AN ABSTRACT OF THE DISSERTATION OF

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Title: Candidate Causes, Consequences, and Estimation of Individual Diet Specialization

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Mark Novak

Diet variation among individuals within populations is widespread. Often diet differences among individuals are attributable to obvious differences among individuals such as age, sex, or morphology. However, growing evidence suggests that individual diet variation is also common among seemingly identical individuals within populations. This phenomenon has been termed individual diet specialization. Individual diet specialization has been documented across a variety of taxa and biomes and theory suggests that diet specialization can potentially alter the structure and strength of predator-prey interactions. This raises two important questions: 1) What are the causes of individual diet specialization?, and 2) What are the potential consequences of diet specialization for populations and communities? In this dissertation, I attempt to address these two questions by combining

mathematical theory, the novel application of statistical methods, and field and laboratory experiments with the intertidal whelk, *Nucella ostrina*.

A potential ultimate cause of variation among individuals is disruptive selection in which natural selection favors individuals with more extreme trait values over individuals with intermediate trait values. Theory has suggested that the availability of alternative resources and intraspecific competition for those resources can drive disruptive selection in consumers and lead to increased diet variation. However, this theory makes several ecologically unrealistic assumptions. In particular, this theory assumes that consumers have linear functional responses and that the trait of the consumer under selection only influences the consumer's attack rates on resources. In Chapter 2, I alleviate these assumptions and show that nonlinear functional responses and traits influencing multiple functional response parameters simultaneously can influence the strength and likelihood of disruptive selection. My results suggest the characteristics of consumers in which disruptive selection in resource-use traits may occur and diet specialization through this mechanism may be most likely.

To empirically evaluate hypotheses on the causes and consequences of individual diet specialization, we need to be able to accurately quantify diet specialization. In Chapter 3, I apply Bayesian hierarchical models to the problem of estimating diet specialization and compare the performance of the Bayesian hierarchical models to currently used methods for estimating diet specialization. Currently used methods infer individual prey preferences using the observed proportion of prey in individuals' diets whereas the Bayesian hierarchical models instead estimate these proportions. I find that the currently used approach tends to overestimate diet specialization compared to the Bayesian hierarchical approach. This is especially the case when sample sizes per individual are low or heterogeneous. In addition, the Bayesian hierarchical approach provides estimates of prey proportions, their variability, and the uncertainty on these estimates in ways that are inaccessible to current methods. These results suggest that the Bayesian hierarchical method can provide an improved method for quantifying diet specialization.

In Chapter 4, I present the results from a field caging experiment examining the proximate ecological mechanisms determining individual diet specialization and its consequences in the intertidal whelk, *Nucella ostrina*. Many of the hypotheses on the ecological causes of diet specialization assume that individuals differ from one another in their prey preferences. However, these hypotheses ignore the potential influence of stochasticity in the foraging process in generating diet variation among individuals. The results of this chapter suggest that changes in the magnitude of diet variation with changes in prey community composition in *Nucella ostrina* can largely be explained by stochastic foraging by individuals with shared prey preferences. In this chapter, I also estimate the consequences of this diet variation for estimates of predator feeding rates through nonlinear averaging (Jensen's inequality) of predator attack rates. The results suggest that nonlinear averaging alters the perceived strength of predator-prey interactions in this system providing one of the first empirical estimates of the potential consequences of diet variation.

Overall, my dissertation provides several insights into the potential causes of diet specialization, provides one of the first empirical estimates of a possibly widespread consequence of diet specialization for populations and communities, and suggests improved statistical methodology for quantifying diet specialization. I believe that this dissertation will lead to a critical assessment of definitions of individual diet specialization, provide guidance towards systems in which diet specialization is the most likely to occur, and encourage further empirical research estimating the effects of diet specialization on populations and communities.

Candidate Causes, Consequences, and Estimation of Individual Diet Specialization

by

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Kyle E. Coblentz, Author

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Dr. Mark Novak assisted with study design and the writing of Chapters 3 and 4. Dr. Adam Rosenblatt provided the American Alligator data analyzed in Chapter 3. Stephanie Merhoff gathered the whelk handling time data used in Chapter 4.

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I dedicate this work to my Great Grandparents the Reverend Claude L. McComas and Jean McComas. I wish you were here.

Yea, though I walk through the valley of the shadow of death, I will fear no evil: for thou art with me; thy rod and thy staff they comfort me.

Thou preparest a table before me in the presence of mine enemies: thou anointest my head with oil; my cup runneth over.

Surely goodness and mercy shall follow me all the days of my life.

Candidate Causes, Consequences, and Estimation of Individual Diet Specialization

1 General Introduction

Variation among individuals is ubiquitous. Evolutionary biologists have long recognized the importance of this variation, as heritable differences among individuals provides the raw material upon which natural selection operates. Similarly, ecologists have long recognized the importance of differences among individuals due to factors such as age and size. However, recent quantification of intraspecific variation has shown widespread intraspecific variation in a variety ecologically relevant traits (Araújo et al., 2011; Bolnick et al., 2003; Violle et al., 2012). Furthermore, theoretical and empirical studies have shown that this variation can have a wide variety of effects on ecological processes such as species interactions and coexistence (Gibert and Brassil, 2014; Hart et al., 2016; Schreiber et al., 2011), food web structure (Araújo et al., 2008; Gibert and DeLong, 2017) , the stability of populations to perturbations(Hughes et al., 2008; Schindler et al., 2010), and eco-evolutionary dynamics (Patel and Schreiber, 2015; Schreiber et al., 2011). In fact, recent meta-analyses have shown that the ecological effects of differences among individuals within a species can have an even greater ecological effect than the differences exhibited among species (Des Roches et al., 2018; Raffard et al., 2018). These realizations have led to a quickly growing body of literature seeking to understand the processes generating and maintaining intraspecific variation and the effects of this variation from populations to ecosystems.

One form of intraspecific variation that has been found to be widespread and is thought to have important implications for the dynamics of populations and communities is individual diet specialization (Araújo et al., 2011; Bolnick et al., 2003). Individual diet specialization occurs when seemingly identical individuals select different subsets of the population's diet despite having the same resources available (Bolnick et al., 2002). This phenomenon has been documented across a variety of invertebrate and vertebrate taxa in terrestrial, freshwater, and marine systems and thus appears to widespread in nature (Araújo et al., 2011; Bolnick et al., 2003). Furthermore, theory suggests that individual diet specialization has the potential to alter the strength of predator-prey interactions (Bolnick et al., 2011; Patel and Schreiber, 2015; Schreiber et al., 2011), the topology and dynamics of ecological networks (Araújo et al., 2008; Bolnick et al., 2011), and can drive eco-evolutionary dynamics (Patel and Schreiber, 2015; Schreiber et al., 2011). Despite the apparent pervasiveness of diet specialization and its potential effects, the factors determining the likelihood and strength of diet specialization are still unclear and empirical measurements of the effects of diet specialization are still lacking.

Many of the hypotheses used to explain changes in the magnitude of diet specialization are drawn from optimal foraging theory (Emlen, 1966; Stephens and Krebs, 1986). These hypotheses assume that individuals differ in their rank preferences for prey and evaluate how variation among individuals in diets should respond given the assumed differences in preferences and changes in prey abundances due to ecological factors (Araújo et al., 2011; Svanbäck and Bolnick, 2005). Although optimal foraging theory has proved useful in explaining diet specialization in some systems (Bolnick, 2004; Svänback and Bolnick, 2007; Tinker et al., 2012), the focus on optimal foraging ignores potential alternative mechanisms that can generate diet differences among individuals. Furthermore, optimal foraging alone cannot explain why individuals differ in rank preferences for prey in the first place. For example, it is possible that in some systems individuals become specialized due to past experience with prey through learning or ingestive conditioning and would remain specialized despite changes in prey abundances (Hall et al., 1982; Tinker et al., 2009). Individuals can also vary in rank preferences for a variety reasons such as differences in prey handling times, search efficiencies, or the criteria individuals are attempting to optimize, yet these underlying causes of differences among individuals are typically unknown (Araújo et al., 2011; Stephens and Krebs, 1986). Altogether, these considerations suggest that our understanding of the causes of diet specialization and why diet specialization might be so widespread is still in its infancy.

Theoretical studies of intraspecific variation and diet specialization have shown that explicitly considering differences among individuals can significantly alter the predictions of theory relative to the typical case of assuming that all individuals are identical or can be represented by mean parameters (Doebeli, 1996; Okuyama, 2008; Schreiber et al., 2011). However, this may not always be the case. It is entirely possible that intraspecific variation may be common, yet is of little consequence in most systems. For example, the general magnitude of variation may be low enough that the use of means is entirely justified and the effect of intraspecific variation is small (Bolnick et al., 2011). It is currently impossible to evaluate the importance of individual variation because we lack empirical measurements its consequences.

My goal in this dissertation was to investigate both the causes and consequences of individual diet specialization and thus fill some of the gaps in our current understanding. Specifically, I developed mathematical theory on potential causes for differences in prey preferences among individuals, applied statistical models to improve our ability to quantify diet specialization, provided empirical evidence for a novel proximate mechanism for variation among individuals, and provided one of the first empirical measurements of a potentially widespread consequence of diet specialization.

One potential explanation for the existence of individual diet specialization is that individuals differ in their resource preferences due to cryptic variation in traits related to resource use or behavior (Araújo et al., 2011; Bolnick et al., 2003). A potential ultimate cause for these individual differences is that they are the product of disruptive selection on consumer populations (Bolnick et al., 2003; Nosil, 2012; Schluter, 2000). Disruptive selection has long been of theoretical interest both evolutionarily and ecologically due to its ability to promote variation within populations and its potential role in speciation (Dieckmann and Doebeli, 1999; Doebeli, 2011; Rueffler et al., 2006; Smith, 1962). However, this body of theory makes several ecologically unrealistic assumptions. In particular, current theory assumes that consumers exhibit linear functional responses on their resources and that consumer traits only influence consumer attack rates. In Chapter 2, I alleviate these assumptions and examine how the parameters of nonlinear functional responses and correlations among the parameters influence the strength and likelihood of disruptive selection. My results suggest the ecological conditions most amenable to disruptive selection and thus the systems in which diet specialization generated through disruptive selection is most likely.

To study diet specialization empirically, we need to be able to accurately quantify it. Typically, individual diet specialization is quantified by comparing the diet preferences of individuals to the preferences of other individuals within the population or to the overall population preference across individuals (Araújo et al., 2008; Bolnick et al., 2002). Current methods equate the observed proportions of each prey type in individual's diets directly to the preferences of individuals (Araújo et al., 2008; Bolnick et al., 2003). This estimate of prey preference is equivalent to the maximum likelihood estimate of the proportions of prey in individual's diets. However, these estimates can be severely biased when sample sizes per individual are low which is a common feature of diet data. In Chapter 3, I compare this currently used method to a Bayesian hierarchical method that estimates the proportions of each prey type in individual's diets rather than using the observed proportions. Through simulated data and the analysis of diet data from American Alligators (*Alligator mississippiensis*) and an intertidal whelk (*Vasula (= Thais) melones*), I find that currently used methods consistently overestimate diet specialization relative to the Bayesian hierarchical approach. Furthermore, the Bayesian hierarchical approach provides estimates of diets, their variation, and the uncertainty of these estimates across scales in ways that are not possible with currently used methods. In general, these results suggest that the Bayesian hierarchical approach for quantifying diet specialization can provide more accurate and robust estimates of diet specialization.

Lastly, in Chapter 4, I use an empirical field study to investigate the proximate ecological mechanisms leading to diet specialization in an intertidal whelk, *Nucella ostrina*, and the effects of diet specialization on the feeding rates of *N. ostrina* through Jensen's inequality. Most hypotheses on the causes diet specialization assume that the observed differences among individuals in diet are due to differences among individuals in diet preferences (Araújo et al., 2011; Bolnick et al., 2003; Svanbäck and Bolnick, 2005). However, less appreciated is the fact that the stochastic nature of the foraging process should also generate differences in diets among individuals even if those individuals share the same prey preferences and experience the same prey availability. Using a caging experiment in the Oregon rocky intertidal, I provide evidence that stochastic foraging among individuals with shared prey preferences provides a better explanation of diet variation in this system than a hypothesis derived from optimal foraging theory. Furthermore, I use the data gathered during the experiment to estimate individual attack rates and the effects of attack rate variation on the perceived strength of predator-prey interactions through Jensen's inequality. Theory predicts variation in attack rates coupled with nonlinear functional responses should weaken predator-prey interactions relative to the case in which there were no variation and all individuals exhibited the mean attack rate (Bolnick et al., 2011). My data provide support for this theory and also suggest that individual variation can interact with other types of variation, such as spatial variation, leading to even greater effects of variation through Jensen's inequality.

2 Nonlinear functional responses and ecological pleiotropy alter the strength of disruptive selection in consumers

Abstract

Much of the theory on disruptive selection has focused on selection in generalist consumers caused by ecological opportunity through the availability of alternative resources and intraspecific competition for those resources. This theory, however, makes several ecologically unrealistic assumptions. First, it assumes consumers have a linear, resource-dependent functional response, ignoring well-documented effects of resource handling times and consumer dependence. Second, it assumes the trait under selection only influences the per-capita attack rates of the consumer, ignoring other effects of the trait that may influence feeding rates and hence, fitness. Here, I develop a one consumer-two resource model to investigate how nonlinear functional responses and ecological pleiotropy (traits with multiple simultaneous ecological effects) influence the strength and likelihood of disruptive selection. I find that handling times and interference among consumers are capable of altering disruptive selection by changing feeding rates differentially across consumer phenotypes. In particular, handling times decrease the strength and likelihood of disruptive selection while the effects of interference depend on the mechanism through which interference occurs. The effects of handling times and

interference, however, depend on whether and how ecological pleiotropy causes correlations between handling times or interference rates and attack rates. Overall, my results suggest that features underlying functional responses of consumers and the relationships among those features determine the likelihood and strength of disruptive selection. In particular, disruptive selection should be strongest in generalist populations with individuals who experience lower handling times and interference rates on the resources for which their attack rates are highest.

2.1 Introduction

Disruptive selection, a process in which natural selection favors individuals with more extreme phenotypes over individuals with intermediate phenotypes, plays important roles in evolution and ecology. Evolutionarily, disruptive selection can cause and maintain genetic and phenotypic variation within populations and can drive speciation and adaptive diversification (Dieckmann and Doebeli, 1999; Doebeli, 2011; Rueffler et al., 2006; Smith, 1962). Ecologically, the intraspecific variation generated by disruptive selection can alter the interactions among species, their coexistence, and their functioning in ecosytems (Barbour et al., 2016; Bolnick et al., 2011; Gibert and Brassil, 2014; Gibert and DeLong, 2017; Hart et al., 2016; Hughes et al., 2008; Schreiber et al., 2011; Svanbäck et al., 2015).

Of the mechanisms generating disruptive selection, much of our knowledge comes from disruptive selection on resource-use traits in generalist consumers. Generally, disruptive selection on resource-use traits is thought to be a product of ecological opportunity through the availability of alternative resources, and intraspecific competition for those resources (Abrams et al., 2008; Nosil, 2012; Schluter, 2000). First, the availability of alternative resources provides a basis for fitness differences among individuals. If individuals with different traits are better able to use different resources, then individuals with phenotypes better matched to available resources will have greater fitness than individuals with intermediate phenotypes. If the mean trait of the consumer population lies between the optima for using the different available resources, disruptive selection will occur as individuals with more extreme phenotypes will have greater fitness than intermediate individuals. Intraspecific competition is then capable of stabilizing this form of disruptive selection by causing the selection to be frequency dependent. Given that different trait values affect individuals' abilities to use different resources, the most common phenotypes will reduce the abundance of their associated resources to the greatest extent. The reduced availability of resources then drives higher rates of intraspecific competition in those common phenotypes. Consumers with less common phenotypes reduce their associated resources to a lesser extent and, all else being equal, experience less competition. The resultant increase in fitness for less common phenotypes leads to negative frequency-dependent disruptive selection because the relative fitness of phenotypes is dependent on their relative abundance in the population (Dieckmann and Doebeli, 1999; Smith, 1962).

Several studies have provided convincing empirical evidence that ecological opportunity through alternative resources and intraspecific competition cause disruptive selection in both the laboratory and field (Bolnick, 2001, 2004; Hendry et al., 2009; Martin and Pfennig, 2009). Yet, previous studies also suggest that the existence and strength of disruptive selection through these mechanisms are dependent on ecological features determining the relative availability of resources and the strength of intraspecific competition. For example, in a survey of fitness landscapes across populations of three-spined stickleback (*Gasterosteus aculeatus*), Bolnick and Lau (2008) showed that differences among populations in the existence and strength of disruptive selection was partially attributable differences in ecological opportunity among populations through differences in the relative availability of benthic versus limnetic habitat. In another survey of fitness landscapes, Martin and Pfennig (2012), showed that the strength of disruptive selection in spadefoot toad tadpoles (*Spea multiplicata*) was associated with the density of conspecifics, a proxy for the strength of intraspecific competition across populations. Together these results suggest that predicting the strength and occurrence of disruptive selection in consumers requires theory incorporating common ecological factors likely to influence ecological opportunity and intraspecific competition.

One factor likely to influence both ecological opportunity and the strength of intraspecific competition is the strength of the underlying consumer-resource interactions (Abrams et al., 2008; Jones and Post, 2013, 2016). For example, for intraspecific competition to influence disruptive selection consumers must deplete resources to an extent that it alters the fitness landscape across phenotypes, but, if the consumer-resource interactions are weak, prey depletion will be minimal and the resulting strength of disruptive selection will be weak (Abrams et al., 2008; Jones and Post, 2013, 2016). Alternatively, if species interactions are strong, consumers can lead resources to local extinction, causing a decrease in ecological opportunity, again, altering strength of disruptive selection (Abrams et al., 2008; Jones and Post, 2013, 2016). One determinant of the strength of consumer-resource interactions largely ignored in current theory on disruptive selection in generalists is the consumer functional response. The consumer functional response defines the relationship between the densities of interacting species and consumer feeding rates and therefore is directly related to the strength of consumer-resource interactions and likely to influence disruptive selection. The vast majority of theory on disruptive selection in consumers assumes that the consumers have a linear, resource dependent functional response (Abrams et al., 2008; Ackermann and Doebeli, 2004; Dieckmann and Doebeli, 1999; Doebeli, 1978; Lawlor and Smith, 1976; MacArthur, 1972). However, linear functional responses are known to be rare (Jeschke et al., 2004). Nonlinearities in functional responses are the product of nearly ubiquitous properties of consumer-resource interactions such as handling times and consumer interference or facilitation (Abrams and Ginzburg, 2000; DeLong and Vasseur, 2011; Holling, 1959; Novak et al., 2017). Given the widespread nature of nonlinear functional responses and their effects on the strength of consumer-resource interactions, incorporating nonlinear functional responses into theory on disruptive selection in consumers may provide some insight into the characteristics of consumers most likely to exhibit disruptive selection.

Incorporating nonlinear functional responses into models of disruptive selection also provides an opportunity to address another assumption of most models: the traits of individuals only influence their per capita attack rates on resources.

It is more likely that traits influencing an individual's attack rates also influence other parameters of the functional response (i.e. handling and interference) causing parameters to be correlated across individuals. The presence of such correlated ecological trait effects has been termed 'ecological pleiotropy' (DeLong, 2017; DeLong and Gibert, 2016; Strauss and Irwin, 2004). Ecologically pleiotropic trait effects are likely to be common in functional responses. For example, a study of protists has shown attack rates, handling times, and interference rates to all covary with one another (DeLong, 2017). In another study, body size has been shown to have allometric relationships with both attack rates and handling times of consumers, at least among species (Vucic-Pestic et al., 2009). Although studies have shown that ecologically pleiotropic trait effects can alter population dynamics (DeLong, 2017) and have examined the evolutionary effects of pleiotropy between functional and numerical responses (Schreiber et al., 2018), it remains unclear how ecological pleiotropy may constrain or promote selection on underlying traits.

Here, I use a one consumer-two resource model to investigate how the parameters of nonlinear functional responses – attack rates, handling times, and interference rates – and potential correlations among them arising from an ecologically pleiotropic trait, influence the existence and strength of disruptive selection. My analyses indicate that nonlinear functional responses alter disruptive selection in ways that are dependent on the correlations between attack rates and handling times or attack rates and interference rates. This suggests that nonlinear functional responses and the presence of ecological pleiotropy can alter disruptive selection generated by intraspecific competition and ecological opportunity, offering a potential explanation for variation in the existence and strength of disruptive selection within and among systems.

2.2 Methods

Below, I first introduce the general one consumer-two resource model used to investigate the relationships between nonlinear functional responses, ecological pleiotropy, and the strength of disruptive selection. I then explain the methods used to analyze the model. Lastly, I introduce the particular nonlinear functional responses investigated and explain how I modeled ecological pleiotropy among functional response parameters.

2.2.1 The General Model

To investigate the effects of nonlinear functional responses and pleiotropy on the strength and likelihood of disruptive selection, I extended a one consumer-two resource model developed by Schreiber et al. (2011) to include nonlinear functional responses. The model begins with the assumption that the consumer population has a quantitative trait, x, that is normally distributed with mean, $\bar{x}$, and variance, σ^2, such that the distribution of x in the population, $p(x, \bar{x})$, is described by,

$$p(x, \bar{x}) = \frac{1}{\sqrt{2\pi\sigma^2}}\mathbf{exp}[-\frac{(x-\bar{x})^2}{2\sigma^2}]. \tag{2.1}$$

Furthermore, I assume that the phenotypic variance of the trait, σ^2, consists of an environmental component, σ_E^2, and a heritable genetic component, σ_G^2, and that the heritable genetic component is positive. The value of an individual's trait, x, is assumed to determine its attack rates, $\alpha_i(x)$, on the two resources, R_i $(i = 1, 2)$, respectively. The maximum attack rate of an individual on the ith resource, $\alpha_{i,max}$, occurs at a trait value of $x = \theta_i$. The attack rate then decreases as the trait value moves away from θ_i in a Gaussian manner,

$$\alpha_i(x) = \alpha_{i,max}\mathbf{exp}[-\frac{(x-\theta_i)^2}{2\tau_i^2}], \tag{2.2}$$

with the rate of decrease determined by τ_i^2. Letting $f_i(R_1, R_2, C, x)$ denote the consumer's functional response on resource i which depends on both resource densities, the trait x, and the consumer's density in models including consumer interference, the mean fitness of the consumer population, $\bar{\omega}(R_1, R_2, C, \bar{x})$, is:

$$\bar{\omega}(R_1, R_2, C, \bar{x}) = \int_{-\infty}^{\infty} \sum_{i=1}^{2} [e_i f_i(R_1, R_2, C, x)] p(x, \bar{x}) dx - m, \tag{2.3}$$

where m is the per capita mortality rate of the consumer and e_i is a linear conversion efficiency of resource i into consumers. Assuming logistic growth in the resources, the dynamics of the consumer and resource populations are:

$$\frac{dR_i}{dt} = r_i R_i \left(1 - \frac{R_i}{K_i}\right) - C \int_{-\infty}^{\infty} f_i(R_1, R_2, C, x) p(x, \bar{x}) dx, \tag{2.4}$$

$$\frac{dC}{dt} = C\bar{\omega}(R_1, R_2, C, \bar{x}). \tag{2.5}$$

where r_i is the intrinsic growth rate of resource i and K_i is its carrying capacity.

