1    Running Head: Feeding rate consistency in space and time

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3    **Food web interaction strength distributions are conserved by greater variation between**

4    **than within predator-prey pairs**

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**Abstract**

Species interactions in food webs are usually recognized as dynamic, varying across species, space and time due to biotic and abiotic drivers. Yet food webs also show emergent properties that appear consistent, such as a skewed frequency distribution of interaction strengths (many weak, few strong). Reconciling these two properties requires an understanding of the variation in pairwise interaction strengths and its underlying mechanisms. We estimated stream sculpin feeding rates in three seasons at nine sites in Oregon to examine variation in trophic interaction strengths both across and within predator-prey pairs. We considered predator and prey densities, prey body mass, and abiotic factors as putative drivers of within-pair variation over space and time. We hypothesized that consistently skewed interaction strength distributions could result if individual interaction strengths show relatively little variation, or alternatively, if interaction strengths vary but shift in ways that conserve their overall frequency distribution. We show that feeding rate distributions remained consistently and positively skewed across all sites and seasons. The mean coefficient of variation in feeding rates within each of 25 focal species pairs across surveys was less than half the mean coefficient of variation seen across species pairs within a given survey. The rank order of feeding rates also remained relatively conserved across streams, seasons and individual surveys. On average, feeding rates on each prey taxon nonetheless varied by a hundredfold across surveys, with some feeding rates showing more variation in space and others in time. For most species pairs, feeding rates increased with prey density and decreased with high stream flows and low water temperatures. For nearly half of all species pairs, factors other than prey density explained the most variation, indicating that the strength of density dependence in feeding rates can vary greatly among a generalist predator's prey species. Our findings show that although individual interaction strengths exhibit

47    considerable variation in space and time, they can nonetheless remain relatively consistent, and

48    thus predictable, compared to the even larger variation that occurs across species pairs. These

49    insights help reconcile how the skewed nature of interaction strength distributions can persist in

50    highly dynamic food webs.

51    **Keywords:** predator-prey, trophic interaction, food web stability, feeding rate, functional

52    response, community dynamics, stream, fish, macroinvertebrate

53    **Introduction**

54         Most attributes of food webs – including species composition and abundances, network

55    topology, and interaction strengths – vary in space and time (Menge et al. 1994, Polis et al.

56    1996). Deterministic drivers of food web variation include both biotic factors such as species

57    introductions or extirpations, population cycles, and organism life history traits (e.g., Boutin et

58    al. 1995, Vander Zanden et al. 1999, de Roos et al. 2003), and abiotic factors such as

59    temperature, nutrients, hydrology, light, and substrate (e.g., Menge 2000, Power et al. 2008,

60    Byers et al. 2017). For example, migrations of anadromous fish can drive predictable seasonal

61    changes in web topology and energy flow (Naiman et al. 2002); tropical storms can rapidly alter

62    interaction strengths on islands (Spiller and Schoener 2007); and climate change is leading to

63    wholesale food web alterations on global scales (Woodward et al. 2010). While increasingly

64    recognized, spatial and temporal food web variation present challenges to predicting and

65    managing community dynamics, particularly in species-rich communities where the relevant

66    intrinsic and extrinsic drivers are poorly resolved (Tylianakis et al. 2008).

67         Although a large body of research shows that food webs are inherently variable, some

68    empirical food web patterns appear to be relatively consistent in space and time (Mora et al.

69    2018). Among these is the skewed frequency distribution of interaction strengths (few strong and

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70    many weak) that has been documented in nearly all studies with field-based quantitative

71    interaction strength measures (e.g., Paine 1992, Fagan and Hurd 1994, de Ruiter et al. 1995,

72    Raffaelli and Hall 1996, Wootton 1997, Woodward et al. 2005, Schleuning et al. 2011, Cross et

73    al. 2013, Bellmore et al. 2015). This pattern appears insensitive to ecosystem type, network

74    complexity, the measure of interaction strength used, and even the type of interaction under

75    study (Wootton and Emmerson 2005, Vázquez et al. 2012). The persistence of the skewed

76    distribution of interaction strengths suggests that either: 1) despite being variable, the strength of

77    each pairwise species interaction shows consistency relative to the variation seen across co-

78    occurring interactions, or 2) the relative position of each pairwise interaction along the

79    distribution is dynamic, but with a distribution-conserving fraction of interactions shifting from

80    strong to weak and vice versa. The latter might occur, for example, if predators are limited by a

81    maximum total feeding rate across all of their prey. Most quantitative measures of species

82    interaction strength lack the spatial or temporal replication to test these ideas for multiple co-

83    occurring interactions in nature.

