3 for details). As for the alligator data, we used WAIC to compare the competing models. The observed proportions method was again applied to the data using RInSp after splitting them to the lowest level of the selected Bayesian hierarchical model. The code and data used for the analysis can be found in Data S6 and S7.

RESULTS

Diet specialization at the individual level

The Bayesian hierarchical model for estimating specialization at the level of each individual outperformed the observed proportions method both when the number of prey items per individual was low (Fig. 2) and when the number of prey items per individual varied among individuals (Fig. 3). With <50 observations per individual, the observed proportions method on average overestimated levels of specialization by underestimating the true values of PS_i (Fig. 2; 77% negative residuals when $n = 5$; 69% when $n = 10$; 62% when $n = 25$; 57% when $n = 50$).

In contrast, the Bayesian hierarchical method estimated PS_i reliably regardless of sample size (Fig. 2; 45% negative residuals when $n = 5$; 48% when $n = 10$; 50% when $n = 25$; 50% when $n = 50$). The observed proportions method also performed poorly when sample sizes varied among individuals (Fig. 3), tending to overestimate specialization most when most individuals had few observations (66% negative residuals). The observed proportions method estimated PS_i more accurately when observations were uniformly distributed among individuals and when most individuals had many observations, but still overestimated specialization in these cases (60% and 57% negative residuals, respectively). In contrast, the Bayesian hierarchical method was not influenced by the variation in the number of observations per individuals, consistently exhibiting an equal number of over- and under-estimates for all scenarios (i.e., 49–50% negative residuals).

Diet specialization at the population level

The IS, WIC/TNW, and $\ln(w)$ indices of population-level specialization were all positively correlated with one another (Fig. 4), but the relationships between IS and either WIC/TNW or $\ln(w)$ were weaker than the relationship between $\ln(w)$ and WIC/TNW (IS and WIC/TNW, $R^2 = 0.59$; IS and $\ln(w)$, $R^2 = 0.72$; WIC/TNW and $\ln(w)$, $R^2 = 0.93$). The latter relationship was weakly nonlinear, with WIC/TNW beginning to saturate as $\ln(w)$ increased. IS tended to imply greater diet specialization than did WIC/TNW and $\ln(w)$. The Bayesian hierarchical model estimated the true values of $\ln(w)$ accurately

