Functional Ecology

BRITISH ECOLOGICAL SOCIETY

Differences among individual predators alter their population feeding rates on prey

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No two individuals are exactly alike. This is as true for other organisms as it is for humans. Despite this fact, ecologists often treat individuals as identical out of convenience or necessity. However, recent developments in ecological theory have identified conditions under which individual differences may play important ecological roles. One of these is when the relationship between the strength of the interaction between two species and a quality of a species that differs among individuals is not linear. Because of a mathematical fact known as nonlinear averaging, differences among individuals can weaken or strengthen the interactions among species with potential consequences for the dynamics of populations over time and whether or not two species may be able to coexist with one another. Here we sought to measure how strong this nonlinear averaging effect was due to differences among individual sea shore snails (*Nucella ostrina*) in two properties that influence their feeding rates on a barnacle (*Balanus glandulus*) and a mussel (*Mytilus trossulus*): their so-called attack rates and handling times. We find that differences among individual snails in their attack rates reduced population feeding rates by up to nine percent. We also estimated that handling time differences among individuals increased population feeding rates but not as much as they were decreased by attack rate differences. Furthermore, we find that individual differences in attack rates can combine

Coblentz et al. show that individual differences among predators, such as the whelk *Nucella ostrina* shown here with its barnacle *prey Balanus glandula*, can alter the population-level strengths of predator-prey interactions.

with differences in the environments experienced by the individuals (the amount of prey available) to reduce population feeding rates by up to twenty nine percent. This combined effect was greater than the effect of individual differences in attack rates or differences in the environment alone. Overall, our study shows that individual differences can have a measurable impact on the strength of predator-prey interactions in the field. Nevertheless, how large this impact is depends on a combination of the average characteristics of species, how different individuals are from one another, their environments, and how these different components interact with one another.

Appendix S1: Derivation of the observational attack rate estimator

for

Coblentz, K.E., Merhoff, S. & Novak, M. Quantifying the effects of intraspecific variation on predator feeding rates through nonlinear averaging. *Functional Ecology.*

Derivation

In the main text, we use an estimator for individual attack rates that combines data on the proportions of observations of individuals that are feeding events on prey species or nonfeeding events, handling times, and prey densities to estimate predator attack rates (main text eqn. 1). Here we provide a derivation of that estimator following Novak *et al.* (2017) but based on longitudinal feeding observations of individuals.

Consider a predator that feeds on S different prey species and, like whelks, can feed on only one prey at a time. Therefore, at any given point in time, the predator is feeding on one of the S prey species or is not feeding. Now, assume that the predator has feeding rates f_i on each prey i where $i = 1, \ldots, S$. Assume also that the predator takes handling time h_i to feed on each prey species i and is readily observable feeding during that handling time. Over a time period T, the predator is expected to eat $f_i T$ individuals of prey species i. During this time, the predator will spend $f_i h_i T$ amount of time handling and observable feeding on prey i. From this, the proportion of the total time the predator spends handling each prey species is $f_i h_i$ and the proportion of time the predator spends not handling prey is $1 - \sum_{j=1}^{S} f_j h_j$.

Now, as in our feeding experiment, we can imagine observing the predator individual n_T total times over some time interval. We assume that these observations are spaced far enough from one another in time that they are independent. Under this assumption, the number of times we observe the individual not feeding (n_0) or the individual feeding on prey i (n_i) will have a multinomial distribution,

$$(n_0, n_1, \ldots, n_S) \sim \text{Multinomial}(p_0 = 1 - \sum_{j=1}^{S} f_j h_j, p_1 = f_1 h_1, \ldots, p_S = f_S h_S; n = n_T)$$

(eqn. S1.1)

where p_i is the proportion of observations that are nonfeeding observations p_0 or feeding observations on prey species $1, \ldots, S$ and n is the total number of observations. This gives us an explicit relationship between the proportions of feeding and nonfeeding observations of the predator and its feeding rates and handling times.

