

2013

Physiological effects of diet mixing on consumer fitness: a meta-analysis

JS Lefcheck

Virginia Institute of Marine Science

MA Whalen

Virginia Institute of Marine Science

TM Davenport

Virginia Institute of Marine Science

JP Stone

Virginia Institute of Marine Science

JE Duffy

Virginia Institute of Marine Science

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Aquaculture and Fisheries Commons](#)

Recommended Citation

Lefcheck, JS; Whalen, MA; Davenport, TM; Stone, JP; and Duffy, JE, "Physiological effects of diet mixing on consumer fitness: a meta-analysis" (2013). *VIMS Articles*. 899.

<https://scholarworks.wm.edu/vimsarticles/899>

Physiological effects of diet mixing on consumer fitness: a meta-analysis

JONATHAN S. LEFCHECK,^{1,3} MATTHEW A. WHALEN,^{1,2} THERESA M. DAVENPORT,¹ JOSHUA P. STONE,¹
AND J. EMMETT DUFFY¹

¹Virginia Institute of Marine Science, College of William and Mary, P.O. Box 1346, Gloucester Point, Virginia 23062-1346 USA

²Department of Ecology and Evolution, University of California, One Shields Avenue, Davis, California 95616 USA

Abstract. The degree of dietary generalism among consumers has important consequences for population, community, and ecosystem processes, yet the effects on consumer fitness of mixing food types have not been examined comprehensively. We conducted a meta-analysis of 161 peer-reviewed studies reporting 493 experimental manipulations of prey diversity to test whether diet mixing enhances consumer fitness based on the intrinsic nutritional quality of foods and consumer physiology. Averaged across studies, mixed diets conferred significantly higher fitness than the average of single-species diets, but not the best single prey species. More than half of individual experiments, however, showed maximal growth and reproduction on mixed diets, consistent with the predicted benefits of a balanced diet. Mixed diets including chemically defended prey were no better than the average prey type, opposing the prediction that a diverse diet dilutes toxins. Finally, mixed-model analysis showed that the effect of diet mixing was stronger for herbivores than for higher trophic levels. The generally weak evidence for the nutritional benefits of diet mixing in these primarily laboratory experiments suggests that diet generalism is not strongly favored by the inherent physiological benefits of mixing food types, but is more likely driven by ecological and environmental influences on consumer foraging.

Key words: *balanced diet; biodiversity; diet mixing; dietary specialism vs. generalism; meta-analysis; nutritional ecology; toxin dilution; trophic transfer.*

INTRODUCTION

The degree of dietary generalism vs. specialism is a central issue in ecology, informing the genesis and maintenance of biodiversity (Chesson et al. 2000), the evolution and consequences of ecological interactions (Futuyma and Moreno 1988), and trophic transfer through food webs (Duffy et al. 2007). At the level of the individual consumer, early foraging theory predicted that energy gain, and thus fitness, would be maximized by feeding on the single most abundant and highest quality food item (Stephens and Krebs 1986). Over evolutionary time, selection on specialists was also expected to drive physiological, morphological, and behavioral adaptations that allowed for more efficient exploitation of such food items. In nature, however, many consumers have generalized diets whose constituents vary widely in their availability, nutritional quality, digestibility, and toxicity (Crawley 1983). Consequently, generalists were predicted to be less efficient overall in their ability to utilize any given food in their diet. This trade-off in quality for quantity has often led the generalist to be called the “jack of all trades, and master of none” (Futuyma and Moreno 1988:212).

Early reviews, however, found little support for the predicted superior fitness of specialists in nature (Smiley 1978, Fox and Morrow 1981), whereas the benefits of a generalized diet have now been documented across a wide range of taxa (Belovsky 1984, Krebs and Avery 1984, Pennings et al. 1993, Bernays et al. 1994, DeMott 1998, Eubanks and Denno 1999, Toft and Wise 1999, Coll and Guershon 2002; but see Bernays and Minkenberg 1997). Generalists have also been shown to be at least as efficient at ingesting and processing food as their specialist counterparts (Scriber and Feeny 1979, Futuyma and Wasserman 1981, Bjorndal 1991). To explain the prevalence of generalized diets, many hypotheses have been proposed. These can be divided into those based on the inherent nutritional quality of the food and the physiology of the consumer, and those involving extrinsic influences on foraging, such as the spatial and temporal availability of prey (MacArthur and Pianka 1966, Westoby 1978) or predation risk (Jeffries and Lawton 1984). We focus here on two hypotheses relating exclusively to prey nutritional content and consumer physiology. First, the *balanced-diet hypothesis* proposes that a diverse prey assemblage contains species that are complementary in their nutritional composition. Thus, a generalized diet provides a more complete range of nutrients, which translates to higher consumer fitness (Pulliam 1975, Raubenheimer and Simpson 1997). An alternative but not mutually exclusive explanation is the

Manuscript received 3 February 2012; revised 28 September 2012; accepted 1 November 2012. Corresponding Editor: B. J. Cardinale.

