



# Relative prey abundance and predator preference predict individual diet variation in prey-switching experiments

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*Abstract.* Individual diet specialization appears widespread and has several ecological ramifications. Hypotheses on the causes of diet specialization generally assume prey preferences differ among predator individuals. They then predict how the magnitude of diet variation should change when ecological factors (e.g., intraspecific competition) alter prey abundances. However, the magnitude of diet variation is expected to change with prey abundances due to stochasticity in the foraging process even if all predators share the same prey preferences. Here I show that the relative prey abundance where diet variation is maximized and the magnitudes of diet variation in prey switching experiments are predicted well by a simple stochastic foraging model based only on relative prey abundances and a shared relative prey preference among predators. These results suggest that the effects of stochasticity during foraging may confound studies of individual diet specialization if these effects are not accounted for in experimental design or interpretation. Furthermore, the stochastic foraging model provides simple baseline expectations for theoretical studies on the ecological consequences of diet variation and offers a way forward on quantitative predictions of how ecological factors influence the magnitude of diet variation when stochasticity during foraging and diet specialization occur simultaneously. Last, this study highlights the continued importance of integrating stochasticity into mechanistic ecological hypotheses.

*Key words:* binomial process; foraging; individual diet specialization; niche variation; predator-prey interactions; stochasticity.

## INTRODUCTION

Individuals within generalist predator populations often differ in their diets. Although various morphological differences among individuals (e.g., ontogenetic niche shifts, sexual dimorphism, resource polymorphisms) can lead to differences in diet, studies focusing on seemingly identical individuals often still find substantial diet variation among individuals (Bolnick et al. 2003, Araújo et al. 2011). This form of intraspecific variation has been termed individual diet specialization and may have several important ecological and evolutionary effects (Bolnick et al. 2011). For example, studies have suggested that diet variation can alter the strengths of predator-prey interactions (Bolnick et al. 2011, Gibert and Brassil 2014), indirect effects among prey and eco-evolutionary dynamics (Schreiber et al. 2011), and coexistence among competitors (Hart et al. 2016).

Most hypotheses on the mechanisms underlying individual diet specialization seek to explain differences in the strength of diet specialization across populations,

species, or experimental treatments using optimal foraging theory (Svanbäck and Bolnick 2005, Tinker et al. 2008, Araújo et al. 2011). Optimal foraging theory predicts which prey species predator individuals should include within their diet to maximize energy intake (Emlen 1966, Stephens and Krebs 1986). In particular, predators should rank prey species according to their profitability, defined as the prey's energy content per unit handling time. Predators should always consume their top-ranked prey when encountered. Predators should include lower-ranked prey in their diet only when the densities of higher-ranked prey fall low enough that ignoring lower-ranked prey would decrease the predator's energy intake rate. Assuming that individual predators differ in their rank preferences for prey, optimal foraging theory offers predictions of how changes in prey availability should alter the magnitude of diet specialization among individuals given individual variation in rank preferences. For example, predictions from optimal foraging theory have been used to develop hypotheses surrounding the effects of intra- and interspecific competition, ecological opportunity, and predation on individual diet specialization (Araújo et al. 2011). Studies that measure diet specialization in different contexts (e.g., populations, experimental treatments) can then compare the observed patterns of diet specialization to

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the predictions derived from optimal foraging theory assuming some pattern of differences in rank preferences among individuals.

Less considered is that stochasticity in the foraging process should also generate predictable changes in the magnitude of diet variation with changes in prey availability, even if predators all share the same prey preferences. To illustrate this, consider a predator population that feeds on two prey species. Assume that all predator individuals have the same relative preferences for prey 1,  $q_1$ , and prey 2,  $q_2$ . Also assume that prey 1 and prey 2 have relative abundances  $R_1$  and  $R_2$ , respectively (note that  $q_2 = 1 - q_1$  and  $R_2 = 1 - R_1$ ). If individuals encounter prey in proportion to their relative abundances and accept prey in proportion to their relative preferences for the prey, the probability of an individual predator eating an individual of prey 1 is  $p_1$ , where

$$p_1 = \frac{q_1 R_1}{q_1 R_1 + (1 - q_1)(1 - R_1)} = \frac{q_1 R_1}{q_1 R_1 + q_2 R_2}. \quad (1)$$