Assuming that the consumer's trait remains normally distributed and that the variance of the consumer's trait remains constant and is not too large, the evolutionary dynamics of the mean of the consumer's trait are described by:

$$\frac{d\bar{x}}{dt} = \sigma_G^2 \frac{d\bar{\omega}(R_1, R_2, C, \bar{x})}{d\bar{x}}, \tag{2.6}$$

where σ_G^2 is the genetic component of the phenotypic variance of the consumer's trait and ${}^{d\bar{\omega}(R_1, R_2, C, \bar{x})}\!/_{d\bar{x}}$ is the fitness gradient (Abrams et al., 1993; Iwasa et al., 1991; Lande, 1976). The fitness gradient describes directional selection on the mean of the consumer's trait. At the ecological and evolutionary equilibrium of the system, there is no directional selection on the consumer's trait and the fitness gradient is zero by definition. The resultant equilibrium is either a fitness maximum or a fitness minimum which can be determined from the curvature of the fitness function at the equilibrium given by the second derivative of the mean fitness with respect to consumer's mean trait evaluated at the equilibrium,

$$\left.\frac{d^2\bar{\omega}(R_1^*, R_2^*, C^*, \bar{x})}{d\bar{x}^2}\right|_{\bar{x}^*}, \tag{2.7}$$

where the asterisks denote equilibrium values. If the curvature of the fitness function evaluated at the equilibrium is negative, the equilibrium is a fitness maximum and there is stabilizing selection on the trait. If the curvature of the fitness function is positive, the equilibrium is a fitness minimum and there is disruptive selection on the trait. The magnitude of the curvature of the fitness function provides a relative measure of the strength of selection. Thus, the curvature of the fitness function can be used to determine the parameters for which stabilizing or disruptive selection occur and the strength of that selection.

2.2.2 Measuring Selection and Methods of Analysis

Here I consider a symmetric version of the above model in which all of the resource specific parameters are equal (e.g. $r_1 = r_2$, $K_1 = K_2$, etc.) except the θ_i's, and the θ_i's are symmetric about zero (i.e. $\theta_2 = -\theta_1$). Given the symmetric model, if the ecological dynamics reach a stable steady state, the evolutionary dynamics reach an equilibrium at $\bar{x} = 0$. The curvature of the fitness function at $\bar{x} = 0$ can then be used to determine the strength of selection and whether it is stabilizing or disruptive.

To determine how nonlinear functional responses and ecological pleiotropy alter the likelihood of disruptive selection, I compared numerical results of the model on the parameters at which selection changed from stabilizing to disruptive selection to analytical results derived by Schreiber et al. (2011). Using a symmetric version of the model with linear consumer functional responses, Schreiber et al. (2011) showed that disruptive selection occurs when,

$$\theta^2 > \sigma^2 + \tau^2. \tag{2.8}$$

Therefore, if the consumers exhibited a linear functional response, selection switches from stabilizing to disruptive selection when $\theta^2 = \sigma^2 + \tau^2$. I use this as a baseline to examine how nonlinear functional responses and ecological pleiotropy change the likelihood of disruptive selection relative to the case of consumers with linear functional responses. Specifically, I alter the value of θ while keeping σ and τ constant, although results are similar when varying σ and τ.

To evaluate how changes in the parameter values of nonlinear functional responses alter the strength and likelihood of disruptive selection, I performed numerical analyses of the model in Mathematica (v. 11.0.1.0). I restricted my analyses to combinations of parameter values for which the consumer-resource interactions reached a fixed point equilibrium (i.e. did not exhibit cycles). After determining that the consumer-resource dynamics were at a fixed point using linear stability analysis, I varied the parameters of interest and calculated the curvature of the fitness function to determine whether selection was disruptive or stabilizing and the strength of selection. Although analytical results for the model were not possible, the results presented below were qualitatively similar across all of the different parameter values investigated that met the above criteria.

2.2.3 Nonlinear Functional Response Due to Handling Times

To determine how handling times influence the strength and likelihood of disruptive selection, I substituted a multispecies Holling Type-II functional response (Holling, 1959),

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x)R_i}{1 + \sum_{i=1}^{2} \alpha_i(x)\eta_i R_i}, \tag{2.9}$$

into equations 3–4, where η_i is the handling time of the consumer when feeding on resource i. I first investigated how handling times in general influenced the likelihood and strength of disruptive selection by assuming that the handling times for both resources were equal (i.e. $\eta_1 = \eta_2$). I then altered the magnitude of the handling times and examined the resulting effects on the likelihood strength of disruptive selection.

2.2.4 Consumer-dependent Functional Responses

Although there are several ‘standard’ functional responses models that include interference, all were developed for a specialist consumer consuming a single resource (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975; Hassel and Varley, 1969). To examine the effects of interference on the likelihood and strength of disruptive selection in the one consumer-two resource model considered here, I extended two of the more mechanistic functional response models including interference – the Beddington-DeAngelis and Crowley-Martin functional responses – to more than one resource (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975).

The Beddington-DeAngelis and Crowley-Martin functional responses make different assumptions about how interference effects consumer feeding rates, and therefore could lead to differences in how they predict interference to alter the likelihood and strength of disruptive selection (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975). The Beddington-DeAngelis functional response model assumes that consumers interfere with one another at a rate, γ, and that interference decreases the time available for searching for resources. These assumptions lead to the following functional response for two resources,

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x) R_i}{1 + \sum_{i=1}^{2} \alpha_i(x) \eta_i R_i + \gamma C}. \tag{2.10}$$

The Crowley-Martin functional response model extends the Beddington-DeAngelis functional response model by assuming that consumers also interfere while handling resources (Crowley and Martin, 1989). Under these assumptions, with a interference rate, λ, the Crowley-Martin functional response extended to two resources is,

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x) R_i}{1 + \sum_{i=1}^{2} \alpha_i(x) \eta_i R_i + \sum_{i=1}^{2} \alpha_i(x) \eta_i \lambda R_i C + \lambda C}. \tag{2.11}$$

Given these two functional responses, I examined how interference in general changed the likelihood and strength of disruptive selection by altering the magnitude of interference and examining the resultant effects.

2.2.5 Ecological Pleiotropy

To determine how an ecologically pleiotropic trait controlling both attack rates and handling times or attack rates and interference rates may influence the likelihood and strength of disruptive selection, I assumed that ecological pleiotropy causes attack rates and handling times or interference rates to covary.

For ecological pleiotropy affecting both attack rates and handling times, I modeled the effects of ecological plieotropy by making the handling times of each resource a linear function of the trait-dependent attack rates,

$$\eta_i(\alpha_i(x)) = \eta_{i,min/max} + \eta_{i,slope} \times \alpha_i(x), \tag{2.12}$$

where $\eta_i(\alpha_i(x))$ is the handling time of an individual on resource i with attack rate $\alpha_i(x)$, $\eta_{i,min/max}$ is the handling time of an individual on resource i when the individual has an attack rate of zero on resource i, and $\eta_{i,slope}$ is the slope of the relationship exhibited across individuals with different trait values between the attack rates and handling times on resource i.

To model the effects of ecological pleiotropy affecting both attack rates and interference rates, I made the interference rate a linear function of the total attack rate of an individual on resources combined. Letting y represent either type of interference examined (i.e. γ for the Beddington-DeAngelis functional response or λ for the Crowley-Martin functional response), I modeled the correlation between interference and attack rates as,

$$y(\alpha_1(x), \alpha_2(x)) = y_{min,max} + y_{slope} \times (\alpha_1(x) + \alpha_2(x)) \tag{2.13}$$

where $y(\alpha_1(x), \alpha_2(x))$ is the interference rate of an individual with attack rates $\alpha_1(x)$ and $\alpha_2(x)$, $y_{min,max}$ is the interference rate that would be experienced if both attack rates were zero, and y_{slope} is the slope of the relationship between the total attack rate interference rates across individuals having different trait values.

I considered both positive and negative correlations between attack rates and handling times and attack rates and interference rates. For positive correlations, $\eta_{i,min/max}$ and $y_{min/max}$ are minimums and $\eta_{i,slope}$ and y_{slope} are positive. For negative correlations, $\eta_{i,min/max}$ and $y_{min/max}$ are maximums and $\eta_{i,slope}$ and y_{slope} are negative. To examine the effects of the correlations between attack rates and handling times or attack rates and interference rates, I altered the strength of the relationship by increasing the magnitude of the slope parameters with a constant maximum or minimum and examined the resulting changes in the likelihood and strength of disruptive selection.

2.3 Results

2.3.1 Handling Times

When there is no correlation between attack rates and handling times, analysis of the model with a multispecies Holling Type-II functional response shows that increasing handling times reduce the parameter space over which disruptive selection occurs relative to consumers with a linear functional response (compare the dashed and solid lines in Figure 2.1A). Increasing handling times also reduce the strength of disruptive selection (Figure 2.1A). This decrease is due to relative changes in feeding rates across the consumer's phenotypes (Figure 2.1B). In particular, as handling times increase, individuals with the highest attack rates show a decrease in feeding rates while individuals with lower attack rates show an increase in feeding rates (Figure 2.1B). This reduces the steepness of the fitness function at the fitness minimum thereby weakening disruptive selection. The relative changes in feeding rates among individuals with different phenotypes are the product of the interaction between attack rates, the saturating effect of handling times, and consequent changes in the equilibrium densities of resources (Figure 2.1B-D). As handling times increase, individuals with the highest attack rates saturate at increasingly lower resource densities (Figure 2.1C). The reduced feeding rates of individuals with the highest attack rates simultaneously increases equilibrium resource densities (Figure 2.1C-D). Individuals with low attack rates experience less saturation from handling times and thus show an increase in feeding rates due to the increase in equilibrium densities of the resources (Figure 2.1E).

The effects of handling time on the likelihood and strength of disruptive selection depend on whether ecological pleiotropy causes a positive or negative correlation between attack rates and handling times. If handling times and attack rates are positively correlated, then the parameter space over which disruptive selection occurs and the strength of disruptive selection decrease as the strength of the relationship increases (Figure 2.2A). In contrast, if handling times and attack rates are negatively correlated, the correlation weakens the effect of handling times on the likelihood and strength of disruptive selection (Figure 2.2C). Under certain parameter values, the negative correlation can increase the parameter space over which disruptive selection occurs relative to the case of linear consumer functional responses (Figure 2.2C). These effects occur because correlations between attack rates and handling times either exacerbate or alleviate the saturating effects of handling times on individuals with high attack rates. When correlations between attack rates and handling times are positive, individuals with high attack rates experience greater saturation with an increase in the strength of the correlation causing a decreasing their feeding rates and increasing the feeding rates of consumers with low attack rates (Figure 2.2B). When correlations are negative, individuals with high attack rates experience less saturation with an increase in the strength of the correlation leading to higher feeding rates and decreases in the feeding rates of individuals with low attack rates (Figure 2.2D).

2.3.2 Interference Rates

When there is no correlation between attack rates and interference rates, the effects of interference on the likelihood and strength of disruptive selection depend on the functional response considered. If interference is modeled using the Beddington-DeAngelis functional response, interference has no effect on the strength of disruptive selection (Figure 2.3A). As interference rates increase, the feeding rates across phenotypes remain constant because equilibrium resource and consumer densities change while feeding rates across phenotypes remain constant (Figure 2.3B). In contrast, if interference is modeled using the Crowley-Martin functional response, increasing interference decreases the parameter space over which disruptive selection occurs and decreases the strength of disruptive selection (Figure 2.3C). In contrast to the Beddington-DeAngelis functional response, interference interacts with the consumer's attack rates and thus phenotype in the Crowley-Martin functional response and alters feeding rates across phenotypes (Figure 2.3D).

As for handling times, the effects of interference on the likelihood and strength of disruptive selection are dependent on whether ecological pleiotropy causes correlations between attack rates and interference rates. Regardless of the functional response considered, a positive relationship between attack rate and interference leads to a decrease in the parameter space over which disruptive selection occurs and the strength of disruptive selection (Figures 2.4A,2.5A). A negative relationship between attack rates and interference leads to an increase in parameter space over which disruptive selection occurs and the strength of disruptive selection (Figures 2.4C,2.5C). These effects occur because the correlation causes the saturating effect of interference to affect consumers differently across phenotypes. For positive relationships between attack rates and interference, phenotypes with the highest attack rates experience the most saturation and reduced feeding rates, while this increases feeding rates for individuals with low attack rates because of increased equilibrium resource densities (Figures 2.4B,2.5B). For negative relationships between attack rates and interference, consumers with high attack rates experience less interference and have increased feeding rates, while consumers with low attack rates experience higher interference and lower equilibrium resource densities causing a decrease in feeding rates (Figures 2.4D,2.5D). For either functional response including interference, negative relationships between attack rates and interference are capable of increasing the parameter space in which selection is disruptive relative to linear functional responses (Figure 2.4C,2.5C).

2.4 Discussion

The mechanisms generating and maintaining disruptive selection in generalist consumers have played a large role in our theoretical understanding of disruptive selection. However, predicting the circumstances under which disruptive selection in consumers is most likely and should be strongest remains difficult as theory on the ecological mechanisms altering ecological opportunity and intraspecific competition in consumers is still being developed. Here I show that two widespread factors influencing the strength of consumer resource interactions – nonlinear functional responses and ecological pleiotropy – are capable of altering the strength and likelihood of disruptive selection in consumers. These results support previous studies asserting that the strength of consumer-resource interactions can influence disruptive selection (Abrams et al., 2008; Jones and Post, 2013, 2016) and suggest that disruptive selection is most likely in consumers whose traits not only determine their attack rates on resources but also reduce their handling times on those resources and their interference rates with other consumers.

The consumer-resource models presented here predict that disruptive selection in generalist consumers should be most common in populations in which handling times and interference are low or negatively correlated with attack rates. Confirmation of this with existing data is difficult, but some of the best known examples of disruptive selection in consumers do exhibit some of these features. For example, disruptive selection in beak size of the medium ground finch (*Geospiza fortis*) of the Galapagos Islands has been shown to be related to the ability of finches with different beak sizes to handle different sized seeds (Hendry et al., 2009; Schluter and Grant, 1984). Thus, attack rates and handling times should be negatively correlated with large-beaked individuals preferring and having lower handling times on large seeds and small-beaked individuals preferring and having lower handling times on small seeds. Another canonical example of disruptive selection is disruptive selection in several traits related to the use of benthic v. limnetic resources in three spine stickleback (Schluter, 1993). Morphological differences among individuals in resource-use traits have been shown to correlate with the feeding efficiency and growth rates of stickleback in benthic versus limnetic habitats (Schluter, 1993, 1995). How interference operates in this system is unclear, but the use of separate habitats may reduce interference by reducing the potential number of competitors or increase interference by concentrating individuals within habitats. Future empirical work should aim to more explicitly examine the relationship between consumer functional responses and natural selection. One possibility for doing so is to use comparative studies across populations or species measuring both functional responses and disruptive selection. Another possibility is to estimate the functional responses of individuals and correlate these functional responses to individual fitness proxies. Recent advances in estimating functional responses from observational data in the field (Novak et al., 2017) and the long history of estimating natural selection (Kingsolver et al., 2001; Lande and Arnold, 1983) should facilitate this effort.

The effects of handling time and interference on the strength of disruptive selection were largely dependent on whether the underlying trait was assumed to have pleiotropic effects that caused correlations between these parameters and the attack rates. The parameters describing nonlinear functional responses are likely to be correlated due to their determination by the same traits, however, the sign and strength of correlations among parameters are likely to be system specific. Some generalizations nevertheless might be possible. Optimal foraging theory, for example, suggests that individuals feeding on energetically equivalent resources should prefer the resources on which they have the lowest handling times (Stephens and Krebs, 1986). This will cause a negative correlation between attack rates and handling times among individuals (e.g. Tinker et al., 2007) which should increase the strength of disruptive selection. Positive correlations seem less likely. One possible source of this pattern could be changes in preferred resource size with consumer body size. For example, relative to mid-sized individuals, large bodied consumers may have higher attack rates on larger prey which require longer handling times, while small bodied consumers may have higher attack rates on smaller bodied resources but have higher handling times due to inefficiencies in handling resources given their size (Hassel et al., 1976).

Interference rates could have both positive or negative correlations with attack rates. For example, positive correlations have been observed in at least one protist system where both parameters were positively related to the swimming speed of the consumer (DeLong and Vasseur, 2013). However, the case could also be made that interference and attack rates should be negatively correlated. For example, attack rates, at least among species, commonly scale with body size (Berlow et al., 2009; Brose, 2010; Rall et al., 2012; Schneider et al., 2012), a trait that often confers an advantage in bouts of interference which could reduce the effects of interference on individuals with high attack rates (Rowland, 1989; Schoener, 1983). Individuals with high attack rates may also use resources more efficiently which may reduce their exposure to interference, at least in the Crowley-Martin functional response. Furthermore, individuals with high attack rates on particular resources may inhabit different habitats. Examples of this occur in several lake fish species, such as three-spined stickleback (*Gasterosteus aculeatus*) which have polymorphisms associated with using either benthic versus limnetic habitats (Lavin and McPhail, 1985; Schluter, 1995). As mentioned above, the use of different habitats may constrain the number of individuals that interfere with one another, thereby leading to an overall reduction in interference relative to the case in which all individuals use the same habitat. Conversely, individuals with high attack rates on the same resource may be concentrated within the same habitat, increasing interference. Unfortunately, data on the correlations among parameters in nonlinear functional responses are sparse, although traits that simultaneously influence multiple functional response parameters should be common.

To model the effects of mutual interference competition on consumer functional responses, I used two of the more ‘mechanistic’ functional response models including interference – the Beddington-DeAngelis and Crowley-Martin functional responses (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975). Which functional response was considered influenced the effects of interference on the strength of disruptive selection. The two functional responses differ primarily in whether or not interference occurs while consumers are handling resources. The most appropriate model for interference therefore is likely dependent on the biology of the particular system. For example, in systems with kleptoparasitism, fighting amongst consumers over already captured resources, or increased handling times in the presence of other consumers, the Crowley-Martin functional response may more appropriate (e.g. Ens and Goss-Custard, 1984; Norris and Johnstone, 1998; Smallegange et al., 2006; Zimmermann et al., 2015). In contrast, in systems where interference occurs largely separate from the handling of resources, or where time spent foraging is distinct from time spent interfering, the Beddington-DeAngelis functional response is likely to be more appropriate (e.g. Getty, 1981; Kratina et al., 2009; Pyke, 1979). Although the Crowley-Martin and Beddington-DeAngelis functional responses are sometimes unable to be distinguished statistically (Lang et al., 2012; Skalski and Gilliam, 2001; Stier and White, 2014; Zimmermann et al., 2015), the models here suggest that distinguishing among them mechanistically may be important to understand the evolutionary consequences of interference. Lastly, the functional responses used here assumed that interference rates, or their relationships with attack rates, were equal for both resources. Recent evidence has suggested that this may not be the case and that interference rates and facilitation effects may be prey-specific in nature (Novak et al., 2017). These results suggest that theory incorporating prey-specific interference rates may be needed to understand the ecological and evolutionary consequences of interference with more than one resource.

There are several potential outcomes of disruptive selection and the particular outcome may be a function of the strength of disruptive selection (Rueffler et al., 2006). Under the quantitative genetics framework, the most likely outcome of disruptive selection is an increase in the phenotypic variation of the consumer's resource-use trait. Patel and Schreiber (2015) have shown that the second derivative of the fitness function used here to measure disruptive and stabilizing selection also determines selection at the evolutionary equilibrium under the adaptive dynamics approach for modeling evolution. Under the adaptive dynamics framework, this theory would predict that evolutionary branching and speciation would occur at the fitness minimum. In general, the outcome of disruptive selection is likely to depend on system specific factors such as the underlying genetics and mating system of the population in concert with the strength of selection. For example, although ecological opportunity and intraspecific resource competition may cause disruptive selection on a trait, opposing directional or stabilizing selection on that trait from other sources, or gene flow, might overwhelm weak disruptive selection (Lande and Arnold, 1983; Nosil, 2012). Future theory explicitly examining how the strength of selection is likely to lead to different evolutionary outcomes will help to further understand how changes to the strength of disruptive selection through ecological factors are likely to manifest in nature.

Overall, my results support the assertions of Abrams et al. (2008) and Jones and Post (2013, 2016) that the strength and likelihood of disruptive selection is dependent on the strength of the underlying consumer-resource interactions. In the model presented here, the effects of nonlinear functional responses and pleiotropy are largely due to how handling resources or interference produces saturation in the feeding rates of the consumers with the highest attack rates. If saturation is increased, the consumer-resource interactions weaken resulting in weakened disruptive selection and vice versa. Abrams et al. (2008) and Jones and Post (2013, 2016), however, have predicted a unimodal relationship between the strength of consumer-resource interactions and the strength of disruptive selection. Their reasoning is that when consumer-resource interactions are very weak there is little depletion of resources, intraspecific resource competition is weak, and thus disruptive selection is weak. In contrast, when consumer-resource interactions are very strong resources associated with the most common consumer phenotypes will go locally extinct, ecological opportunity will decrease, and disruptive selection will weaken. Allowing for this effect would require extending the theory here to models with a continuous distribution of resources such as the MacArthur model which has been used widely to model disruptive selection in consumers (MacArthur, 1972). Caution should be taken in doing so. The MacArthur model with linear functional responses has been shown to have a stable global equilibrium (Chesson, 1990). Nonlinear functional responses, however, can lead to cycling in population dynamics which may alter evolutionary dynamics (Svanbäck et al., 2009). Nevertheless, the incorporation of nonlinear functional responses and pleiotropy into these models would be worthwhile.

Lastly, consumer-resource models similar to those used to examine disruptive selection have also been used to study other topics such as the coevolution of competitors and character displacement (Case, 1981; Doebeli, 1978; Roughgarden, 1976; Taper and Case, 1992). As I have shown here that nonlinear functional responses and ecological pleiotropy can alter the likelihood and strength of disruptive selection, these factors may also influence phenomena such as character displacement. Previous studies have also suggested as much. For example, Abrams (1980), has shown that nonlinear functional responses alter the strength of competition among consumers in a two consumer-two resource system. Further incorporation of nonlinear functional responses and ecological pleiotropy into evolutionary theory will provide insight into how these widespread ecological factors influence evolutionary dynamics beyond disruptive selection.