³ E-mail: jslefcche@vims.edu

toxin-dilution hypothesis, which proposes that diet mixing limits the quantity of toxins ingested from any one species, lessening their collective negative effect on fitness across a range of toxic prey (Freeland and Janzen 1974, Bernays et al. 1994).

In addition to these direct fitness consequences for individual foragers, diet breadth also has important consequences for communities and ecosystems. Hill-Brand and Cardinale (2004) and Edwards et al. (2010) showed using meta-analysis that the top-down impact of consumers on the aggregate biomass or abundance of their prey tends to decrease as the number of species in the prey assemblage increases, although these conclusions were primarily drawn from consumer-removal experiments rather than manipulations of prey richness. In contrast, much less attention has focused on corresponding bottom-up effects, or how prey diversity influences trophic transfer to higher levels (Duffy et al. 2007). If a varied diet enhances consumer fitness, then the degree of trophic transfer through food webs may in turn depend on the diversity of available prey.

Despite the implications of diet mixing at the individual, community, and ecosystem levels for both basic and applied ecology, there has been no comprehensive quantitative analysis of the fitness consequences of diet mixing. Several summaries do exist for particular consumer taxa. Bernays and Minkenberg (1997) reviewed 12 studies that manipulated diet diversity in grasshoppers, all of which reported significant, but weak, benefits of diet mixing. This pattern was not upheld in their own experiments with caterpillars and true bugs, where they found no evidence that mixtures yielded higher fitness than single food types (Bernays and Minkenberg 1997). Coll (1998) reviewed the benefits of including plants in the diets of predatory beetles and found generally positive effects, but their data set was restricted primarily to agroecosystems. Both reviews also employed a “vote-counting” approach that provides no quantitative estimate of effect size.

Here, we report the results of a meta-analysis synthesizing 161 peer-reviewed publications from a variety of taxa and systems, yielding 493 experiments that varied diet diversity and measured the change in consumer fitness while holding most other ecological and environmental constraints constant. We used this data set to address three general questions: (1) Do mixed diets promote consumer fitness relative to a single-species diet, as predicted by the balanced-diet hypothesis? (2) Do mixed diets enhance fitness when the prey assemblage includes chemically defended species, consistent with the toxin-dilution hypothesis? (3) Are the effects of diet mixing similar across taxa, trophic levels, and habitats?

METHODS

We conducted a literature search using ISI Web of Science on 8 February 2011 using the follow keyword search: (prey OR diet* OR food OR alga* OR

nutrition*) AND (mix* OR divers* OR choice OR general* OR special*) AND (fitness OR growth OR surviv* OR reproduc* OR fecund*) AND (experiment* OR manipul* OR assay). To ensure that we did not systematically omit relevant bodies of literature by restricting ourselves to a single database, we repeated the same keyword search using CSA/Proquest, restricting the date range to the same as in the ISI search. We examined the abstract and the text of each publication to select studies that met the following criteria. The study must: (1) be published in a peer-reviewed journal, (2) be a controlled and replicated experiment, (3) present fitness data for a diet treatment consisting of equal densities of two or more prey taxa, as well as for diets consisting of each of those prey taxa alone, and (4) measure some component of consumer fitness as a function of diet treatment, specifically survivorship, growth, reproduction, and/or population growth. We note that in some cases, individual diets were actually strains of a single algal species or functional groups of multiple similar species. Since this subset of studies did not produce results that were qualitatively different from those that manipulated species-level diversity, we hereafter simply refer to diet items offered alone as “single-species diets.” We excluded studies that used humans as consumers and studies that included prey items the consumer would not encounter naturally, such as enhanced or artificial foods. Finally, we examined the Literature Cited section of each study retained from the keyword searches and added those studies that met the above criteria to the database.

For each experiment in the final database we recorded all estimates of fitness reported by the authors in the text, figures, or tables. In instances where the authors reported multiple responses for the same fitness component, we chose the one that was measured more directly, or generated composite traits when the composite trait represented a more holistic measure of fitness than either individual trait—for instance, egg production \times number of hatchlings = total reproductive success. For each fitness component in each experiment, we extracted the mean response under each treatment, as well as the sample size and variance when reported. In the case of repeated-measures designs, we recorded the last date for which all treatments were measured, in order to fairly compare them to studies that did not employ repeated measures. Finally, we recorded consumer taxon, trophic level (based solely on the identity of the prey items offered during the experiment), and habitat (e.g., terrestrial grassland, marine benthos), as well as whether the prey assemblage included chemically defended species (as identified by the authors of the original publication) and the number of prey species (richness) included in the mixture.