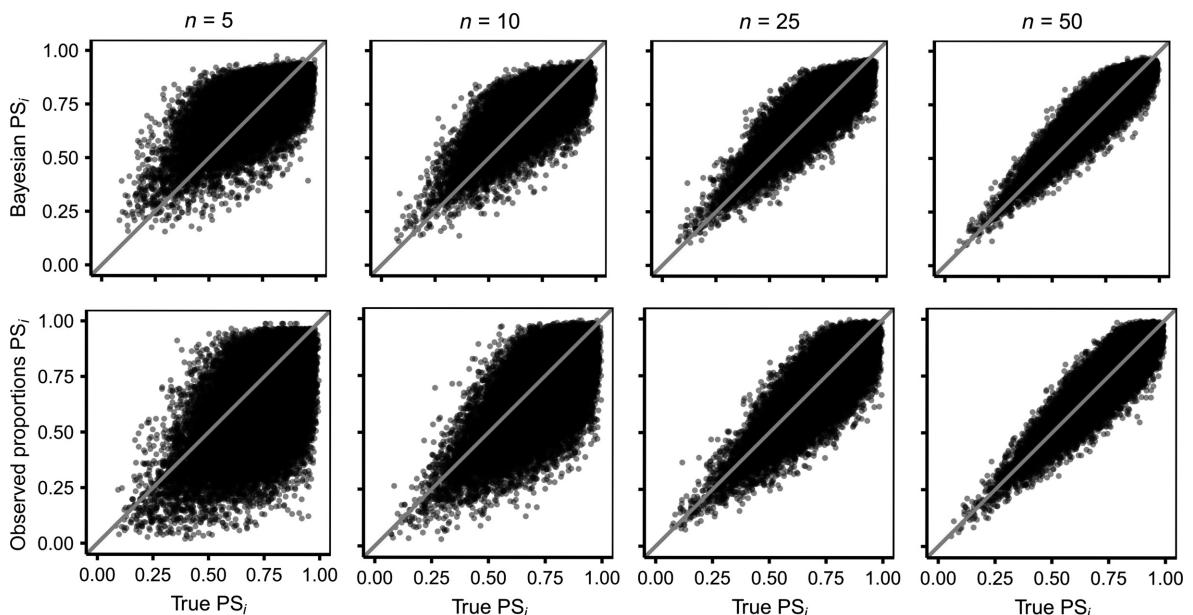


FIG. 2. The observed proportions method led to the overestimation of individual diet specialization (the underestimation of proportional similarity index, PS_i) at low numbers of observations per individual. As the number of observations per individual increases, the estimates from the observed proportions method and the Bayesian hierarchical models converge and perform equally well at estimating PS_i . Estimates of PS_i from simulated data are plotted against the true PS_i values for 5, 10, 25, and 50 observations per individual. The gray line in each graph reflects the line of equality between the true and estimated values.

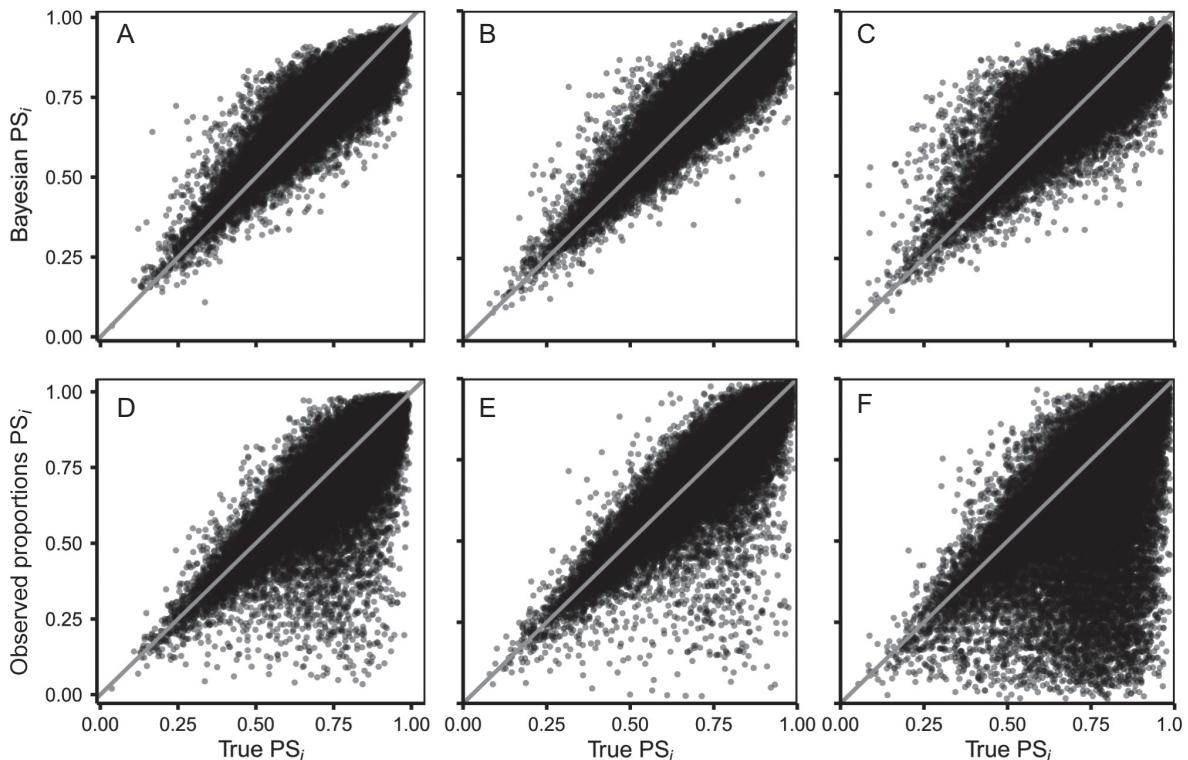


FIG. 3. Simulations with varying numbers of prey per predator individual following one of three distributions, (A, D) a uniform distribution, (B, E) a distribution with most individuals having a large number of observations, or (C, F) a distribution with most individuals having few observations, showed that the observed proportions method overestimates specialization when the number of prey per individual varied across individuals. In contrast, the Bayesian hierarchical models estimated prey proportions more accurately in all situations. The gray line in each graph is the line of equality between the true and estimated PS_i values.

despite the heterogeneous distribution of sample sizes we simulated (Fig. 4, $R^2 = 0.97$). The observed proportions method estimated IS and WIC/TNW precisely, but consistently underestimated both indices by average values of 0.04 and 0.03, respectively (Fig. 4).