Figures

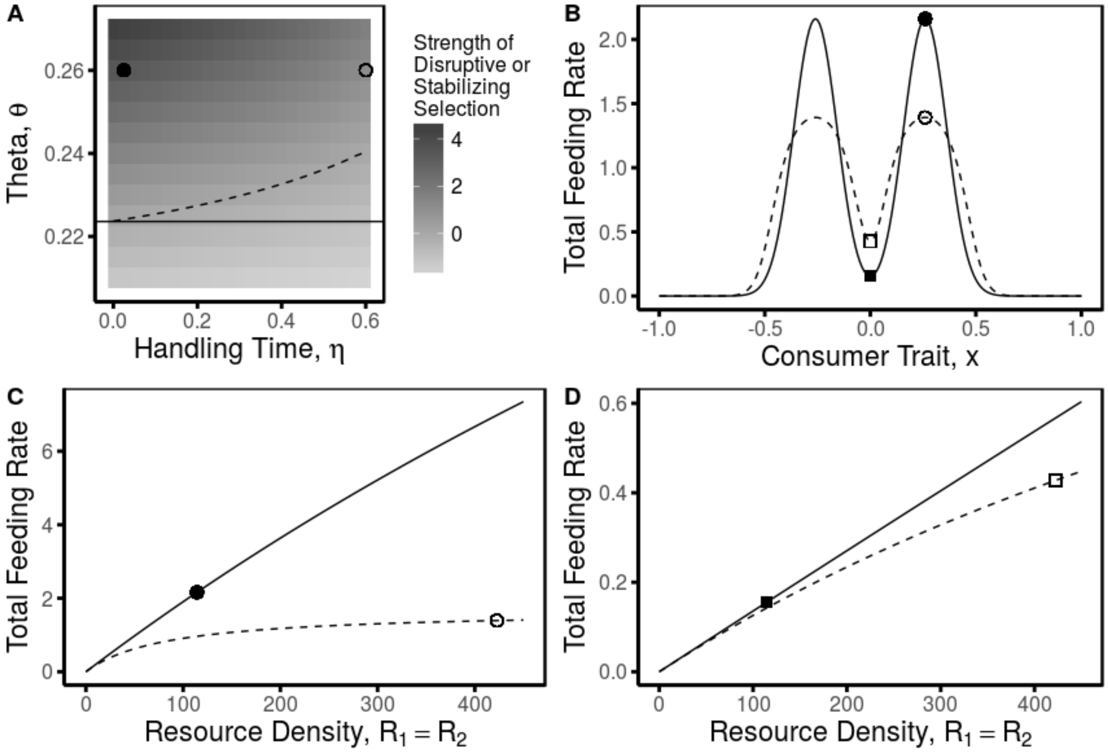

Figure 2.1: Larger handling times are associated with weaker disruptive selection (**A**). Larger handling times are also associated with a reduced parameter space over which disruptive selection occurs (above the dashed line in **A**) relative to the case in which consumers have linear functional responses (above the solid line in **A**). Handling times reduce the strength of disruptive selection by differentially affecting consumer feeding rates across the consumer's phenotypes (compare feeding rates of consumers with low handling times in **B** (solid dot in **A**, solid lines in **B-D**) to feeding rates of consumers with high handling times (open dot in **A**, dashed lines in **B-D**)). For individuals with high attack rates (dots in **B** and **C**), feeding rates decrease with higher handling times despite an increase in equilibrium resource densities due to saturation caused by handling times (**C**). Individuals with low attack rates (squares in **B** and **D**) are less affected by the saturating effects of handling times and feeding rates increase with the increasing equilibrium resource densities (**D**). These changes in feeding rates reduce the potential gain in fitness associated with disruptive selection. Parameter used in the figure are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.02, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.5$.

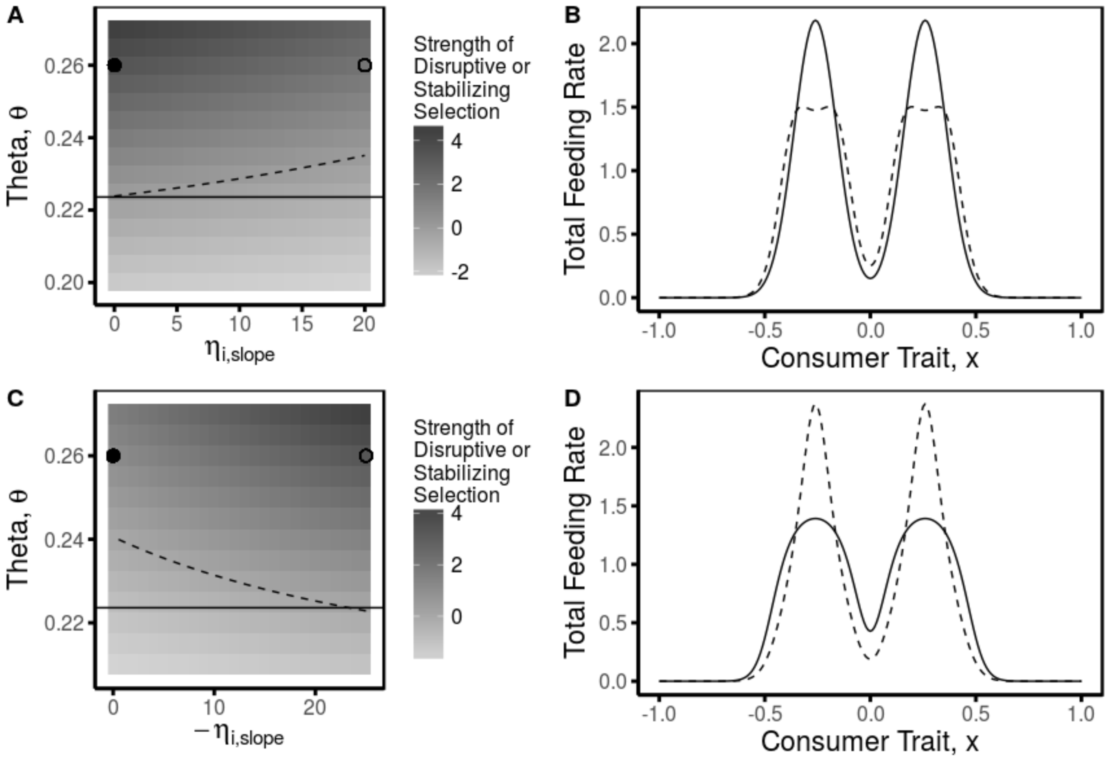

Figure 2.2: Ecological pleiotropy leading to correlations between attack rates and handling times alters the strength of disruptive selection (**A,C**). Positive correlations lead to a decrease in the strength of disruptive selection (**A**), while negative correlations lead to an increase in the strength of disruptive selection (**C**). The correlations also alter the parameter space over which disruptive selection occurs in this model (above the dashed lines in **A** and **C**) relative to the case in which consumers have linear functional responses (above the solid line in **A** and **C**). Changes in selection are due to changes across the consumer's phenotypes in feeding rates as the correlation is changed from weak (solid dot in **A** and **C**, solid line in **B** and **D**) to strong (open dot in **A** and **C**, dashed line in **B** and **D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.02, \theta_1 = -\theta_2 = 0.3, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.5$, and $\eta_{1,min} = \eta_{2,min} = 0.01$ in **A** and **B**, and $\eta_{1,max} = \eta_{2,max} = 0.4$ in **C** and **D**.

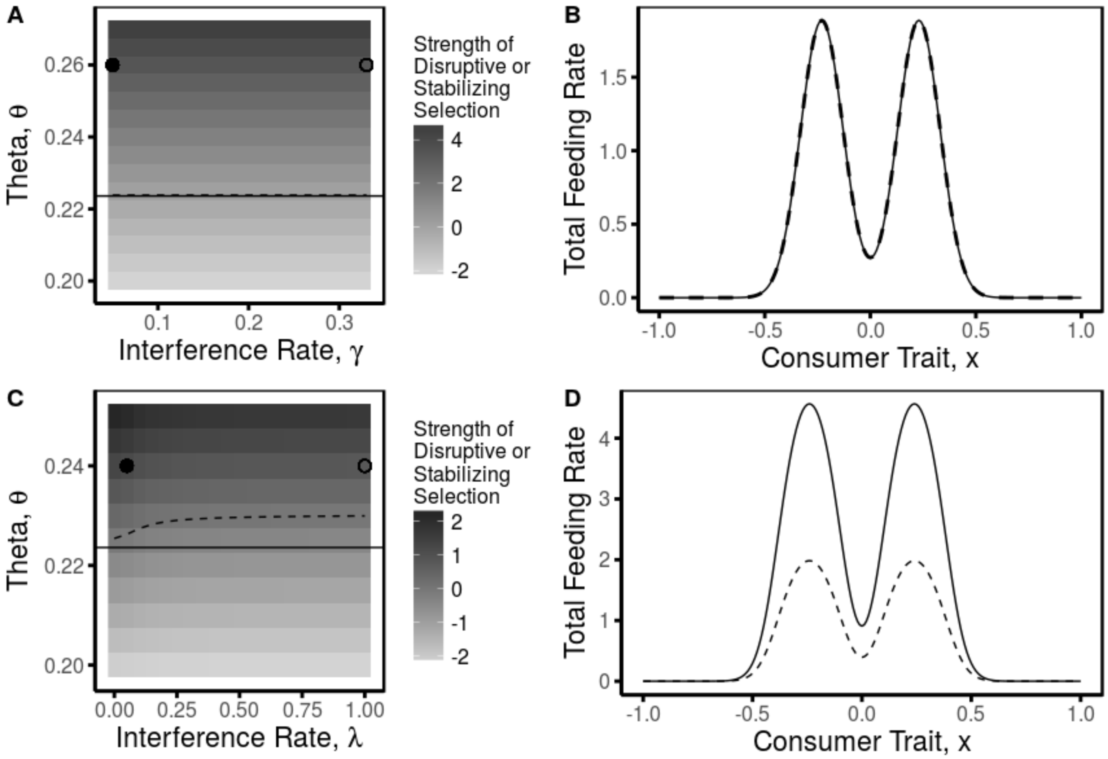

Figure 2.3: The effects of interference on the strength of disruptive selection are dependent on which functional response is considered (**A** – Beddington-DeAngelis functional response,**C** – Crowley-Martin functional response). The interference rate of the Beddington-DeAngelis functional response, (γ), has no effect on the strength of disruptive selection (**A**) and the parameter space over which disruptive selection occurs in this model (above the dashed line in **A**) compared to the case in which consumers have linear functional responses (above the solid line in **A**). This is because the interference rate but has no effect on the feeding rates of the consumers across their phenotypes (low interference: solid dot in **A**, solid line in **B**; high interference: open dot in **A**, dashed line in **B**). The interference rate of the Crowley-Martin functional response (λ) decreases the strength of disruptive selection (**C**) and parameter space over which disruptive selection occurs in this model (above the dashed line in **C**) relative to the model with linear consumer functional responses (above the solid line in **C**). The interference rate of the Crowley-Martin functional response differentially effects the feeding rates of consumers across the consumers phenotype (low interference: solid dot in **C**, solid line in **D**; high interference: open dot in **C** and dashed line in **D**). Parameter values used in the Beddington-DeAngelis figures are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.3, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.2, \eta_1 = \eta_2 = 0.01$. Parameter values used in the Crowley-Martin figures are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.1, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 100, e = 0.5, m = 0.5, \eta_1 = \eta_2 = 0.1$.

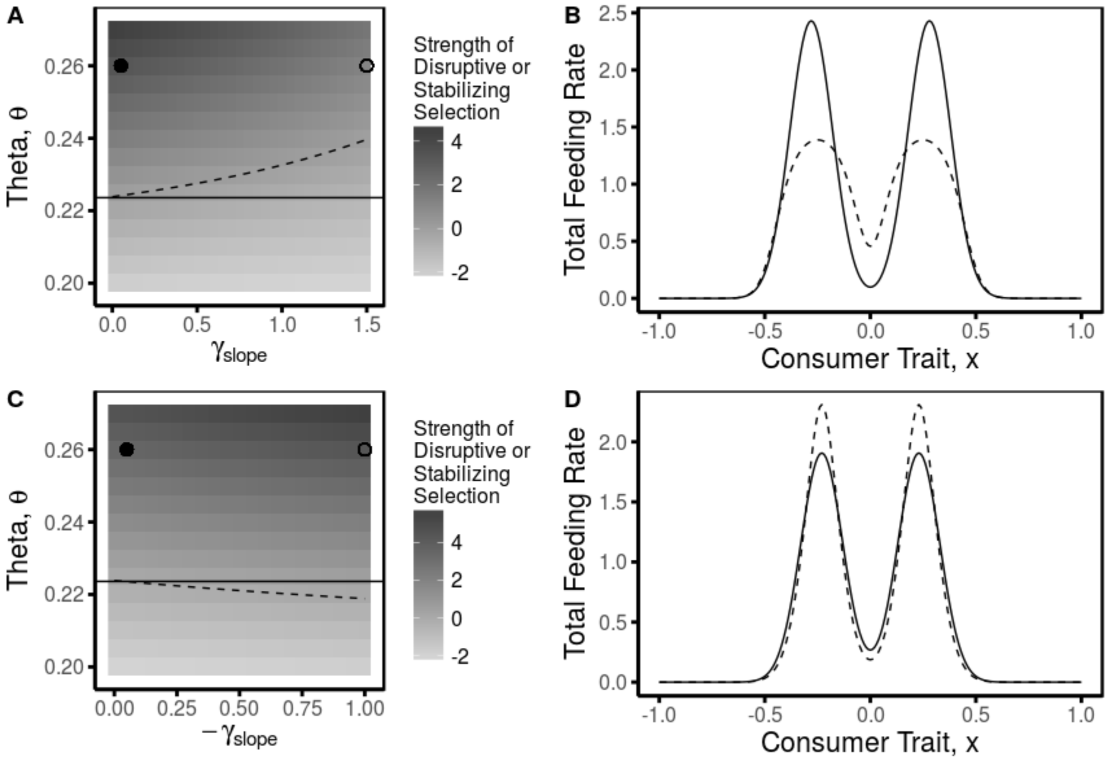

Figure 2.4: Ecological pleiotropy leading to correlations between attack rates and interference rates in the Beddington-DeAngelis functional response alters the strength of disruptive selection (**A, C**). Positive correlations lead to a decrease in the strength of disruptive selection (**A**), while negative correlations lead to an increase in the strength of disruptive selection (**C**). The correlations also alter the parameter space over which disruptive selection occurs in this model (above the dashed lines in **A** and **C**) relative to the case in which consumers have linear functional responses (above the solid line in **A** and **C**). Changes in selection are due to changes across the consumer's phenotypes in feeding rates as the correlation is changed from weak (solid dot in **A** and **C**, solid line in **B** and **D**) to strong (open dot in **A** and **C**, dashed line in **B** and **D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.3, \theta_1 = -\theta_2 = 0.3, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.2, \eta_1 = \eta_2 = 0.01$, and in **A** and **B** $\gamma_{1,min} = \gamma_{2,min} = 0.01$ and in **C** and **D** $\gamma 1, max = \gamma_{2,max} = 0.3$.

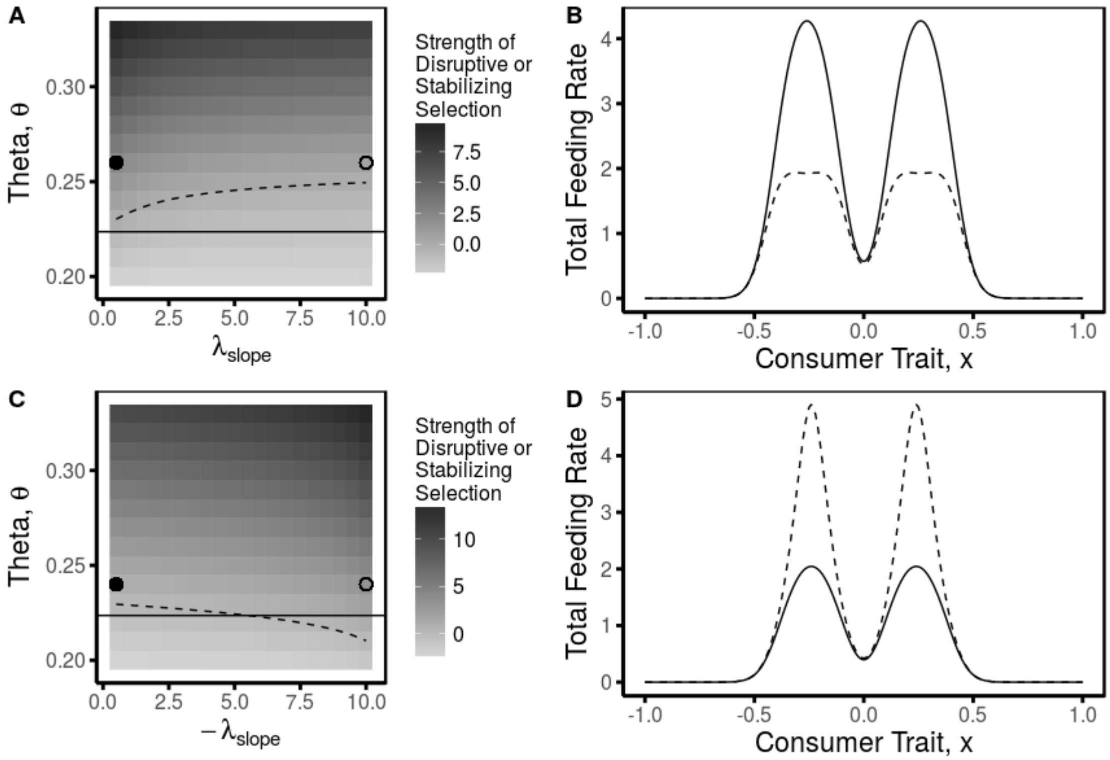

Figure 2.5: Ecological pleiotropy leading to correlations between attack rates and interference rates in the Crowley-Martin functional response alters the strength of disruptive selection (**A, C**). Positive correlations lead to a decrease in the strength of disruptive selection **A**, while negative correlations lead to an increase in the strength of disruptive selection (**C**). The correlations also alter the parameter space over which disruptive selection occurs in this model (above the dashed lines in **A** and **C**) relative to the case in which consumers have linear functional responses (above the solid line in **A** and **C**). Changes in selection are due to changes across the consumer's phenotypes in feeding rates as the correlation is changed from weak (solid dot in **A** and **C**, solid line in **B** and **D**) to strong (open dot in **A** and **C**, dashed line in **B** and **D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma = 0.2, \alpha_{1,max} = \alpha_{2,max} = 0.1, \tau_1 = \tau_2 = 0.1, r_1 = r_2 = 0.2, K_1 = K_2 = 100, e = 0.5, m = 0.5, \eta_1 = \eta_2 = 0.1$ and in **A** and **B** $\lambda_{1,min} = \lambda_{2,min} = 0.01$ and in **C** and **D** $\lambda_{1,max} = \lambda_{2,max} = 1$.

3 The application of Bayesian hierarchical models to quantify individual diet specialization

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3.1 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.

3.2 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 (Araújo et al., 2011; Bolnick et al., 2011, 2003). 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; Gibert and Brassil, 2014; Schreiber et al., 2011). 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. Rosenblatt et al., 2015; Semmens et al., 2009) 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 individuals 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, $\mathrm{PS}_i = 1 - 0.5 \sum_j |p_{ij} - v_j|$, 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 (Feinsinger et al., 1981; Schoener, 1968). 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 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 B) . 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).

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 WIC/TNW index (Appendix B) 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 (Clark, 2005; Ellison, 2004) 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 re-analyze two published empirical data sets of individual diets to highlight the differences in inferences that the observed proportions and Bayesian hierarchical approaches provide.

3.3 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

$$\vec{y_i} \sim \text{Multinomial}(\vec{p_i}, n_i) \tag{3.1}$$

$$\vec{p_i} \sim \text{Dirichlet}(\vec{q} \times w) \tag{3.2}$$

(Fordyce et al., 2011), where $\vec{y_i}$ 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, $\vec{p_i}$ is a vector of the individual's diet proportions (to be estimated), $\vec{q}$ 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 (Figure 3.1). The concentration parameter thereby reflects the degree of diet specialization that exists within the population. When no previous knowledge exists on the $\vec{q}$ and w parameters, uniform priors, such as

$$\vec{q} \sim \text{Dirichlet}(\vec{1}) \tag{3.3}$$

$$w \sim \text{Uniform}(0, c), \tag{3.4}$$

may be used. Here $\vec{1}$ 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 re-analyses we expanded upon this model to include more grouping levels by including additional equations like eqns. 3.2-3.4 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.

3.3.1 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 4 different prey types. Second, because in studies of individual predator diets the number of prey items observed per individual varies considerably among 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, Beta($\alpha = 1$, $\beta = 1$); a skewed distribution of observations per individual whereby most individuals were observed with few prey items, Beta(0.5,1); or a skewed distribution of observations per individual whereby most individuals were observed with a large number of prey items, 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 to 101 prey items per individual (see Appendix B for details).

For each simulation we implemented the Bayesian hierarchical model (eqns. 3.1 - 3.4) 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$_i$ greater than 50% as a measure of a given method's tendency to overestimate diet specialization.

3.3.2 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, $\ln(w)$ (Figure 3.1), 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 eqns. 3.1-3.2 to simulate multinomial data for 1000 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 B). For each population we then implemented the Bayesian hierarchical model (eqns. 3.1 - 3.4), implemented the observed proportions method using 'RInSp', 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.

3.3.3 Analysis of empirical data

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

3.3.3.1 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: (*i*) a two-level model with all individuals grouped into a single population (eqns. 3.1-3.4), (*ii*) a three-level model with individuals nested within site, and (*iii*) a four-level model with individuals nested within sex nested within site (see Appendix C 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 (Gelman et al., 2014; Vehtari et al., 2016; Watanabe, 2010). 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 (Gelman et al., 2014; Watanabe, 2010). 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.

3.3.3.2 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 5 prey observations per individual and categorized the whelks into three size classes.

We fit three Bayesian hierarchical models to these data: (*i*) a two-level model with all individuals grouped into a single population (eqns. 3.1-3.4), (*ii*) a three-level model with individuals categorized by size class, and (*iii*) a four-level model with individuals categorized by size class nested within site (see Appendix C 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.

3.4 Results

3.4.1 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 (Figure 3.2) and when the number of prey items per individual varied among individuals (Figure 3.3). With less than 50 observations per individual, the observed proportions method on average overestimated levels of specialization by underestimating the true values of PS_i (Figure 3.2; 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 (Figure 3.2; 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 (Figure 3.3), 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).