84         Estimates of predator feeding rates are useful for addressing the extent to which species

85    interaction strengths and their frequency distributions are dynamic or consistent over space and

86    time. Moreover, there is a rich literature that seeks to mechanistically describe the factors driving

87    variation in feeding rates (Jeschke et al. 2002). For example, functional response models

88    generally predict that feeding rates should increase (often nonlinearly) with prey density (Holling

89    1959), such that fluctuations in prey should be a primary factor determining variation. Predator

90    density, predator and prey traits (e.g., body size), and environmental conditions are also linked to

91    variation in feeding rates (e.g., Skalski and Gilliam 2001, Rall et al. 2012, Kalinoski and DeLong

92    2016), with changes in each having the potential to alter interaction strengths and their frequency

93    distribution in space and time.

94         In the present study we address two related questions using replicated *in situ* feeding rate

95    estimates of a focal generalist predator, the reticulate sculpin (*Cottus perplexus*). First, we ask

96    how dynamic are prey-specific sculpin feeding rates in space and time? To address this question,

97    we use the variation seen in sculpin feeding rates across their diverse prey community as a

98    relative measure to compare against the variation seen within species pairs over space and time.

99    Variation within species pairs across space and time that is consistently less than variation across

100   species pairs at a given point in space and time would suggest that pairwise species interaction

101   strengths show consistency, which could underlie the consistency of community-wide interaction

102   strength frequency distributions. A conserved rank order of prey-specific feeding rates would

103   also support this idea. Second, we ask what factors are driving within species-pair variation in

104   feeding rates over space and time?  To address this question we quantify variation in space and

105   time for each interaction individually and determine the extent to which changes in prey density,

106   conspecific predator density, prey body mass, or abiotic factors can explain this variation. Our

107   results show that, despite considerable within-pair variation in feeding rates, 'strong' interactions

108   tend to remain 'strong' while 'weak' interactions tend to remain 'weak'. As a result, interaction

109   strengths distributions show consistency in space and time. Our results also show that while prey

110   density is a primary factor driving within-pair variation in feeding rates for many prey taxa,

111   factors including prey body mass, water temperature, and stream discharge frequently exhibit

112   even greater effects for other taxa.

113   **Methods**

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114     *Study sites* – We estimated feeding rates of reticulate sculpin (*Cottus perplexus*) on its

115     macroinvertebrate prey at nine stream sites within Oregon State University's McDonald-Dunn

116     Research Forest northwest of Corvallis, Oregon. The nine sites were each ~45 m in length and

117     were nested within three streams (Berry, Oak, and Soap Creeks, see Preston et al. 2018). The

118     three study streams were > 4km apart from one another, and the sites within each stream were on

119     average 336 m apart (min = 87 m, max = 950 m). The ecology of streams in the McDonald-Dunn

120     Research Forest has been well studied, including extensive work on the diverse (>325 species)

121     macroinvertebrate community (e.g., Anderson and Lehmkuhl 1968, Kerst and Anderson 1975,

122     Grafius and Anderson 1979), community interactions (e.g., Davis and Warren 1965, Hawkins

123     and Furnish 1987), and ecosystem functioning (e.g. Warren et al. 1964). In addition to reticulate

124     sculpin, other resident aquatic vertebrates at our sites include cutthroat trout (*Oncorhyncus*

125     *clarkii*), Pacific giant salamanders (*Dicamptodon tenebrosus*), and brook lamprey (*Lampetra*

126     *richardsoni*).

127     *Estimating feeding rates* – We estimated feeding rates in an *in situ* manner by combining

128     gut contents data from field surveys with information on the time period over which prey items

129     remain identifiable in a sculpin's stomach (hereafter the 'prey identification time'). Prey-specific

130     sculpin feeding rates were estimated for each survey as

131     $$\hat{f}_i = \frac{n_i}{p}\frac{1}{d_i}, \qquad [1]$$

132     where $\hat{f}_i$ is the average sculpin's feeding rate (prey consumed predator$^{-1}$ time$^{-1}$), $n_i$ is the number

133     of prey items of species $i$ found in a sample of $p$ predator stomachs, and $d_i$ is prey $i$'s estimated

134     identification time (see also Novak and Wootton 2008, Novak et al. 2017, Wolf et al. 2017 and

135     Preston et al. 2018). This approach explicitly accounts for differences in the amount of time that

136     prey items persist in stomach contents, which when unaccounted for, will bias inferences about

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137    trophic interactions made from diet data (Hyslop 1980, Fairweather and Underwood 1983,

138    Novak 2010, Preston et al. 2017).

139         *Field surveys* – To collect sculpin diet information ($n_i$ and $p$ in eqn. 1), we surveyed each

140    of the nine stream sites in summer (June/July 2015), fall (September 2015), and spring (April

141    2016) (27 total site-by-season replicates). Sculpin were surveyed systematically throughout the