Analysis of empirical data

Alligator data.—The comparison of the three Bayesian hierarchical models indicated that the three-level model that included site as a grouping variable and the four-level model that included both site and sex as grouping variables were indistinguishable by WAIC (Table 1, Appendix S3). We therefore analyzed the simpler three-level model which suggested that sites differed in their average diet proportions (Fig. 6A, $\ln(w_{\text{sites}}) = 1.13$ (95% credible interval 0.83–1.43)). While the majority of sites showed evidence of diet specialization at the individual level, sites also varied substantially in their $\ln(w)$ values indicating that diet specialization was stronger within some populations than others (Fig. 5B, Fig. 6B–D). Estimates of $\ln(w)$ showed weak but positive correlations with the observed proportions method estimates of IS ($R^2 = 0.30$, Fig. 5B) and WIC/TNW ($R^2 = 0.47$, Fig. 5C). Estimates of PS_i from the Bayesian

hierarchical model and those of the comparable observed proportions method evidenced little correspondence, with the observed proportions method suggesting substantially higher levels of diet specialization than the Bayesian hierarchical method for many individuals (Fig. 5A). Estimates of diet proportions at the site and individual level suggested that differences among sites were primarily attributable to differences in the diet contributions of invertebrates (especially molluscs) and fishes, with one site showing a large diet proportion of reptiles. The prey taxa responsible for within-site variation in diet proportions varied between sites.

Whelk data.—The three Bayesian hierarchical models considered were indistinguishable from one another using WAIC, so we selected the simplest two-level model that implied no difference among size classes and sites in whelk diet proportions (Table 1, Appendix S3). The PS_i estimates from this model and the observed proportions method were strongly positively correlated ($R^2 = 0.93$; Fig. 5E). However, the observed proportions method consistently implied greater specialization. The model suggested dispersion among individual diet proportions ($\ln(w) = 0.99$, 95% CrI = (0.67–1.29), Fig. 6E) that was driven primarily by differences in individual's apparent