3.4.2 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 (Figure 3.4), 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 despite the heterogeneous distribution of sample sizes we simulated (Figure 3.4, $R^2 = 0.97$). 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 (Figure 3.4).

3.4.3 Analysis of empirical data

3.4.3.1 Alligator data

The comparison of the three Bayesian hierarchical models indicated that the 3-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 3.1, Appendix C). We therefore analyzed the simpler 3-level model which suggested that sites differed in their average diet proportions (Figure 3.6A, $\ln(w_{\text{sites}}) = 1.13$ (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 (Figure 3.5B, Figure 3.6B-D). Estimates of $\ln(w)$ showed weak but positive correlations with the observed proportions method estimates of IS ($R^2 = 0.30$, Figure 3.5B) and WIC/TNW ($R^2 = 0.47$, Figure 3.5C). 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 (Figure 3.5A). 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.

3.4.3.2 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 3.1, Appendix C). The PS_i estimates from this model and the observed proportions method were strongly positively correlated ($R^2 = 0.93$; Figure 3.5E). 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), Figure 3.6E) that was driven primarily by differences in individual's apparent preference for either *Ostrea* spp. oysters, *Siphonaria maura* limpets, or serpulid polychaetes.

3.5 Discussion

A prerequisite for gaining insights into the causes and consequences of diet specialization is the ability to accurately quantify specialization (Araújo et al., 2011; Bolnick et al., 2011, 2003). 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 re-analyses of two empirical data sets. Furthermore, our analysis of the empirical data sets highlights the flexibility of hierarchical methods and illustrates the ability of 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 A).

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 re-analyses 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 D). 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) and citations within). 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 B). 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 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 D). 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 (Araújo et al., 2011; Novak, 2010). 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 ($\vec{q}$; 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 D). 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.

Organism and model	WAIC	SE	Δ WAIC
Alligator Individuals nested within site and sex	9008.5	138.6	0
Individuals nested within site	9016.7	137.0	8.2
All individuals within the same hierarchical level	9381.6	125.6	373.1
Whelk Individuals nested within size class and site	905.2	30.0	0
All individuals within the same hierarchichal level	916.0	29.2	10.8
Individuals nested within size class	925.5	31.7	20.3

Table 3.1: 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.

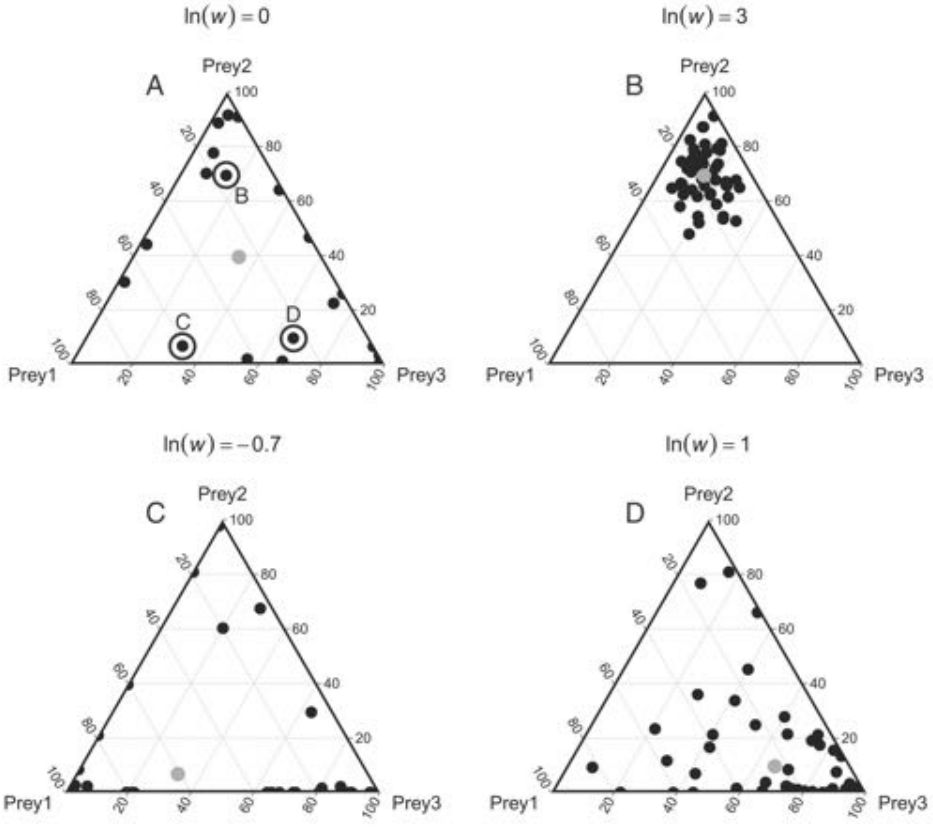

Figure 3.1: Hypothetical data illustrate the hierarchical nature of the Bayesian models and the properties of the Dirichlet distribution. In **A**, the black points represent the mean diet proportions of population sub-groups (e.g. sites or treatments) and the gray point denotes the population mean over all sub-groups. The labeled points in **A** represent the mean diet proportions of the sub-groups illustrated in **B**-**D**. In **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 **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 **A**); values greater than 1 ($\ln(w) > 0$) represent a more concentrated distribution (as illustrated in **B** and **D**); values less than 1 ($\ln(w) < 0$) represent a more dispersed distribution (as illustrated in **C**).

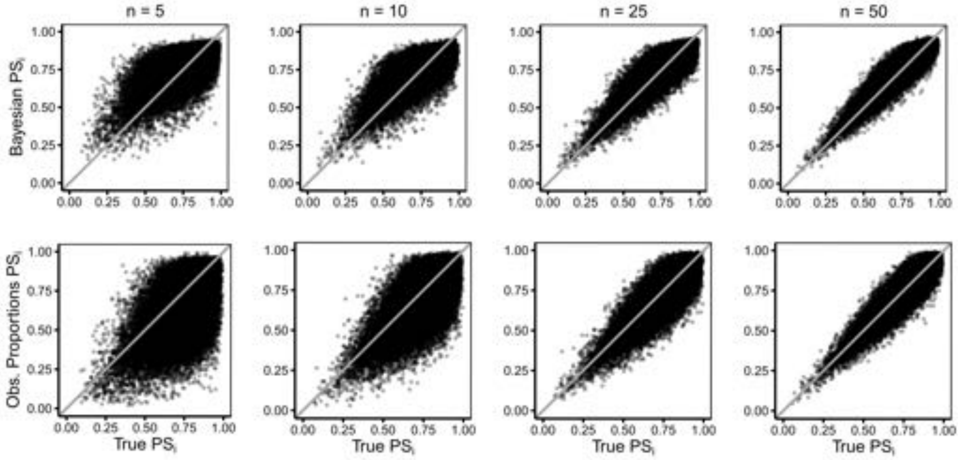

Figure 3.2: The observed proportions method led to the overestimation of individual diet specialization (the underestimation of PS$_i$) at low numbers of observations per individual. As the number of observations per individual increases, the estimates from the observed proportions method and the Bayesian 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.

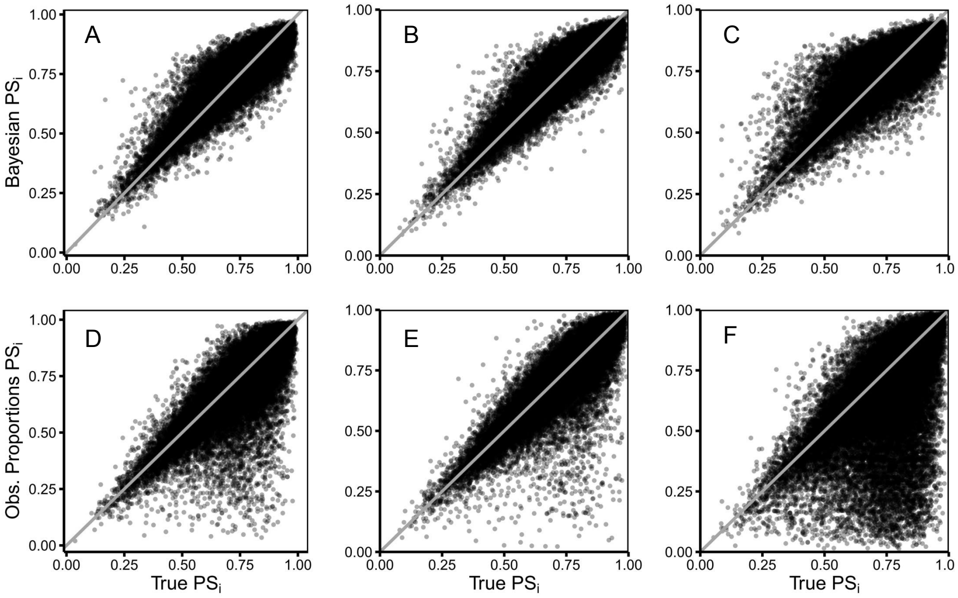

Figure 3.3: Simulations with varying numbers of prey per predator individual following one of three distributions – (**A**,**D**) a uniform distribution, (**B**,**E**) a distribution with most individuals having a large number of observations, or (**C**,**F**) a distribution with most individuals having 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 accurately in all situations. The gray line in each graph is the line of equality between the true and estimated PS_i values.

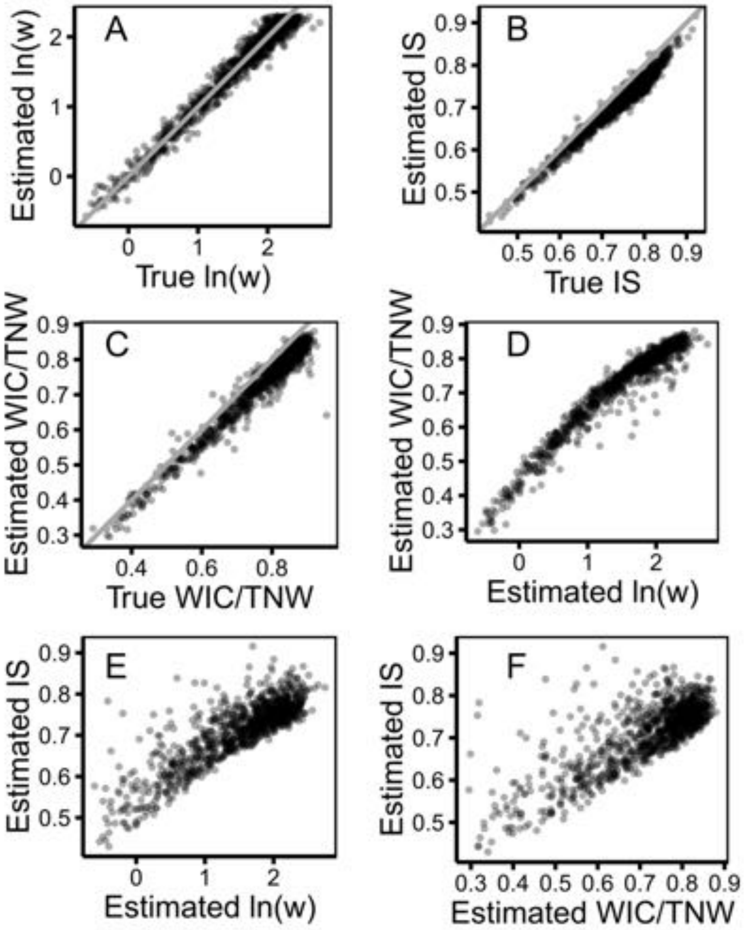

Figure 3.4: (**A**) Estimates of relative diet specialization within groups from simulated data showed that the Bayesian hierarchical models provide a faithful estimate of the true value of the Dirichlet concentration parameter, w. (**B,C**) Simulations also showed that the observed proportions method 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.

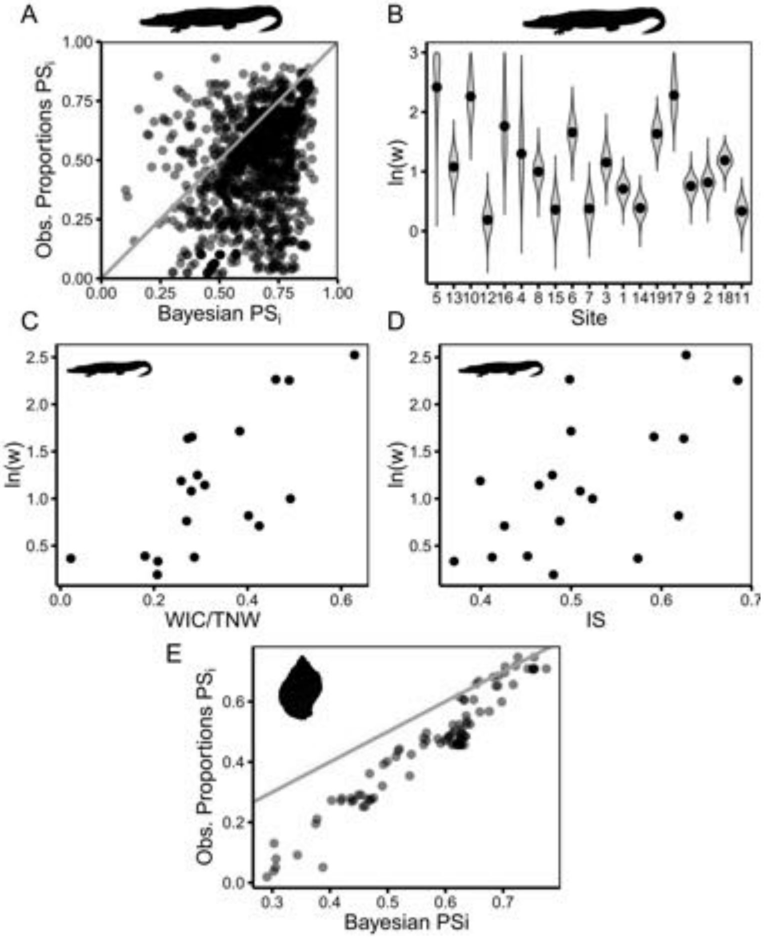

Figure 3.5: (**A**) Individual-level estimates of diet specialization in American alligators were frequently higher when inferred by the observed proportions method than the Bayesian model which differentiated sites but not sexes. (**B**) Site-level estimates of specialization from the Bayesian model 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 **A** and **E** represent the line of equality between estimates from the Bayesian model and the observed proportions method.

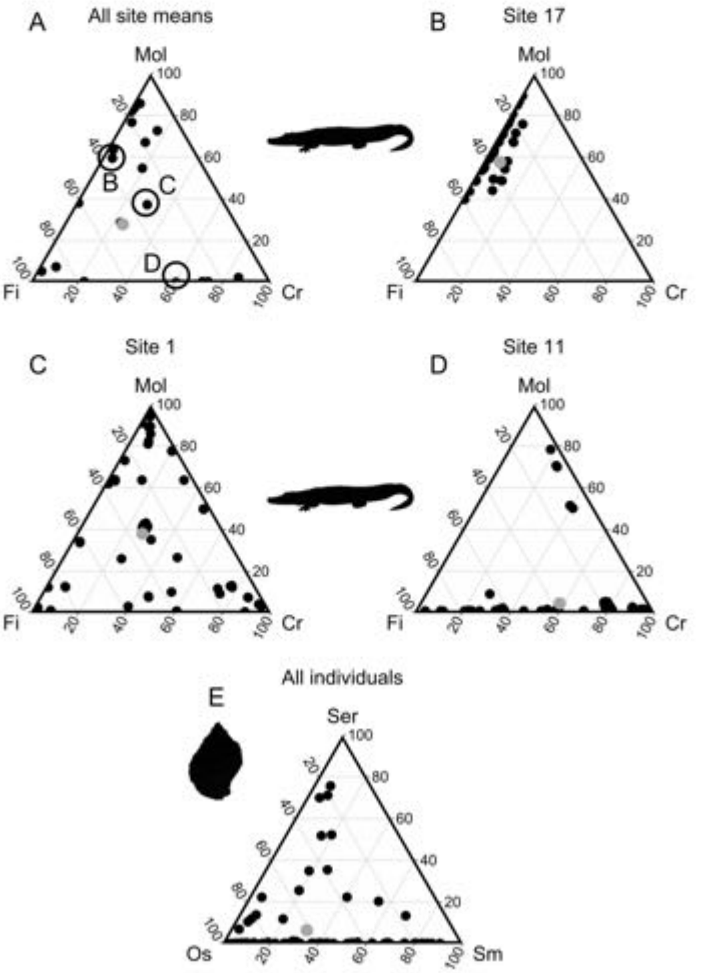

Figure 3.6: (**A**) American alligators showed variation in the mean proportion of the three most consumed prey items (Fi = Fish, Mol = Mollusc, Cr = Crustacean) among sites ($ln(w_{sites}) = 1.13$) as well as among individuals, as illustrated by three exemplary sites (**B**: $\ln(w_{17}) = 2.27$, **C**: $\ln(w_1) = 0.71$), and **D**: $\ln(w_{11}) = 0.34$). The labeled points within **A** show the site means for the three sites illustrated in **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**).

4 Changes in diet variation with prey community composition alter the perceived strength of predator-prey interactions

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4.1 Abstract

Diet variation among even seemingly identical individuals appears to be widespread and has been hypothesized to have important ecological and evolutionary effects. Many hypotheses surrounding the causes of this individual diet variation center around the assumption that individuals vary among one another in their prey preferences. However, chance alone, even if individuals have the same preferences, should also cause diet variation and the magnitude of variation should change predictably with the relative densities of prey. Here, we show support for this stochastic foraging hypothesis in an intertidal whelk, *Nucella ostrina*, feeding on barnacles and mussels. We show further that the variation in diets among individuals associated with both preference variation and variation in feeding propensity alter mean feeding rates on prey through Jensen's inequality. Furthermore, the effects of variation through Jensen's inequality are magnified when considering both diet variation among individuals and spatial variation in prey densities. These results highlight the importance of considering the stochastic nature of predator foraging in studies of diet specialization and variation and show that variation at multiple scales is capable of changing the perceived strength of predator-prey interactions through nonlinear averaging.

4.2 Introduction

Individuals within generalist predator populations often differ from one another in terms of diet. Although among individual differences in diet can often be attributed to various causes (e.g. ontogenetic niche shifts, sexual dimorphism, resource polymorphisms, etc.), studies focusing on seemingly identical individuals often still find substantial variation among individuals in diets (Araújo et al., 2011; Bolnick et al., 2003). This variation could have important ecological and evolutionary effects (Bolnick et al., 2011). For example, recent theoretical studies have suggested that diet variation can alter the strengths of predator-prey interactions (Bolnick et al., 2011; Gibert and Brassil, 2014), the eco-evolutionary dynamics of predator-prey systems (Schreiber et al., 2011), and the coexistence of competitors (Hart et al., 2016). Given the apparent prevalence of individual diet variation and its potential consequences, ecologists are increasingly attempting to understand the factors that cause it and assess its empirical effects.

Many hypotheses surrounding the ecological causes of individual diet variation are derived from optimal foraging theory (Araújo et al., 2011; Svänback and Bolnick, 2007; Tinker et al., 2008). Optimal foraging theory predicts the prey species that individuals should consume to maximize energy intake (Emlen, 1966; Stephens and Krebs, 1986). Under optimal foraging theory, predators should rank prey species according to their profitability, defined as the prey's energy content per unit handling time. The highest ranked prey item should be consumed whenever it is encountered. Lower ranked prey should only be included when the density of higher ranked prey falls below a threshold at which 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 has been used to make predictions for how changes in prey densities and individual variation in rank preferences alters the magnitude of consequent diet variation. These predictions underlie several hypotheses regarding the effects of intra- and interspecific competition, ecological opportunity, and predation on the focal predator on individual diet variation (Araújo et al., 2011; Svänback and Bolnick, 2007; Tinker et al., 2008).

Although prey preference differences among individuals is one source of diet variation, diet variation can also be observed when all individuals share the same prey preferences. It is recognized for example, that diet variation can result when some individuals are able to monopolize resources or if individuals forage in different habitats that differ in prey availability (Bolnick et al., 2003). What has not been generally considered is the extent to which the stochastic nature of predator foraging influences the real and perceived magnitude of diet variation even when individual prey preferences and experienced prey densities are the same. The effects of this stochasticity on diet variation are predictable: consider a population of predators in which all individuals have the same and equal preferences for two prey species. If one prey species is rare while the other is abundant, the diets of individuals will mostly consist of the abundant species and diet variation will be low. However, when both prey species are common, individual diets will vary along a spectrum from nearly all of one prey species to nearly all of the other prey species, thus increasing the amount of diet variation (Figure 4.1). It is unknown how common this mechanism may be for generating diet variation, but its generality suggests that diet variation through stochastic foraging should be common.

A potentially important and pervasive effect of diet variation is the alteration of predator feeding rates due to Jensen's inequality (Bolnick et al., 2011). Jensen's inequality states that, for a concave function f of a variable x the mean of the function, $\overline{f(x)}$, will be less than or equal to the function evaluated at the mean of the variable ,$f(\overline{x})$. The opposite is true for convex functions. Because predator functional responses (the relationship between prey densities and predator feeding rates) are almost always nonlinear functions (Jeschke et al., 2004), variation among individuals in functional response parameters is expected to alter population-level feeding rates relative to the scenario in which all individuals exhibit the same functional response parameters. For example, the commonly used Holling Type II functional response (Holling, 1959) is a concave function of the predator attack rate and a convex function of predator handling times. If predators vary in their attack rates, then the realized mean feeding rate of predators should be less than or equal to the expected feeding rate of the predators if all individuals exhibited the mean attack rate (Figure 4.2). The opposite is true for variation in predator handling times. Because individual variation and nonlinear functional responses should be common, so should effects of Jensen's inequality on feeding rates (Bolnick et al., 2011). Despite the strong theoretical argument for effects of Jensen's inequality, we currently lack empirical data measuring this effect.

Here we used a manipulative field caging experiment with an intertidal whelk, *Nucella ostrina* to examine relative support for an optimal foraging hypothesis vs. a stochastic foraging hypothesis as causes of diet variation. We also estimate the effects of diet variation on feeding rates through Jensen's inequality. Our data show greater support for the stochastic foraging hypothesis than the optimal foraging hypothesis as the explanation for diet variation in this system. As predicted, we find that attack rate variation among individuals within cages decreases the mean feeding rate of whelks relative to the scenario in which all individuals exhibited the same mean attack rate within the cage. The total magnitude of this effect was small. In contrast, we find up to an order of magnitude larger effect of attack rate variation among individuals and heterogeneity in resource densities among cages through Jensen's inequality, suggesting that spatial variation in prey abundances must be considered in concert with individual variation in attack rates to appropriately scale between individual- and population-level feeding rates.

