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Quantifying the effects of intraspecific variation on predator feeding rates through nonlinear averaging

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Abstract

1. Theory suggests that intraspecific trait variation will alter species interaction strengths through nonlinear averaging when interaction strengths are nonlinear functions of individuals' traits. This effect is expected to be widespread, yet what factors mediate its magnitude in nature and hence its potential effects on ecosystems and communities are unclear.

2. We sought to quantify how nonlinear predator functional responses, variation in prey densities and counteracting variation in attack rates and handling times among predator individuals of similar body size alter their population-level feeding rates through nonlinear averaging in a natural system, and to determine the processes influencing the net magnitude of this effect.

3. We used a field caging experiment in the rocky intertidal of Oregon, USA to quantify attack-rate variation and feeding rates of the whelk *Nucella ostrina* on its barnacle and mussel prey. We also used empirically parameterized simulations to examine the effects of handling-time variation among individuals on population-level feeding rates.

4. Within cages, individual attack-rate variation reduced population-level whelk feeding rates. However, the magnitude of this reduction differed among prey species and cages depending on cage-specific magnitudes of attack-rate variation and functional-response nonlinearity. The inferred effects of handling-time variation among individuals were of smaller magnitude than those of attack-rate variation, yet counteracted them to cause a net weakening of the effect of individual attack-rate variation on population-level feeding rates. Across cages, attack-rate and prey-density variation had non-additive effects that produced greater feeding-rate reductions at the experiment scale relative to the cage scale.

5. Our results indicate that the effects of trait variation via nonlinear averaging depend critically on the features of systems that determine the magnitudes of nonlinearities and trait variation. Because of counteracting trait variation, nonlinear-averaging effects may be quite complex, involving both the variances and covariances of all traits and environmental variables influencing the ecological process of interest.

KEYWORDS
diet variation, feeding rates, functional response, intraspecific trait variation, Jensen's inequality, rocky intertidal, species interactions

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1 | INTRODUCTION

Trait variation among individuals within populations is ubiquitous, and its importance in ecology and evolution has long been known (Darwin, 1859; Polis, 1984). Renewed interest in intraspecific variation has led to several additional insights into trait variation's potential consequences, particularly in community ecology (Bolnick et al., 2003, 2011; Violle et al., 2012). For example, recent theory shows that trait variation can influence the coexistence among competitors (Hart et al., 2016), the strength and dynamics of predator–prey interactions (Gibert & Brassil, 2014; Schreiber et al., 2011) and the structure of food webs (Gibert & DeLong, 2017). However, the development of theory on the ecological consequences of intraspecific variation has outpaced empirical studies, limiting our understanding of how trait variation is likely to affect ecological systems in nature.

A potentially widespread consequence of individual trait variation is the effect of nonlinear averaging on species interaction strengths (Bolnick et al., 2011; Gibert & Brassil, 2014; Okuyama, 2008). Nonlinear averaging is likely to influence species interaction strengths whenever interaction strengths are nonlinear functions of individuals' traits. When coupled with nonlinear functions, variation in traits leads to nonlinear averaging because, for a nonlinear function of a trait, $f(x)$, the average of the function over the traits of individuals, $\overline{f(x)}$, will not equal the function evaluated at the average of the trait, $f(\overline{x})$ (Figure 1). For concave down functions, the average of the function applied to all individual traits will be less than the function evaluated at the average trait (Figure 1a), while for concave up functions, the average of the function will be greater than the function evaluated at the average (Figure 1b; this effect is also known as Jensen's inequality (Ruel & Ayres, 1999)). In terms of species interaction strengths, nonlinear averaging means that the overall strength of an interaction between species (i.e. at the population level) is dependent not only on the average trait value exhibited by the individuals of the population, but also on the magnitude of trait variation among individuals and the shape of the relationship between the trait and the strength of the interaction. Furthermore, in terms of estimating population-level averages, nonlinear averaging means that using among-individual averages or assuming all

individuals are equivalent can lead to misleading population-level estimates.

Although nonlinear averaging is expected to influence many different interaction types, predator–prey interaction strengths are especially likely to be shaped by nonlinear averaging (Bolnick et al., 2011; Gibert & Brassil, 2014; Okuyama, 2008). This is because predator functional responses, which describe predator feeding rates, are almost universally nonlinear functions (Jeschke et al., 2004). In particular, predator functional responses are generally concave down with respect to predator attack rates and resource densities, and concave up with respect to predator handling times (as is the case in the Type II functional response of Holling (1959); Figure 1a,b). Therefore, while variation among individuals in attack rates, as well as spatial or temporal variation in resource densities, should reduce a predator population's overall feeding rates, variation in handling times should increase the population's overall feeding rates for a given average attack rate, resource density or handling time (Bolnick et al., 2011; Okuyama, 2008).

While theory provides qualitative expectations on how individual variation in attack rates, handling times and resource densities should alter population-level feeding rates, it remains unclear how strong the effects of nonlinear averaging are likely to be under conditions in the field. Furthermore, it is also unclear under what circumstances the overall net effects of nonlinear averaging over individual trait variation are likely to decrease or increase feeding rates at the population level. This is particularly the case in the context of individual variation that is not associated with obvious traits. For example, intraspecific diet specialization is a widespread form of intraspecific variation whereby individuals with otherwise apparently identical characteristics (e.g. similar body sizes) specialize on different resources and differ simultaneously in attack rates and handling times (Bolnick et al., 2003). In addition to such innate specialization, stochasticity itself—either in space or in time—can lead to diet differences among individuals and will be reflected in each individual's realized attack rates and handling times (Coblentz, 2020). While most readily observable differences among individuals, such as body size, have well-known relationships with predator attack rates and handling times and, therefore, predictable consequences through nonlinear averaging (Vucic-Pestic et al., 2010), the importance of more cryptic
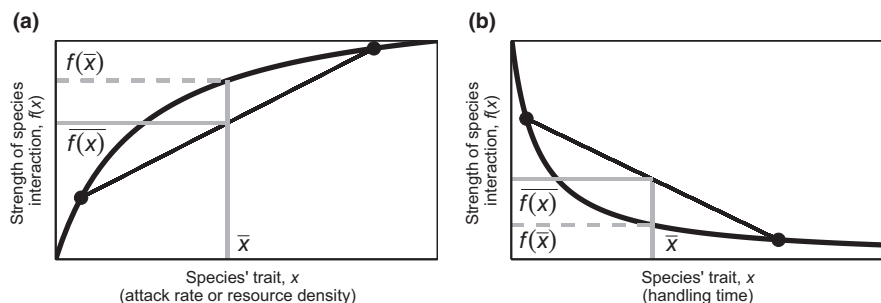
FIGURE 1 When species interaction strengths are nonlinear functions of a species' trait, $f(x)$, then the average interaction strength across the values of the species' trait, $\overline{f(x)}$, will not be equal to the interaction strength evaluated at the average of the species' trait $f(\overline{x})$. (a) When the nonlinear function is concave up, $\overline{f(x)} < f(\overline{x})$, as is the case for predator feeding rates as a function of attack rates or resource densities. (b) When the nonlinear function is concave down, $\overline{f(x)} > f(\overline{x})$, as is the case for predator feeding rates as a function handling times