We estimated the effects of diet diversity on consumer fitness using log response ratios, hereafter LRs, a dimensionless response metric commonly employed in ecological meta-analysis (Hedges et al. 1999). We

TABLE 1. Candidate mixed models proposed to explain the effect of diet diversity on four fitness components as a function of seven predictors.

Model	Predictors included in the model						
	Study	Habitat	Trophic level	Defense	S_{\max}	$T \times S_{\max}$	$D \times S_{\max}$
0	x						
1	x	x					
2	x		x				
3	x			x			
4	x				x		
5	x	x		x			
6	x		x	x			
7	x			x	x		
8	x		x		x	x	
9	x			x	x		x
10	x	x	x	x	x		
11	x	x	x	x	x	x	x

Notes: The predictors are study (random term), habitat, trophic level, defense (the presence of chemically defended prey), S_{\max} (the number of prey species in the mixture), $T \times S_{\max}$ (the interaction between trophic level and prey richness), and $D \times S_{\max}$ (the interaction between prey defense and prey richness). The rationale behind each model is as follows: model 0 is the null model (includes only the random intercept); models 1–4 are the univariate models, including only the random term (study) and each fixed factor; models 5–7 estimate the other fixed factors while accounting for the presence of defended prey; model 8 tests whether the effect of diet mixing on fitness changes as a function of trophic level; model 9 tests whether the effect of diet mixing on fitness changes when defended prey are present; model 10 is the global model without interactions; and model 11 is the global model with interactions.

calculated two LRs for each measure of fitness, which we treated as two separate responses in our analysis: (1) the *mean log response ratio* (LR_{mean}), which compares consumer fitness on the mixed diet to fitness averaged across all diets that offered single species alone, and (2) the *maximum log response ratio* (LR_{max}), which compares fitness on the mixed diet to that on the single prey species that supported the highest fitness. For both metrics a positive LR indicates that the prey mixture outperformed the diet of single prey species (whether average or best), whereas a negative LR indicates the opposite. Individual LRs were averaged across all experiments to produce a grand mean LR, $\overline{LR}_{\text{mean}}$ and $\overline{LR}_{\text{max}}$, for each fitness component with 95% confidence intervals derived using the sample variance of the LRs.

To determine if LR_{mean} or LR_{max} varied as a function of consumer trophic level, habitat, prey richness, and/or prey defense, we constructed linear mixed-effects models, allowing the intercept to vary by study. We used varying-intercept models because our data set contains studies of varying rigor and complexity, and we wished to account for within-study variation in the effect size when estimating the overall regression coefficients (Gelman and Hill 2007). We created a candidate set of models to address specific biological hypotheses (Table 1). Using an information-theoretic approach, we calculated Akaike weights to identify the model(s) with the greatest support given the data and the candidate set of models (Burnham and Anderson 2002). A term was considered significant in the model (i.e., different from zero) if it was greater than twice its reported standard error (Gelman and Hill 2007). All analyses were performed in R 2.15.1 (R Development Core Team 2012).

To evaluate sources of potential bias in the data, we conducted two additional analyses. First, we tested whether studies that reported multiple experiments dominated the results by randomly sampling a single experiment from each study, repeating this draw 10 000 times, and then averaging the LRs across all subsampled data sets. Second, we investigated how the precision of studies influenced the results by repeating the analyses after weighting each individual LR by the inverse of its variance or sample size (Hedges et al. 1999). For a detailed discussion of search terms and construction of the log response ratios, linear mixed models, and tests for bias, see Appendix A.

RESULTS

The ISI search generated 3487 peer-reviewed studies, of which 76 studies met our criteria. The CSA/Proquest search generated 3440 peer-reviewed studies, of which 23 studies met our criteria and were not in the original ISI search. An additional 62 studies were obtained from the Literature Cited of these papers. The database and Literature Cited searches together yielded a total of 161 studies from 1973 through 2010 representing 493 experiments and 664 measures of fitness. The full list of publications can be found in Appendix B.

The consumers in the data set were diverse, including protists ($N = 8$ studies, 30 experiments), rotifers ($N = 5$, 32), molluscs ($N = 38$, 123), annelids ($N = 1$, 6), arthropods ($N = 95$, 435), echinoderms ($N = 7$, 16), chordates ($N = 8$, 21), and a parasitic plant ($N = 1$, 1). The experiments spanned freshwater ($N = 21$, 116), marine ($N = 95$, 314), and terrestrial habitats ($N = 45$, 234) and a variety of trophic levels: parasites ($N = 1$, 1),