142    whole area of the reach by a crew of four researchers using a backpack electroshocker (Smith-

143    Root LR20B), a block net (1.0 x 1.0 m) and two dip nets (0.30 x 0.25 m). Block nets at each end

144    prevented movement in and out of the reach during surveys. We anesthetized, weighed,

145    measured, and nonlethally lavaged each sculpin with a 60 cc syringe and blunt 18-gauge needle

146    to obtain gut contents. Sculpin were then held in aerated stream water and released after recovery

147    from anesthesia. We preserved stomach contents in 70% ethanol and in the laboratory identified

148    and measured prey for total body length. To estimate dry mass, we used a conversion factor

149    based on wet mass for sculpin (Lantry and O'Gorman 2007) and length-to-mass regressions for

150    invertebrates (Table S1). At each site, we also estimated prey densities by collecting

151    macroinvertebrates with ten Surber samples (0.093 $m^2$ in area) evenly spaced along the length of

152    each reach. Surber samples were preserved in 70% ethanol and invertebrates were measured for

153    body length and identified using Merritt et al. 2008. We quantified abiotic variables at each site,

154    including stream discharge, canopy openness, substrate size, water temperature, and stream

155    width (Supplemental Materials). Lastly, we estimated sculpin densities by correcting our

156    electroshock sculpin counts using catch efficiency estimates from habitat-specific (pool or riffle)

157    mark-recapture surveys conducted at each stream (Supplemental Materials).

158         *Prey identification times* – Our estimates of prey identification times ($d_i$ in eqn. 1) were

159    based on functions from laboratory trials during which individual sculpin were fed invertebrate

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160    prey and then lavaged over time to determine the rate at which prey became unidentifiable as a

161    function of covariates. Our approach for estimating prey identification times is provided in detail

162    in Preston et al. (2017) and is summarized in Preston et al. (2018). Here we provide an overview.

163           We estimated the prey-specific identification times for common prey types observed in

164    sculpin diets, including mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies

165    (Trichoptera), flies (Diptera), beetles (Coleoptera), worms (Annelida), and snails (*Juga plicifera*)

166    (Table S2). Our approach therefore incorporated differences in prey traits across taxonomic

167    groups that affect rates of digestion by sculpin. In the laboratory trials, we varied water

168    temperature (10°C to 20°C), prey size for each taxon (Table S2), and predator size (32 mm to 86

169    mm sculpin) in a continuous and randomized manner, and then fit Weibull survival curves to the

170    observed prey status (identifiable or not) as a function of the covariates (Klein and Moeschberger

171    2005). The time periods over which sculpin were lavaged after feeding ranged from 10 min to

172    100 hrs depending on the prey type. The estimated laboratory coefficients from the Weibull

173    survival functions were used with observed covariate information from our field surveys (i.e.,

174    predator and prey sizes and water temperatures) to estimate prey identification times for each

175    prey item recovered from a sculpin's stomach. For each prey item, the identification time was

176    estimated as the mean of the probability density function that corresponded to the Weibull

177    survival function under the observed covariate values (Preston et al. 2017). We then used the

178    average prey-specific detection times within each survey to calculate the prey-specific sculpin

179    feeding rates using eqn. 1. For prey types other than the aforementioned seven taxa, we used

180    survival function coefficients from morphologically similar prey types (Table S3).

181           *Analyses* – We first assessed changes in the overall distribution of all feeding rates in

182    each survey by examining the distribution parameters including the mean, standard deviation,

183     skewness and kurtosis. We then quantified the within-pair variation in feeding rates seen across

184     space and time and compared it to the variation in feeding rates seen across species pairs at a

185     given site and time. Within-pair variation was quantified as the coefficient of variation for each

186     species pair using the mean and standard deviation of the prey-specific feeding rates across

187     surveys. Not all prey taxa were observed in sculpin diets from all surveys, hence these

188     calculations included up to 9 sites x 3 seasons = 27 feeding rate estimates for each species pair

189     (Table S3). Across-pair variation was quantified for each survey as the coefficient of variation

190     calculated using the mean and standard deviation of the survey's prey-specific feeding rates. To

191     quantify variation within and across species pairs we focused on the 25 prey taxa (i.e., pairwise

192     interactions with sculpin) for which we had at least two feeding rate estimates per season and at

193     least 10 estimates total across all site-season combinations (mean = 20.7 estimates; Table S3).

194     Together, these taxa represented 88% of the individual prey items that we recovered (see

195     *Results*).

196         Next we evaluated the consistency in the rank order of prey-specific feeding rates

197     using Spearman's correlation coefficients. We did this by ordering the 25 focal feeding rates by

198     their overall means across all surveys and assessing deviations from this ordering in each of the

199     individual surveys (n = 27 surveys). We also assessed deviations in the rank order across seasons

200     (n = 3 seasons) and streams (n = 3 streams) using their respective mean values.