forms of individual variation through nonlinear averaging is unclear. Quantitative estimates of the importance of these latter forms of individual variation would be useful for establishing baseline expectations for the magnitude of nonlinear-averaging effects.

Here, our goal was to quantify the effects of nonlinear averaging on predator feeding rates in the field. We use a field caging experiment with the whelk *Nucella ostrina* feeding on the barnacle *Balanus glandula* and the mussel *Mytilus trossulus* to quantify the effects of nonlinear averaging on predator feeding rates. At the cage level, we use feeding observations of individuals to quantify individual attack rates and estimate the discrepancy between population-level feeding rates estimated using the average feeding rate across individuals ($\overline{f(x)}$) and the average feeding rate estimated using the average of individual attack rates ($f(\overline{x})$; Figure 1a). Because we were unable to directly estimate individual handling times in the field, we used data from laboratory experiments and simulations to examine the potential effects of individual handling-time variation. Lastly, we contrasted the effects of nonlinear averaging on feeding rates within cages to the effect of joint attack-rate variation among individuals and prey densities across cages to gain insight into the relative importance of individual-level and environmental variation.

2 | MATERIALS AND METHODS

To quantify the effects of nonlinear averaging on whelk feeding rates, we combined data from a field caging experiment with measurements of whelk handling times from a laboratory study. Below, we first describe the study system and field caging experiment. We then describe our observational method for estimating individual-level attack rates (combining individual feeding observations and measurements of prey densities from the field experiment with handling-time measurements from the laboratory experiment), and how we used these estimates to quantify the effects of individual attack-rate variation within the cages of our experiment. We then describe how we combined field-estimated attack rate, prey density and mean handling times with observed variation in handling times from the laboratory experiment to parameterize simulations with which we inferred the potential magnitudes of variation in handling times that could counteract the effects of attack-rate variation on nonlinear averaging. Finally, we describe how we combined the individual attack-rate estimates, prey density estimates across cages and mean handling-time estimates to estimate the effects of simultaneous variation among individuals in attack rates and prey densities on the experiment-wide feeding rates of whelks, contrasting these experiment-wide effects with the effects we inferred at the within-cage level.

2.1 | Study system

Nucella ostrina is a common intertidal predator on rocky shores of the Northeast Pacific, feeding on a wide variety of different invertebrate species. On the Oregon coast, its primary prey are the acorn barnacle *Balanus glandula* and the mussel *Mytilus trossulus* (hereafter referred to as barnacles and mussels; Novak et al., 2017). Several features make this system amenable to studying individual variation. First, *N. ostrina* feeds on barnacles and mussels by drilling through their shells or prying open their valves or opercula over the course of several hours, allowing for the identification of feeding events while predators are feeding. Second, because the barnacles and mussels are sessile, resource densities are easily estimated and manipulated. Third, whelks' shells are easily tagged, allowing individuals to be distinguished and tracked over time. Fourth, prior field studies have inferred the presence of individual diet variation in this and similar whelk species not attributable to observable traits (Burrows & Hughes, 1990; West, 1986, 1988; but see Coblentz et al., 2017).

2.2 | Field experiment

To examine the effects of nonlinear averaging on the strength of interactions between *N. ostrina* and its prey, we used a caging experiment in the rocky intertidal at Yachats, Oregon, USA (44.3°N, 124.1°W). In June 2015, we bolted twenty 25 cm × 35 cm stainless steel mesh cages with galvanized steel mesh lids into an early successional patch in the mid-intertidal. To ensure differences among cages in prey densities, we divided each cage into a grid of ten 7 cm × 12.5 cm rectangles and applied one of five treatments to four cages each, scraping either zero, two, four, six or eight randomly selected rectangles to bare rock.

Following the prey density manipulation, we added 30 individually tagged whelks from the surrounding area to each cage. All whelks measured 14.5–16.5 mm from their shell's apex to the base of the aperture, reflecting the median size of whelks at this site during the summer months. Reducing whelk size variation will have reduced individual overall attack-rate variation but was done to bring focus to the residual effects of diet specialization and stochasticity (Bolnick et al., 2003; Coblentz, 2020). We gathered individual feeding data by performing 22 low-tide surveys in mid-June through August and 19 low-tide surveys in September for a total of 41 surveys. During each survey, we recorded whether each whelk was feeding or not. If the whelk was feeding, we recorded the identity and size of the prey and the method by which the whelk was feeding (drilling or prying). At the beginning, middle and end of the experiment, we took photographs of the cage interiors and estimated prey densities using ImageJ (Schneider et al., 2012). We kept whelk densities constant within cages by replacing individuals that escaped or died.