To arrive at the attack rate estimator in eqn. 1 of the main text, we now need to provide an explicit model for the predator's feeding rate (i.e. its functional response). We use the multispecies Holling Type II functional response (Holling, 1959) because it has been shown to be a good characterization of whelk feeding rates when whelk densities are constant, as they were in our experiment (Novak *et al.*, 2017). The multispecies Holling Type II functional response describes the feeding rate of the predator on prey i as

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$$f_i = \frac{a_i R_i}{1 + \sum_{j=1}^{S} a_j h_j R_j} \qquad \text{(eqn. S1.2)}$$

where a_i is the attack rate of the predator on prey i and R_i is the density of prey i. Substituting eqn. S1.2 into eqn. S1.1 gives

$$(n_0, n_1, \ldots, n_S) \sim \text{Multinomial}(p_0 = 1 - \frac{\sum_{j=1}^{S} a_j h_j R_j}{1 + \sum_{j=1}^{S} a_j h_j R_j}, p_1 = \frac{a_1 h_1 R_1}{1 + \sum_{j=1}^{S} a_j h_j R_j}, \ldots,$$
$$\text{(eqn. S1.3)}$$

$$p_S = \frac{a_S h_S R_S}{1 + \sum_{j=1}^{S} a_j h_j R_j}; n = n_T)$$

As in the main text, we assume that we have estimates of the handling times for each prey and that we can measure resource densities in a way that reflects resource densities over the course of time the individual predator was observed. If this is the case, the only unknown parameters in eqn. S1.3 are the individual's attack rates. To get to the attack rate estimator in eqn. 1 of the main text, we first recognize that $\frac{1}{p_0} = 1 + \sum_{j=1}^{S} a_j h_j R_j$. We can see this with some algebraic manipulation of the first term of the multinomial distribution in eqn. S1.3:

$$\frac{1}{p_0} = \frac{1}{1 - \frac{\sum_{j=1}^{S} a_j h_j R_j}{1 + \sum_{j=1}^{S} a_j h_j R_j}} \qquad \text{(eqn. S1.4a)}$$

$$\frac{1}{p_0} = \frac{1}{\frac{1 + \sum_{j=1}^{S} a_j h_j R_j}{1 + \sum_{j=1}^{S} a_j h_j R_j} - \frac{\sum_{j=1}^{S} a_j h_j R_j}{1 + \sum_{j=1}^{S} a_j h_j R_j}} \qquad \text{(eqn. S1.4b)}$$

$$\frac{1}{p_0} = \frac{1}{\frac{1}{1 + \sum_{j=1}^{S} a_j h_j R_j}} \qquad \text{(eqn. S1.4c)}$$

$$\frac{1}{p_0} = 1 + \sum_{j=1}^{S} a_j h_j R_j \qquad \text{(eqn. S1.4d)}$$

We can then plug this into the equation for the proportion of feeding events for prey i (i.e. the ith term of the multinomial in eqn. S1.3) to get,

$$p_i = \frac{a_i h_i R_i}{\frac{1}{p_0}} \qquad \text{(eqn. S1.5)}$$

With estimates of the predator's handling time on prey i and the density of prey i over the time period the predator was observed, the only unknown in eqn. S1.5 is the predator attack rate. Solving for the attack rate, a_i gives the attack rate estimator in eqn. 2 of the main text:

$$a_i = \frac{p_i}{p_0} \times \frac{1}{h_i R_i}. \qquad \text{(eqn. S1.6)}$$

Eqn. S1.6 matches eqn. 2 in the main text with $a_i = a_{ijk}$, $p_i = p_{ijk}$, $p_0 = p_{0jk}$, and $R_i = R_{ik}$.

References

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* **91**, 385–398.

Novak, M., Wolf, C., Coblentz, K.E. & Shepard, I.D. (2017) Quantifying predator dependence in the functional response of generalist predators. *Ecology Letters* **20**, 761–769.

Appendix S2: Laboratory handling time experiment

for

Coblentz, K.E., Merhoff, S. & Novak, M. Quantifying the effects of intraspecific variation on predator feeding rates through nonlinear averaging. *Functional Ecology*.