Under these assumptions, the number of prey 1 in the diet of an individual is binomially distributed,  $\text{Binomial}(p_1, n)$ , where  $n$  is the total number of prey consumed. Under the binomial distribution, the variance is maximized when  $p_1 = 0.5$ . This occurs in the model when  $q_1 = 1 - R_1$  or when the relative preference for prey 1 is equivalent to the complement of the relative abundance of prey 1. Therefore, even if all individuals share the same relative preferences for two prey, the amount of diet variation among individuals should change predictably with the relative densities of the two prey (this model and its implications can also be extended to more than two prey; see Appendix S1). Hereafter, the above model will be referred to as the “stochastic foraging model.”

I wanted to examine whether stochasticity in the foraging process was capable of explaining diet variation empirically. Prey-switching experiments provide a convenient source of data to do so. Prey switching occurs when predators include a disproportionately large amount of a prey species in their diet when that prey is common and a disproportionately small amount of that prey in their diet when it is rare (i.e., frequency-dependent predation; Murdoch 1969). Experiments evaluating prey switching typically do so by varying the relative abundances of two prey and recording the proportions of the prey in predators’ diets at each relative abundance. These experiments also typically include multiple trials at each relative prey abundance providing an estimate of the amount of variation in the proportion of prey in predators’ diets at each relative abundance. As the stochastic foraging model predicts changes in the amount of diet variation at different relative abundances of prey, these studies offer a simple “proof of concept” test of the stochastic foraging model’s ability to predict diet variation in empirical studies.

Overall, I find that the stochastic foraging model is indeed able to predict both the relative density at which diet variation is the greatest and the magnitude of diet variation well. Support for the stochastic-foraging model suggests that changes in the magnitude of variability among individuals with changes in prey abundances can potentially affect inferences in studies of diet specialization if this effect is not accounted for. Furthermore, these results suggest the connection between individual diet specialization theory and empirical studies may benefit from the direct inclusion of stochasticity as has theory on extinction risk (Dennis 1989, Lande 1993), population and community dynamics (Hubbell 2001, Turchin 2003, Fukami 2015), and ecological stability (Ives et al. 2003, Nolting and Abbott 2016).

## METHODS

### *Gathering data*

I located potential switching experiments to evaluate the stochastic foraging model by examining the 1,169 citations of the seminal paper on prey switching on Google Scholar (Murdoch 1969; as of December 4, 2018). All experimental papers in this list were examined for those including data on (1) the proportion of the focal prey in the predators’ diets for each relative prey availability, (2) a measure of variance among individuals or experimental groups (for studies including more than one predator per trial) in the proportion of focal prey consumed, and (3) data on or a way to estimate the average total number of prey consumed by individuals or experimental groups. Including the Murdoch (1969) paper itself, I found 20 studies that provided the required information. Some of these studies included multiple switching experiments using different predator species, prey species, or experimental conditions giving a total of 36 usable experiments. See Table 1, for a table giving the characteristics of each of the studies. In most cases, the necessary data were extracted from figures using WebPlotDigitizer (Rohatgi 2011). In a few cases, raw data was given in tables within the publication (Table 1).

After extracting the data, I evaluated the ability of the stochastic foraging model to make two predictions: (1) the relative prey abundance at which the maximum diet variation occurred in each experiment, and (2) the magnitude of diet variation at each relative prey abundance in each study.

### *Predicting the relative abundance at which maximum diet variation occurs*

According to the stochastic foraging model, diet variation should be maximized when the relative abundance of the focal prey is equal to one minus the predator’s relative preference for the focal prey. For all but two

TABLE 1. This table provides the 20 prey-switching studies used to evaluate the ability of a stochastic foraging model to predict the magnitude of individual diet variation and provides relevant information to the analyses performed.