2.3 | Statistical methods

2.3.1 | Quantifying individual attack rates and cage-level effects of nonlinear averaging

To translate from the observational feeding surveys of individual whelks to measures of individual attack rates, we used the

attack-rate estimator derived by Novak and Wootton (2008) and Wolf et al. (2017). This estimator works by connecting feeding rates with the time period over which feeding events are detectable to an observer because these together determine the expected proportion of time that individuals will be observable feeding (Novak et al., 2017). Although this approach has previously only been applied at the population level, it may also be applied at the level of individuals when longitudinal surveys are performed on the same individuals (see Appendix S1). Specifically, under the assumption that whelks exhibit a multispecies Holling Type II functional response (an appropriate characterization of whelk feeding rates when whelk densities are constant; Novak, 2010; Novak et al., 2017), the number of non-feeding observations of individual j in cage k (n_{0jk}) and feeding observations on barnacles (n_{bjk}) and mussels (n_{mjk}) follow a multinomial distribution:

$$(n_{0jk}, n_{bjk}, n_{mjk}) \sim \text{Multinomial}\left(p_{0jk} = 1 - \frac{\sum_{i\in b,m} a_{ijk}h_i R_{ik}}{1 + \sum_{i\in b,m} a_{ijk}h_i R_{ik}}, \; p_{bjk} = \frac{a_{bjk}h_b R_{bk}}{1 + \sum_{i\in b,m} a_{ijk}h_i R_{ik}}, \; p_{mjk} = \frac{a_{mjk}h_m R_{mk}}{1 + \sum_{i\in b,m} a_{ijk}h_i R_{ik}}\right), \quad (1)$$

where p_{ijk} is the proportion of surveys of individual j in cage k in which it was observed feeding on prey i, p_{0jk} is the proportion of surveys of individual j in cage k that were non-feeding observations, h_i is the handling time for prey i and R_{ik} is the density of prey i in cage k (Appendix S1). With estimates of each of the proportions, handling times and resource densities, one can solve for an estimate of the individual attack rates:

$$a_{ijk} = \frac{p_{ijk}}{p_{0jk}} \times \frac{1}{h_i R_{ik}}. \quad (2)$$

Below, we explain how we estimated each of these components and combined them to estimate individual attack rates and the effects of their variation on feeding rates within cages.

We used a Bayesian approach to estimate the proportions of feeding and non-feeding observations p_{ijk} and p_{0jk} rather than using the raw (i.e. observed) proportions because the latter can be biased (Coblentz et al., 2017). We did so by modelling each individual's numbers of feeding and non-feeding observations as being multinomially distributed following Wolf et al. (2017). We further assumed that all individual-level proportions had a cage-level Dirichlet distribution and then used a uniform Dirichlet prior to fit this model with the program JAGS (v. 4.3.0) through the R package 'RJAGS' (v. 4.10, R version 4.0.3; Plummer, 2003, 2019; R Core Team, 2019). To approximate the posterior distributions of the model parameters, 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 model samples and the Gelman–Rubin statistic for the parameters (Gelman & Rubin, 1992).

As measurements of the prey densities in each cage, R_{ik}, we used weighted averages of the prey densities over the course of the experiment. We did so because the feeding surveys took place over months and, therefore, the feeding observations reflect individuals' feeding rates integrated over that time period. However, prey

densities were not constant in cages over time: barnacle densities tended to increase due to recruitment and mussel densities tended to decrease through mortality. Furthermore, the feeding surveys themselves were not evenly spread over the length of the experiment, with half of the surveys taking place within the last month of the experiment. Therefore, we used a weighted average of the densities of the prey in each cage, with the final measurement of prey densities given twice the weight of the prey density measurements from the beginning and middle of the experiment. Because we used an average over the prey density measurements, we also restricted the whelk individuals included in the analysis to those that were observed in at least 30 of the 41 surveys to ensure that the weighted average prey densities reflected the prey densities experienced by the whelks. Our inferences were robust to the use of different values for this cut-off.

To estimate field-based handling times on barnacles and mussels (h_i in Equation 1), we combined data from the field-based feeding surveys with the measurements of whelk handling times obtained from a laboratory experiment. The handling times of individuals in the field could not be measured because individuals can only be observed for a short period of time during low tide and whelk handling times on mussels and barnacles can regularly exceed 24 hr (Novak et al., 2017). In the laboratory experiment, the details of which can be found in Appendix S2, we measured whelk handling times on barnacles and mussels, then used regressions to determine their relationship with prey size, predator size and feeding method (e.g. drilling versus prying). We then used the regression coefficients from the laboratory experiment to estimate the handling time of each feeding observation made in the field experiment given the sizes of the whelk and prey and the method of feeding involved in each observed foraging event. We then averaged across all these individual handling times to generate an experiment-wide characteristic handling time for each prey species. (Below, we also describe simulations to evaluate the effects of individual handling-time variation around the mean handling-time values.)

To quantify the effects of nonlinear averaging on feeding rates due to individual attack-rate variation, we first calculated individual attack rates. We did so by calculating attack rates using the estimator (Equation 1) for each iteration of the Markov chain Monte Carlo process used to approximate the posterior distribution of the proportions of feeding and non-feeding events. For each iteration of the Markov chain Monte Carlo process, we also quantified individual feeding rates on barnacles and mussels by plugging the individual attack rates into the multispecies Type II functional response along with the resource density and handling-time estimates. We then calculated the average feeding rate on the barnacles and mussels in each cage in two ways. First, we calculated the cage-specific average of the individual feeding rate calculated with the individual-level attack-rate estimates. This corresponds to the average of the

function across observations ($\overline{f(x)}$ in Figure 1a). Second, we calculated the cage-specific average feeding rate by plugging the average of the individual-level attack rates into the Type II functional response. This corresponds to the function evaluated at the average of the observations ($f(\bar{x})$ in Figure 1a). The difference between these two estimates provided our measure for the effect of nonlinear averaging on feeding rates due to individual attack-rate variation.

2.3.2 | Quantifying the potential effects of nonlinear averaging through handling-time variation

Handling-time variation among individuals is expected to counteract the effect of attack-rate variation on population-level feeding rates (Figure 1). We therefore wanted to quantify whether empirically plausible levels of individual handling-time variation were large enough to cancel or reverse the effect of the attack-rate variation that we estimated directly. We did so using simulations. As a baseline for the magnitude of handling-time variation among individuals, we used the variation among barnacle and mussel handling times measured in the laboratory handling-time experiment (Appendix S2). The variation observed in the laboratory handling-time experiment provides a useful comparison because we purposefully attempted to maximize variation in handling times in these experiments. For example, although our field experiment minimized variation due to predator size by employing similarly sized whelks, our laboratory experiment used ranges of predator and prey body sizes that included small whelks feeding on large prey (a 9-mm whelk feeding on a 21 mm mussel) and large whelks feeding on small prey (a 21-mm whelk feeding on a 1 mm barnacle). Thus, it is unlikely that variation in handling times among the similarly sized individuals in the caging experiment would exceed the handling-time variation that occurred in the laboratory experiment.