Introduction and Methods

Estimating individual attack rates requires estimates of predator handling times on prey. To determine the handling times of the whelk *Nucella ostrina* on the acorn barnacle *Balanus glandula* and the mussel *Mytilus trossulus* (hereafter barnacles and mussels), we used a laboratory experiment to parameterize a regression model quantifying the relationship between handling times, 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 clear plastic aquaria (dimensions 21.844cm x 21.844cm x 17.526cm), we placed a single whelk between 4mm and 21mm into an aquarium with several barnacles between 1mm and 5mm or several mussels between 4mm and 25mm. All whelks and prey were collected at Yachats, OR at the same site in which the caging experiment took place. The flow-through system replicated semidiurnal tides by alternately draining and refilling the aquaria every six hours. Security cameras (Model DS-2CD2622FWD-IZS, Hikvision, China) mounted above the aquaria filmed the whelks and we monitored whelks several times per day to determine whether the whelks 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 had fed on the prey item (drilled or pried for barnacles, drilled the valve, drilled 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 regression models in a Bayesian framework. 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 the barnacle's flesh remaining 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. We fit both models using 'Stan' through the R package 'rstanarm' (Carpenter et al. 2017, Stan Development Team 2016). For the barnacle model, we placed a Normal($\mu = 0$, $\sigma = 10$) prior on the intercept, a Normal(0, 2.5) prior on 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 (see documentation for the 'rstanarm' package for an explanation of the LKJ distribution). For the mussel model, we placed a Normal(0, 10) prior on the intercept, Normal(0, 5) priors on the coefficients, and a 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).

Results

We analyzed 163 handling times on barnacles across 68 individuals with an average handling time of 0.6 days. Whelk handling times increased with prey size, decreased with predator size, and were lower when

whelks pried barnacles rather than drilling them (Supplementary Online Material (SOM) Table 1.1, SOM Figure 1.1). For mussels, we analyzed 46 handling times across 40 individuals with an average handling time of 1.68 days. Whelk handling times 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 mussel valve relative to drilling through the side of the valve (SOM Table 1.2, SOM Figure 1.2). The median regression coefficient estimates in SOM Tables 1.1 and 1.2 are the coefficients used to estimate the handling times of each feeding observation in the caging experiment. The average handling times across the estimates for each feeding observation provided the characteristic handling time estimates across the experiment.

Literature Cited

Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt, M., *et al.* (2017). Stan: A probabilistic programming language. *J. Stat. Softw.,* 76.

Gelman, A., Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Stat. Sci.*, 7:457—511**.**

Stan Development Team (2016). rstanarm: Bayesian applied regression modeling via Stan. *http://mc-stan.org*.

Tables and Figures

Table S2.1: Estimated regression parameters and associated 95% credible intervals for the regression model of log whelk handling times on barnacles

Parameter	Median Estimate	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 S2.2: Estimated regression parameters and associated 95% credible intervals for the regression model of log whelk handling times on mussels

Parameter	Median Estimate	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)