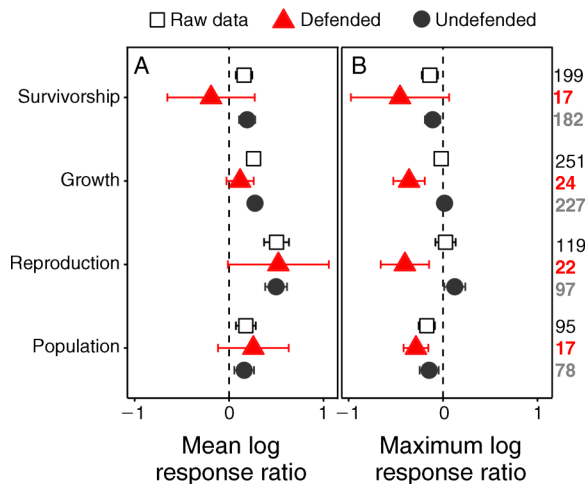


FIG. 1. Effects of diet mixing on the four fitness components for the full data set (solid circles), for the subset of studies with chemically defended prey (red triangles), and for the subset of studies with undefended prey (open squares). (A) The mean log response ratio represents the grand mean log ratio ($\bar{L}R_{\text{mean}} \pm 95\%$ CI) of fitness on the mixed diet relative to that on the average of single-species diets. (B) The maximum log response ratio represents the grand mean log ratio ($\bar{L}R_{\text{max}} \pm 95\%$ CI) of fitness on the mixed diet relative to that on the best single prey species. Numbers to the right indicate the number of measurements of fitness used in each calculation.

detritivores ($N = 2, 6$), herbivores ($N = 107, 454$), carnivores ($N = 29, 94$), and omnivores ($N = 22, 109$). Roughly one-fifth of the studies included at least one defended prey species ($N = 29, 80$).

Considering the data set as a whole, a mixed diet significantly enhanced fitness relative to the average of single-species diets for individual survivorship (grand mean $\bar{L}R_{\text{mean}} = 0.158$, corresponding to a 17% increase in fitness on a mixed diet), growth ($\bar{L}R_{\text{mean}} = 0.260, +30\%$), reproduction ($\bar{L}R_{\text{mean}} = 0.502, +65\%$), and population growth ($\bar{L}R_{\text{mean}} = 0.177, +19\%$). Significance was determined by nonoverlap of 95% confidence intervals with zero (Fig. 1A). In contrast, none of the fitness components were higher on the mixed diet than on the best single-species diet when averaged across studies (Fig. 1B). In fact, survivorship was significantly less on the mixed diet than on the best single-species diet ($\bar{L}R_{\text{max}} = -0.140, -13\%$), as was population growth ($\bar{L}R_{\text{max}} = -0.172, -16\%$). Thus, there was no evidence for a consistent advantage of a mixed diet on consumer fitness for the data set as a whole. When the data set was partitioned by subcategory, there was only one scenario in which fitness on the mixed diet significantly exceeded that on the best single-species diet (reproduction in marine habitats, $\bar{L}R_{\text{max}} = 0.230, +26\%$, $N = 45$ experiments). The full summary of LRs by subcategory can be found in Appendix D: Table D1.

A substantial proportion of studies included chemically defended prey species, which may be expected to decrease fitness in mixtures. To evaluate whether these experiments influenced the overall pattern, we partitioned the data set

into studies that included defended prey vs. those that did not. When studies with only undefended prey were considered, the patterns were nearly identical to the trends from the full data set, with the exception of reproduction relative to the best single-species diet, which was slightly significantly positive (Fig. 1). Oppositely, when studies with only defended prey were considered, there was no advantage of a mixed diet relative to the average of single-species diets (Fig. 1A), and fitness was significantly reduced relative to the best single-species diet in all cases except survivorship (Fig. 1B).

Focusing on the grand mean LRs across the entire data set obscures the fact that LRs for individual experiments varied widely. This variance can be divided into three categories that represent different physiological phenomena, represented by quadrants in a plot of $L\bar{R}_{\text{mean}}$ against $L\bar{R}_{\text{max}}$ (Fig. 2A). For experiments falling in quadrant I, both LRs are positive, indicating that performance on the mixed diet exceeded that on both the average and the best single-species diet. We considered points in this quadrant to exhibit *diet complementarity*, since the effects of mixing foods were positive and synergistic. For studies in quadrant III, both LRs are negative, indicating that performance on the mixed diet was worse than on both the average and the best single-species diet. We considered points in this quadrant to exhibit *diet interference*, since feeding on a mixed diet negated any benefits from the other items in the diet. Finally, for studies in quadrant IV, $L\bar{R}_{\text{mean}}$ is positive and $L\bar{R}_{\text{max}}$ is negative, indicating that performance on the mixed diet was better than on the average of single-species diets, but inferior to that on the best single-species diet. We considered points in this quadrant to exhibit *diet neutrality*, since they present no evidence of aggregate negative or positive interactions among food types. Because no scenario exists where the mixed diet can enhance performance relative to the best but not the average of single-species diets, points are bounded below the 1:1 line. Considering the data set as a whole, approximately half of all experiments measuring growth and reproduction exhibited diet complementarity (Fig. 2C, D). A substantial number of studies exhibited diet complementarity for survivorship and population growth as well, but these tended to be counterbalanced by a similar number of studies that exhibited diet interference. Studies with defended prey almost always exhibited diet neutrality or diet interference (Fig. 2B–E).