To perform the simulations, we first drew handling times for barnacles and mussels for each individual within a cage from log-normal distributions parameterized using the mean field experiment-wide handling times (the handling times used for h_i in the attack-rate variation analysis) and the standard deviations of handling times from the laboratory experiment (a mean of 0.49 days and a standard deviation of 0.52 days for barnacles and a mean of 0.77 days and a standard deviation of 1.2 days for mussels). We used log-normal distributions to avoid negative handling times and because handling times appeared log-normally distributed in the laboratory handling-time experiment. We then calculated the feeding rate of each individual on the focal prey using the multispecies Type II functional response with the average attack rates and prey densities for that cage. The average of these feeding rates on each prey gave the average feeding rate including individual handling-time variation ($\overline{f(x)}$ in Figure 1b). We also calculated the average feeding rate on each prey using the average handling time among individuals ($f(\bar{x})$ in Figure 1b). We then subtracted the two population-level average feeding rates to calculate the increase in the average feeding rate due to

TABLE 1 Abbreviations for each of the experiment-wide average feeding rates calculated, their definitions and empirical scenarios of when such averages arise in either calculating population averages or producing nonlinear-averaging effects

Abbreviation	$\overline{f(a_i, R_c)}$	$\overline{f(a_i, \bar{R})}$	$\overline{f(\bar{a}, R_c)}$	$f(\bar{a}, \bar{R})$
Definition	Average experiment-wide feeding rate incorporating …			
	the among-individual attack-rate variation (a_i) and among-cage resource-density variation (R_c) and their covariance	the among-individual attack-rate variation (a_i) and the among-cage resource-density averages ($\bar{R}$)	the among-individual attack-rate averages ($\bar{a}$) and among-cage resource-density variation (R_c)	the among-individual attack-rate averages ($\bar{a}$) and the among-cage resource-density averages ($\bar{R}$)
Typical empirical scenario—calculating population averages	Researchers calculate an average accounting for …			
	individual trait differences (e.g. body size) and differences in environments experienced by individuals (e.g. temperature) and their covariance	individual trait differences (e.g. genotype) but assume that all individuals experienced the same average environment (e.g. precipitation)	differences in environments experienced by individuals (e.g. predation pressure) but assume all individuals have the average trait of the population (e.g. activity level)	no among-individual variation by assuming all individuals have the same average trait value (e.g. leaf area) and experience the same environment (e.g. sunlight)
Typical empirical scenario—biological effects of nonlinear averaging	Average when individuals …			
	vary and covary in traits and the environments they experience	vary in traits but all experience the same environment	exhibit no trait variation but experience different environments	exhibit no trait variation and all experience the same environment

handling-time variation through nonlinear averaging for each prey. We performed 10,000 simulations for each cage. After performing the simulations, we compared the reductions in the average feeding rates estimated due to attack-rate variation in each cage to the increases in average feeding rates due to handling-time variation across the simulations.

2.3.3 | Estimating the effects of nonlinear averaging at the experiment scale

Our just-described methods for quantifying the magnitude of nonlinear averaging were performed at the cage level and focused on the effect of attack-rate and handling-time variation among individuals within each cage. We also quantified the magnitude of nonlinear averaging across cages (at the level of the entire experiment) to understand the effect of joint among-individual attack-rate variation and among-cage variation in resource densities. To do so, we calculated the average experiment-wide feeding rate on barnacles and mussels in four ways. First, we calculated the average feeding rate by averaging across all individual feeding rates thus incorporating individual attack-rate variation and among-cage resource-density variation ($\overline{f(a_i, R_c)}$, see Table 1 for definitions of abbreviations of the averages and typical empirical scenarios they describe). Second, we calculated the average feeding rates incorporating individual attack-variation but using the average resource densities among cages to calculate each feeding rate ($\overline{f(a_i, \overline{R})}$). Third, we calculated the average feeding rates incorporating among-cage variation in resource densities but using the average attack rates across individuals ($\overline{f(\overline{a}, R_c)}$). Fourth, we calculated the average feeding rates using the average attack rates among individuals and the average among-cage resource densities ($f(\overline{a}, \overline{R})$). We then made three contrasts among the average feeding-rate estimates to determine the effects of nonlinear averaging at the scale of the entire experiment due to: (a) simultaneous variation and covariation in attack rates and resource densities ($f(\overline{a}, \overline{R}) - \overline{f(a_i, R_c)}$), (b) individual attack-rate variation alone ($f(\overline{a}, \overline{R}) - \overline{f(a_i, \overline{R})}$) and (c) among-cage resource-density variation alone ($f(\overline{a}, \overline{R}) - \overline{f(\overline{a}, R_c)}$). We

generated 95% credible intervals (CrI) for the experiment-scale feeding rates and contrasts using the Markov chain iterations of the Bayesian model we used for estimating the proportions of individual feeding and non-feeding events.

3 | RESULTS

In total, the experiment generated 23,864 total observations for 719 individual whelks of which 3,185 observations were feeding observations. Focusing on the 550 individuals that were observed in at least 30 of the 41 total surveys reduced the number of observations to 21,638 of which 2,918 were feeding observations. The average number of feeding observations per individual was 5.3 and ranged from 1 to 17. Of the 2,918 feeding observations, the vast majority were on barnacles and mussels, with only 10 feeding observations on the acorn barnacle *Chthamalus dalli* and one feeding observation on the limpet *Lottia pelta*. These observations were removed prior to analysis.

3.1 | Cage-level nonlinear averaging due to individual attack-rate variation

Across cages, individual attack-rate variation led to a reduction in cage-level feeding rates that ranged from 0.43 to 3.1 barnacles per whelk per 100 days and from 0.046 to 0.57 mussels per whelk per 100 days. These reductions correspond to a 3.5% to 8.7% reduction in barnacle feeding rates (Figure 2a) and a 2.4% to 7.9% reduction in mussel feeding rates (Figure 2b) relative to the case in which all individuals within a cage exhibited the mean cage-level attack rate.