4.3 Methods

4.3.1 Study System

N. ostrina is a common intertidal predator on rocky shores of the Northeast Pacific coast and feeds on several marine invertebrate species including acorn barnacles, mussels, limpets, littorine snails, and gooseneck barnacles(Palmer, 1984; Spight, 1981). Its primary prey are the acorn barnacle, *Balanus glandula*, and the mussel, *Mytilus trossulus*, hereafter referred to as barnacles and mussels, respectively, unless otherwise noted.

Given this knowledge, we developed two hypotheses that make different predictions of how the magnitude of diet variation should change given changes in the total and relative abundances of the whelk's preferred prey. The first hypothesis is drawn from optimal foraging theory and assumes that individuals differ in their rank preferences for barnacles versus mussels. Under this hypothesis, diet variation should be highest when both prey are at similarly high densities, intermediate when the total density of prey is high, but prey evenness is low, and lowest when the total prey density is low regardless of prey evenness. Under the stochastic foraging hypothesis, when all individuals have the same prey preferences and relative preferences are intermediate, diet variation should increase as prey evenness increases regardless of the total prey densities (Figure 4.1).

4.3.2 Experimental Methods

To empirically evaluate our two hypotheses, we used a field caging experiment manipulating the total and relative densities of prey. In June 2015, we bolted twenty 25x35mm stainless steel mesh cages with galvanized steel mesh lids into an early successional disturbance patch within a California Mussel (*Mytilus californianus*) bed in the mid-intertidal at Yachats, Oregon, USA (44.3°N, -124.1°W) (Novak et al., 2017). Disturbed patches within California Mussel beds occur naturally and in their early successional stages contain high densities of the preferred prey of whelks. To modify total prey densities, we divided each cage into a grid of ten 7x12.5cm rectangles and applied one of five treatments to four cage replicates, scraping either zero, two, four, six, or eight randomly selected rectangles to bare rock. As cages naturally varied in the composition of prey, the removal of prey led to continuous variation across cages in both the composition of the prey community and the total number of prey available.

To each cage we added 30 individually-tagged whelks from the surrounding area. The size of the whelks chosen (15.5-16.5mm) reflects the median size range of whelks at this site in the summer months. We then performed biweekly surveys during the lowest low tides of June through August and on 19 of 30 days in September for a total of 41 surveys. Feeding whelks were recorded along with the identity of the prey being eaten, the size of the prey, and the method by which the whelk was feeding on the prey (drilled or prying). Every two weeks we recorded whelk sizes were recorded every two weeks and photographed of the cage interiors. Photographs from the beginning, middle, and end of the experiment were used to estimate prey densities using ImageJ (Schneider et al., 2012). Any individuals dying or escaping from the cages were replaced with a new individually tagged whelk within the size range of the other whelks. This design provided longitudinal samples of individual whelk diets over the course of four months and estimates of prey densities across cages varying in both prey composition and total density.

4.3.3 Statistical Methods

4.3.3.1 Estimating Diet Variation

We estimated diet variation among individuals using a Bayesian hierarchical model modified from Coblentz et al. (2017). We assumed that the number of barnacles observed in an individuals diet was binomially distributed. Because the handling times for mussels are generally longer than the handling times for barnacles, we added a correction for the bias in observing a feeding event on mussels versus barnacles by accounting for the relative difference in handling times between the two prey. Handling times and their relationship with prey size, predator size, and feeding method were estimated from a laboratory experiment, the details of which can be found in Appendix E. Handling times for each feeding observation were estimated using regression coefficients from the laboratory experiment and averaged for barnacles and mussels to generate a characteristic handling time for each prey species across the experiment. Although estimating handling times this way ignores possible effects of individual differences in handling times on diet variation and its effects through Jensen's inequality, we were unable to estimate handling times of individuals, as individuals were only observed for a short period of time during low tides. After correcting proportions for bias due to differences among prey in handling times, we then assumed that the corrected proportion of barnacles in individuals' diets within a cage were described by a Beta distribution, the variance of which we used as our measure of diet variation within each cage. We used a uniform Beta prior for the mean of each Beta distribution and weak Gamma priors on the variance of the Beta distributions, and estimated the parameters from the model in R using the program 'JAGS' through the R package 'rjags' (Plummer, 2003, 2016).

We used model comparison to determine the relative support for two statistical models encapsulating the differences between the optimal foraging and stochastic foraging hypotheses. The optimal foraging hypothesis predicts that diet variation should be related to the total density of barnacles and mussels, the relative density of mussels to barnacles, and the interaction between these. Thus, we represent this hypothesis with a multiple linear regression including terms for the total density, relative density, and their interaction, with the variance of the cage-level beta distributions estimated above as the response variable. The stochastic foraging hypothesis predicts that diet variation should be associated with the relative densities of prey regardless of the total density of prey available. Thus, we represent this hypothesis with a simple linear regression between diet variation and relative prey densities.

To perform model comparison, we fit both models using the median point estimates of diet variation from the hierarchical model in a Bayesian regression framework using the R package 'rstanarm' (Carpenter et al., 2017; Stan Development Team, 2016), then calculated the Widely Applicable Information Criterion (WAIC), a Bayesian analogue to the Akaike Information Criterion (AIC) (Watanabe, 2010). To better meet model assumptions, we fit the models using the natural log of diet variation and total prey density. The relative density of mussels to barnacles was left untransformed. We used weakly informative priors on all of the regression parameters (details can be found in Appendix F).

4.3.3.2 Estimating the Effects Variation on Feeding Rates through Jensen's Inequality

To estimate the effects of variation through Jensen's inequality on feeding rates, we first estimated individual attack rates and used these individual attack rates to estimate each individual's feeding rate. Using the individual feeding rates, we then calculated the observed mean feeding rate across individuals within each cage and across all cages. We also used the individual attack rate estimates to calculate the mean attack rate within each cage and across all cages and calculated the mean feeding rate assuming that all individuals exhibited the same mean attack rate. Comparing the observed mean feeding rates to the feeding rates calculated assuming all individuals exhibited the same mean attack rate allowed us to measure the effects of variation on the perceived feeding rates on prey through Jensen's inequality within each cage and across cages (Figure 4.1). To estimate individual attack rates, we used the attack rate estimator derived by Novak and Wootton (2008) and Wolf et al. (2017) assuming a Holling Type II predator functional response. Although this estimator has previously only been applied to snapshot feeding surveys across individuals, it can also be applied to individuals given longitudinal samples of individual feeding and nonfeeding events (Novak et al., 2017). Following Wolf et al. (2017), we modeled the number of feeding events on barnacles and mussels and nonfeeding events for each individual as multinomially distributed. The proportions of feeding and nonfeeding events for each individual were assumed to have a cage-level Dirichlet distribution with a uniform Dirichlet prior. Using estimates of the proportion of feeding events of individual j in cage k on prey i, p_{kji}, the individual's proportion of nonfeeding events, p_{kj0}, the density of prey i in cage k, R_{ki}, and the handling time of prey i, h_i, the attack rate estimator for the individual on prey i, α_{kji}, is

$$\alpha_{kji} = \frac{p_{kji}}{p_{kj0}} \times \frac{1}{h_i R_{ki}}. \tag{4.1}$$

We assumed that the densities of resources in each cage and the handling times of prey were known and were estimated as in the above analysis of diet variation. To calculate individual feeding rates, we substituted the estimated attack rates, handling times, and resource densities into Holling Type II multispecies functional responses for barnacles and mussels. From these individual feeding rate estimates, we then estimated the mean feeding rate within each cage and across the entire experiment by averaging the individuals feeding rates across individuals within each cage or across the entire experiment respectively. Similarly, we estimated the mean feeding rate using the mean attack rate for each cage and the mean attack rate across the experiment. In calculating the feeding rate across the entire experiment from the mean attack rate, the average resource densities across the cages were used in the functional response. Thus the effect of Jensen's inequality at the experiment level is due to both variation among individuals in feeding rates and variation among cages in resource densities. We measured the effect of Jensen's inequality by subtracting the feeding rate as estimated using the mean attack rate from the mean feeding rate as averaged across all individual feeding rates. Therefore, a negative difference corresponds to an overestimation of cage or population feeding rates when individual variation is ignored.

Lastly, because individuals can differ in attack rates due to variation in diet (the p_{kji}'s) and variation in the proportion of nonfeeding events (p_{kj0}, hereafter feeding propensity variation), we examined how these two types of variation were related to the effects of Jensen's inequality across cages. To do so, we performed regressions on the relationships between diet variation and feeding propensity variation and the effects of Jensen's inequality on feeding rates for barnacles and mussels. To estimate feeding propensity variation, we used the same model used to estimate diet variation but with the total number of feeding events modeled as binomially distributed. Diet variation was defined and measured using the variance of the cage-specific beta distributions, just as measured above. Attack rates were estimated using the program 'JAGS' through the R package 'rjags' (Plummer, 2003). The regressions of the effects of Jensen's inequality on diet and feeding propensity variation were performed using the program 'Stan' through the R package 'rstanarm' (Carpenter et al., 2017; Stan Development Team, 2016).

Details of all of the statistical models used can be found in Appendix F.

4.4 Results

In total, the experiment generated 24,673 total observations for 719 individuals of which 4,067 observations were feeding observations. Because prey densities within the cages changed over the course of the experiment with increases in barnacles due to recruitment and decreases in mussels from predation, we limited the analysis to individuals for which the mean densities of prey over the course of the experiment were representative of the average prey densities experienced by individuals. Thus, we focused on the 513 individuals that were observed in at least 35 of the total 41 surveys and had at least one feeding observation. Results were similar when using different cutoffs for the minimum number of observations per individual. The 513 focal individuals had a total of 20,313 observations of which 2,713 were feeding observations. The average number of feeding observations per individual was 5.2 and ranged from 1 to 15. Of the 2,713 feeding observations, the vast majority were feeding observations on barnacles or mussels with only 10 observations of individuals feeding on another species of acorn barnacle *Chthamalus dalli* and one observation of an individual feeding on the limpet *Lottia pelta.* These observations were removed prior to the analysis.

4.4.1 Causes of Diet Variation

Overall, cages differed in both the mean and variance of the proportion of barnacles in the diets of individuals (Figure 4.3). Model selection using WAIC suggested greatest support for the stochastic foraging hypothesis (WAIC Stochastic Foraging Hypothesis = 31.3, WAIC Optimal Foraging Hypothesis = 33.4, Difference in WAIC (Standard Error) = 1.1 (0.4)), with the magnitude of diet variation being positively associated with the relative densities of mussels to barnacles (Figure 4.4A). Total density of prey was not associated with the magnitude of diet variation and there was no clear indication of an interaction between total prey density and the relative density of mussels and barnacles influencing the magnitude of diet variation (Figure 4.4A,4.4B).

4.4.2 Effects of Jensen's Inequality on Feeding Rates

For both barnacles and mussels, individual variation in attack rates within cages led to mean feeding rate estimates that were lower than the feeding rate estimated from the cage-specific mean attack rate (Figure 4.5A-C, 4.6A-C). The mean discrepancies in feeding rate estimates for barnacles ranged from -0.1 to -1.4 barnacles per individual per 100 days. The estimated percent reduction in feeding rates on barnacles ranged from 1.5 to 4.8%. The mean discrepancies in feeding rates for mussels ranged from 0.003 to -0.33 mussels per individual per 100 days. The estimated percent reduction of feeding rates on mussels ranged from -0.2 to 5.1%. Discrepancies in feeding rate estimates for barnacles increased with the amount of feeding propensity variation (slope = 0.0028, 95% CrI = (0.0021, 0.0035)) and decreased with the amount of diet variation (slope = 0.005, 95%CrI = (-0.0053, -0.004);Figure 4.5B-C). The magnitude of the discrepancies in feeding rate estimates for mussels increased with diet variation (slope = -0.001, 95%CrI = (-0.0015, -0.0004)) and showed no relationship with feeding propensity variation (slope = -0.0004, 95%CrI =(-0.001,0.0002), Figure 4.6B-C).

At the site scale, Jensen's inequality also led to mean feeding rate estimates that were lower than the feeding rates estimated from the mean attack rates (Figure

4.5D, 4.6D). The mean estimated discrepancies at the site-scale were -4.8 barnacles and -1.0 mussels per predator per 100 days. The estimated percent reduction in feeding rates was 19.6% for barnacles and 21.2% for mussels.

4.5 Discussion

Intraspecific diet variation is a widespread phenomenon in generalist predators that is hypothesized to have important ecological and evolutionary consequences (Araújo et al., 2011; Bolnick et al., 2011, 2002). Using the intertidal whelk, *Nucella ostrina*, as our focal predator, we investigated the drivers of diet variation in this system and estimated the effects of individual variation on feeding rates through Jensen's inequality. Our results suggest that diet variation in this system can be explained by individuals foraging randomly on available prey. We also find that variation among individuals in attack rates reduces the mean feeding rates of whelks. Furthermore, at the scale of the experiment, variation in attack rates along with variation in resource densities reduces the mean feeding rates of the whelks further. These results suggest that significant diet variation among individuals can occur as a product of stochasticity and provides empirical affirmation of previous theory on the effects of intraspecific variation on predator feeding rates through Jensen's inequality.

Much of the recent interest in intraspecific diet variation focuses on individual diet specialization (Araújo et al., 2011; Bolnick et al., 2003). Individual diet specialization occurs when the diets of individuals are narrower than the diet of the population and the difference in diet cannot be explained by sex, age, or obvious morphological differences (Bolnick et al., 2003). Although the variation in diets of whelks in many cases within our experiment fits this definition, the fact that our data provide strongest support for diet variation being driven by random foraging of whelks makes us hesitant to use the term 'specialization'. Although it is possible that some individuals were indeed specialized on either mussels or barnacles, we cannot rule out that individual diets consisting of either mostly barnacles or mostly mussels happened by chance. Ideally, studies of diet specialization would sample prey communities concurrently with samples of individual diets. Doing so would allow researchers to distinguish between variation due to random foraging and variation due to diet specialization with the random foraging hypothesis acting as a null model. In contrast, current null model approaches determine the probability of the observed variation in diet among individuals if all individual's diets were random samples of the population-level diet using Monte Carlo techniques (Bolnick et al., 2002). Using the random foraging hypothesis as a baseline for comparison instead asks whether the observed variation could be explained by assuming that all individuals share the population-level preference for prey but differ in diets from random prey choice. Doing so should allow for a better distinction of whether significant variation among individuals in diets is truly due to individual specialization.

Besides the occurrence of the expected relationship between the ratio of mussels to barnacles under the random foraging hypothesis, other lines of evidence for the random foraging hypothesis within the data may help researchers to distinguish between variation due to random foraging and diet specialization. First, the variation among individuals is relatively continuous. If individuals were specialized, one would expect more discrete variation. For example, under the optimal foraging hypothesis, if total and relative densities of prey were high enough, we would expect to see some bimodal distributions of proportions of barnacles in diets. The lack of bimodality in the estimates of our study is not a product of our chosen statistical analyses, as the beta distribution used can take a bimodal form. The optimal foraging hypothesis also predicts that if barnacle density is high enough, individuals that prefer barnacles over mussels should ignore mussels and consume only barnacles. Yet, complete barnacle specialists were absent in some cages which contained thousands of barnacles. Another possible pattern supporting the random foraging hypothesis that could not be assessed here is that the random foraging hypothesis predicts that diet variation should be unimodal with respect to the ratio of mussels and barnacles. Overall, distinguishing between random foraging and diet specialization should be possible by combining statistical analyses of how variation changes with prey densities with patterns of individual diet composition.

Random foraging is likely to be more difficult to assess in other generalist species that may incorporate tens of species into their diets. Multivariate techniques, partitioning prey into categories during the analysis, and stable isotope analysis, however, should be useful. For example, ordination methods such as principal components analysis or nonmetric multidimensional scaling applied to the individual diets could provide evidence for clusters of individuals with similar diets. A lack of clear clustering of individual diets might provide evidence for the random foraging hypothesis, whereas clustering that is unable to be explained by prey densities might provide evidence for diet specialization. If there are a priori expectations of how individuals are likely to differ in diets, the dimensionality of the diet could be reduced by grouping prey species and then looking for evidence of diet specialization or random foraging given differences among individuals in the grouped prey. For example, a common specialization in fishes is on either benthic or limnetic prey (e.g. Ehlinger and Wilson, 1988; Robinson et al., 1993; Schluter, 1995; Svanbäck and Eklöv, 2002). After grouping prey as either benthic or limnetic, one could then determine whether variation among individuals in proportions of the grouped prey were more likely a product of the relative densities of the grouped prey and random foraging or diet specialization. Lastly, if individuals are foraging randomly, they may appear to be specialists over a given period of time but, over a longer period of time, are likely to have a generalist diet. By sampling tissues with different turnover rates for stable isotope analysis or analyzing tissues produced sequentially over time, it should be possible to distinguish between true specialization or variation among individuals due to random foraging.

Regardless of the cause of diet variation among individuals, we show that variation among individuals in attack rates is associated with reductions in feeding rates through Jensen's inequality as predicted by theory (Bolnick et al., 2011). Although the effect of variation through Jensen's inequality on feeding rates was detectable, the magnitude of the effect was relatively small. The overall effect of variation through Jensen's inequality is dependent on the amount of variation among individuals and the nonlinearity of the function. Therefore, the effect should be greater in systems with larger variation among individuals such as systems with strong diet specialization and in which the relationship between attack and feeding rates is more strongly nonlinear. The effect of variation in attack rates in whelks through Jensen's inequality is also likely to be greater than measured, as we purposefully minimized variation that could arise from size differences among whelks so that this variation did not confound estimates of individual diet variation. Unfortunately, because we could not estimate individual handling times, we could not estimate the effects of handling time variation on feeding rates through Jensen's inequality. As handling time variation should have the effect of strengthening feeding rates on barnacles and mussels, handling time variation could cancel out the effect of attack rate variation or cause the net effect of individual variation to be an overall strengthening of feeding rates. Future studies accounting for both attack rate and handling time variation across naturally occurring variation among individuals will be necessary to understand the net outcome of Jensen's inequality and individual trait variation.

Our results highlight that the effect of attack rate variation through Jensen's inequality is a product of variation in both diet composition (what we have referred as simply diet variation) and feeding propensity variation . Furthermore, these two types of variation can have different effects on the magnitude of the the reduction in feeding rates. For example, the effect of variation through Jensen's inequality on barnacle feeding rates was greater with higher feeding propensity variation and was dampened by diet variation. Cages with the largest effects of variation on barnacle feeding rates were those in which diet variation was low with most individuals feeding on barnacles. Because most individuals were feeding on barnacles, variation in attack rates was largely attributable to feeding propensity variation among individuals. As diet variation increased and more individuals incorporated mussels into their diets, variation in attack rates on barnacles declined and the consequent effects of attack rate variation through Jensen's inequality weakened. The effect of attack rate variation through Jensen's inequality on mussel feeding rates was only associated with the amount of diet variation. This was due to the greatest amount of attack rate variation for mussels occurring when individuals varied in the proportion of mussels within their diets. It is possible that these associations might be flipped if cages had been dominated by mussels. The fact that feeding propensity variation alters attack rate variation widens the scope of potential effects of variation through Jensen's inequality on feeding rates beyond diet variation. For example, variation in feeding propensity among specialist individuals should also lead to the application of Jensen's inequality. Although variation in feeding propensity could arise randomly, feeding propensity variation could also be the product of consistent behavioral or physiological differences among individuals. Several examples exist of consistent individual differences in traits such as behavior and metabolism (For reviews see Biro and Stamps, 2010; Dall et al., 2004; Sih et al., 2004). If these differences lead to differences among individuals in the amount of prey they consume, then Jensen's inequality should be relevant even in specialist predators.

Combining the results that diet variation changes with prey densities and that variation influences the strength of species interactions raises the possibility of an indirect interaction between prey mediated by the effects of their densities on predator variation. For example, while mussels are rare, feeding rates through the whelk functional response will be high on barnacles and low on mussels. However, because of low diet variation and high feeding propensity variation, feeding rates on barnacles will be weakened by Jensen's inequality. As mussel densities increase, feeding rates on mussels will increase due to the functional response. Diet variation will also increase which should weaken the effects of variation through Jensen's inequality on barnacle feeding rates and increase the effects of variation through Jensen's inequality on mussel feeding rates, thus modifying feeding rate changes through the functional response. It is possible that the direction of these effects may be reversed if mussels dominated the system and barnacle densities were increased. Altogether, this suggests that changes in whelk diet variation as a product of changes in prey densities could cause an interaction modification (*sensu* Wootton (1993)) by mussels on the whelk-barnacle interaction and vice versa. Although this effect is likely to be weak in this system, changes in feeding rates mediated by changes in predator variation due to prey availability is hence another of a myriad of ways in which prey that share predators may indirectly interact (Abrams and Matsuda, 1996; Holt, 1977).

At the level of the experiment, variation among individuals in feeding rates and variation among cages in prey densities combined to produce a greater effect of Jensen's inequality than at the cage level. This effect stems from the nonlinear relationships between both attack rates and prey densities with feeding rates in the Holling Type II functional response. Our estimates suggest that the difference in feeding rate estimates were 0.048 for barnacles and 0.001 for mussels per predator per day. Over enough individuals or time, these differences suggest a possibly substantial effect of the combined variation among individuals and variation in prey densities. This suggests that even if a researcher is able to account for individual variation in attack rates when estimating feeding rates, they also should account for variation in resource availability for those individuals. In our study, individuals were confined to cages, so estimating the average densities experienced by individuals was simple. For non-confined animals, the spatial scale over which to determine prey densities is more complex. One option might be to estimate the local prey density for each feeding event or sample of an individual. Alternatively, one could sample the prey community at the scale at which the individual could have foraged over the temporal scale for which the individual was sampled. Given that both spatial and individual variation are likely to influence the strength of predator-prey interactions across scales, it may be useful to extend scale transition theory to include individual trait variation. Scale transition theory is a method developed to scale processes from samples at small spatial scales to larger spatial scales by accounting for variability in species densities and the interaction of this variability with nonlinearities (Chesson, 1998, 2012; Melbourne and Chesson, 2006). It may be possible to take advantage of this theory to scale from the level of the individual to the level of the population to account for individual trait variation and its effects on ecological processes.

4.6 Conclusions

Diet variation is generally considered as the result of differences among individuals in their prey preferences. However, substantial variation among individuals can occur purely through stochastic prey choice by individuals. Furthermore, variation through stochastic foraging changes predictably with prey densities. Studies of diet variation, particularly individual diet specialization, should examine whether stochastic foraging is able to explain diet differences among individuals and be aware that stochastic foraging could confound inference on other ecological causes of diet variation. Jensen's inequality is thought to have widespread application in ecology due to the prevalence of nonlinearities in ecology. We provide evidence that the effect of variation through Jensen's inequality on feeding rates is measurable in this system at multiple scales. Future studies incorporating individual trait variation and its scaling to effects at the population level will give us a greater understanding of how individual differences might alter the dynamics of populations and when these effects are likely to be important.