The mixed-model analysis showed that different combinations of factors best predicted the effect of diet mixing on the four fitness components (Table 2). The model with the highest Akaike weight (and thus the greatest support) for survivorship included prey richness, trophic level, and their interaction (Model 8). The parameter estimates for the trophic level-by-prey richness interaction term predicted a significant decrease in survivorship for omnivores and carnivores compared to herbivores with each additional prey item added to the mixture (Appendix C). In other words, in terms of their survivorship, herbivores were predicted to benefit more

from adding species to their diet than higher trophic levels. This prediction held for fitness on the mixture relative to both the average and best single-species diets, although the decreasing trend for carnivores relative to the average of single-species diets was not considered significant. Model 8 was also identified as the best model for growth. The model output showed that the effect of prey richness on growth for carnivores and omnivores was no different than for herbivores, relative to both the average and best single-species diets. The selection of this model as the best of the candidates for growth was driven by the inclusion of detritivores, which only appeared in experiments that measured growth. Their growth was predicted to increase significantly with increasing prey richness, compared to both the average and best single-species diet (Appendix C). However, we note that this prediction was based on only six experiments and two levels of richness. For both survivorship and growth, the global model with interactions (Model 11) was also supported for fitness on the mixture relative to the best single-species diet, but we consider it a less parsimonious alternative to Model 8. Five separate models were identified as having some level of support for reproduction, four of which included prey defense as a predictor. Similarly, six separate models were identified as having some level of support for population growth, three of which also included prey defense.

To evaluate the influence of bias on our results, we began by first subsampling the data set to consider only a single experiment from each study, which produced identical patterns to those of the complete data set (Appendix C: Fig. C2). Next, we compared variance-weighted, sample size-weighted, and equally weighted grand mean LRs. Weighting based on sample size did not change our interpretation, but weighting by variance showed that survivorship was significantly lower on a mixed diet and reproduction significantly higher compared to the equally weighted grand mean LRs (Appendix C: Fig. C3). Given the substantial loss of information associated with variance weighting—only 59% of estimates reported variance—we decided to draw inferences from the full data set, as it is likely to be more robust and represents a much wider range of taxa and habitats. For a full discussion of mixed-model results and tests of bias, including variance-weighting, see Appendix C.

DISCUSSION

Our analysis of 493 experiments and 664 estimates of consumer fitness showed that, generally, a mixed diet including several prey types supported higher fitness than the average of single prey species diets, but only exceeded the best single prey species in less than half of published cases. As a result, diet mixing did not significantly enhance any fitness component beyond the single best single-species diet when averaged across studies (Fig. 1B). Because our conclusions are drawn from experiments that were largely conducted in the laboratory, we emphasize that our results primarily reflect the inherent nutritional quality of the

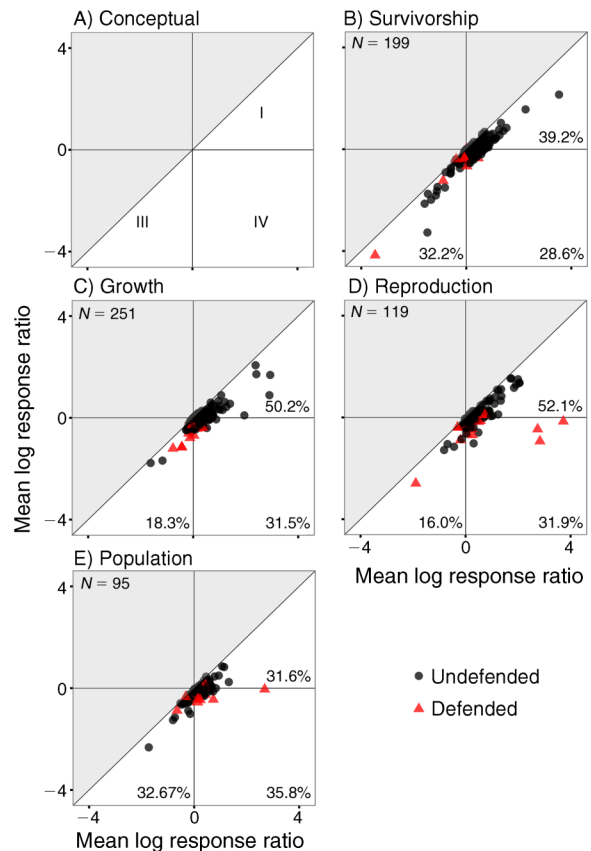


FIG. 2. Relationship between the mean log response ratio (LR_{mean}) and the maximum log response ratio (LR_{max}) across individual experiments. (A) Conceptual figure showing the three quadrants that correspond to (I) diet complementarity, (III) diet interference, and (IV) diet neutrality, as defined in Results. Panels (B)–(E) show LRs for individual experiments plotted for (B) individual survivorship, (C) growth, (D) reproduction, and (E) population growth. Solid circles denote studies with undefended prey; red triangles denote studies with chemically defended prey. The total number of experiments (N) for each component is given in each panel's top left corner, and the percentage of total experiments (both defended and undefended) occurring in each quadrant is given at the bottom right.