3.2 | Potential cage-level nonlinear averaging due to individual handling-time variation

Across cages, simulated variation in individual handling times led to an increase in average feeding rates that ranged from 0.07
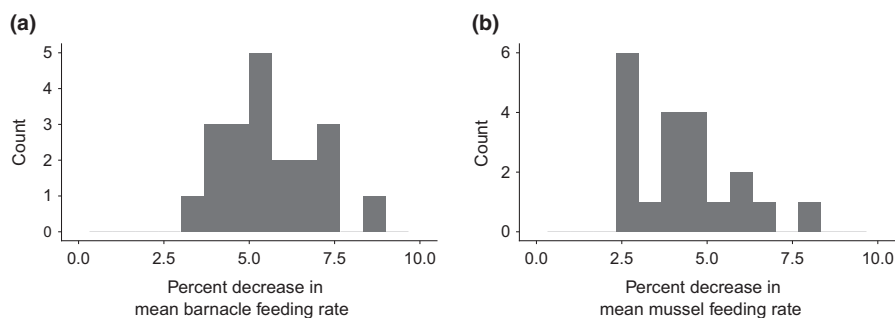

FIGURE 2 Among-individual attack-rate variation reduced the average feeding rates of whelks within cages on (a) barnacles and (b) mussels. Counts reflect the number of cages in which a given percent decrease in average feeding rate due to nonlinear averaging was estimated to have occurred relative to the hypothetical situation in which all individuals within a cage exhibited the same mean attack rate

to 0.8 barnacles per whelk per 100 days and from 0.03 to 0.19 mussels per whelk per 100 days, respectively, corresponding to 0.6% to 2.5% and 0.6% to 2.3% increases in mean feeding rates (Figure 3). None of the increases in average feeding rates due to handling-time variation exceeded the magnitude by which average feeding rates were reduced by attack-rate variation (Figure 3).

3.3 | Experiment-level nonlinear averaging due to attack-rate and resource-density variation

The effect of nonlinear averaging at the experiment scale, including both among-individual attack-rate variation and among-cage resource-density variation, was greater than the effect of nonlinear averaging through within-cage attack-rate variation for both barnacles and mussels (Figure 4). The difference between the experiment-scale feeding rates including among-individual attack-rate variation