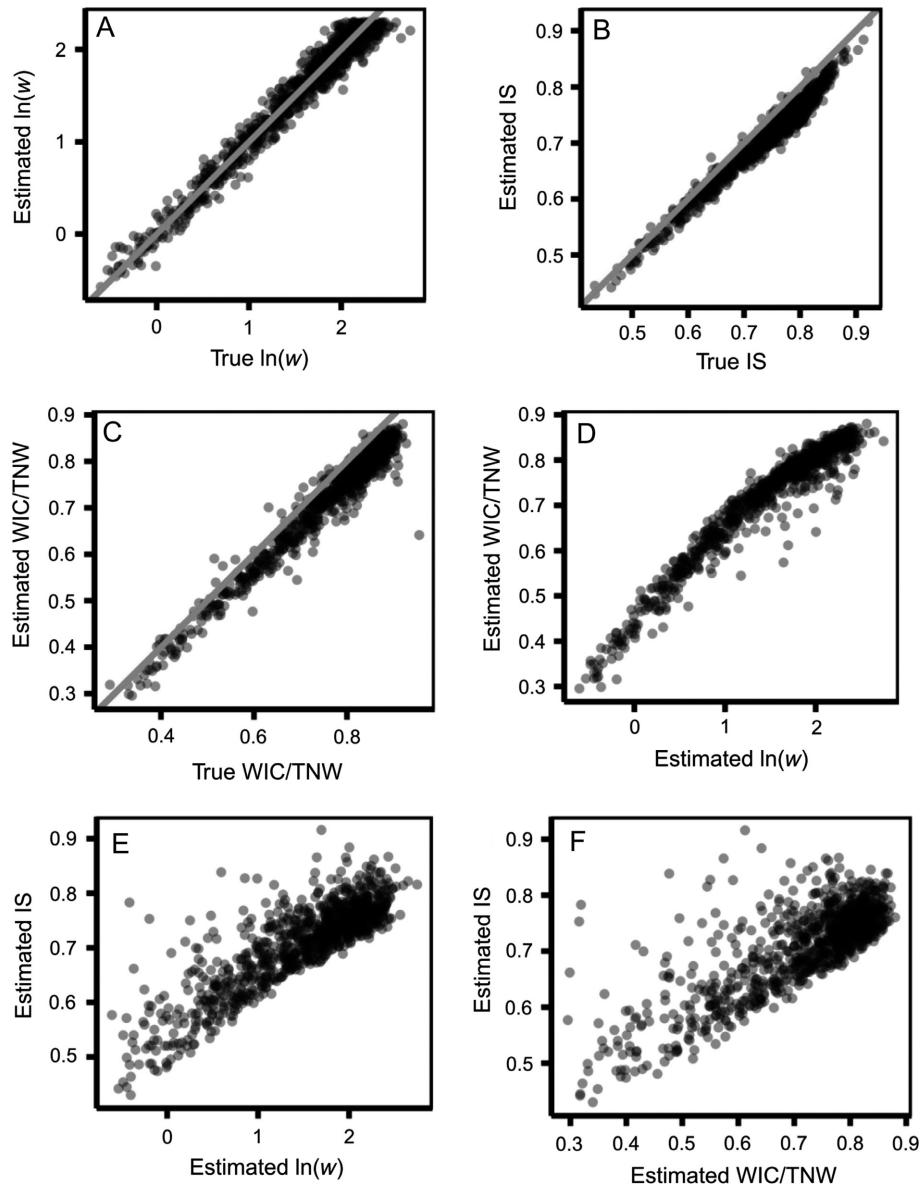


FIG. 4. (A) Estimates of relative diet specialization within groups from simulated data showed that the Bayesian hierarchical models provide a faithful estimate of the true value of the Dirichlet concentration parameter, w . (B, C) Simulations also showed that the observed proportions method provides precise estimates that consistently underestimate the true values of IS and WIC/TNW. The gray line reflects the line of equality between the true and estimated values. (D–F) The three measures of population-level diet specialization within groups, $\ln(w)$, IS, and WIC/TNW, were all positively correlated, but $\ln(w)$ and WIC/TNW show a higher correlation than does either with IS.

preference for either *Ostrea* spp. oysters, *Siphonaria maura* limpets, or serpulid polychaetes.

DISCUSSION

A prerequisite for gaining insights into the causes and consequences of diet specialization is the ability to accurately quantify specialization (Bolnick et al. 2003, 2011, Araújo et al. 2011). Here, using simulated and empirical data, we show that Bayesian hierarchical models are less

prone to the overestimation of diet specialization than the currently used frequentist observed proportions approach, especially when the numbers of prey observed per individual are low or are heterogeneous among individuals. Low sample sizes per individual and heterogeneity in sample sizes are two common features of predator diets whose influences were also observed in our reanalyses of two empirical data sets. Furthermore, our analysis of the empirical data sets highlights the flexibility of hierarchical methods and illustrates the ability of

TABLE 1. The widely applicable information criterion (WAIC) suggested that the models for the alligator data which had individuals nested within site and individuals nested within site and sex were indistinguishable (within 1 standard error (SE) of one another), but were preferred over the model with all individuals in the same hierarchical level. For the whelk data, WAIC suggested that all of the models fit to the data were indistinguishable. When WAIC was unable to distinguish among models, we chose to analyze the simplest model (bolded). Δ WAIC represents the difference between the model with the lowest WAIC score and the other models considered.

Organism and model	WAIC	SE	Δ WAIC
Alligator			
Individuals nested within site and sex	9,008.5	138.6	0
Individuals nested within site	9,016.7	137.0	8.2
All individuals within the same hierarchical level	9,381.6	125.6	373.1
Whelk			
Individuals nested within size class and site	905.2	30.0	0
All individuals within the same hierarchical level	916.0	29.2	10.8
Individuals nested within size class	925.5	31.7	20.3

the method to provide quantitative descriptions of diets and diet specialization for individuals and groups under a single framework.