Study	Predator species	Number of relative prey abundances	Replicates per relative abundance	How variation was reported	Prey replaced	Predators per trial	Method for estimating total number of prey eaten	Number of experiments
Akre and Johnson (1979)	<i>Anomalagrion hastatum</i> , Odonate larva	6	5	Data provided for each replicate	No	1	Estimated from functional response experiments	2
Bayliss (1982)	<i>Lepsiella vinosa</i> , whelk	3	6	Raw data provided	Yes	2	Raw data provided	3
Bell et al. (1999)	<i>Pomatomus saltatrix</i> , fish	3	3	Standard errors reported	No	4	Number of attacks and proportion of successful attacks given	1
Blois-Heulin (1990)	<i>Anax imperator</i> , Odonate larva	5	10	Confidence interval reported	Yes	1	Mean number of prey eaten at absolute prey density reported	2
Buckel and Stoner (2000)	<i>Pomatomus saltatrix</i> , fish	5	3	Standard errors reported	No	3	Estimated from functional response experiments	2
Butler and Burns (1991)	<i>Piona exigua</i> , mite	5	8 or 4 (two experiments)	Data provided for each replicate	No	1	Estimated from functional response experiments	2
Cuthbert et al. (2018)	<i>Gammarus duebeni celticus</i> , amphipod	7	6	Standard errors reported	Yes	1	Estimated from functional response experiments	1
Daly and Long (2014)	<i>Paralithodes camtschaticus</i> , crab	5	4–12	Standard errors reported	No	1	Estimated from functional response experiments	2
Dinis et al. (2016)	<i>Calathus capitata</i> and <i>Pterostichus globosus</i> , beetles	7	25	Standard errors reported	No	1	Estimated from functional response experiment	2
Ejdung and Elmgren (2001)	<i>Saduria entomon</i> , isopod	3	6	Data provided for each replicate	No	1	Estimated from prey depletion experiment	1
Flinn et al. (1985)	<i>Reduviolus americanoferus</i> , hemipteran	7	6	Standard errors reported	Unclear	1	Estimated from functional response experiments	1
Hill and Elmgren (1992)	<i>Saduria entomon</i> , isopod	3	5	Data provided for each replicate	No	1	Mean number of prey eaten at absolute prey density reported	1
Johansson and Johansson (1992)	<i>Aeshna juncea</i> , Odonate larva	5	4	Standard deviations reported	No	1	Estimated from functional response experiments	1
Katz (1985)	<i>Urosalpinx cinerea</i> , whelk	5	5	Standard errors reported	No	1	Estimated from functional response experiments	1
Long et al. (2012)	<i>Callinectes sapidus</i> , crab	7	3–14	Standard errors reported	No	1	Estimated from functional response experiments	1
Mattila and Bonsdorff (1998)	<i>Platichthys flesus</i> , fish	3	8	Standard errors reported	No	1	Estimated from functional response experiments	1
Murdoch (1969)	<i>Thais (Nucella) emarginata</i> and <i>Acanthina spirata</i> , whelks	5	5	Data provided for each replicate in one experiment, standard errors reported in other	Yes	2	Total number of prey eaten reported for one experiment and estimated from functional response experiments in the other	2

TABLE 1. (Continued)

Study	Predator species	Number of relative prey abundances	Replicates per relative abundance	How variation was reported	Prey replaced	Predators per trial	Method for estimating total number of prey eaten	Number of experiments
Murdoch and Marks (1973)	<i>Coccinella</i> sp., ladybird	5	6–7	Raw data provided	No	1	Raw data provided	3
Murdoch et al. (1975)	<i>Poecilia reticulata</i> , fish	4	11	Standard errors reported	Yes	1	Number of prey eaten per trial controlled	1
Sherratt and Harvey (1989)	<i>Pantala avescens</i> , Odonate larva	3	6	Data provided for each replicate	Yes	1	Mean number of prey eaten reported	3
Vantornhout (2006)	<i>Iphiseius degenerans</i> , mite	3	20	Standard errors reported	No	1	Mean number of prey eaten reported	4

experiments, I estimated the predator's relative prey preference by using the mean proportion of the focal prey in predators' diets when the two prey were offered in equal abundances. The remaining two experiments did not include a trial with prey offered in equal abundances (Murdoch et al. 1975, Akre and Johnson 1979). These papers did include an estimate of relative preference obtained by fitting a linear model with a zero intercept to data on the ratio of prey available and the ratio of prey consumed. The slope of this line gives the predator's preference in terms of the expected ratio of the two prey in the diet (Murdoch 1969). For these studies, I estimated the predator's relative preference by converting this ratio to a proportion. I then calculated the predicted relative abundance at which diet variation should be the greatest for each experiment as one minus the predator's relative preference.