and among-cage resource-density variation versus the feeding rate calculated using the average attack rates and resource densities $(f(\overline{a}, \overline{R}) - \overline{f(a_i, R_c)})$ was 6.1 barnacles per whelk per 100 days and 1.9 mussels per whelk per 100 days, corresponding to a 22% and 29% reduction in feeding rates (Figure 4b,d). The difference between the experiment-scale feeding rates calculated with among-individual attack-rate variation and average among-cage resource densities versus the feeding rates calculated using the average attack rates and resource densities $(f(\overline{a}, \overline{R}) - \overline{f(a_i, \overline{R})})$ was 3.15 barnacles per whelk per 100 days and 0.8 mussels per whelk per 100 days, corresponding to 11% and 12% reduction in feeding rates (Figure 4b,d). The difference between the experiment-scale feeding rates calculated with among-cage resource-density variation but using the average among-individual attack rate versus the feeding rates calculated using the average attack rates and resource densities $(f(\overline{a}, \overline{R}) - \overline{f(\overline{a}, R_c)})$ was 0.8 barnacles per whelk per 100 days and 0.26 mussels per whelk per 100 days, corresponding to 3% and 4% reductions in feeding rates (Figure 4b,d).
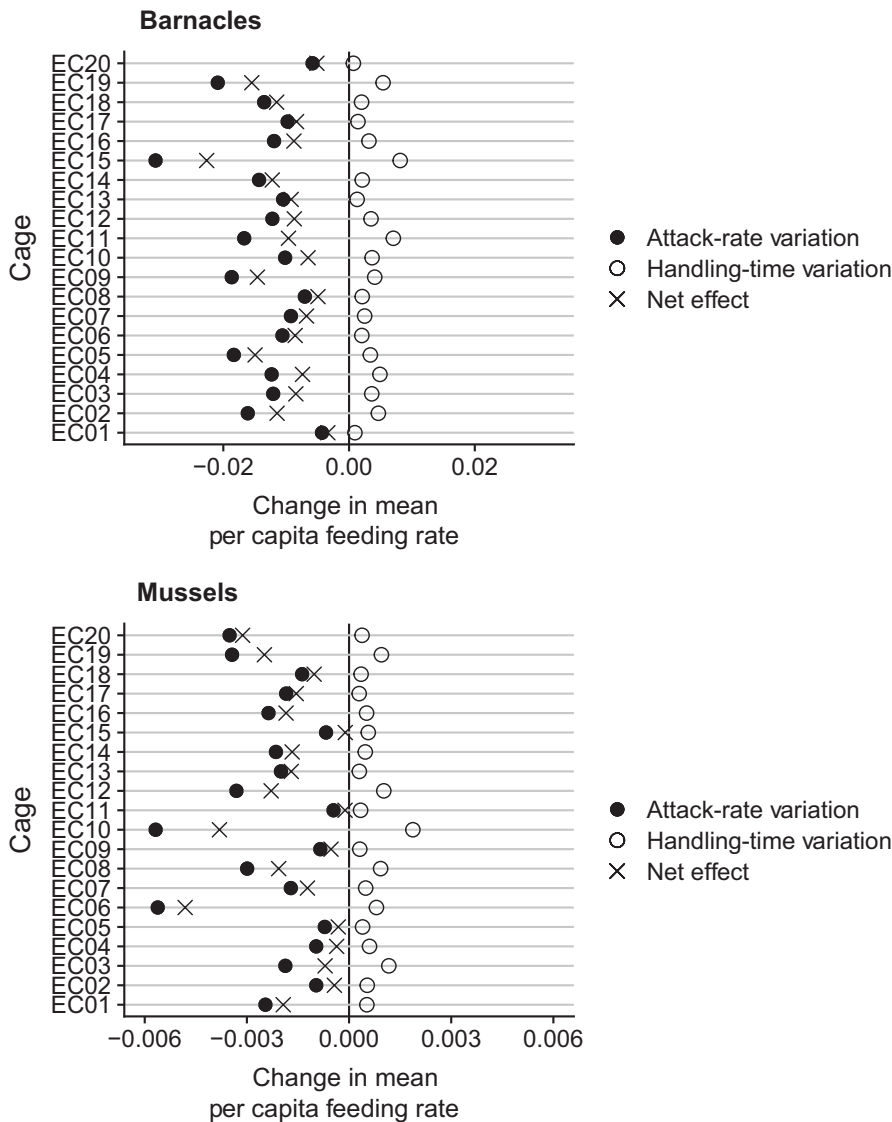
FIGURE 3 Simulations based on the combination of information from field and laboratory experiments show that individual handling-time variation increases the average feeding rates of whelks on both barnacles and mussels in each cage. However, these increases do not outweigh the decreases in average feeding rates due to attack-rate variation. Therefore, in all cages, the net effect of individual variation in both attack rates and handling times is a reduction in mean feeding rates
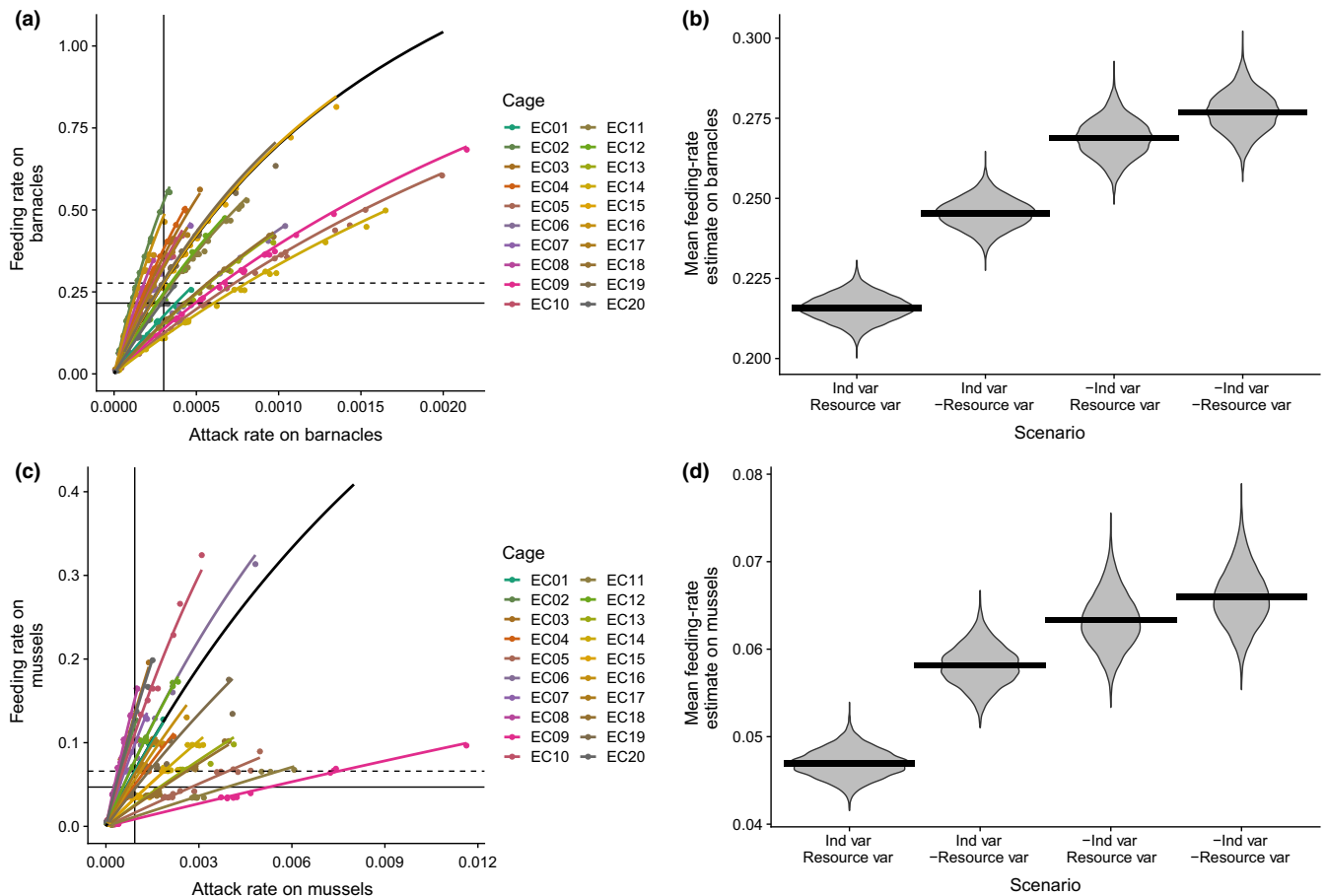
FIGURE 4 Across the experiment, among-individual variation in attack rates and among-cage variation in barnacle and mussel densities led to a difference in the average feeding rate across individual whelks (the solid horizontal lines in (a) and (c)) and the feeding rate calculated using the among-individual average attack rate and the among-cage average resource densities (the dashed horizontal lines in (a) and (c)). The vertical line in (a) and (c) represents the average attack rate across cages, and the curved solid black line represents the relationship between attack rates and feeding rates that would be expected at the among-cage average resource densities. The coloured lines in (a) and (c) represent the relationships between attack rates and feeding rates for each cage. The posterior distributions of average feeding-rate estimates at the experiment scale were lowest for rates that were estimated including individual variation in attack rates and among-cage variation in resource densities $(\overline{f(a_i, R_c)})$, were intermediate for rates estimated including attack-rate variation but using the average resource densities $(\overline{f(\overline{a}, R_c)})$ as well as when using the average among-individual attack rate but including among-cage resource densities $(\overline{f(a_i, \overline{R})})$ and were highest for rates estimated using the average among-individual attack rates and average among-cage resource densities $(f(\overline{a}, \overline{R}))$. The black lines in (b) and (d) represent the means of the posterior distributions