food and the physiology of the consumers. However, laboratory experiments allow for direct tests of two important hypotheses regarding prey nutritional content and consumer fitness by controlling for other ecological and environmental influences on foraging. First, we investigated the balanced-diet hypothesis, which suggests that a mixture of prey species provides a more complete range of nutritional resources than any single prey species. Overall, we found a high prevalence of diet neutrality in our analysis, where fitness on the mixed diet was higher than the average but not than the best single-species diet. This result is inconsistent with the balanced-diet hypothesis, which predicts that energy gain and thus fitness will be highest on the mixture of prey items (Pulliam 1975). But this average trend masks the prevalence of diet complementarity, where fitness on the mixed diet exceeds even the

TABLE 2. The results of the model selection. Candidate models and their predictors are described in Table 1.

Model and statistic	Survivorship		Growth		Reproduction		Population	
	LR _{mean}	LR _{max}	LR _{mean}	LR _{max}	LR _{mean}	LR _{max}	LR _{mean}	LR _{max}
Model 0								
<i>k</i>	3		3		3		3	
AIC _c	330.4	302.4	279.5	146.5	243.4	187.4	128.4	106.2
<i>w_i</i>	0.00	0.00	0.00	0.00	0.37	0.01	0.30	0.04
Model 1								
<i>k</i>	5		5		5		5	
AIC _c	333.1	305.8	282.8	149.6	247.2	187.6	131.0	105.7
<i>w_i</i>	0.00	0.00	0.00	0.00	0.06	0.01	0.08	0.05
Model 2								
<i>k</i>	5		6		5		5	
AIC _c	328.0	303.4	273.5	136.8	246.1	189.6	132.2	102.3
<i>w_i</i>	0.00	0.00	0.05	0.02	0.10	0.00	0.05	0.26
Model 3								
<i>k</i>	4		4		4		4	
AIC _c	327.8	298.4	280.3	140.9	245.1	180.4	129.4	106.3
<i>w_i</i>	0.00	0.01	0.00	0.00	0.16	0.50	0.18	0.04
Model 4								
<i>k</i>	4		4		4		4	
AIC _c	322.4	301.1	277.8	148.5	245.2	189.5	129.4	106.4
<i>w_i</i>	0.02	0.00	0.01	0.00	0.15	0.01	0.19	0.03
Model 5								
<i>k</i>	6		6		6		6	
AIC _c	330.3	301.7	248.0	144.6	249.1	182.9	132.7	106.0
<i>w_i</i>	0.00	0.00	0.00	0.00	0.02	0.14	0.04	0.04
Model 6								
<i>k</i>	6		7		6		6	
AIC _c	327.4	300.6	275.1	132.8	248.0	183.8	133.5	101.1
<i>w_i</i>	0.00	0.00	0.02	0.18	0.04	0.09	0.02	0.47
Model 7								
<i>k</i>	5		5		5		5	
AIC _c	320.2	297.1	278.5	142.8	246.9	182.5	129.9	107.1
<i>w_i</i>	0.05	0.03	0.00	0.00	0.07	0.17	0.15	0.02
Model 8								
<i>k</i>	8		10		8	
AIC _c	314.7	291.3	267.9	130.8	252.5	195.3
<i>w_i</i>	0.75	0.49	0.88	0.50	0.00	0.00
Model 9								
<i>k</i>	6		6		6	
AIC _c	322.0	298.8	280.4	144.8	249.1	184.7
<i>w_i</i>	0.02	0.01	0.00	0.00	0.02	0.06
Model 10								
<i>k</i>	9		10		9		9	
AIC _c	322.3	303.3	278.0	137.5	254.4	188.8	138.1	105.5
<i>w_i</i>	0.02	0.00	0.01	0.02	0.00	0.01	0.00	0.05
Model 11								
<i>k</i>	12		14		12	
AIC _c	317.9	291.5	275.4	132.0	261.5	194.9
<i>w_i</i>	0.15	0.44	0.02	0.27	0.00	0.00

Notes: An AIC score (AIC_c) was computed for each model (where *k* = the number of estimated parameters), which was then used to derive an Akaike weight (*w_i*), or the probability of that model being the best model given the candidate set of models and the data. For each measure of fitness (predictor), two log response ratios (LRs) were calculated: the mean LR, which compares consumer fitness on the mixed diet to fitness averaged across all diets that offered single species alone; and the maximum LR, which compares fitness on the mixed diet to that on the single prey species that supported the highest fitness. Cells with ellipses indicate models that could not be fit due to insufficient representation in the data set.

best single-species diet, in over half of cases for growth and reproduction (Fig. 2B–E). Thus, while the grand mean trend across studies does not support the balanced-diet hypothesis, it is corroborated in a substantial number of individual cases and appears not to be isolated to any particular system or taxa (Appendix D: Table D1).