Box 1: Stochastic Foraging and Diet Variation

Although many hypotheses regarding the ecological causes of diet variation assume that individuals differ in their prey preferences, diet variation among individuals is expected even if all individuals share the same prey preferences and experience the same prey densities. This stochastic mechanism can be illustrated by considering the foraging process of a population of predators feeding on two prey as a binomial process. Assume that all predator individuals have the same relative preferences for prey one, q_1, and for prey two, q_2. Prey one and prey two also have relative abundances in the environment, r_1 and r_2, respectively. Assume that individuals randomly encounter individuals of each prey species in proportion to their relative abundances and accept prey in proportion to their preference for that prey. Under these assumptions, we can treat the number of prey one in the diet of a predator as a binomially distributed random variable with the probability of consuming an individual of prey one , p,as:

$$p = \frac{q_1 r_1}{q_1 r_1 + q_2 r_2}.$$

By definition, the variance of a binomially distributed random variable is $np(1-p)$, where n is number of trials (in this case, the total number of prey items consumed). Assuming a constant n, the variance is maximized when $p = 0.5$. Thus, if all individuals have the same preferences for prey, the amount of diet variation among individuals is maximized when the relative preferences for each prey q_i are equal to the reciprocals of the relative densities of each prey $\frac{1}{r_i}$. For example, if all predators have equal preference for both prey $q_1 = q_2 = 0.5$, then diet variation is maximized when $r_1 = r_2 = 0.5$. These results also hold for more than two prey where foraging can be considered as a multinomial process and the total variance (defined as the sum of the diagonal of the variance-covariance matrix) is maximized.

Figure 4.1: Text box providing an explanation of the generation of individual diet variation through stochastic foraging.

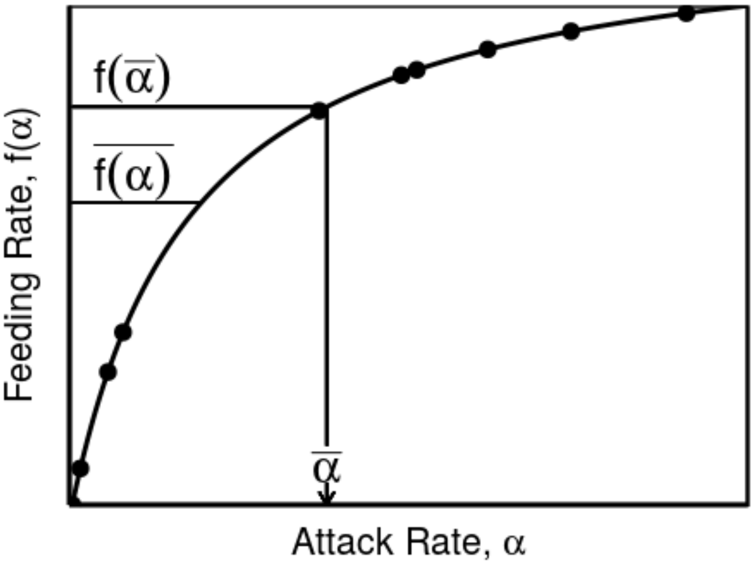

Figure 4.2: The Holling Type II functional response f is a concave function of the attack rate α. Variation among individuals in attack rates causes the average feeding rate among individuals $\overline{f(\alpha)}$ to be less than the feeding rate evaluated at the average attack rate $f(\overline{\alpha})$.

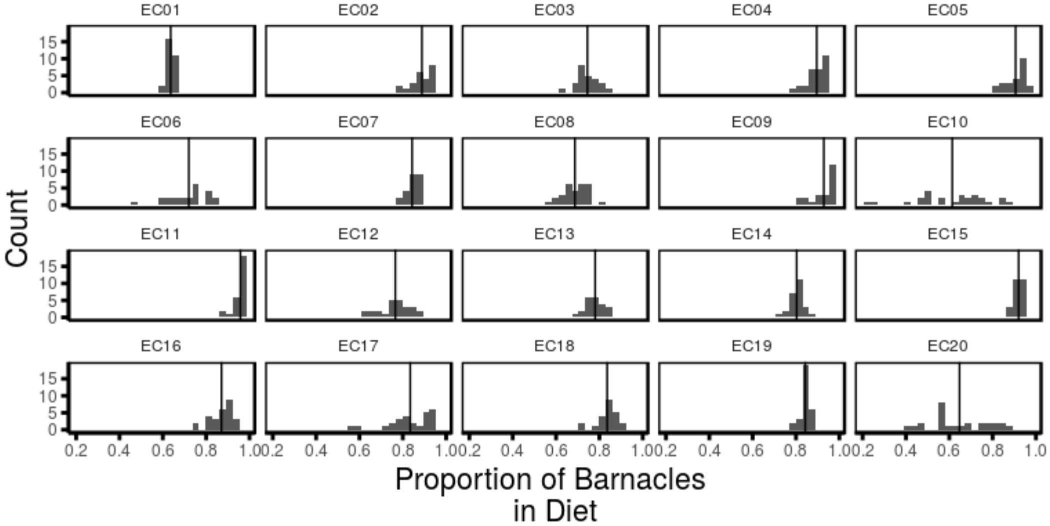

Figure 4.3: The mean and variance of the proportion of barnacles in the diets of individuals differed across cages varying in the ratio of mussels to barnacles and the total densities of prey. The vertical line in each histogram denotes the mean proportion of barnacles observed across individuals.

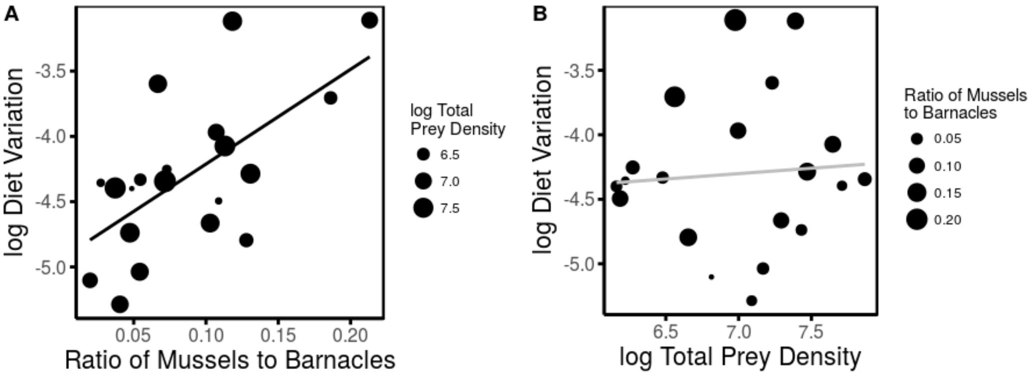

Figure 4.4: In support of the stochastic foraging hypothesis, the magnitude of variation among individual whelks in the propotion of barnacles in their diets showed a positive relationship with the ratio of mussels to barnacles (**A**), no relationship between the total density of prey (**B**), and no clear evidence of the effect of an interaction between the ratio of mussels to barnacles and total prey density (**A,B**).

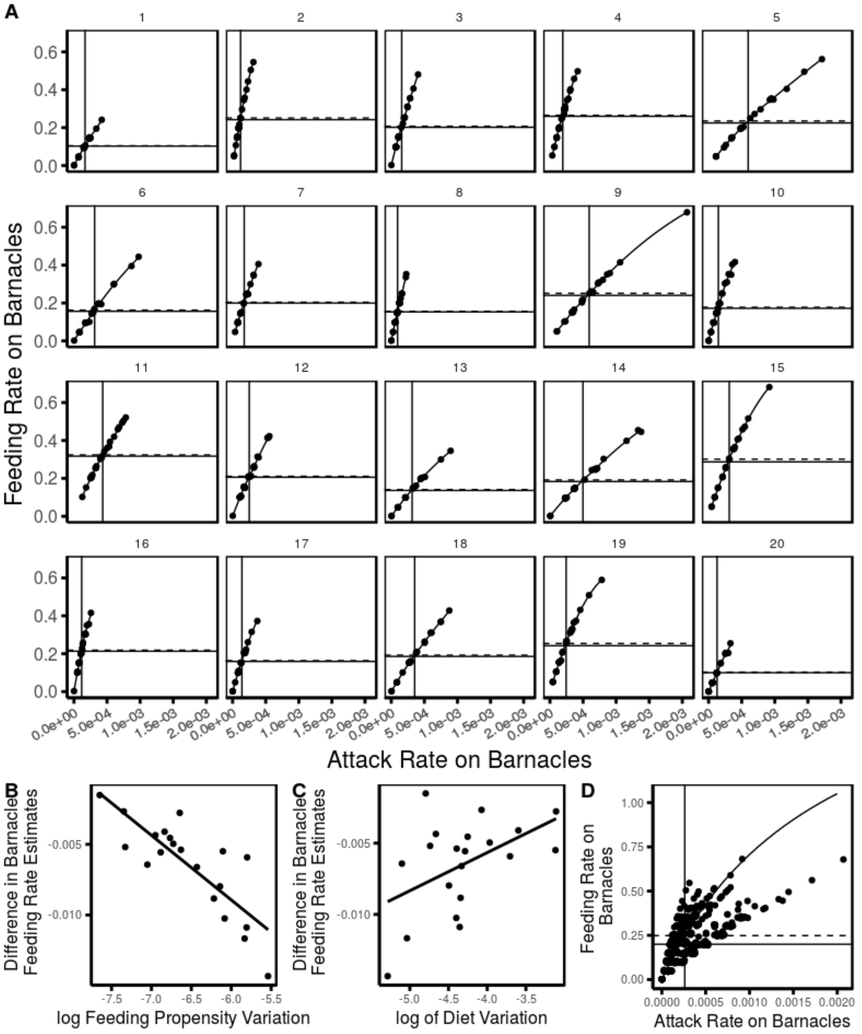

Figure 4.5: Individuals across cages vary in their attack and feeding rates on barnacles (**A**). Attack rate variation among individuals leads to differences between the mean feeding rates of individuals (the solid horizontal lines) and the mean feeding rate (the dotted horizontal lines, which may overlap the solid horizontal lines) evaluated at the mean attack rate (the solid vertical lines) due to Jensen's inequality. The differences in the feeding rate estimates become more negative (greater effect of Jensen's inequality) as the variation among individuals in feeding propensity increases (**B**) and less negative as the amount of diet variation increases (**C**). At the experiment scale, variation among individuals in attack rates coupled with variation across cages in prey densities again leads to differences between the mean feeding rates across individuals (the solid horizontal line) and the mean feeding rate (the dashed horizontal line) evaluated at the mean attack rate across individuals (the solid vertical line; **D**). The curved line in **D** gives the relationship between attack rates and feeding rates on barnacles at the mean prey densities across cages.

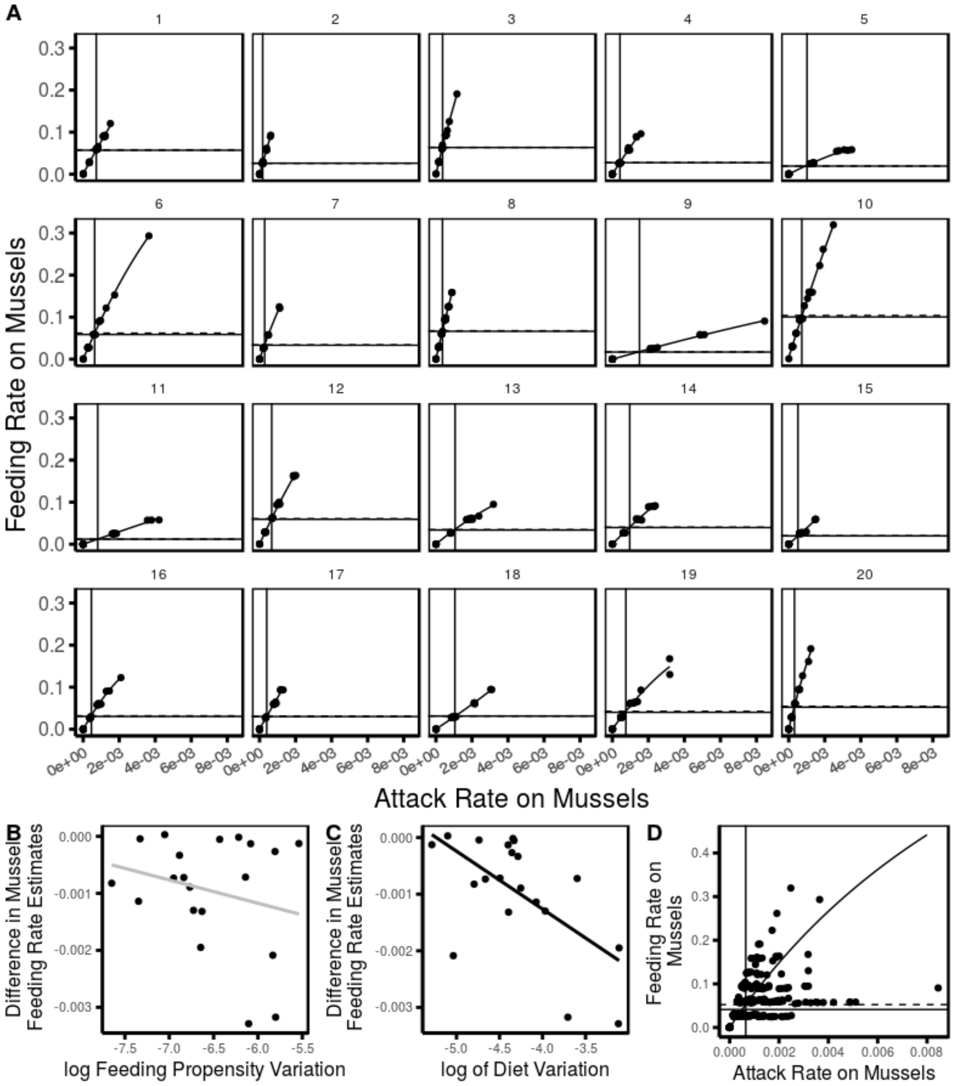

Figure 4.6: Individuals across cages vary in their attack and feeding rates on mussels (**B**). Attack rate variation among indivdiuals leads to differences between the mean feeding rates of invdividuals (the solid horizontal lines) and the mean feeding rate (the dotted horizontal lines, which may overlap the solid horizontal lines) evalutated at the mean attack rate (the solid vertical lines) due to Jensen's inequality. The differences in feeding rate estimates shows no relationship with variation in feeding propensity (**B**) but become more negative (greater effects of Jensen's inequality) with increasing individual diet variation (**C**). At the experiment scale, variation among individuals in attack rates coupled with variation across cages in prey densities again leads to differences between the mean feeding rates across individuals (the solid horizontal line) and the mean feeding rate (the dashed horizontal line) evaluated at the mean attack rate across individuals (the solid vertical line; **D**). The curved line in **D** gives the relationship between attack rates and feeding rates on mussels at the mean prey densities across cages.

5 Conclusions

Variation among individuals in many traits is widespread, including diet. The phenomenon in which diet differences among individuals cannot be attributed to obvious differences among individuals has been termed individual diet specialization. Emprical surveys of predator populations have suggested that this phenomenon is widespread (Araújo et al., 2011; Bolnick et al., 2003), while theoretical studies have suggested that diet specialization may have important consequences for populations and communities (Bolnick et al., 2011; Hart et al., 2016; Patel and Schreiber, 2015; Schreiber et al., 2011). In this dissertation I have attempted to address some outstanding issues in the litterature regarding the causes, consequences, and estimation of diet specialization. Overall, my dissertation simultaneously provides both critiques and support for some ideas in the field and suggests some ways forward.

One of the motivations underlying the study of individual diet specialization has been the large number of studies suggesting that individual diet specialization is commonplace in a variety of taxa and biomes (Araújo et al., 2011; Bolnick et al., 2003). However, one concern is that the magnitude of diet specialization may be overestimated in these studies. In Chapter 3, I showed that current methods for estimating diet specialization are biased towards the overestimation of diet specialization. This overestimation is particularly severe when sample sizes per individual are low or are heterogeneous among individuals which is a common feature of diet data. This suggests that diet specialization may not be as widespread as previously purported. Future studies should guard against this overestimation by either adopting methods such as those presented in Chapter 3 with shrinkage estimators (Coblentz et al., 2017) or by excluding individuals with low sample sizes. However, there are likely biological situations in which diet specialization itself lead to some individuals having low sample sizes. For example in some fishes, individuals differ in their degree of piscivory (Svanbäck et al., 2015). Piscivorous individuals will show low sample sizes while individuals consuming invertebrates will have higher sample sizes. This suggests that, in general, the adoption of hierarchical models are likely the better solution in many systems.

An additional concern beyond overestimation of diet specialization is that many studies may not be estimating diet specialization in the strict sense. In the seminal paper defining diet specialization, Bolnick et al. (2003), individual specialists were defined as ‘an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete (a priori) morphological group.’ However, it is difficult to assess whether many studies of diet variation are able to determine whether an individuals ‘niche is substantially narrower’ from their samples of individuals diets. In fact, in a companion paper, Bolnick et al. (2002), several of the issues involved in inferring diet specialization were outlined. For example, ‘true’ diet specialization should be temporally consistent and should not be the product of differential resource availability for individuals (Araújo et al., 2011; Bolnick et al., 2002). Although several studies have provided evidence for diet specialization in this strict sense, the majority do not. I suggest that the term diet specialization be limited to the cases in which there is evidence for consistent limited diets of individuals relative to the population and when this is not the case diet variation be referred to as simply diet variation.

Despite these concerns, the estimation of variation's effect on feeding rate estimates through Jensen's inequality in Chapter 4 suggests that diet variation that does not meet the strict definition of diet specialization can still have important ecological effects. As shown in Chapter 4, diet variation among whelks was unlikely due to specialization. However, diet variation still influenced the attack rate variation among indviduals. This variation in attack rates interacting with nonlinear functional responses altered the perceived strength of predator-prey interactions. Furthermore, the variation among individuals interacted with variation in resource densities to produce greater differences in the perceived strength of interactions. Overall, this suggests that diet variation that is not specialization is still ecologically relevant. Therefore, research into causes and consequences of variation caused by mechanisms not leading to specialization, such as stochastic foraging or habitiat/resource availability, is still important.

In terms of systems exhibiting 'true' diet specialization, my dissertation provides some insight into ecological features of consumer-resource interactions that are likely to produce disruptive selection, a potential ultimate cause of diet specialization. First, disruptive selection requires that resources require sufficiently different traits or behavior of the consumers to use well (Patel and Schreiber (2015); Schreiber et al. (2011), Chapter 2). Second, disruptive selection should be stronger when handling times and interference are low for individuals with the highest attack rates. However, this is dependent on the nature of interference among consumers. Lastly, Chapter 2 suggests that considering the effects of traits on multiple features of consumer-resource interactions is important in determining the evolution of traits. In terms of disruptive selection, the theory in Chapter 2 suggests that disruptive selection is most likely in traits that alter the ability of an individual to use particular resources, decrease the handling time of that individual on a consumer, and decrease the interference experienced by the individual.

In summary, my dissertation suggests several ways forward for the study of diet specialization. First, the definitions used in defining diet specialization and the evidence used to provide support for diet specialization within systems are often mismatched. However, my results also suggest that variation that may not meet the definition of diet specialization is nonetheless important. Furthermore, this suggests that the development of theory and empirical work into understanding alternative causes and consequences of variation in diet are also important. This dissertation also provides some insight into which systems should be targeted in attempting to understand diet specialization. In particular, systems likely to exhibit diet specialization due to disruptive selection on resource-use traits may eventually provide model systems in which to examine the potential consequences of diet specialization. Lastly, by providing an example of a way in which to empirically measure a consequence of diet variation, in particular the effect of variation and nonlinear functions through Jensen's inequality, I hope that my research will increase the attention given to understanding what effects this variation may have and the situations in which variation is most likely to alter our understanding species interactions and ecological and evolutionary dynamics.

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APPENDIX

Appendix A Estimates of diet specialization using individual to individual comparisons

In the main text, we focus on indices of diet specialization that compare individual diet proportions to those of the population. However, some authors have used indices such as the E index that compare the diet proportion of each individual to the diet proportions of each other individual to estimate diet specialization (Araújo et al., 2008; Novak and Tinker, 2015). E_i is calculated by computing the PS_i index for each individual compared to each other individual then averaging across those values and subtracting the resulting value from 1. For a group level estimate, the index E can be calculated by averaging across all of the individual E_i estimates. As defined by Araújo et al. (2008), E_i and E range from a value of 1 when there is complete diet specialization to 0 when all individuals have the same diet. However, for consistency with the other indices we report, which have lower diet specialization with increasing values, we report 1-E_i as E_i.

Because each estimate of individual diet proportions under the observed proportions method is expected to be associated with error at low sample sizes, we predicted that comparisons of individuals to individuals would be associated with higher overestimation for the observed proportions method than the Bayesian hierarchical method. Hence, we ran simulations where the true values of E_i were known and then estimated E_i using the observed proportions and Bayesian hierarchical methods under various sample sizes per individual and with heterogeneous sample sizes among individuals.

We used simulations to compare the true E_i values to those estimated by the observed proportions and Bayesian hierarchical methods under different sample sizes per individual and with variation in sample sizes among individuals. First, we investigated the effects of sample size with all indviduals having the same number of observations. We simulated 50 populations of 100 individuals feeding across four prey types with each individual feeding on either 5, 10, 25 or 50 prey items. For each simulation, we first drew the true population diet preference from a uniform Dirichlet distribution. We then drew the Dirichlet concentration parameter from a Uniform(1,10) distribution. Using the Dirichlet distribution defined by the population preference and the concentration parameter, we then randomly drew preferences for each individual. Then, we used the individual level preferences to draw multinomial data for each individual with the appropriate number of observations. Using the individual preferences, we then calculated the true values of E_i and estimated E_i using the observed proportions method in the R package 'RInSp' with the function Eindex (Zaccarelli et al., 2013) and a two level Bayesian hierarchical model (eqns. 1-4 in the main text) implemented in BUGS using the R package 'R2OpenBUGS' (Lunn et al., 2000; Sturtz et al., 2005). To obtain the Bayesian posterior estimates we used a burn-in period of 200 iterations followed by 1000 sampling iterations from every fifth iteration of the model for each of three chains. The burn-in period, number of samples, and thinning were chosen after applying the model to several simulated data sets and examining the convergence of the model, the mixing of the chains, and the autocorrelation between iterations within chains. To compare the accuracy with which the two methods estimated E_i, we plotted the true and estimated values against one another and calculated the percentage of negative residuals (i.e. the percentage of points falling below the 1:1 line). If a method over and underestimates a value at equal frequencies, we would expect to have 50% negative residuals. Therefore, we interpret values of negative residuals above 50% as a measure of the extent to which a method overestimates diet specialization.