At the individual level, the observed proportions method consistently estimated higher diet specialization than the underlying true values in the simulated data, whereas the Bayesian method appeared unbiased. The observed proportions method also estimated greater diet specialization for individuals within the empirical data sets, suggesting that the observed proportions method may lead to biased inferences of diet specialization in these cases. Our simulations showed that overestimation by the observed proportions method is particularly severe when sample sizes per individual are low or variable across individuals. Indices that compare individuals to individuals (e.g., the E index [Araújo et al. 2008]) exacerbate this overestimation of diet specialization (Appendix S1).

Hierarchical models provide so-called shrinkage estimators for which estimates are pulled towards population-level means. The degree to which shrinkage occurs is dependent on the sample size or amount of information that estimates are based upon (Gelman et al. 2013). The Bayesian hierarchical method thereby gives less weight to observations with low sample sizes whereas the observed proportions method gives all observations equal weight regardless of sample size. For instance, when an individual is observed feeding on three prey items of the same prey type, the observed proportions method will infer this individual to be a complete specialist. In contrast, the Bayesian hierarchical method will associate some non-zero probability to each of the unobserved but potential alternative prey depending on the assumed prior and the population-level diet proportion estimates. At high

sample sizes the observed proportions and Bayesian hierarchical models will converge. In our simulations, this occurred when individuals were observed feeding on between 25 to 50 prey items, which exceeds the median individual sample sizes in both empirical data sets we analyzed. Although we did not consider the influence of the number of prey types fed on across individuals, this is unlikely to influence the estimation of diet proportions in a fundamentally different manner than assessed here given sufficient sample sizes.

In our reanalyses of the two empirical data sets, both individual- and population-level estimates of the observed proportions method exhibited a much higher correspondence with those of the Bayesian hierarchical method for the whelks than for the alligators. Both data sets exhibited heterogeneity in sample sizes, with the majority of individuals having low sample sizes and few individuals having large sample sizes (Appendix S4: Figures S1 and S2). However, the range of sample sizes was vastly different in the two data sets, with the whelks having been observed consuming between 4 and 18 prey items per individual and the alligators having been observed with between 1 and 2335 items in each individual's gut. Several populations of alligators also had individuals with low sample sizes who had fed on rarely observed prey types. The combination of these patterns means that the alligator diets were much more heterogeneous, which is likely why the two approaches showed better correspondence when applied to the whelk data set.

Contrasts of diet specialization between groups of individuals is a common goal in studies of diet specialization. Although the three metrics of population-level specialization we examined all exhibited positive correlations with one another, the $\ln(w)$ and WIC/TNW indices showed a higher correlation with one another than did either index with the IS index. This result is likely driven by the fact that IS reflects the average overlap between individual diets and the population diet, whereas WIC/TNW and $\ln(w)$ are based on the variation in population diets explained by differences among individuals. We advocate using $\ln(w)$ as a measure of specialization for three reasons. First, there is a large body of statistical literature on the Dirichlet distribution and its concentration parameter (see Agresti 2002). In contrast, the statistical properties of WIC/TNW are unknown. Second, (Roughgarden 1979) used the Shannon Diversity Index as an analog for the variance of discrete data in calculating WIC/TNW (Appendix S2). The use of Shannon's Diversity Index requires taking the log of proportions, which is known to cause the overestimation of diet specialization if some individuals have consumed only a single prey type (Bolnick et al. 2002). Third, combining $\ln(w)$ with the estimates of the diet proportions of individuals and groups allows for the determination of the levels at which most variation in diet occurs, and the particular prey that are responsible for that variation among individuals and/or groups. For example, our reanalysis of the whelk diet data provided insufficient