Second, many organisms produce toxic chemical compounds that deter consumers. The toxin-dilution

hypothesis proposes that diet mixing benefits consumers by limiting the ingestion of toxic compounds from any one defended species. Our results were inconsistent with this prediction on several counts. First, a large proportion of studies with toxic species exhibited diet interference, where fitness on the mixed diet was even lower than for the average of single-species diets (Fig. 2B–E). These values suggest that, in the majority of

cases, toxic prey detracted from fitness even in mixtures. This result was further reflected in the grand mean LRs for studies with defended species (Fig. 1A). Second, and not surprisingly, fitness on a mixed diet including defended prey was generally worse than on the best single prey item (Fig. 1B). This outcome might be expected when studies included a mixture of defended and undefended prey, as fitness will almost always be highest on the undefended prey (Freeland and Janzen 1974). Because of designs that incorporated both toxic and nontoxic species, the majority of studies included in our data set may not be the fairest test of the toxin-dilution hypothesis. Only two studies included all defended prey (Steinberg and van Altena 1992, Hägele and Rowell-Rahier 1999), but the effect of diet mixing was still negative relative to the best single-species diet in these experiments. The strong and pervasive negative effects of diversity in experiments with defended prey presumably explain why prey defense was included in seven of the supported mixed models (Table 2).

Our mixed-model analysis also revealed that the effect of mixing food types on survivorship was highest for herbivores, then carnivores and omnivores. This difference in diet-diversity effects among trophic levels may be attributable to the well-documented heterogeneity in the nutritional quality of plants (Dearing and Schall 1992) and, to a lesser extent, of herbivores (Fagan et al. 2002). Since the average plant species is less nutritious than the average animal species, herbivores may compensate by incorporating a greater variety of plant species into their diet (Newman 2007) as opposed to feeding on a single, nutritionally unbalanced item. In fact, the latter option may actually incur fitness costs through the overingestion of certain nutrients (Raubenheimer and Simpson 1997). We observed the greatest effect of diet diversity on growth for detritivores, which could also be explained by the trend towards increasing food quality and homogeneity with increasing trophic level (Bowen et al. 1995), but we are reticent to draw any conclusions from such a small number of experiments ($N = 6$). These results appear counter to the results of studies such as Krebs and Avery (1984), as well as the predictions of Denno and Fagan (2003), who suggested that diet mixing may be equally important for higher trophic-level predators. However, Denno and Fagan (2003) developed their hypothesis in reference to carnivores supplementing their diet of herbivores with other carnivores (i.e., intraguild predation) as a way to increase their nitrogen intake. While the small representation of intraguild predators in our data set precludes us from being able to adequately test this alternative prediction ($N = 3$ experiments), it is a topic that merits future attention.

The generally weak evidence for the benefits of diet mixing based on the intrinsic properties of food highlights the fact that consumer food choice depends on many additional factors, including food distribution and abundance, foraging behavior, and ecological interactions, such as competition and predation risk

(Stephens and Krebs 1986, Singer and Bernays 2003). The experiments we reviewed were primarily conducted in homogeneous laboratory environments where individual consumers were offered food ad libitum (i.e., routinely replenished to initial values) and in densities equalized across treatments. Because these conditions minimized many of the behavioral or ecological influences that drive consumer choice of foods in nature, they primarily measured the inherent nutritional benefits of mixing food types. The laboratory setting of the experiments included in our analysis may explain the prevalence of diet neutrality in our analysis, as the advantages of diet generalism may manifest more frequently under more realistic foraging scenarios.

Overall, our meta-analysis of 161 peer-reviewed publications, spanning a wide range of systems, taxa, and fitness components, revealed relatively little support for the predicted benefits of diet mixing based on the inherent nutritional properties of the food and the physiology of the consumer. While consumer growth and reproduction were enhanced by a mixed diet in about half of published studies, consistent with the balanced-diet hypothesis, consumer fitness was generally higher when feeding on the single optimal food item. We also found no evidence that a mixed diet negates the impact of chemically defended foods, refuting the toxin-dilution hypothesis. We did find that the benefits of diet diversity were greater for herbivores than for higher trophic levels. The large size and robustness of our data set suggest that these conclusions well represent the available published data on consumers feeding on natural foods. The general weakness of nutritional benefits derived from diet mixing suggests that explanations of diet generalism must continue to be sought in the broader ecological context of consumer foraging.