To examine the accuracy with which the observed proportions and Bayesian hierarchical methods estimated E_i with heterogeneous sample sizes among individuals, we simulated diets of individuals with known preferences. The methods for simulating and analyzing the effects of heterogeneity in sample sizes across individuals was the same for the analysis of the effects of sample sizes when all individuals had the same sample size with one exception. Rather than the sample sizes per individual being predetermined, each individual's sample size was determined by a random draw from one of three beta distributions multiplied by 100 and rounded to the next highest integer. The three beta distributions (Beta(1, 1), Beta(0.5, 1), and Beta(1, 0.5)) were chosen to represent three possible cases for the distribution of sample sizes among individuals: a uniform distribution of sample sizes, a distribution of sample sizes skewed towards many individuals having few observations, and a distribution of sample sizes skewed towards many individuals having many observations.

As expected, the observed proportions method consistently overestimated diet specialization at low sample sizes (A.1) and when sample sizes among individuals were heterogeneous (A.2). Although the observed proportions estimates of E_i were estimated more accurately as the sample size per individual increased to 50, the percentage of overestimation by the maximum likelihood method remained high (A.1; % negative residuals, n=5, 91.5%; n=10, 86.1%; n=25, 78.4%; n=50, 71.0%). In contrast, the Bayesian hierarchical method by a sample size of 10 prey items per individual began to over- and underestimate the values of E_i at a nearly equal frequency (A.1; % negative residuals, n=5, 41.3%; n=10, 48.4%; n=25, 48.5%; n=50, 49.0%). With heterogeneous sample sizes among individuals, the maximum likelihood method performed poorly by overestimating diet specialization in all three of the cases examined (A.2). The overestimation was highest for the case in which most individuals had few observations (92.8% negative residuals). However, significant overestimation still occurred for uniform distributions of sample sizes across individuals (80.8% negative residuals) and when sample sizes were skewed towards many observations per individual (74.1% negative residuals). Heterogeneity in sample sizes among individuals had less influence on the Bayesian hierarchical method in terms of over- and underestimation of diet specialization as the percentage of negative residuals ranged from 52.0% in the case of sample sizes skewed towards few observations per individual to 47.9% in the case of a uniform distribution of observations per individual.

Our simulations show that indices of diet specialization that use individual to individual comparisons of diet proportions rather than individual to population diet proportions using the observed proportions method also overestimate diet specialization when sample sizes per individual are low or heterogeneous. The overestimation of the E_i index using the observed proportions method is larger than that of the indices using the individual to population estimates. This is because at low sample sizes the maximum likelihood estimates of the diet proportions are associated with error. In the case of the E_i index, one is comparing estimates of diet proportions that are each associated with error. In the case of indices that compare individual to population level estimates, the population level estimates are associated with higher sample sizes and therefore less error. Thus, the observed proportions method overestimates diet specialization more often with indices that compare individual-level estimates. The estimates of E_i using the Bayesian hierarchical method were associated with nearly equal under- and overestimation. Again, this is because of the shrinkage estimators provided by hierarchical methods which perform better at low sample sizes but converge to maximum likelihood estimates at large sample sizes. As group level estimates constructed from E_i simply take the average of the E_i values, these estimates follow the same general pattern of overestimation for the maximum likelihood method (not shown).

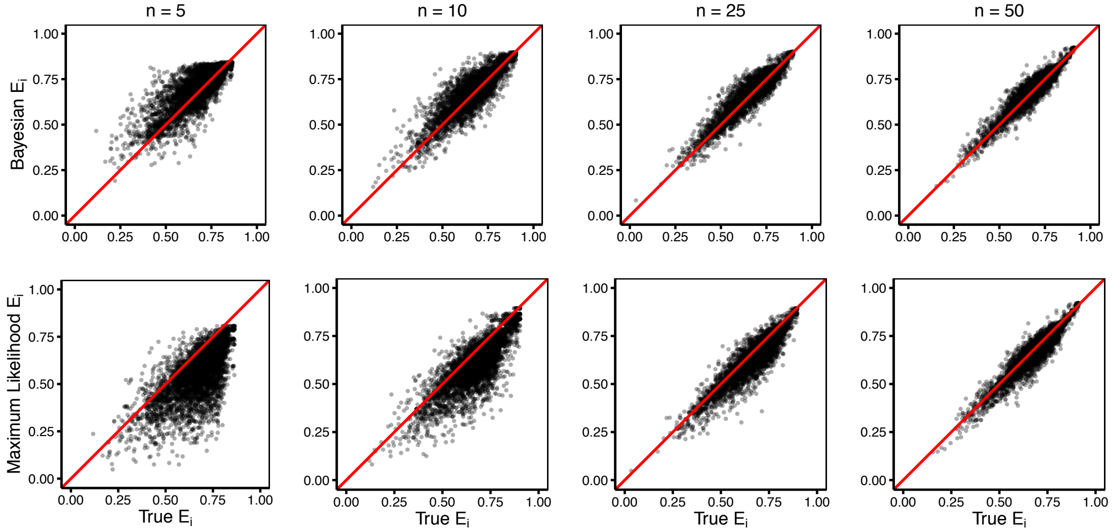


Figure A.1: The maximum likelihood method using the observed diet proportions of individuals tends to overestimate E_i when sample sizes per individual are low. The estimates become more accurate as the sample size per individual increases, but the method still tends to overestimate E_i values. The Bayesian hierarchical method shows equal over- and underestimation of E_i for sample sizes ten or larger. Estimates of E_i from simulated data are plotted against the true E_i values for 5, 10, 25, and 50 observations per individual. The red line in each graph reflects the line of equality between the true and estimated values

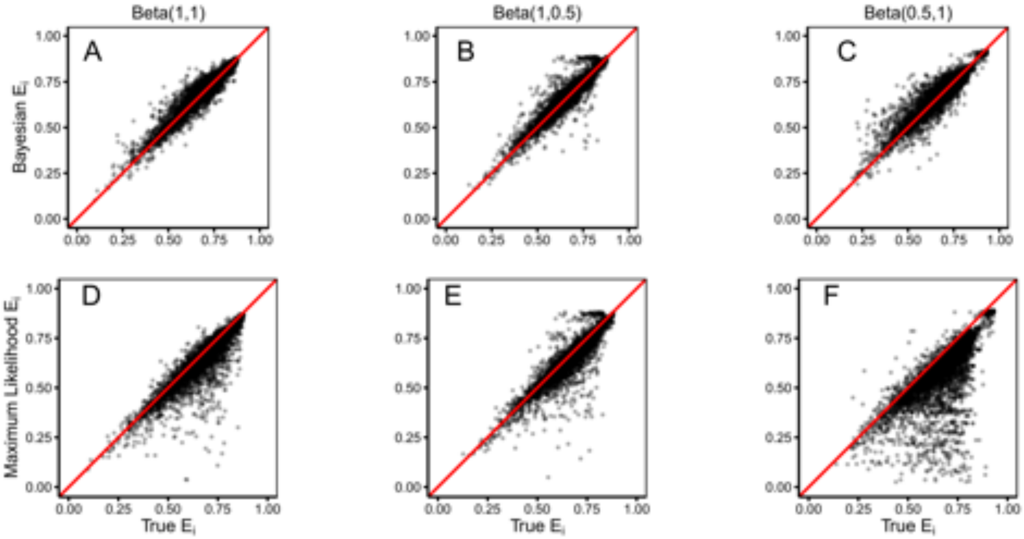


Figure A.2: Simulations with varying numbers of prey per predator individual following one of three distributions – (**A**,**D**) a uniform distribution, (**B**,**E**) a distribution with most individuals having a large number of observations, or (**C**,**F**) a distribution with most individuals having few observations – show that the maximum likelihood method overestimates specialization when the number of prey per individual varies across individuals. By contrast, the Bayesian hierarchical models estimate prey proportions accurately in all situations. The red line in each graph is the line of equality between the true and estimated E_i values.

Appendix B Details for the simulation of data and the analysis of simulated data

B.1 Estimating individual diet specialization across sample sizes per individual

For each of the 500 populations simulated at 5, 10, 25, and 50 observations per individual, we first drew a single sample from a uniform Dirichlet distribution to determine the population diet preferences. To allow for differences among populations in the amount of diet specialization, we then drew a concentration parameter for the population from a Uniform(1,10) distribution. Then, for each of the 100 individuals in the population, we drew the individual's diet preferences from the Dirichlet distribution defined by the random population preferences and concentration parameter. Each individual was then given the appropriate number of observations from a random draw from a multinomial distribution with the probabilities of each prey item being observed defined by the individual's prey preferences. The individual's true PS_i value was calculated using the true population and individual prey preferences.

The simulated data was first analyzed using the Bayesian hierarchical method implemented in OpenBUGS through the package 'R2OpenBUGS' (Lunn et al., 2000; Sturtz et al., 2005) with the following model,

$$\vec{\mathrm{y}}_i \sim \mathrm{Multinomial}(\vec{\mathrm{p}}_i, \mathrm{n}_i) \tag{B.1}$$

$$\vec{\mathrm{p}}_i \sim \mathrm{Dirichlet}(\vec{\mathrm{q}} \times \mathrm{w}) \tag{B.2}$$

with priors,

$$\vec{\mathrm{q}} \sim \mathrm{Dirichlet}(\vec{1}) \tag{B.3}$$

$$\mathrm{w} \sim \mathrm{Uniform}(0.1, 30) \tag{B.4}$$

where $\vec{y_i}$ 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, $\vec{p_i}$ is a vector of the individual's diet proportions, $\vec{q}$ is a vector of the population's diet proportions, and w is the concentration parameter. We chose uniform priors for the model to minimize the influence of priors on the resulting posterior distributions. We used a burn-in period of 200 iterations followed by 1000 sampling iterations from every fifth iteration of the model for each of three chains. The burn-in period, number of samples and thinning were chosen from results of applying the model to several simulated data sets and examining the convergence of the model, the mixing of chains, and the autocorrelation between iterations within chains. For each iteration, PS_i was calculated so that we could estimate the variance of PS_i. After fitting the model, we saved the median values of the posterior for PS_i of each individual and calculated the variance of PS_i from the posterior distribution of PS_i.

We then estimated PS_i using the observed proportions method with the R package 'RInSp' (Zaccarelli et al., 2013). We used the function 'PSicalc' with the population diet determined by taking the average of the diet proportions of individuals so that the results between the observed proportions and Bayesian hierarchical methods would be comparable. After estimating PS_i and the variance of PS_i, the values were saved.

B.2 Estimating individual specialization with heterogeneity in sample sizes among individuals

The simulation and analysis methods for estimating individual diet specialization with heterogeneity in sample sizes among individuals was the same as the methods for simulation and analysis for estimating diet specialization across different sample sizes per individual with one exception. Rather than the sample sizes per individual being predetermined, each individual's sample size was determined by a random draw from one of three beta distributions multiplied by 100 and rounded to the next highest integer. The three beta distributions (Beta(1, 1), Beta(0.5, 1), and Beta(1, 0.5)) were chosen to represent three possible cases for the distribution of sample sizes among individuals: a uniform distribution of sample sizes, a distribution of sample sizes skewed towards many individuals having few observations, and a distribution of sample sizes skewed towards many individuals having many observations (Figure B.1).

B.3 Estimating individual specialization at the population level

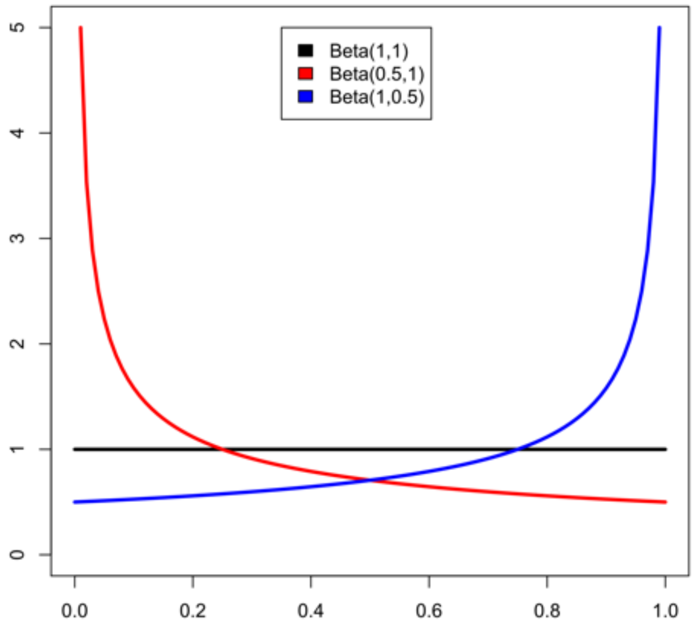
To compare estimates of individual specialization at the population level, we estimated three indices of relative diet specialization at the group level: IS, WIC/TNW, and $\ln(w)$. IS is defined as the average of the PS_i values within the group (see main text for the definition of PS_i). WIC/TNW is based on equations for within-species niche partitioning derived by Roughgarden (1979). This method, when applied to discrete diet data, decomposes the diet data into a Within-Individual Component (WIC), a Between-Individual Component (BIC), and the Total Niche Width (TNW) using the Shannon Diversity Index of the observed diet proportions of each prey item as an analog for variance. The three components are given by

$$\begin{aligned}
\mathrm{WIC} &= \sum_i (p_i \times -\sum_j p_{ij} \ln p_{ij}) && \text{(B.5)}\\
\mathrm{TNW} &= -\sum_j v_j \ln v_j && \text{(B.6)}\\
\mathrm{BIC} &= \mathrm{TNW} - \mathrm{WIC}, && \text{(B.7)}
\end{aligned}$$

where p_i is the proportion of the total number of the aggregated population's prey that are consumed by individual i, p_{ij} is the proportion of prey type j in the diet of individual i, and v_j is the proportion of prey type j in the diet of the population. The WIC/TNW index ranges from 0 to 1, where a value of 0 represents no overlap in the diet of individuals and a value of 1 represents total overlap in the diets of all individuals. Lastly, ln(w) is the natural log of the concentration parameter of the Dirichlet distribution describing the population diet.

The basic process of simulating data for the analysis of the relative diet specialization of populations was the same as the process of simulating data for the analysis estimating diet specialization across different sample sizes per individual, with some exceptions. First, for greater coverage for evaluating the accuracy with which the Bayesian hierarchical model estimates ln(w), the concentration parameter was drawn from a Uniform(0.5, 10) distribution. Sample sizes per individual were drawn from a Uniform(3, 50) distribution and rounded to the nearest integer. Lastly, to estimate WIC/TNW, the function 'WTdMC' was used with the population preferences estimated as the average observed proportions of individuals in the population (Zaccarelli et al., 2013). After the analyses, we saved the true and estimated values of w, WIC/TNW, and IS.

Figure B.1: Probability density functions (pdf's) of the three Beta distributions from which individual sample sizes were drawn for simulating heterogeneity in sample sizes among individuals.



Appendix C Details of the process used to estimate diet specialization from empirical data

C.1 American alligator data

To determine the most appropriate Bayesian hierarchical model for analyzing the alligator gut content data, we fit three different models to the data and then used the Widely Applicable Information Criterion (or Watanabe-Akaike Information Criterion; WAIC) to select among the three models (Gelman et al., 2014; Vehtari et al., 2016; Watanabe, 2010). The models we examined were: 1) all individuals analyzed at the same hierarchical level, 2) individuals nested within site, and 3) individuals nested within sex and site. The models are given below:

C.1.1 Individuals at the same hierarchical level

$$\vec{\mathrm{y}}_i \sim \mathrm{Multinomial}(\vec{\mathrm{p}}_i, \mathrm{n}_i) \tag{C.1}$$

$$\vec{\mathrm{p}}_i \sim \mathrm{Dirichlet}(\vec{\mathrm{q}} \times \mathrm{w}) \tag{C.2}$$

with priors,

$$\vec{\mathrm{q}} \sim \mathrm{Dirichlet}(\vec{1}) \tag{C.3}$$

$$\mathrm{w} \sim \mathrm{Uniform}(0, 30) \tag{C.4}$$

where, $\vec{\mathrm{y}}_i$ is the observed diet of alligator i, $\vec{\mathrm{p}}_i$ is the vector of estimated preferences for alligator i, n_i is the number of prey items observed in the gut of alligator i, $\vec{\mathrm{q}}$ is the vector of the estimated population preference, w is the concentration parameter of the Dirichlet distribution describing the distribution of alligator preferences, and $\vec{1}$ is a vector of ones the same length as the total number of prey items observed for the population.

C.1.2 Individuals nested within site

$$\vec{\mathrm{y}}_{ik} \sim \mathrm{multinomial}(\vec{\mathrm{p}}_{ik}, \mathrm{n}_{ik}) \tag{C.5}$$

$$\vec{\mathrm{p}}_{ik} \sim \mathrm{Dirichlet}(\vec{\mathrm{q}}_k \times \mathrm{w}_k) \tag{C.6}$$

$$\vec{\mathrm{q}}_k \sim \mathrm{Dirichlet}(\vec{\mathrm{q}} \times \mathrm{w}) \tag{C.7}$$

with priors,

$$
\begin{aligned}
\mathrm{w}_k &\sim \text{Uniform}(0, 30) && \text{(C.8)}\\
\mathrm{w} &\sim \text{Uniform}(0, 30) && \text{(C.9)}\\
\vec{\mathrm{q}} &\sim \text{Dirichlet}(\vec{1}) && \text{(C.10)}
\end{aligned}
$$

where $\vec{\mathrm{y}}_{ik}$ is the observed diet data for alligator i from site k, $\vec{\mathrm{p}}_{ik}$ is the vector of estimated preferences for alligator i from site k, n_{ik} is the number of prey items observed in the gut of alligator i from site k, $\vec{\mathrm{q}}_k$ is the vector of the average preferences for alligators in site k, w_k is the concentration parameter of the Dirichlet distribution describing the distribution of alligator preferences within site k, $\vec{\mathrm{q}}$ is the vector of the average prey preferences across all of the sites, and w is the concentration parameter of the Dirichlet distribution describing the site level alligator preferences, $\vec{1}$ is a vector of ones the same length as the total number of prey items observed for the population.

C.1.3 Individuals nested within sex and site

$$
\begin{aligned}
\vec{\mathrm{y}}_{isk} &\sim \text{multinomial}(\vec{\mathrm{p}}_{isk}, \mathrm{n}_{isk}) && \text{(C.11)}\\
\vec{\mathrm{p}}_{isk} &\sim \text{Dirichlet}(\vec{\mathrm{q}}_{sk} \times \mathrm{w}_{sk}) && \text{(C.12)}\\
\vec{\mathrm{q}}_{sk} &\sim \text{Dirichlet}(\vec{\mathrm{q}}_k \times \mathrm{w}_k) && \text{(C.13)}\\
\vec{\mathrm{q}}_k &\sim \text{Dirichlet}(\vec{\mathrm{q}} \times \mathrm{w}) && \text{(C.14)}
\end{aligned}
$$

with priors,

$$\mathrm{w}_{sk} \sim \mathrm{Uniform}(0,30) \tag{C.15}$$

$$\mathrm{w}_{k} \sim \mathrm{Uniform}(0,30) \tag{C.16}$$

$$\mathrm{w} \sim \mathrm{Uniform}(0,30) \tag{C.17}$$

$$\vec{\mathrm{q}} \sim \mathrm{Dirichlet}(\vec{1}) \tag{C.18}$$

where $\vec{\mathrm{y}}_{isk}$ is the observed diet of alligator i of sex s from site k, $\vec{\mathrm{p}}_{isk}$ is the vector of estimated preferences for alligator i of sex s from site k, n_{isk} is the number of prey in the gut of alligator i of sex s from site k, $\vec{\mathrm{q}}_{sk}$ is the estimated preference of sex s from site k, w_{sk} is the concentration parameter of the Dirichlet distribution describing the distribution of individual alligator preferences of sex s from site k, $\vec{\mathrm{q}}_{k}$ is the estimated preference across sexes from site k, w_{k} is the concentration parameter of the Dirichlet distribution describing the distribution of prey preferences of sexes from site k, $\vec{\mathrm{q}}$ is the vector of the average prey preferences across all of the sites, and w is the concentration parameter of the Dirichlet distribution describing the site level alligator preferences, $\vec{1}$ is a vector of ones the same length as the total number of prey items observed for the population.

C.1.4 Process of model fitting and selection

For each of the three models, we used the program 'jags' through R using the package 'rjags' to fit the model to the data (Plummer, 2003, 2016). To avoid numerical computation issues 0.05 was added to each term of the Dirichlet distributions (M. Plummer, *Pers. communication*). We used a burn-in period of 100,000 iterations to avoid drawing samples not from the posterior distribution of the parameters. After the burn-in period, 2000 samples were collected per parameter by sampling once every 100 iterations. We used three simultaneous Markov chains for sampling. To ensure that the model had converged and that the chains had adequately mixed, we visually inspected plots of the samples. To compare across the models, we used the R package 'loo' to calculate WAIC from a matrix of the pointwise log-likelihood values at each iteration of the model (Vehtari et al., 2016). The WAIC values suggested that the model of alligators nested within site provided the most parsimonious result.

C.2 Whelk data

To determine the most appropriate Bayesian hierarchical model to analyze the whelk data, we again used WAIC to choose among three models. For the whelk data, the models are identical to those used to analyze the alligator data, but with differences in interpretation. The three models we examined were all individuals at the same hierarchical level, individuals nested within size class, and individuals nested within size class and site.

We fit each model to the whelk data using the program ‘jags’ implemented in R using the package ‘rjags’ (Plummer, 2003, 2016). To avoid numerical computation issues 0.05 was added to each term of the Dirichlet distributions (M. Plummer, *Pers. communication*). We used a burn-in period of 10,000 iterations and then sampled the posterior of each distribution 2,000 times by drawing a sample once every 100 iterations. We used three simultaneous Markov chains for sampling. To ensure that the model had converged and that the chains had adequately mixed, we visually inspected plots of the samples. Using WAIC, we found that the model containing all individuals within the same hierarchical level was the most parsimonious model.