If switching experiments included all possible relative abundances of prey, it would be simple to compare the predicted relative abundance at which diet variation should be greatest to the observed abundance at which it occurred. However, the experiments used a minimum of three and a maximum of seven relative prey abundances (Table 1). It is unlikely that the predicted relative abundance where the maximum variation should occur was included in the experiment. For the studies with only three relative abundances, I compared the predicted relative abundance where the maximum diet variation should occur to the observed relative abundance at which the maximum occurred. For the experiments containing more than three relative abundances, I fit a spline to the observed variances and used the relative abundance at which the maximum of the spline occurred as the estimate of the relative abundance at which the maximum variation occurred. If the maximum variation occurred at either the lowest or highest relative abundance considered, the spline predicted that the maximum variation occurred at a relative abundance of zero or one. In these cases, I used the relative abundance at which the greatest variation occurred in the experiment as the estimate of the observed relative abundance at

which the maximum occurred. Separately for the experiments with three relative abundances and more than three relative abundances, I plotted the predicted vs. observed relative abundances at which the maximum diet variation occurred and calculated the coefficient of determination ( $R^2$ ) of the 1:1 line.

#### Predicting the magnitude of diet variation

The stochastic foraging model also provides a prediction of the magnitude of diet variation at each relative prey abundance. Under the binomial distribution, the expected variance in the proportion of successes (the proportion of the focal prey consumed) is

$$\frac{p(1-p)}{n} \quad (2)$$

where  $n$  is the total number of trials (the total number of prey consumed). With  $p$  defined as  $p_1$  in Eq. 1, the magnitude of diet variation can be predicted given the estimate of the predator's relative preference, the focal prey's relative abundance, and the total number of prey consumed. The relative preference of consumers was estimated as above by using the mean proportion of focal prey in the diet of the predator when prey were offered at equal abundances or, in the case of the two studies that did not include a treatment offering the prey in equal abundances, using the reported preference value. Relative abundances were given in each experiment. For studies that gave the raw data,  $n$  was estimated at each relative abundance by averaging the number of prey eaten across all of the individuals at that relative density. For studies including functional response experiments, in which the abundances of prey are varied and the number of prey consumed is recorded, the abundances of the prey used in the switching experiment were matched with the functional response experiments to provide an estimate of the total number of prey consumed. Last, some studies provided the mean number of

prey consumed at each relative abundance of prey (Table 1).

After calculating the predicted variance, I used simulations to generate a 95% confidence interval (CI) around the predicted variance. For each relative prey abundance, I performed 10,000 simulations. In each simulation, I drew a number of samples from a binomial distribution equal to the number of individuals or experimental groups used in the experiment. The binomial distribution was parameterized using the probability calculated from the relative preference and relative prey abundance and the  $n$  given by the total number of prey consumed. I then calculated the proportion of the focal prey within each of the simulated diets and calculated the variance of the proportions across the simulated diets. I then used the 0.025 and 0.975 quantiles of the variances across the 10,000 simulations as the 95% CI for the predicted variance and determined whether the observed variance fell within the CI.

Although here I estimate diet variation using the variance of the proportion of focal prey in diets, studies of diet variation typically measure diet variation using indices of diet specialization (e.g., the individual specialization (IS) index, the ratio of within individual variation (WIC) to the total niche width (TNW; WIC/TNW), etc.; Bolnick et al. 2002). For a subset of the switching experiments that provided the raw data or proportions of prey in individuals' diets, I analyzed the ability of the stochastic foraging model to predict the magnitude of IS. The values of IS and the variance in the proportion of focal prey within diets were strongly correlated and the results of the analysis for IS were similar to the results for the variance of the proportion of the focal prey within diets and can be found in Appendix S2.

All of the calculations were performed in the program R (R Core Team 2018; v. 3.4.4). All of the code and data are available (see *Data Availability*).