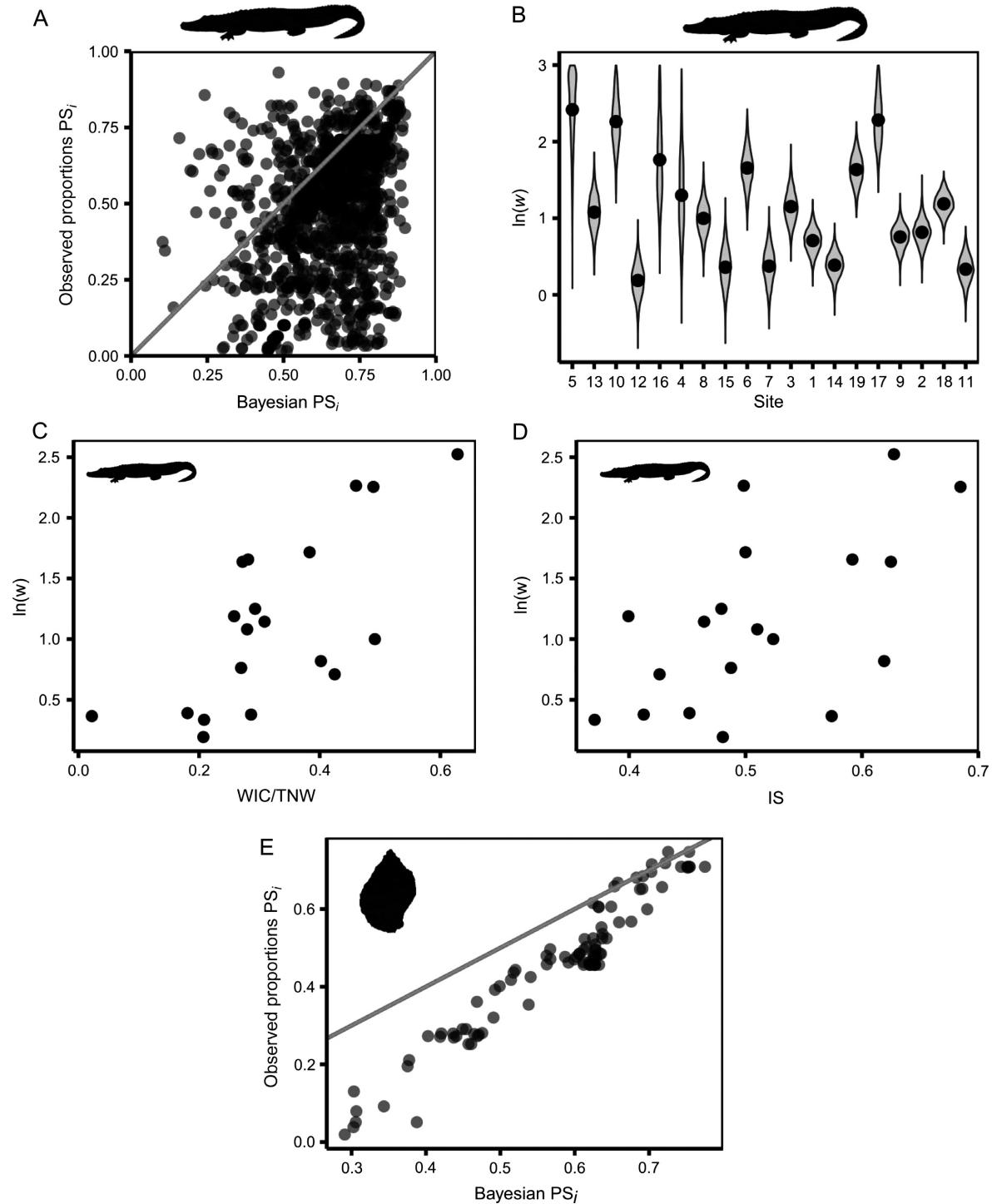


FIG. 5. (A) Individual-level estimates of diet specialization in American alligators were frequently higher when inferred by the observed proportions method than by the Bayesian model, which differentiated sites but not sexes. (B) Site-level estimates of specialization from the Bayesian model differed across sites and were only weakly correlated with the corresponding observed proportions estimates (C) WIC/TNW and (D) IS. (E) For whelks, the most parsimonious model did not differentiate sites and whelk sizes. Its estimates of individual-level diet specialization were positively correlated with the observed proportions estimates, but the latter consistently estimated higher levels of specialization. The gray lines in panels A and E represent the line of equality between estimates from the Bayesian model and the observed proportions method.