201         We examined the relative roles of space and time in contributing to the variation seen

202     within each species pair (n=25) using a generalized linear mixed model (GLMM) with log-

203     transformed feeding rates as the response (Zuur et al. 2009). Our model included the fixed

204     effects of reach identity (i.e. 'space') and of season (i.e. 'time'), and random intercept terms for

205     stream (three reaches per stream) and prey taxonomic identity (up to 27 feeding rates per prey

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206    taxon). Diagnostic plots and comparisons to a model without random intercept terms indicated

207    that inclusion of the random effects was justified (Supplemental Materials). To assess the

208    contributions of 'space' and 'time' fixed effects, we compared the full model to 1) a model with

209    season only, 2) a model with reach identity only, and 3) an intercept-only null model. We

210    compared model performance using small sample size adjusted Akaike Information Criterion

211    scores (AICc) (Burnham and Anderson 2002) and evaluated model fit using marginal and

212    conditional R-squared values (Nakagawa and Schielzeth, 2013); marginal R-squared represents

213    variance explained by fixed effects and conditional R-squared represents variance explained by

214    fixed and random effects. To further examine feeding rate variation in space and time, we also

215    calculated coefficients of variation for feeding rates on each of the 25 focal taxa across the nine

216    sites (using mean feeding rates per site) and across the three seasons (using mean feeding rates

217    per season).

218        Our next goal was to assess the capacity of prey density, predator density, prey body

219    mass, and abiotic factors to explain the variation in prey-specific feeding rates we observed over

220    space and time. These analyses focused on 20 of the 25 previously-considered prey taxa as 5 taxa

221    (Dixidae, Ceratopogonidae, Copepoda, Ostracoda, Polycentropodidae) were sometimes not

222    detected in surber samples, precluding estimates of their density. The analyses entailed using

223    general linear models for each focal taxon, including a full model (all four hypothesized drivers

224    included), models with each of the four predictors alone, and an intercept-only null model (six

225    total models per prey taxon). While many other biologically reasonable models (i.e., variable

226    combinations) are plausible, our primary goal was to determine the univariate explanatory power

227    of the four variables rather than develop a predictive mechanistic model. Exploratory models

228    also included a random intercept term for reach identity nested within stream, but these

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229     decreased relative model performance (based on AICc scores) and were thus not included in the

230     final analysis (Supplemental Materials). Abiotic factors were incorporated as the first principal

231     component from a PCA analysis of stream discharge, canopy openness, substrate size, water

232     temperature, and stream width, using mean values per survey. Prey masses were from the Surber

233     data and not the sculpin diet data. When a prey taxon was not detected in the Surber samples of a

234     given survey, the corresponding feeding rate was omitted from the analysis. Feeding rates and all

235     predictor variables other than the PC scores were log-transformed to improve conformance to

236     model assumptions. For each prey taxon, we used AICc and $R^2$ values to compare the six

237     models. Lastly, we examined the overall univariate explanatory power of each of the four

238     predictor variables across all taxa combined by summing the AICc scores of each variable's

239     prey-specific models. Plots showing covariate correlations and model residuals are shown in the

240     Supplemental Materials (Figs. S1, S2).

241     **Results**

242         *Feeding rate variation* – The frequency distributions of feeding rates were positively

243     skewed in all seasons and at all sites, exhibiting a consistent pattern of a few strong and many

244     weak interactions (Fig. 1 and Fig. S3). Estimates of distribution skewness ranged from 1.4 to 5.4

245     (mean = 3.7) across surveys. These and the other distribution moments we measured did not

246     differ consistently across streams or reaches, but did show seasonal differences in that all were

247     generally highest in the summer (Table S4).

248         In total, we collected 15,471 identifiable prey items from 2,068 sampled sculpin. The 25

249     focal prey taxa accounted for 13,564 prey items (88% of the total). The majority of these focal

250     prey items belonged to the orders Ephemeroptera (45%), Diptera (37%), Trichoptera (9%), and

251     Plecoptera (5%). Mean prey-specific feeding rates across the focal taxa varied by over three

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252 orders of magnitude, with the highest mean feeding rates being on Baetidae mayflies and

253 Chironomidae midges, and the lowest being on *Juga* snails (Fig. 2).

254     Overall, the variation in feeding rates across species pairs within a survey was greater

255 than the variation across surveys within a species pair (Fig. 2 inset). The mean coefficient of

256 variation was 2.31 across species pairs (min = 1.27, max = 3.53, median = 2.38; n=27 surveys),

257 versus 1.05 for variation within species pairs (min = 0.71, max = 1.63, median = 1.01; n = 25

258 prey taxa). The within-pair difference from the lowest to highest feeding rates across all surveys

259 in space and time averaged a 102-fold increase, ranging from 14-fold (Psychodidae flies) to

260 1093-fold (Annelid worms).