## RESULTS

### *Predicting the relative abundance at which maximum diet variation occurs*

The predicted relative abundance at which the maximum variance should occur from the stochastic foraging model was positively correlated with the observed relative abundance at which the maximum diet variation occurred in experiments including three relative abundances (Fig. 1A) and those including more than three relative abundances (Fig. 1B). The coefficient of determination ( $R^2$ ) of the 1:1 line between predicted and observed diet variation for studies with three relative abundances was 0.33 and was 0.79 for studies with more than three relative abundances.

### *Predicting the magnitude of diet variation*

Overall, the studies used included 161 observed variances. The predicted and observed variances were positively correlated (Pearson correlation coefficient,  $\rho = 0.59$ ,  $P < 0.001$ , Fig. 2). Of the 161 variances, 79.5% (128 variances) fell within the 95% CI's of the predicted magnitude of variance from the stochastic foraging model (Fig. 3). Of the 33 variances not covered by the 95% CI's, the stochastic foraging model underestimated the diet variation in 25 of the cases and overestimated variance in the remaining eight cases.

## DISCUSSION

Many hypotheses on the causes of individual diet specialization predict how the magnitude of individual diet variation should change with changes in prey abundances when individuals differ in their prey preferences. My analyses show that the magnitude of diet variation

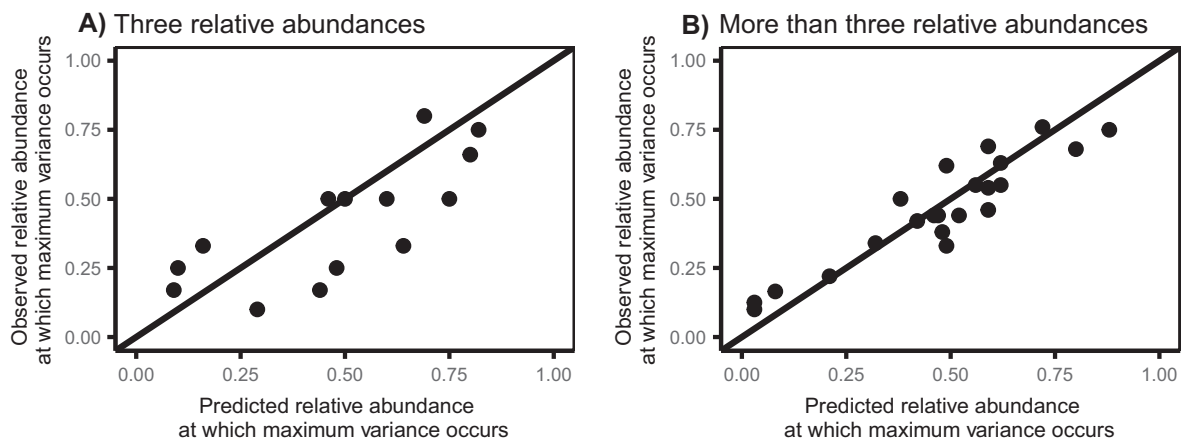


FIG. 1. The relative abundances of prey at which the maximum diet variation occurs in prey switching experiments including (A) three relative prey densities and (B) more than three relative prey densities is predicted well by a stochastic foraging model assuming all predators share the same relative prey preferences.

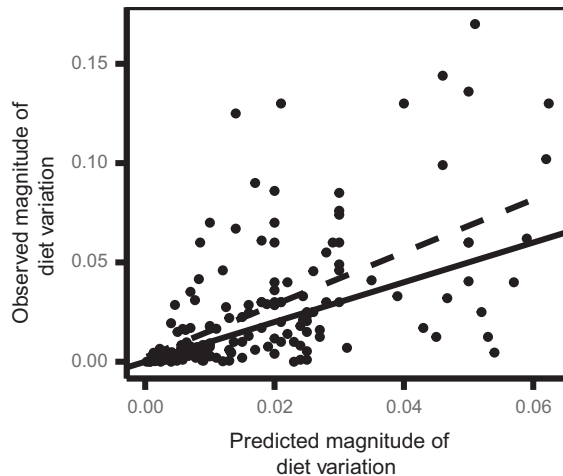


FIG. 2. The magnitude of diet variation measured in prey-switching experiments is correlated with the predicted magnitude of diet variation from a stochastic foraging model assuming all predators share the same relative prey preferences (Pearson correlation coefficient,  $\rho = 0.69$ ). The solid line is the 1:1 line between the predicted and observed diet variation whereas the dashed line is a linear model fit between the predicted and observed diet variation (intercept = 0.002, slope = 1.32).