Appendix D Chapter 3: Supplementary figures

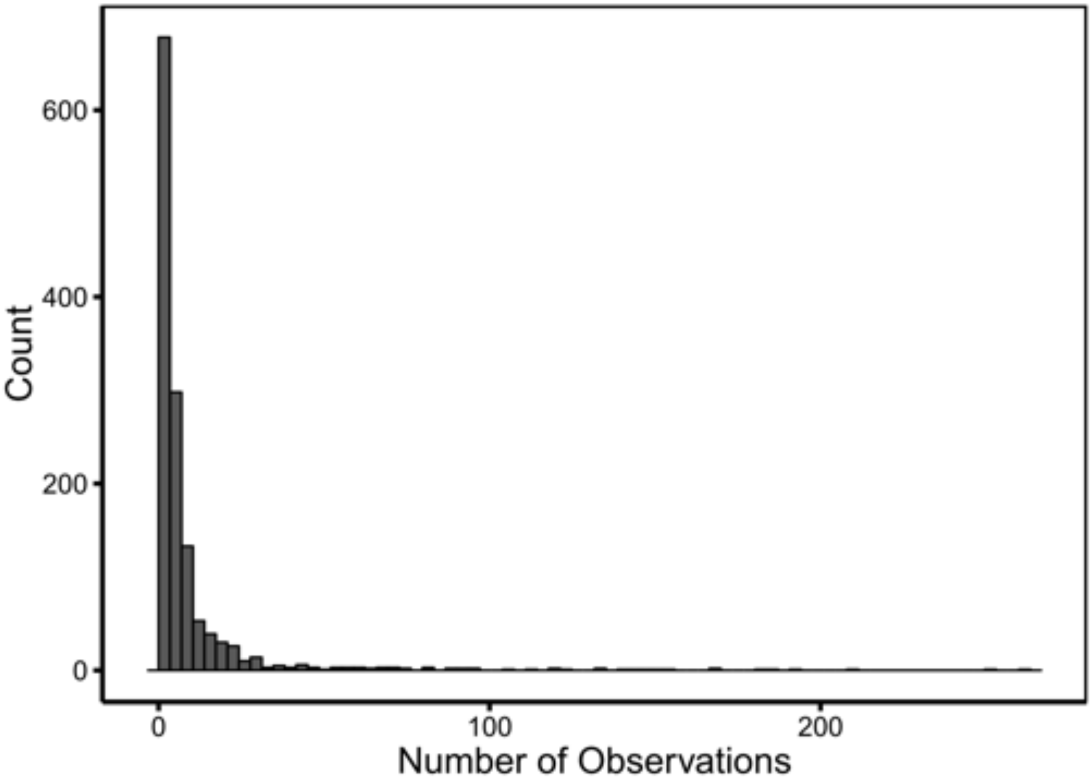


Figure D.1: The distribution of individual sample sizes for American alligators with less than 500 observations.

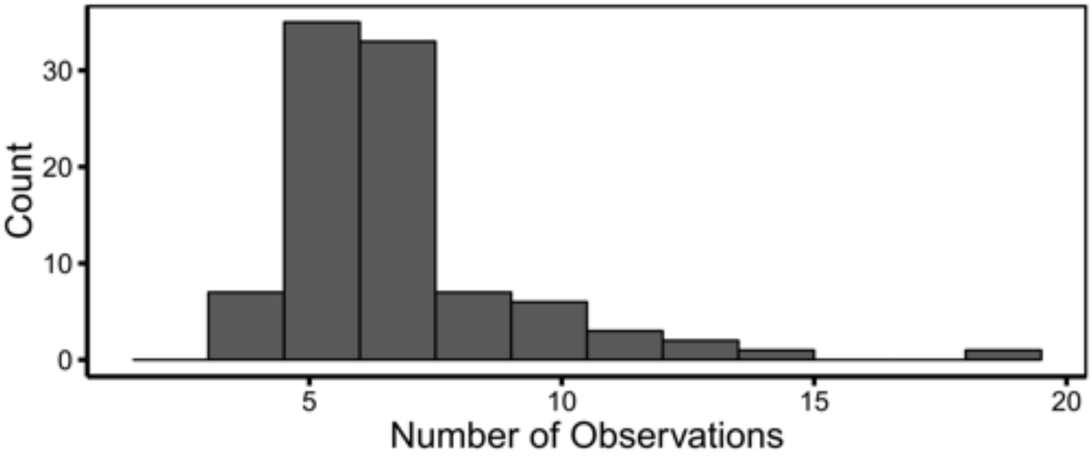


Figure D.2: The distribution of the number of feeding observations per individual whelk.

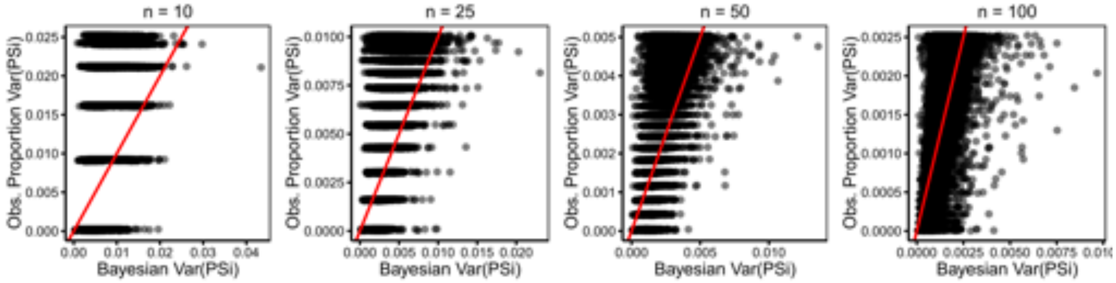


Figure D.3: The estimated variance of PS_i from the Bayesian hierarchical method and the observed proportions method. The red line represents the line of equality between the estimates from the Bayesian hierarchical method and the observed proportions method.

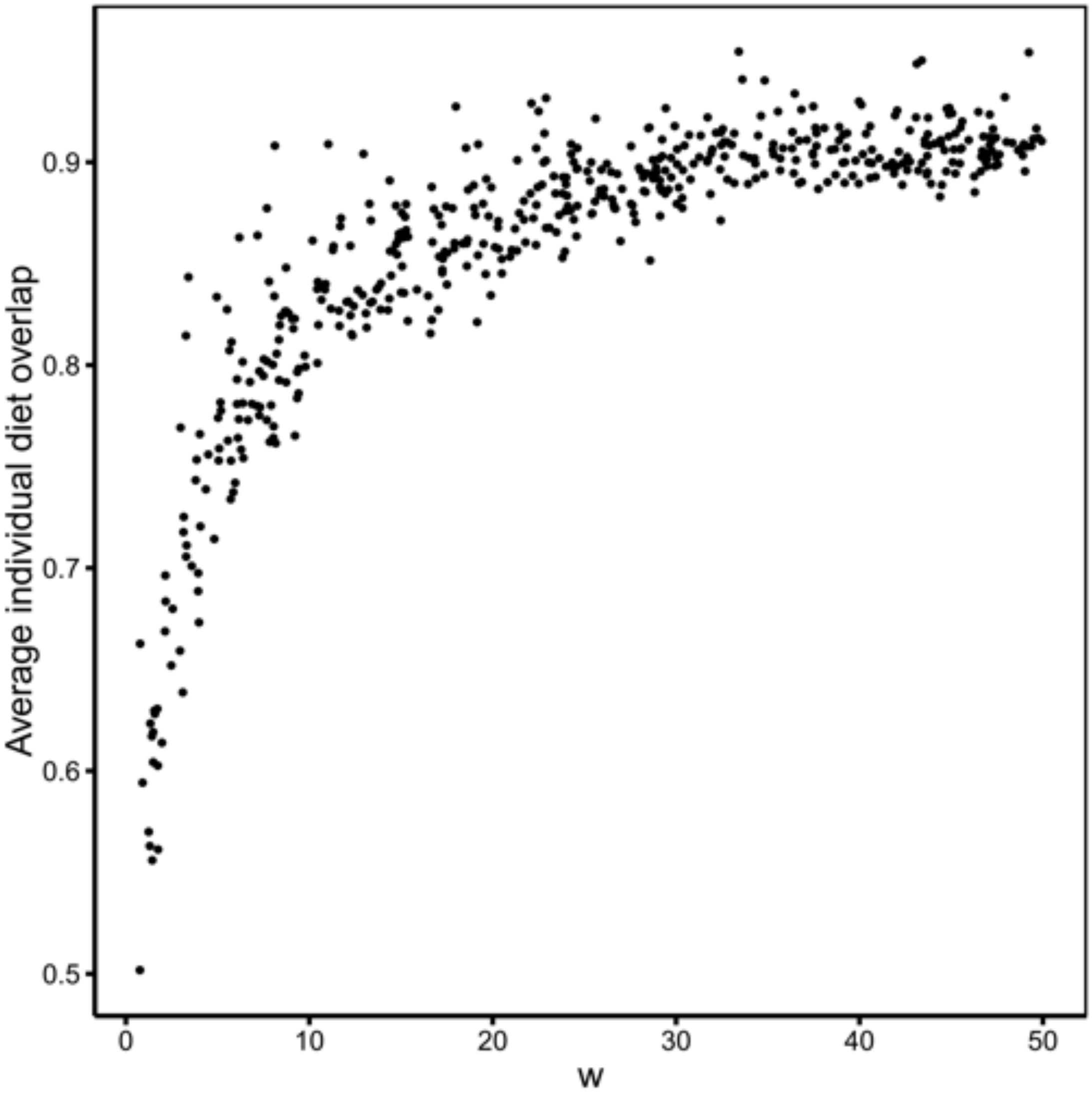


Figure D.4: We justify using a maximum of 30 for the uniform prior in our analyses because the relationship between the mean overlap of individuals within a population and the concentration parameter of the Dirichlet distribution asymptotes at approximately 30. Thus considering higher values for the maximum of the prior on the concentration parameter is unlikely to qualitatively influence the results because this range covers the biologically relevant variation in diet overlap.

Appendix E Laboratory experiment to estimate whelk handling times on barnacles and mussels

E.1 Introduction and Methods

Accounting for bias in estimates of individual diets in the whelk, *Nucella ostrina*, and determining the attack rates of individual whelks requires estimates of whelk handling times on barnacles, *Balanus glandula*, and mussels, *Mytilus trossulus*. To determine the handling times of whelks on barnacles and mussels, we used a laboratory experiment to parameterize a regression model quantifying the relationship between handling times on the prey, predator size, prey size, and the method by which whelks handled prey. We performed the laboratory experiment in flow-through aquaria within a temperature controlled room at the Hatfield Marine Science Center (Newport, OR, USA). In each of the aquaria, we placed a single whelk between 4-21mm into an aquarium with several barnacles between 1-5mm or several mussels from 4-25mm. All whelks and prey were collected from the same site as the caging experiment, Yachats, OR. Security cameras mounted above the aquaria filmed the whelks and we monitored the whelks several times daily to determine whether or not the whelk individuals were feeding. Once a whelk finished feeding, we used the video to determine the start and stop time of the feeding event. We also examined the prey item to determine how the whelk fed on the prey item (drilled or pried for barnacles, drilled the valve, drilled through the edge of the valve, or pried for mussels) and the percent of flesh remaining in the prey item.

To quantify the relationships between handling times, predator size, prey size, and the method of handling, we used Bayesian regression. For barnacles, we used a linear mixed effects model because most individuals had more than one measurement and we wanted to account for the non-independence of observations from the same individual. We also log transformed handling time, predator size, and prey size. Any observations in which there was more than 10% of flesh remaining in the barnacle were thrown out. For mussels, most individuals did not have repeat observations, so we used a simple linear regression treating the few repeat observations as independent measurements. As with the barnacle model, we log transformed handling time, prey size, and predator size. For mussels, any observations with more than 25% of the flesh remaining was thrown out. We fit both models using 'Stan' through the R package 'rstanarm'. For the barnacle model, we placed a Normal($\mu = 0$, $\sigma = 10$) prior on the intercept, a Normal(0, 2.5) prior on each of the coefficients, a half-cauchy distribution with location equal to zero and scale equal to five on the residual variance, and a uniform LKJ distribution on the random effects covariance matrix. For the mussel model, we placed a Normal(0, 10) prior on the intercept, Normal(0, 5) priors on the coefficients, and half-cauchy distribution with location equal to zero and scale equal to five on the residual variance. For each model, the posterior distribution was approximated with 1,000 samples from four Markov chains each after a burn-in period of 1,000 samples. We examined trace plots and the Gelman-Rubin statistics to assure that the chains had converged (Gelman and Rubin, 1992).

E.2 Results

We analyzed 163 handling times on barnacles across 68 individuals with an average handling time of 0.6 days. Whelk handling times on barnacles increased with prey size, decreased with predator size, and were lower when whelks pried barnacles rather than drilling them (Table E.1, Figure E.1). For mussels, we analyzed 46 handling times across 40 individuals with an average handling time of 1.68 days. Whelk handling times on mussels also increased with prey size, decreased with predator size, and decreased nearly the same amount if whelks pried or drilled at the edge of the mussels valves relative to drilling through the side of the valve (Table E.2, Figure E.2). The median regression coefficient estimates in Tables E.1 and E.2 are the coefficients used to estimate the handling time of each feeding observation in the caging experiment. The average handling times across the estimates for each feeding observation provided the characteristic estimates handling time across the experiment.

Parameter	Median	95% Credible Interval
Intercept	0.312	(-0.48,1.05)
log Whelk Size	-0.24	(-0.55,0.08)
log Barnacle Size	0.61	(0.465,0.847)
Barnacle Pried	-1.1	(-1.46, -0.62)
Residual Standard Deviation	0.5	(0.48,0.60)
Standard Deviation of Random Intercept	0.1	(0.03,0.16)

Table E.1: Estimated coefficient values and associated 95% credible intervals for the regression model of whelk handling times on barnacles

Parameter	Median	95% Credible Interval
Intercept	1.35	(0.15,2.51)
log Whelk Size	-1.38	(-1.95,-0.83)
log Mussel Size	1.12	(0.73,1.49)
Mussel Pried	-0.53	(-0.89, -0.16)
Mussel Valve Edge Drilled	-0.52	(-0.89,-0.16)
Residual Standard Deviation	0.6	(0.47,0.69)

Table E.2: Estimated coefficient values and associated 95% credible intervals for the regression model of whelk handling times on mussels

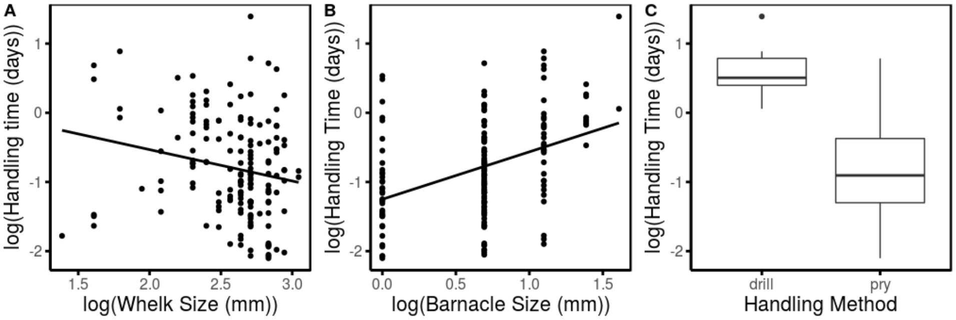


Figure E.1: The handling times of whelks on barnacles decrease with whelk size (**A**), increase with barnacle size (**B**), and are lower when whelks pry open their prey as opposed to drilling (**C**).

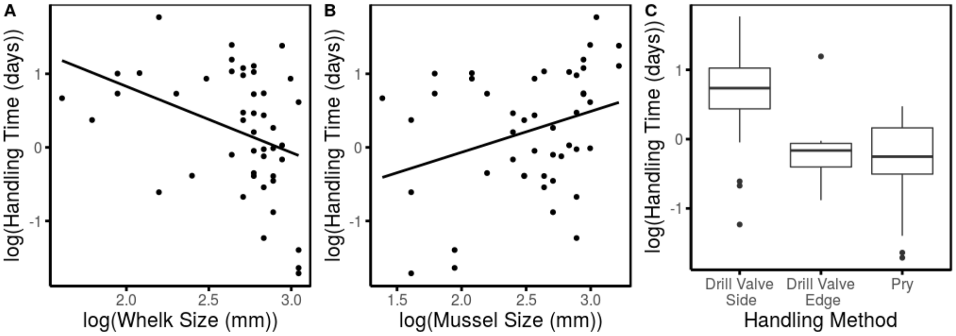


Figure E.2: The handling times of whelks on mussels decrease with whelk size (**A**), increase with mussel size (**B**), and are lower when whelks pry open or drill the edges of the valves of mussels as opposed to drilling through the sides of the valves (**C**).

Appendix F Details of the statistical models used in Chapter 4

F.1 Estimating the proportions of barnacles in individual diets and diet variation within cages

To estimate individual diets and the magnitude of diet variation among individuals, we used a Bayesian hierarchical model. We assumed that the number of barnacles in the diet of individual i in cage j, y_{ij} is binomially distributed,

$$y_{ij} \sim Binomial(p_{ij}, n_{ij}), \tag{F.1}$$

where p_{ij} is the estimated proportion of barnacles in the diet of individual i in cage j and n_{ij} is the total number of feeding observations for individual i in cage j. Because the time required to handle mussels is generally longer than the time required to handle barnacles, feeding events on mussels are more likely to be observed. To account for this bias, we performed a correction on the proportion of barnacles in an individual's diet by accounting for the differences in handling times for barnacles and mussels (for information on the handling time estimates, see the main text and Appendix E). The correction we used is,

$$p_{ij} = \frac{q_{ij} h_B}{q_{ij} h_B + (1 - q_{ij}) h_M}, \tag{F.2}$$

where q_{ij} is the corrected proportion of barnacles in the diet of individual i in cage j, h_B is the average handling time on barnacles across the experiment, and h_M is the average handling time on mussels across the experiment. After correcting for the bias due to handling time differences among prey, we assumed that the corrected estimates of the proportions of barnacles in individual's diets had a cage-level beta distribution,

$$q_{ij} \sim Beta(\alpha_j, \beta_j) \tag{F.3}$$

with shape parameters α_j and β_j. Rather than placing priors directly on the shape parameters, we instead used moment matching to place priors on the mean and variance of the Beta distribution. Defining α_j and β_j in terms of the mean of the Beta distribution, μ and the variance of the Beta distribution σ^2, gives,

$$\alpha_j = \frac{(\mu_j^2 - \mu_j^3 - \mu_j\sigma_j^2)}{\sigma_j^2} \tag{F.4}$$

and

$$\beta_j = \frac{\mu_j - 2\mu_j^2 + \mu_j^3 - \sigma_j^2 + \mu_j\sigma_j^2}{\sigma_j^2}. \tag{F.5}$$

We then placed a uniform Beta prior on the mean of the Beta distribution, μ_j and a weakly informative Gamma prior on the variance of the Beta distribution,

$$\mu_j \sim Beta(1, 1) \tag{F.6}$$

and

$$\sigma_j \sim Gamma(1, 20). \tag{F.7}$$

The model was fit using the program 'JAGS' through the R package 'rjags' (**?**). To approximate the posterior distribution, we used 2,000 samples each from three Markov chains after a burn-in period of 10,000 iterations. We verified that the Markov chains had converged by examining trace plots of the sampling and the Gelman-Rubin statistic for the parameters (Gelman and Rubin, 1992).

F.2 Optimal and stochastic foraging regressions

To compare support for the optimal and stochastic foraging hypotheses as causes of diet variation in this system, we performed regressions using the program 'Stan' through the package 'rstanarm' (Carpenter et al., 2017; Stan Development Team, 2016). The optimal foraging hypothesis was represented by a model in which the log diet variation among cages was a function of the log total density of prey, the relative density of mussels to barnacles, and their interaction. The stochastic foraging hypothesis was represented by a simple linear regression in which log diet variation was a function of only the relative density of mussels to barnacles. For both models, a Normal($\mu = 0$, $\sigma = 10$) prior was placed on the intercept, Normal(0, 5) priors were placed on the coefficients, and a half-Cauchy prior with location zero and shape parameter equal to five was placed on the residual standard deviation. To approximate the posterior distribution, we used 1,000 samples each from four Markov chains after a burn-in period of 1,000 iterations. We verified that the Markov chains had converged by examining trace plot of the sampling and the Gelman-Rubin statistic for the parameters. After fitting the models, WAIC values for model comparison were calculated for each model using the R package 'loo' (Vehtari et al., 2016).

F.3 Estimating individual attack rates

To estimate the attack rates of individuals on barnacles and mussels, we needed estimates of the proportion of observations for each individual j in cage k that were feeding events on barnacles or mussels and proportion of observations that were non-feeding events. Following Wolf et al. (2017), we first assumed that the number of observations that were feeding events on barnacles and mussels and the number of observations that were non-feeding events, $\vec{y}_{jk}$, was multinomially distributed,

$$\vec{y}_{jk} \sim Multinomial(\vec{p}_{jk}, n_{jk}), \tag{F.8}$$

where $\vec{p}_{jk}$ is a vector containing the estimated proportion of feeding events on barnacles and mussels and non-feeding events, and n_{jk} is the total number of observations for individual j in cage k. We then assumed that individual proportion estimates were described by a cage-level Dirichlet distribution,

$$\vec{p}_{jk} \sim Dirichlet(\vec{q}_k), \tag{F.9}$$

where $\vec{q}_k$ is the vector describing the mean proportions of feeding events on barnacles and mussels and non-feeding events. Lastly we assume that the cage-level vector has a uniform Dirichlet prior,

$$\vec{q}_k \sim Dirichlet(\vec{1}), \tag{F.10}$$

where $\vec{1}$ is a vector of all one's of length three. This model was fit using the program 'JAGS' through the R package 'rjags' (Plummer, 2003). To approximate the posterior distribution, we used 2,000 samples each from three Markov chains after a burn-in period of 100,000 iterations. We verified that the Markov chains had converged by examining trace plots of the sampling and the Gelman-Rubin statistic for the parameters (Gelman and Rubin, 1992). Using the estimates of the proportion of feeding events on barnacles and mussels and the proportion of nonfeeding events and assuming that the handling times and resource densities of barnacles and mussels were known, we used equation 4.1 to estimate the attack rates of each individual.

F.4 Estimating the relationships between diet and feeding propensity variation and differences in feeding rate estimates due to Jensen's inequality

After estimating the differences in feeding rate estimates due to Jensen's inequality, we used multiple linear regression to examine the relationships between the magnitude of the feeding rate differences and variation among individuals in diet and feeding propensity. The estimates of diet variation were the same as those used to examine support for the optimal and stochastic foraging models. Feeding propensity variation was estimated using the same model as for estimating diet variation but with the number of barnacles observed replaced by the number of observations that were feeding events, the number of total feeding events replaced by the number of total observations, and no correction for bias. The differences in feeding rate estimates for barnacles and mussels were then regressed against the diet and feeding propensity variation estimates. We used the same priors and methods as for the earlier regressions in section F.2.