Figure S2.1: The handling times of whelks on barnacles decrease with whelk size (A), increase with barnacle size (B), and are lower when whelks pry open barnacles' opercula as opposed to drilling (C).
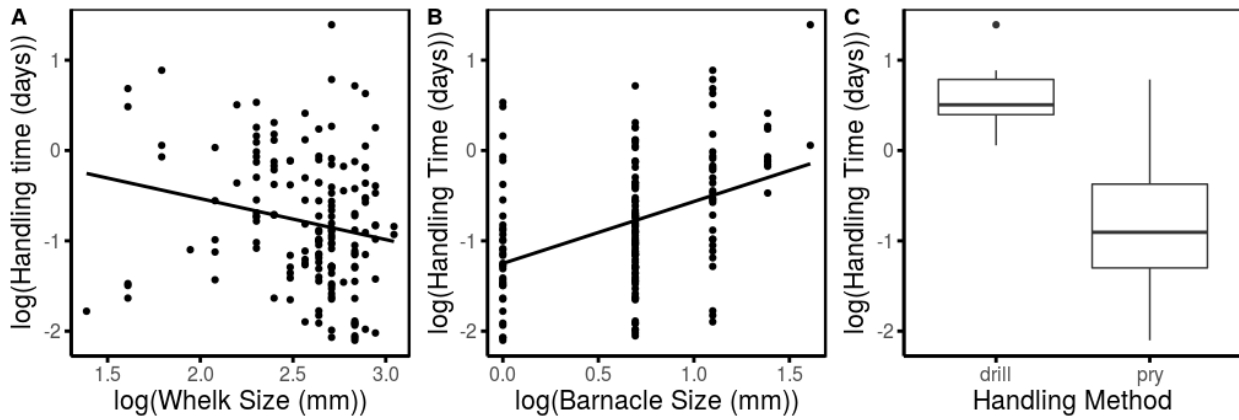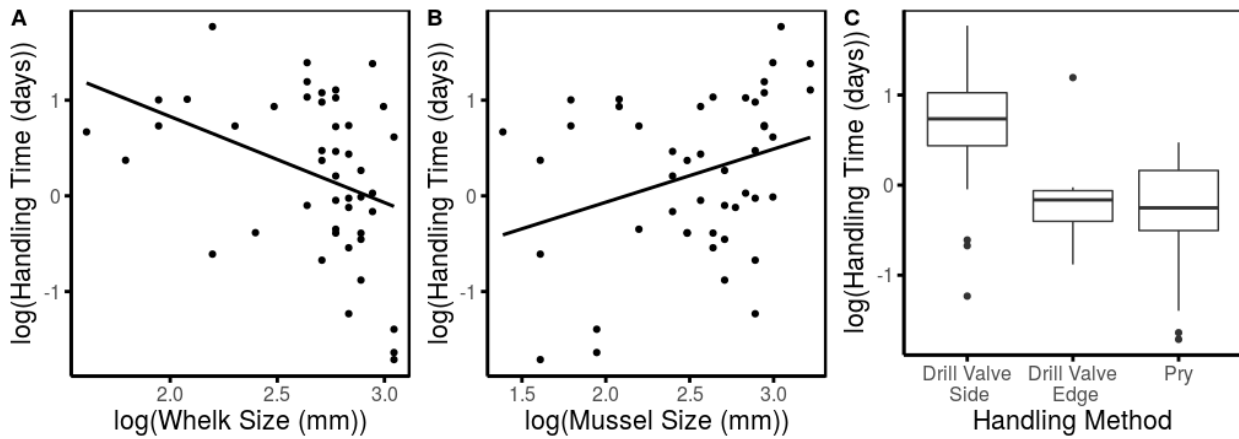

Figure S2.2: The handling times of whelks on mussels decrease with whelk size (A), increase with mussel size (B), and are shorter when whelks pry open or drill the edges of the valves of mussels as opposed to drilling through the sides of the mussels' valves (C).

for

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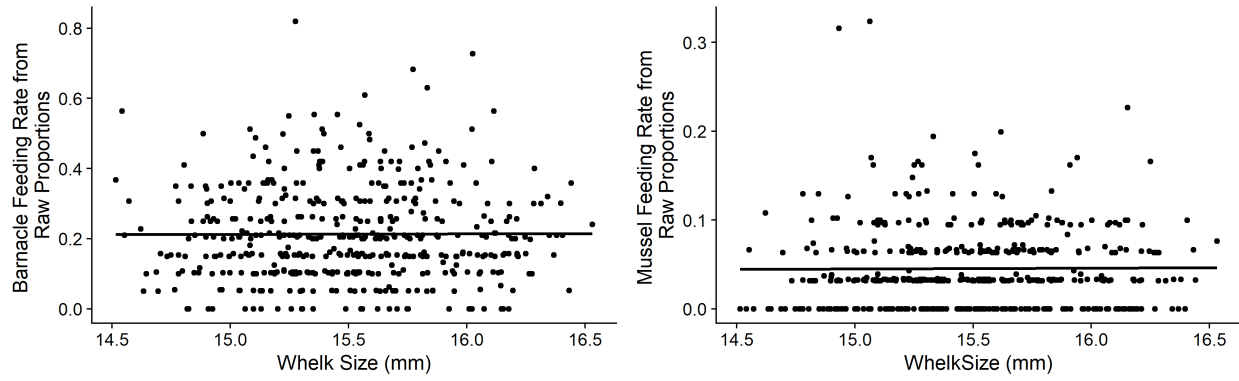