among individuals is likely to change with prey abundances even if all predators have identical preferences due to stochasticity in the foraging process. Changes in the magnitude of diet variation among individuals with identical preferences can potentially confound studies of diet specialization if the effects of stochasticity are not considered in the design or interpretation of experiments. For example, consider a population exhibiting diet specialization in which there are two groups of individuals that differ in prey preferences. Under relative prey abundances that cause a large amount of stochastic within-group variation, this within-group variation may mask the preference differences among the two groups, hampering inference of diet specialization. Furthermore, when prey relative abundances differ across samples or treatments, changes in both the mean diets of the groups that share preferences and variation within those groups with prey abundances will determine the observed differences in specialization across the samples or treatments. Because of this, as has been pointed out previously in the ecological literature on measuring interspecific diet overlap, studies should measure and account for prey availability when possible (Hurlbert 1978). Last, one can view the variance predicted by the stochastic foraging model as the predicted amount of variation among individuals sharing prey preferences or the predicted variation in repeated samples of an individual when its prey preferences and the prey abundances remain constant. Therefore, in studies that repeatedly measure the diets of individuals (e.g., Rhoades et al. 2018) the amount of within-individual variation relative to between-individual variation may depend on the

abundances of prey used in the experiment. Recognizing that stochastic variation in diet may change with prey availability and predator preferences will help in the design and interpretation of individual diet specialization studies.

A related issue in studies of diet specialization is that the stochastic foraging model and optimal foraging theory can also make identical predictions of how the magnitude of diet variation should change with prey abundances. For example, one of the most widely considered hypotheses on causes of individual diet specialization is intraspecific competition (e.g., Svanbäck and Persson 2004, Svanbäck and Bolnick 2006, Tinker et al. 2008). A simple version of this hypothesis assumes that individuals all have the greatest preference for one prey species but differ among one another in their preferences for alternative prey. As the predator's density increases, exploitation competition reduces the density of the most preferred prey species. In turn, individuals switch to consuming their different alternative prey increasing the amount of diet variation. However, if individuals share a high preference for one prey species and exhibit no differences in preference for alternative prey, the stochastic foraging model also predicts that the amount of diet variation among individuals should increase as abundance of the most preferred prey decreases. If the variation among individuals is due purely to stochasticity, existing Monte Carlo methods for assessing diet specialization should show that this variation is not statistically significant (Bolnick et al. 2002, Zaccarelli et al. 2013). However, the pattern of changes in the magnitude of diet variation with prey abundances may be identical. This highlights the importance of assessing whether differences among individuals in diets are due to stochasticity and assuring that best practices for inferring diet specialization are followed such as minimizing spatial and temporal variation in the sampling of individual diets (Araújo et al. 2011), ensuring prey items represent independent foraging decisions by the predator (Araújo et al. 2011), and accounting for the fact that the observed proportions of prey in predator diets can overestimate individual diet specialization (Coblentz et al. 2017).

Distinguishing between situations in which diet variation is due to actual specialization or not is important in terms of the potential consequences of diet variation for populations, communities, and ecosystems. For example, the potential eco-evolutionary consequences of diet variation require that prey preference differences among individuals are heritable (Schreiber et al. 2011, Patel and Schreiber 2015). Therefore, these consequences will only occur in systems with individual diet specialization due to heritable trait differences among individuals. On the other hand, other potential consequences will occur regardless of whether diet variation is due to specialization. One example of this is the alteration of the strength of predator-prey interactions due to nonlinear averaging (Jensen's Inequality; Bolnick et al. 2011). Diet variation