4 | DISCUSSION

Because trait variation among individuals is common and species interactions are often nonlinear functions of species' traits, it has been supposed that nonlinear averaging 'might be of ubiquitous importance in ecology' (Bolnick et al., 2011, p. 185). Although the conditions for nonlinear averaging to influence species interactions may be ubiquitous, whether these effects are strong enough to have ecologically significant consequences, and what determines their strength, remains rarely tested. We directly estimated how nonlinear averaging and intraspecific attack-rate variation affected the strength of whelk interactions with their barnacle and mussel prey. We estimated that intraspecific attack-rate variation reduced whelk feeding rates within cages by up to 9% relative to the hypothetical case in which all whelks were equivalent and exhibited

the same mean attack rate. Simulations showed that an increase in mean whelk feeding rates due to individual handling-time variation was unlikely to outweigh the decrease due to individual attack-rate variation. We also showed that, at the experiment scale, the effect of nonlinear averaging due to both variation among individuals in attack rates and variation among cages in resource densities was larger than that at the cage level (22% reduction in feeding rates for barnacles and 27% for mussels). Furthermore, the effect of nonlinear averaging at the experiment scale was greater than the sum of the effects of individual attack-rate variation and resource-density variation alone, indicating that the effects of these two sources of variation are not additive. These results provide the first estimates of nonlinear-averaging effects on feeding rates due to intraspecific variation in the field and illustrate the complex interactions among variation, covariation and nonlinearities that determine the

overall net effects of nonlinear averaging on the strength of species interactions.

Prior to our analysis, we had several reasons to expect that attack-rate variation among whelks would cause a large effect of nonlinear averaging. First, other whelk species have been shown to exhibit individual diet specialization unexplained by attributes such as body size, which should be reflected by large individual variation in attack rates (Burrows & Hughes, 1990; West, 1986, 1988). Second, whelks generally exhibit strongly nonlinear functional responses in manipulative cage and laboratory experiments (Katz, 1985; Murdoch, 1969; Novak et al., 2017). However, our data showed no signature of strong individual diet specialization among whelks in their attack rates. Furthermore, the relationships between whelk attack and feeding rates were only weakly nonlinear (Figure 4a,c). This weak nonlinearity is the product of the magnitude of the whelks' attack rates and handling times and the prey densities they experienced. We limited whelk size variation to examine the residual effects of individual diet specialization and stochasticity to provide a baseline estimate of the magnitude of nonlinear-averaging effects on predator feeding rates in the absence of size variation, the consequences of which are now well-characterized (Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic et al., 2010). This will have reduced the amount of attack-rate variation among individuals. However, we note that even with increased attack-rate variation due to the inclusion of size variation, the effects of nonlinear averaging may not have increased substantially due to the weakly nonlinear relationships between attack and feeding rates (Figure 4a,c). In general, we therefore conclude that expectations on the strength of nonlinear-averaging effects must consider both how much trait variation is likely among individuals, and how nonlinear relationships between traits and interaction strengths are likely to be under conditions organisms experience in the field (see also Beardsell et al., 2021; Novak, 2010; Preston et al., 2018; Wootton & Emmerson, 2005).

Even though the effects of nonlinear averaging were not as large as expected, the effects were detectable even with variation in predator size was minimized. We also note that the variation in whelk size that did exist did not account for any variation in diet proportions (Figure S3.1 in Appendix S3). Of course, whether the magnitudes of the effects should be considered to be weak or strong are likely to depend on perspective; a 9% change in an estimate of prey mortality due to predation could be viewed as large or small depending on the natural history of the species involved (e.g. whether predation is a large or small source of total mortality for the prey, and how large a change in mortality it represents relative to prey growth rates (Novak & Wootton, 2010)). However, weak effects of intraspecific variation through nonlinear averaging are consistent with several recent studies in which nonlinear averaging was a potential mechanism producing the effects of intraspecific variation (Dibble & Rudolf, 2019; Start, 2019; Start & Gilbert, 2019). For example, Start and Gilbert (2019) used mesocosm experiments to examine the effects of individual activity-rate variation in dragonfly larvae on community and ecosystem properties. They found that differences among treatments in mean activity rate had large

effects, whereas differences in the magnitude of intraspecific variation in activity rates had relatively minor effects. The weak effects of intraspecific variation in their experiment align with our estimates of nonlinear-averaging effects on whelk feeding rates. Nonetheless, more measurements of nonlinear-averaging effects are necessary before generalizing about their importance.

Our simulations suggest that increases in whelk feeding rates through individual handling time are unlikely to be greater than the decreases due to attack-rate variation. Although we assumed in our simulations that individual variation in handling times on barnacles and mussels among the whelks was equivalent to that observed in the laboratory handling-time experiment, these variances are quite large relative to what would be expected for similarly sized whelks feeding on similarly sized prey (standard deviations of 0.52 and 1.2 days for barnacles and mussels respectively). The weaker effects of nonlinear averaging through individual handling-time variation can again be explained by the weak nonlinearity of the relationship between handling times and feeding rates at the attack rates, handling times and resource densities occurring in the system (Figure 5). In systems with low attack rates such as our focal study system, the effects of handling-time variation are likely to be weak unless prey densities are quite large. This is because attack rates determine the slope of functional responses near the origin, whereas handling times determine the asymptote of functional responses at high prey densities (Holling, 1959). Thus, with low attack rates, prey densities must be quite large before the relationship between handling times and feeding rates becomes nonlinear enough for handling-time variation to have strong effects. In other systems where predators exhibit higher attack rates and/or resources exhibit higher densities, handling-time variation is likely to play a larger role in shaping population-level feeding rates through nonlinear averaging. In these cases, individual handling-time variation may outweigh the effects of individual attack-rate variation to cause net increases in population-level feeding rates.