Figure S3.1. Individual whelk feeding rates calculated using the raw (non-estimated) proportions of feeding and non-feeding events (see Appendix 1) show no relationship with individual whelk sizes over the range of whelk sizes included in the experiment.
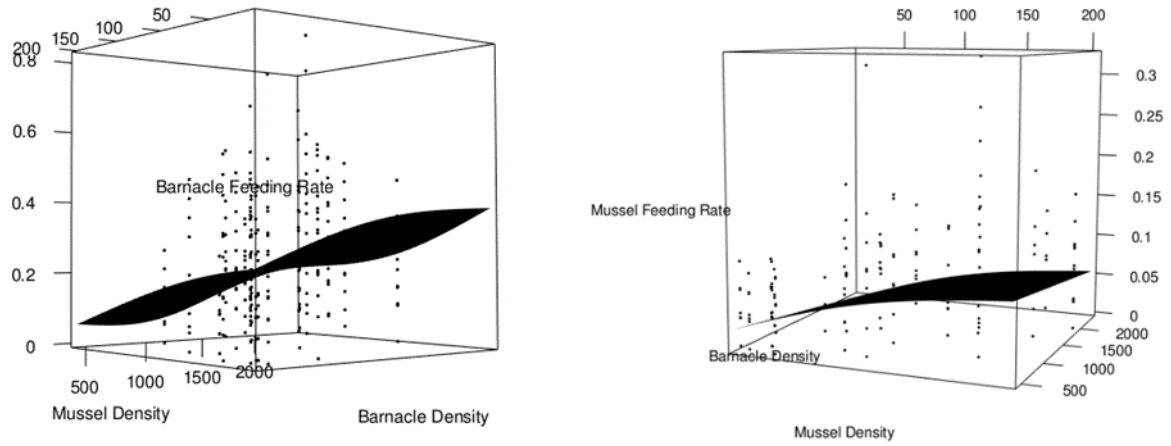
Figure S3.2. Mean whelk feeding rates calculated using the raw (non-estimated) proportions of feeding and non-feeding events (see Appendix 1) increased with focal prey densities and decreased with non-focal prey densities.
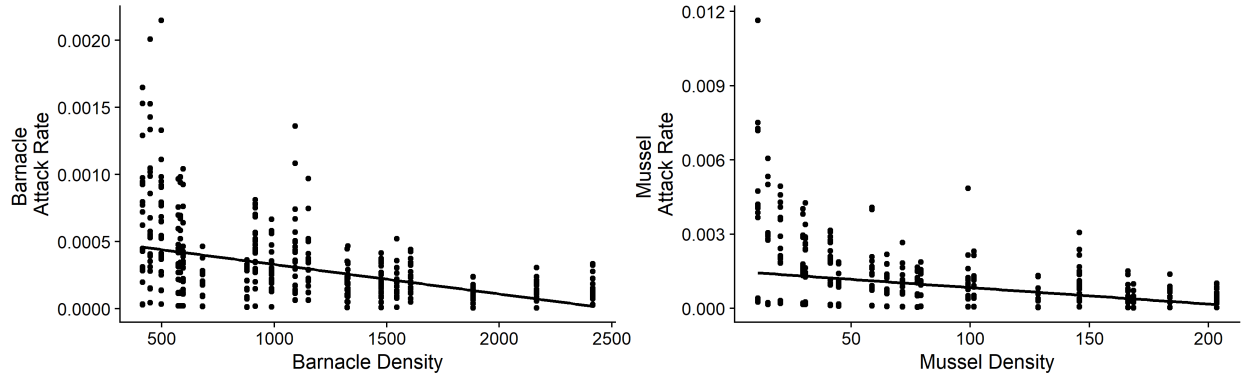
Figure S3.3. Individual whelk attack rates on barnacles and mussels decreased with increasing barnacle and mussel densities.