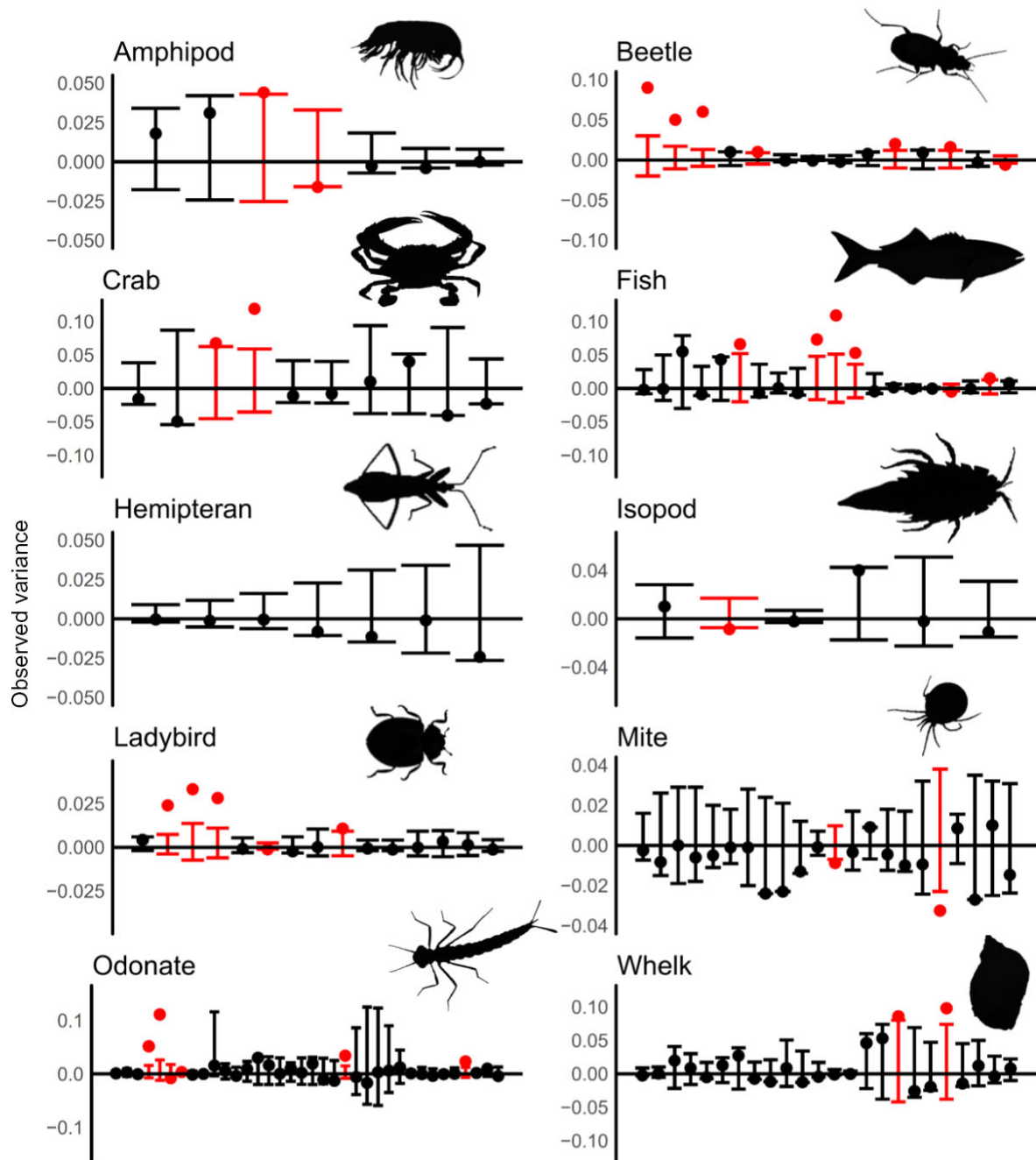


FIG. 3. Across several taxa, The magnitude of diet variation in prey-switching experiments is predicted well by a stochastic foraging model assuming all predators share the same relative prey preference. In 161 observed variances, 79.5% (the 128 variances shown in black) fell within the 95% confidence intervals of the predictions from the stochastic foraging model (the variances outside the 95% confidence intervals are shown in red). The 95% confidence intervals were generated by simulation. See the Methods for details. Note there is no  $x$ -axis. Each point on the  $x$ -axis is one of the 161 observed variances.

among individuals, regardless of its cause, is reflected in differences among individuals in their attack rates. Because the feeding rates of predators are typically non-linear functions of attack rates, this variation will typically alter the strength of predator–prey interactions relative to the case that all individuals had the same

mean attack rate (Bolnick et al. 2011). Although this effect should occur regardless of the cause of diet variation, the effect may be stronger in cases of individual diet specialization. For effects of diet variation that do not depend on variation being the result of diet specialization, the stochastic foraging model may provide a

baseline expectation for the minimum expected magnitude of the effect and its relationship with prey availability.