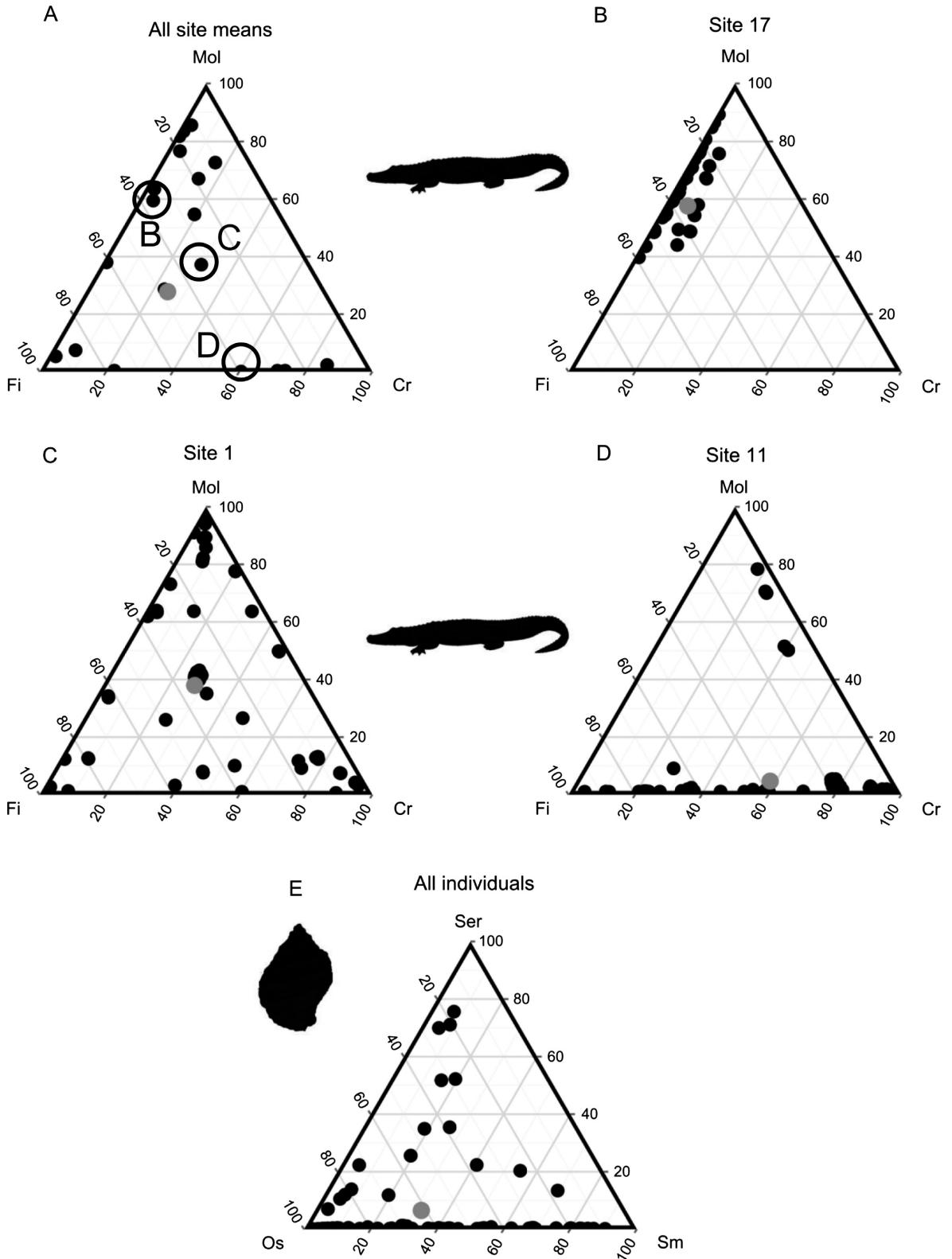


FIG. 6. (A) American alligators showed variation in the mean proportion of the three most consumed prey items (Fi, fish; Mol, mollusc; Cr, crustacean) among sites ($\ln(w_{\text{sites}}) = 1.13$) as well as among individuals, as illustrated by three exemplary sites (B, $\ln(w_{17}) = 2.27$; C, $\ln(w_1) = 0.71$; D, $\ln(w_{11}) = 0.34$). The labeled points within panel A show the site means for the three sites illustrated in panels B–D. (E) Whelks similarly showed variation in the proportion of the three most frequently consumed items (Os., *Ostrea* spp. Oysters; Ser, serpulid polychaetes; Sm, *Siphonaria maura* limpets). The gray points in each ternary plot represent either the average population-level proportions (A, E) or the site-level average proportions (B–D).

support for the hypothesis that diets differed across sites or size classes, yet individuals still differed in the proportions of common prey types that they consumed. Similarly, our analysis showed equivocal support for sex specific differentiation in alligator diets, yet diets differed significantly among sites and among individuals within sites. In this case, our analysis revealed that fishes and invertebrates played primary roles in explaining the individual differences in diets.