Our inferences of feeding rates calculated at the experiment level illustrate how the effects of intraspecific variation through nonlinear averaging can be scale dependent when there is covariance between intraspecific variation and other sources of variation influencing species interactions. The effects of nonlinear averaging on feeding rates were greater when considering both individual variation in attack rates and among-cage variation in resource densities. This was true for both barnacles and mussels. Furthermore, the joint effects of variation among individuals in attack rates and variation among cages in resource densities were greater than the sum of the effects of each source of variation alone. This may have been the result of negative covariance between prey densities and attack rates despite increases in mean predator feeding rates with increases in focal prey abundances (Figure S3.2, S3.3 in Appendix S3). We suggest that a fruitful way for future work to integrate variation among individuals, variation in the environment and the covariation among them into ecological theory is scale transition theory (Chesson, 1998a, 1998b, 2012). Scale transition theory was developed to account for the effects of nonlinear averaging on regional-scale population dynamics
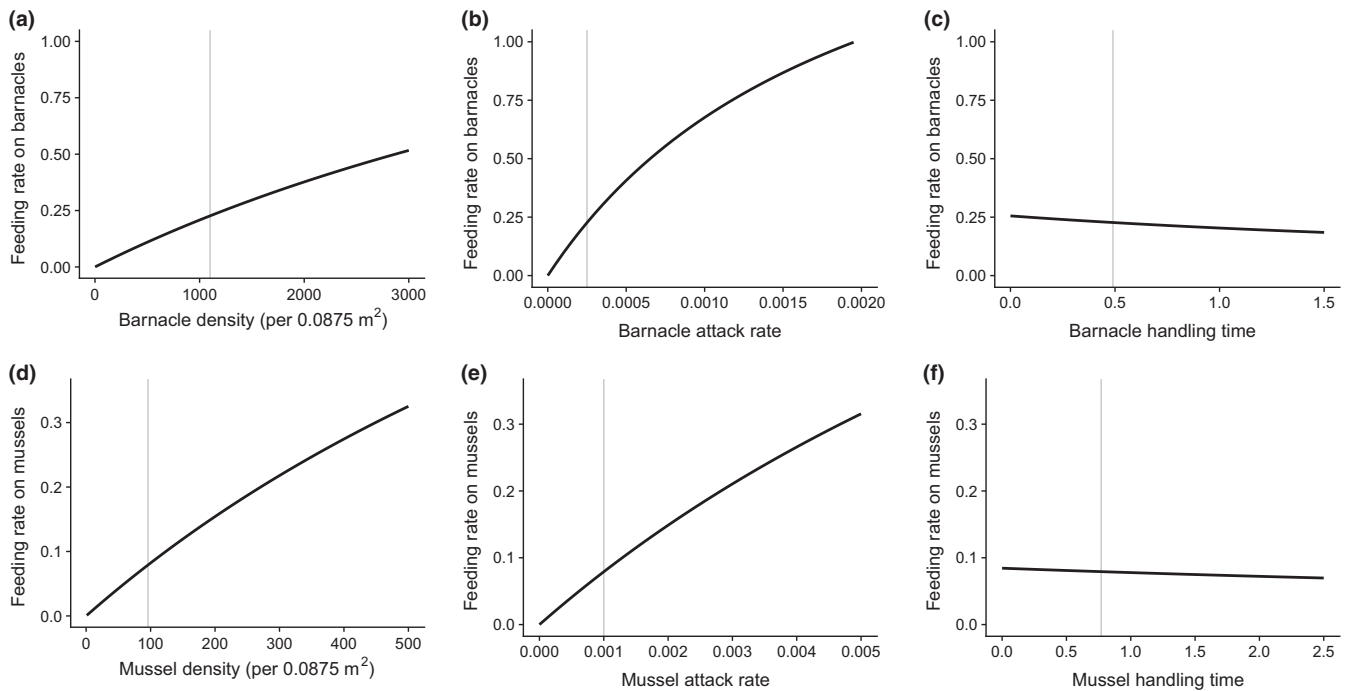
FIGURE 5 The relationships between feeding rates and prey densities (a, d), attack rates (b, e) and handling times (c, f) illustrate the weak nonlinearity observed between them. Each of the panels uses the experiment-wide averages for all of the parameters excepting the parameter being varied on the *x*-axis. The vertical grey line in each panel represents the experiment-wide mean of the parameter on the *x*-axis

due to local-scale nonlinear population dynamics and spatial variation. As scale transition theory already provides a way of incorporating spatial variation into models of population dynamics, modifying scale transition theory to include variances and covariances between sources of intraspecific variation and environmental variation will provide a way to explicitly incorporate the effects of nonlinear averaging through intraspecific variation. The explicit derivations of the effects of variation and covariation on nonlinear averaging will help to identify the circumstances under which some sources of variation are likely to counteract variation in others and when certain sources of variation may be particularly important.

Although we aimed to directly examine how nonlinear averaging influences population-level feeding rates, our approach still required that we use averages for some parameters which will have influenced our estimates of variation. More specifically, to estimate individual attack rates, we required a measure of prey densities associated with the feeding surveys. Because estimating attack rates at the individual level required longitudinal surveys, we used average prey densities over the course of the experiment as our measure of prey densities. Doing so will have influenced our individual attack-rate estimates by not accounting for the temporal variation in prey densities as well as the nonlinear relationship between prey densities and the attack-rate estimator. It was nonetheless necessary to implement our approach. Given that whelk functional responses were only weakly nonlinear and the within-cage variation in prey densities that occurred, we do not believe this will have greatly influenced our overall inferences. However, recognition of these limitations does highlight that the sources of nonlinear averaging that are accounted for can often be subjective and constrained by the goals and methods of a study. Furthermore, the existence of logistical constraints on which sources of variation can even be considered by a study highlights the importance of developing a priori expectations of what sources of variation are likely to have large effects through nonlinear averaging and under what circumstances ignoring them will matter.

5 | CONCLUSIONS

Theory predicts that trait variation among individuals could have widespread ecological and evolutionary effects by altering species interaction strengths through nonlinear averaging (Bolnick et al., 2011; Gibert & Brassil, 2014; Okuyama, 2008). Although the necessary components for nonlinear averaging to affect species interactions may be common, our data highlight that, in practice, the strength of these effects is dependent on how nonlinear the functions that link species' traits to their interactions are and how variable individuals are in their traits. Determining whether any generalizations can be made about the strength of nonlinear-averaging effects will require further concurrent estimates of nonlinear interactions and intraspecific variation in the field. Nevertheless, that we were able to estimate the detectable effects of intraspecific variation on predator feeding rates through nonlinear averaging encourages an explicit incorporation of variation into theoretical models, as well as empirical work to uncover the processes generating variation, nonlinearities and the statistical interactions among them.

AUTHORS' CONTRIBUTIONS

K.E.C. and M.N. developed the ideas herein; K.E.C. performed the field experiment, analysed the data and wrote the first draft of the manuscript; S.M. performed the laboratory handling-time experiment. All the authors contributed to the manuscript revisions.

DATA AVAILABILITY STATEMENT

Data available from zenodo https://doi.org/10.5281/zenodo.4633995 (Coblentz et al., 2021).

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