261     The rank order of prey-specific feeding rates remained relatively consistent across

262 seasons, streams, and individual surveys (Fig. 2 and Fig. S4). The ordering of mean feeding rates

263 across the three seasons ($\rho$ = 0.92 in summer; 0.84 in fall; 0.80 in spring) and the three streams

264 ($\rho$ = 0.86 at Berry Creek; 0.91 at Oak Creek; 0.86 at Soap Creek) did not differ greatly from the

265 ordering of the overall means (Fig. S4). Across surveys the mean Spearman's correlation

266 coefficient was 0.71 (range = 0.45 to 0.93), with deviations from the order of the mean feeding

267 rates driven primarily by variation in the lowest feeding rates.

268     *Effects of space and time on within-pair variation* – Many prey-specific feeding rates

269 showed strong seasonal variation. Summer corresponded to the highest feeding rates for 17 of

270 the 25 prey taxa, followed by spring (7 taxa), and fall (1 taxon) (Fig. 3). Feeding rates on flies

271 (Figs 3a to 3g) and worms (Fig. 3t) showed relatively little seasonal change, while mayflies

272 (Figs. 3h to 3j), stoneflies (Figs. 3k to 3m), and caddisflies (Figs. 3n to 3r) showed larger

273 seasonal differences. Among the largest seasonal changes in mean feeding rates were those

274 observed on mayflies, including Baetidae (a 4-fold decrease in mean feeding rates from summer

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275   to fall; Fig. 3h) and Heptageniidae (a 10-fold increase in mean feeding rates from fall to spring;

276   Fig. 3i). General linear models fit to all 25 prey-specific feeding rates combined supported the

277   idea that feeding rate variation was more strongly associated with season than reach identity

278   (Table S5). The top-performing model included season alone. Nevertheless, even in the top-

279   performing model, the fixed effect of season explained relatively little variation in feeding rates

280   (marginal $R^2 = 0.04$) compared to the random effect of prey taxon (conditional $R^2 = 0.63$).

281        The coefficients of variation for feeding rates in space versus time reflected the different

282   effects of season on each prey taxon. The CVs were higher across sites than across seasons for 7

283   of 8 fly and worm taxa (Fig. S5). In contrast, for mayflies, stoneflies, and caddisflies, the CVs

284   were higher across seasons than across sites for 8 of 11 taxa (Fig. S5). In general, the taxa with

285   high variation across seasons showed consistent differences in mean seasonal feeding rates (Fig.

286   3), whereas taxa showing higher variation in space were not necessarily associated with

287   consistent differences in mean reach- or stream-level feeding rates.

288        *Drivers of within-pair variation* – The four hypothesized explanatory variables for

289   within-pair variation in feeding rates (i.e., prey density, prey body mass, predator density, and

290   abiotic factors) varied more across seasons than across sites for most prey taxa. The densities for

291   9 of the 20 taxa considered in these prey-specific analyses were highest in summer, while

292   another 9 were highest in fall and two were highest in spring (Fig. S6). Nine of the 20 taxa had

293   the largest mean body size in spring (Fig. S7). Of the abiotic variables measured, water

294   temperature and stream discharge showed the largest variation, with low flows (mean = 0.01

295   $m^3s^1$) and warm temperature (mean =15°C) in summer, followed by lower temperatures (mean

296   =10°C) and higher flows (mean = 0.09 $m^3s^{-1}$) in spring (Fig. S8). The first principal component

297   from the PCA analysis, which was associated with 41% of the variation in the abiotic data, was

298     positively associated with lower water temperatures and higher discharge (Fig. S9). Sculpin

299     densities were highest in summer (mean = 2.8 m$^{-2}$) and decreased slightly in fall and spring

300     (mean = 2.1 m$^{-2}$ for both) (Fig. S10).

301             Variation in prey density and abiotic factors showed relatively consistent directional

302     associations with within-pair variation in feeding rates. Feeding rates increased with prey density

303     for 18 of the 20 prey taxa (Fig. 4, Table S6); the two exceptions being Empididae flies and

304     Hydracharina mites which showed negative relationships. The first principal component of our

305     PCA analysis of abiotic variables was negatively associated with feeding rates for 14 of the 20

306     taxa (Fig. 6, Table S6), indicating that feeding rates decreased at lower temperatures and higher

307     flows.