A further benefit of Bayesian methods is the ability to estimate the variation around point estimates of diet specialization and prey preferences. Markov chain Monte Carlo methods provide estimates of posterior variance even in situations where it is otherwise difficult to derive variance estimators directly or where asymptotic approximations are required (Gelman et al. 2013). For example, some authors have called into question the variance estimators for PS_i provided by Feinsinger et al. (1981; Bolnick et al. 2002). Indeed, estimates of the variance of PS_i from the Bayesian method showed little correspondence with the variance estimated using Feinsinger et al.'s equations (Appendix S4: Figure S3). Furthermore, although variance can be estimated for IS and $\ln(w)$, there is no variance estimate for WIC/TNW. Although Monte Carlo simulations have been used to determine the significance of WIC/TNW and IS relative to null models of feeding (Bolnick et al. 2002), these will also be prone to low sample size problems (Efron and Tibshirani 1993).

Future extensions to the Bayesian hierarchical models presented here will help to address further questions surrounding the mechanisms underlying diet specialization. For example, groups may appear to display higher diet specialization relative to others due to differences in the availability or handling times of prey rather than differences in individual diet preferences and specialization per se (Novak 2010, Araújo et al. 2011). The Bayesian hierarchical model can be extended to explicitly address this possibility by modeling the concentration parameters as a function of such group-level attributes. A similar approach could also be used to examine the role of intraspecific competition in promoting diet specialization by modeling the concentration parameters as a function of resource availability relative to predator abundance. Several other possibilities, such as including individual-level covariates to determine the influence of individual traits on diet specialization, make Bayesian hierarchical models well-suited for addressing hypothesis-driven questions regarding diet specialization and predator foraging more generally.

It is important to note, however, that Bayesian posterior distributions are a compromise between the assumed

prior distribution and the data-dependent likelihood function, with the latter carrying more weight as sample sizes increase (Gelman et al. 2013). We used uniform priors on the parameters describing the population level diet (\bar{q} ; Dirichlet($\vec{1}$)) and the concentration parameters (w ; Uniform(0, c)). For the analysis of both empirical data sets, we chose a maximum value of $c = 30$ for the uniform prior on the concentration parameters because the effects of increasing w on the proportional overlap among individual diets saturated near 30 (Appendix S4: Figure S4). Thus considering higher maximum values would not likely qualitatively influence our inferences. Nevertheless, it is important to allow for large enough values of w so as not to artificially limit it to small values that could inflate estimates of diet specialization. Further analyses of intraspecific diet specialization within the Bayesian hierarchical framework are needed to allow ecologists to develop more empirically-grounded prior choices.

For methods of model fitting and parameter estimation to be useful and generally applicable, it is important to consider issues involved in implementing the method. For example, we had difficulty fitting the hierarchical model to the alligator gut content data with prey identities resolved to the family level due to the sparsity of these data. To address this problem, we grouped the prey items into functional groups. Although the general influence of lumping prey into functional groups is unknown for estimating diet specialization because no systematic analyses have been performed, it is a common practice that ought to reduce the inferred strength of specialization. That said, previous investigations have observed no qualitative and only weak quantitative effects (Bolnick and Paull 2009, Novak and Tinker 2015). Furthermore, models with particularly rare prey taxa may face numerical issues involving the division by probabilities very close to zero. These issues can be resolved by adding a small constant to each probability estimate or by only considering taxa that appear in the diet over a certain abundance threshold, but the influences of these choices needs further study.

Finally, it should be recognized that the Bayesian models presented here are more difficult and require more work to implement than many of the currently used observed proportions methods. As an example, in Bayesian analyses, the user must examine several model diagnostics to ensure that the Markov Chains have converged and are well mixed, that the burn-in period specified is long enough so as not to bias the posterior distributions of parameters, and that posterior estimates are reasonable (Gelman et al. 2013). Despite these added complications, our study suggests that the inference of diet specialization from Bayesian hierarchical

models is more reliable and provides greater ecological insight into the diets of individuals and populations. Thus, even when compared to the ease with which the observed proportions methods may be implemented, the Bayesian hierarchical method offers several advantages that ultimately outweigh its additional complexity.

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