Overall the stochastic foraging model predicted the magnitude of diet variation in switching experiments well. However, this comes with some caveats. First the switching experiments used to evaluate the stochastic foraging model represent very simplified situations in terms of the ecology and diet variation. For example, all but one study (Katz 1985) were performed under controlled laboratory conditions with generally only a single predator per trial. These conditions remove many of the factors known to lead to niche expansion and increased diet variation such as interactions with individuals of the same and other species, spatial variability, and ecological opportunity (Semmens et al. 2009, Rosenblatt et al. 2015, Costa-Pereira et al. 2018). Therefore, it is unclear how well the stochastic foraging model would be able to predict diet variation under more realistic conditions. Furthermore, for 33 of the 161 measured variances, the 95% confidence intervals generated did not include the observed variance. However, several methodological considerations may explain why the stochastic foraging model performed poorly in these cases: (1) individuals may have varied in their relative preferences, (2) all but one study violated the model assumption that all individuals consumed the same amount of prey, (3) most studies did not replace prey as they were eaten meaning that relative prey densities were not constant throughout the experiment, and (4) most studies included few replicates at each relative density. Despite these caveats, changes in diet variation with prey availability were consistent with stochasticity in the foraging process in most cases.

The explicit relationships between individual diets, preferences, and prey abundances within the stochastic foraging model may also help improve studies of diet specialization. For example, diet specialization often implies that diet differences among individuals reflect prey preference differences among individuals (Bolnick et al. 2003, Araújo et al. 2011). However, as shown here, individual diets reflect both individual prey preferences and prey availability. In studies in which prey availability can be estimated, the relationships between diets, preferences, and prey abundances could be used to directly estimate individual preferences, thus facilitating comparisons among individuals using a common currency rather than one that may be biased by differences in prey availabilities experienced by individuals. Similarly, the stochastic foraging model may help generate more nuanced inferences on the causes of diet specialization. Consider an experiment examining the role of intraspecific competition in generating diet specialization comparing the amount of diet variation among individuals in low predator density treatments to the amount of diet variation in high predator density treatments (e.g., Svanbäck and Bolnick 2006). An observed increase in the magnitude of diet variation with

predator density could be due to changes in the preferences of individuals or changes in resource abundances. A possible way to distinguish between these scenarios would be to estimate individual preferences in the low predator density treatments from the individual diets and prey availabilities. Using these preferences, one could then perform simulations to create a null expectation of the amount of diet variation among individuals if individual prey preferences remained identical to the low predator density treatments, but prey densities changed as observed in the high predator density treatments. These sorts of methods may lead to a more mechanistic understanding of the ecological causes of individual diet specialization and facilitate more meaningful comparisons of diet differences among individuals.

## CONCLUSIONS

Individual diet variation in generalist consumers appears widespread and has several potential ecological consequences (Bolnick et al. 2003, 2011, Araújo et al. 2011). Here I have shown that, when this variation is due to stochasticity in the foraging process, the magnitude of diet variation may be predictable given the predator's relative prey preferences, the relative densities of prey, and the number of prey consumed. These results suggest that the existence of stochastic foraging's effect on diet variation should be considered in the design and interpretation of experiments and offer simple expectations for the magnitude of diet variation and its relationship with prey availability in the absence of diet specialization. Lastly, the incorporation of stochastic processes into ecological theory has helped refine our understanding of several ecological phenomena and provides a bridge between deterministic theory and real world observations (e.g., Lande 1993, Hubbell 2001, Ives et al. 2003, Turchin 2003, Fukami 2015, Nolting and Abbott 2016). The continued integration of stochastic processes into theory on individual diet specialization should help to bring a closer link between theory and empirical studies.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2911/supinfo>

## DATA AVAILABILITY

Code and data are available on Zenodo: <https://doi.org/10.5281/zenodo.3422007>