308             The directional nature of the relationships between feeding rates and variation in prey

309     mass and sculpin density differed widely across the 20 taxa. Prey body mass was positively

310     associated with feeding rates for 13 taxa and negatively associated for 7 taxa, without a clear

311     taxonomic divide in either the sign or magnitudes of correlations (Fig. 5, Table S6). Sculpin

312     densities were positively associated with feeding rates for half of the taxa and negatively

313     associated with feeding rates for the other half (Fig. 7, Table S6).

314             The ability of prey density, prey body mass, predator density, and abiotic factors to

315     explain variation in feeding rates differed widely across the 20 prey taxa (Table S7). For 3 taxa

316     (Baetidae, Hetpageniidae, Semisculcospiridae), the top-performing model was the full model

317     with all four covariates. For 2 taxa (Psychodidae and Chloroperlidae), the intercept-only model

318     outperformed all other models. Of the other 15 taxa, the top model included only prey density for

319     7 taxa (Elmidae adults, Chironomidae, Tipulidae, Leptophlebidae, Nemouridae, Perlidae,

320     Lepidostomatidae), abiotic factors for 5 taxa (Empididae, Annelida, Glossosomatidae,

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321    Hydropsychidae, Rhyacophilidae), and prey mass for 3 taxa (Hydracharina, Elmidae larvae,

322    Simulidae). The variation explained by the top models averaged 37% ($R^2$ range: 0.14 to 0.81)

323    after excluding the two taxa for which the intercept-only model performed best (Table S7).

324    Summing the AICc scores across the 20 taxa resulted in the model including only abiotic factors

325    having the best relative performance, followed by models including only prey density ($\Delta$AICc =

326    6.1), prey mass ($\Delta$AICc = 47.1), the intercept-only model ($\Delta$AICc = 66.7), the full model ($\Delta$AICc

327    = 90.2), and only predator density ($\Delta$AICc = 98.9).

328    **Discussion**

329        Ecologists are increasingly grappling with the dynamic nature of species interactions and

330    the consequences of food web variation for the structure and functioning of communities (Poisot

331    et al. 2015, Lopez et al. 2017, Tylianakis and Morris 2017). Alongside this growing appreciation

332    for variation, there remains the now longstanding realization that many properties of

333    communities are conserved. This includes the recurrently observed skewed distribution of

334    interaction strengths (many weak, few strong), which has often been linked to the stability of

335    species-rich communities (McCann et al. 1998, Borrvall et al. 2000, Wootton and Emmerson

336    2005, Gellner and McCann 2016). This leads to an interesting inconsistency: if interactions in

337    food webs are highly dynamic, why is the skewed distribution of interaction strengths apparently

338    conserved? Our results help to reconcile the seemingly contradictory nature of these two food

339    web properties by showing how the ecological scale of inference shapes conclusions about

340    whether species interactions are dynamic or consistent. We show that, from the perspective of

341    community-wide variation in interaction strength, the pairwise interactions in our study system

342    are relatively consistent in space and time; 'strong' interactions remain 'strong' and 'weak'

343    interactions remain 'weak'. Although within-pair variation averaged a 100-fold difference from

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344     the lowest to highest observed feeding rate, it was much smaller than the variation seen across

345     pairs, leading to a consistent rank order and overall frequency distribution of species interaction

346     strengths. Our results therefore emphasize how food webs encompassing dynamic interactions

347     can yield properties that are nonetheless conserved in space and time.

348          The consistency of the pairwise interactions relative to community-wide variation has

349     several implications. Among these is that it suggests the existence of fundamental characteristics

350     that drive interaction strengths within versus between interacting species pairs. That is, while

351     within-pair variation was explained by distinct prey-specific factors (especially abiotic variables

352     and prey density), the variation seen across species pairs suggests a more fundamental role of

353     prey identity in driving variation (Preston et al. 2018). Clearly, species identity is associated with

354     a wide range of attributes of relevance to foraging predators (e.g., life history traits) that will

355     have shown consistent differences across prey taxa over the spatiotemporal scale of our surveys.

356     The relative consistency of the pairwise interactions also provides mechanistic insight into

357     processes underlying other conserved food web properties beyond the skewed distribution of

358     interaction strengths. For instance, the persistence of common structural characteristics in food

359     webs, such as motif frequencies and "backbone" interactions (Mora et al. 2018), may be

360     explained by the relative consistency of species interaction strengths at the community scale.

361     Thus, while our findings should be interpreted within the spatial, temporal, and ecological (i.e.,

362     focal prey community) scale of our surveys, they collectively suggest that from a community-

363     wide perspective, interaction strengths may be more predictable than commonly assumed.

364          The relative consistency of the pairwise interactions seen in our study is nonetheless

365     striking given that we focused on a generalist predator in species-rich streams that typically show

366     large variation in biotic and abiotic factors (Fisher et al. 1982, Power et al. 2008, Death 2010).