ACKNOWLEDGMENTS

We thank the graduate students in the VIMS Evolutionary Ecology class of Fall 2010 for initially exploring this topic with us, two anonymous reviewers for their comments, and the National Science Foundation (OCE-1031061 to J. E. Duffy) for partial support of this work. This paper is VIMS contribution #3260.

LITERATURE CITED

- Belovsky, G. E. 1984. Herbivore optimal foraging: a comparative test of three models. *American Naturalist* 124:97–115.
- Bernays, E. A., K. L. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997–2006.
- Bernays, E. A., and O. P. J. M. Minkenberg. 1997. Insect herbivores: different reasons for being a generalist. *Ecology* 78:1157–1169.
- Bjorndal, K. A. 1991. Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. *Ecology* 72:1234–1241.
- Bowen, S. H., E. V. Lutz, and M. O. Ahlgren. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76:899–907.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.

- Coll, M. 1998. Living and feedings on plants in predatory heteroptera. Pages 89–130 in M. Coll, and J. R. Ruberson, editors. *Predatory Heteroptera: their ecology and use in biocontrol*. The Entomological Society of America, Lanham, Maryland, USA.
- Coll, M., and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* 47:267–297.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal–plant interactions*. University of California Press, Berkeley, California, USA.
- Dearing, M. D., and J. J. Schall. 1992. Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. *Ecology* 73:845–858.
- DeMott, W. R. 1998. Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* 79:2463–2481.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory in carnivorous arthropods? *Ecology* 84:2522–2531.
- Duffy, J. E., B. J. Cardinale, K. E. Frane, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.
- Edwards, K. F., K. M. Aquilino, R. J. Best, K. L. Sellheim, and J. J. Stachowicz. 2010. Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. *Ecology Letters* 13:194–201.
- Eubanks, M. D., and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* 80:1253–1266.
- Fagan, W. F., E. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. *American Naturalist* 160:784–802.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? *Science* 211:887–893.
- Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108:269–289.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19:207–233.
- Futuyma, D. J., and S. S. Wasserman. 1981. Food plant specialization and feeding efficiency in the tent caterpillars *Malacosoma disstria* and *M. americanum*. *Entomologia Experimentalis et Applicata* 30:106–110.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York, New York, USA.
- Hägele, B. F., and M. Rowell-Rahier. 1999. Dietary mixing in three generalist herbivores: Nutrient complementation or toxin dilution? *Oecologia* 119(4):521–533.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
- Hillebrand, H., and B. J. Cardinale. 2004. Consumer effects decline with prey diversity. *Ecology Letters* 7:192–201.
- Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23:269–286.
- Krebs, J., and M. Avery. 1984. Chick growth and prey quality in the European Bee-eater (*Merops apiaster*). *Oecologia* 64:363–368.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- Newman, J. 2007. *Herbivory*. Chapter 6. Pages 175–221 in D. W. Stephens, J. S. Brown, and R. C. Ydenberg, editors. *Foraging: behavior and ecology*. University of Chicago Press, Chicago, Illinois, USA.
- Pennings, S. C., M. T. Nadeau, and V. J. Paul. 1993. Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. *Ecology* 74:879–890.
- Pulliam, H. R. 1975. Diet optimization with nutrient constraints. *American Naturalist* 109:765–768.
- R Development Core Team. 2012. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raubenheimer, D., and S. J. Simpson. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews* 10(1):151–179.
- Scriber, J. M., and P. Feeny. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. *Ecology* 60:829–850.
- Singer, M. S., and E. A. Bernays. 2003. Understanding omnivory needs a behavioral perspective. *Ecology* 84:2532–2537.
- Smiley, J. 1978. Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* 201:745–747.
- Steinberg, P. D., and I. van Altna. 1992. Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australia. *Ecological Monographs* 62:189–222.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Toft, S., and D. H. Wise. 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 119:191–197.
- Westoby, M. 1978. What are the biological bases of varied diets? *American Naturalist* 112:627–631.

SUPPLEMENTAL MATERIAL

Appendix A

Detailed description of data collection (including full search string) and detailed methods for construction of log response ratios, mixed-model analysis, and tests of bias ([Ecological Archives E094-048-A1](#)).

Appendix B

List of publications used in the meta-analysis ([Ecological Archives E094-048-A2](#)).

Appendix C

Detailed results for mixed-model analysis and tests of bias ([Ecological Archives E094-048-A3](#)).

Appendix D

Supplementary table of log response ratios partitioned by consumer attributes ([Ecological Archives E094-048-A4](#)).