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367    Pairwise interaction strengths in streams are expected to be dynamic because interaction-strength

368    altering abiotic drivers themselves vary greatly over time (Power et al. 1988, Peckarsky et al.

369    1990, Wootton et al. 1996, Tonkin et al. 2017). Spatial heterogeneity in stream habitat can also

370    shape community structure over small spatial scales (Palmer and Poff 1997), and the life-

371    histories of many stream organisms result in fluctuating population abundances and size

372    structures across seasons (Huryn and Wallace 2000). The observed variation in prey-specific

373    feeding rates in our study is usefully interpreted in the context of these factors.

374         When considered in a univariate fashion, abiotic factors explained the most variation in

375    feeding rates for five prey taxa, suggesting that knowledge traditionally seen as vital to the nature

376    of predator functional responses was of little utility for these species. The importance of abiotic

377    conditions was further underscored by the result that the prey-specific models including only

378    abiotic factors had the lowest total score when their AICc scores were summed across the 20 taxa

379    that this analysis included. This role of abiotic factors in driving feeding rate variation was less

380    apparent in our previous single-season study (Preston et al. 2018), which emphasizes the

381    importance of spatiotemporal replication and scale-dependence in considering interaction

382    strength variation and its drivers. Here, we observed a 33% decrease in water temperature and a

383    9-fold increase in stream flows from summer to the following spring, which far exceeded the

384    abiotic variation in our previous study. Prey-specific sculpin feeding rates correlated negatively

385    with stream flow and positively with water temperatures, consistent with expected effects of

386    these variables on energetic demands, activity levels, and possibly foraging conditions for fishes

387    (e.g., ability to locate and consume prey under high flow and low water clarity) (Elwood and

388    Waters 1969, Kishi et al. 2005). These relationships with abiotic variables were particularly

389    strong for feeding rates on caddisflies. More broadly, the observed role of abiotic factors in our

17

390    study supports the idea that predation should be stronger (and more consistent) in low stress

391    environments and weaker in high stress environments (Peckarsky 1983, Menge and Sutherland

392    1987, Peckarsky 1990).

393         We found that univariate prey-density models had the second best performance behind

394    models with abiotic variables in explaining within-pair feeding rate variation. For most prey (18

395    of 20 taxa), prey-specific feeding rates increased as prey-specific density increased, suggesting

396    that sculpin are opportunistically consuming prey that they encounter, especially at low prey

397    densities. The relative role of prey density across pairwise interactions was associated with the

398    life histories of the prey taxa, such as voltinism and length of the nymphal period. These factors

399    also contributed to differences in variation associated with space versus time. In general, the

400    seasonal patterns in feeding rates on mayflies, stoneflies, and caddisflies were likely driven by

401    their mostly univoltine lifecycles, where densities and size distributions change markedly over

402    the season and often peak in spring and summer (Anderson and Wold 1972, Kerst and Anderson

403    1974). For instance, the large seasonal changes in feeding rates on Baetid mayflies (highest in

404    summer) and Heptageniid mayflies (highest in spring) corresponds with peak emergence periods,

405    after which decreases in nymphal densities due to emergence result in lower feeding rates

406    (Lehmkuhl 1968, 1969). Feeding rates on prey taxa that showed less seasonal variation may in

407    turn be related to longer larval periods or multiple generations per year that result in less

408    temporal fluctuation in prey density and size (e.g., many dipterans; Dudley and Anderson 1987).

409         The slopes of the within-pair relationships between feeding rates and the densities of each

410    prey taxon are informative because they allow comparisons with predictions from predator

411    functional response models. These slopes were less than one on the log-log scale for all but one

412    prey taxon (for which the slope was approximately one)(Table S6) reflecting decelerating

18

413    positive (i.e., saturating) relationships on the natural scale (Menge et al. 2018). This finding is

414    consistent with nearly all parametric models of predator functional responses (Jeschke et al.

415    2002). The mechanisms underlying the saturation of prey-specific feeding rates, however, are not

416    necessarily clear in that an accelerating (non-saturating) slope between feeding rates and prey

417    densities was observed when considering the relationship across all prey species combined

418    (Preston et al. 2018 and Fig. S2). In other words, feeding rates increased with within-species

419    differences in prey density in a decelerating (saturating) form but increased with between-species

420    differences in prey density in an accelerating (non-saturating) fashion. Further lines of evidence

421    also suggest that the overall feeding rates of sculpin are not limited by either handling or

422    digestion times, which are the typically invoked rate-limited steps for generating saturating

423    functional responses. For instance, the mean number of prey observed per sculpin was less than

424    30-times the maximum observed, suggesting that most sculpin are able to consume far more prey

425    than is observed in their stomachs (a widespread characteristic of fishes; Armstrong and

426    Schindler 2011). It is also noteworthy that for most taxa (13 of 20) the top-performing model did

427    not include prey density, and that for 8 taxa prey body mass or abiotic factors explained more of

428    the univariate variation in within-pair feeding rates. Together, these findings suggest that

429    functional response models that focus only on within-prey variation in density may poorly

430    predict feeding rates in the field, and that current functional response models (developed on the

431    basis of within-prey variation) may not be as easily scaled-up to predicting total or between-prey

432    variation in feeding rates as currently assumed. Future work is needed to develop and test

433    functional response models for species-rich contexts that can better characterize and assess the

434    interdependencies between the prey-specific feeding rates of generalist predators (Abrams 2001,

435    Novak et al. 2017).

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436    Prey mass was most closely associated with feeding rate variation for relatively few prey

437    taxa (3 of 20), suggesting that efforts to infer interaction strengths based on pairwise predator-

438    prey size relationships should be applied to food webs containing generalist predators with

439    caution. Across the entire feeding rates dataset, there appears to be an 'optimal' prey mass

440    associated with the highest feeding rates (Preston et al. 2018 and Fig. S2). In general, predators

441    are thought to select for prey of intermediate predator-prey body size ratios, thereby increasing

442    energetic gains from prey while avoiding large prey that are less efficiently consumed (Brose

443    2010, Kalinkat et al. 2013). This could result in either monotonic positive or negative

444    relationships between feeding rates and prey size within a given prey taxon depending on where

445    a prey type lies relative the optimum. We observed both positive and negative correlations

446    between prey mass and prey-specific feeding rates in our analysis, but the direction of the

447    relationships were not consistent with a single optimal prey mass across all prey taxa. Some prey

448    likely showed negative relationships between mass and feeding rates because large prey

449    individuals present challenges for consuming and digesting prey. For instance, limitations on

450    sculpin gape width and digestibility likely play a role in the low feeding rates on large *Juga*

451    snails (Semisulcospiridae) (Preston et al. 2017). For other feeding rates that showed strong

452    relationships with prey size (e.g., Elmidae beetle larvae), feeding rates were highest when prey

453    were largest. While for some taxa the specific mechanisms underlying this pattern are not clear,

454    it is possible that prey size is correlated with other traits (e.g., anti-predator behaviors, propensity

455    to drift) that could contribute to the different direction of correlations between size and feeding

456    rates across taxa. Recent research also indicates that differences in the mean and the standard

457    deviation of predator-prey size relationships across food webs are likely linked to changes in

458    overall prey availability (Costa-Pereira et al. 2018). While we did not examine interactions

20

459    between explanatory variable (e.g., prey density and prey mass), this provides an interesting area

460    for future work.

461         Predator (i.e., sculpin) density was not a primary factor underlying variation in prey-

462    specific feeding rates in our dataset. The presence and relative importance of predator

463    dependence has been a debated topic in the literature (Abrams and Ginzburg 2000, Baraquand

464    2014), with relatively few studies having assessed predator dependence in field settings (Novak

465    et al. 2017). The lack of a relationship for most prey taxa is interesting given that 1) we observed

466    a negative correlation between sculpin density and feeding rates in the dataset across all

467    combined prey taxa from summer (Preston et al. 2018), and 2) sculpin in streams are known to

468    be territorial such that increases in density are expected to increase intraspecific interactions and

469    decrease time spent feeding (Grossman et al. 2006). It is possible that wider variation in predator

470    densities, beyond what was observed naturally at our sites would be more effective at revealing

471    whether or not predator interference occurs in this system. That said, our results suggest that over

472    the observed range of species densities predator dependence is unlikely to strongly shape sculpin

473    feeding rates relative to other factors.

474         Several aspects of our study are of relevance in evaluating the generality of our results

475    and the degree to which they can be extrapolated to other food webs. We focused on a single

476    predator species and, for most analyses, only a subset of its prey taxa. While sculpins are

477    generalists, as are most predators, focusing on other predators in our system could have altered

478    some conclusions. For instance, our own preliminary evidence suggests that cutthroat trout in our

479    streams show less consistency in their prey-specific feeding rates across seasons due to highly

480    variable terrestrial prey availability (Falke et al. in prep). Similarly, although our focus on a

481    subset of the sculpin prey taxa was necessitated by the lack of replicated feeding rate estimates

482     for many prey taxa, consideration of the entire prey community would likely increase both

483     within and across-pair variation in feeding rates. Furthermore, while streams in general are

484     highly dynamic, our sites typically do not dry completely in late summer unlike some

485     Mediterranean climate streams and they no longer support anadromous fishes, both of which can

486     drive wholesale food web alternations (Gasith and Resh 1999, Naiman et al. 2002). Nonetheless,

487     we do not expect any of these study system choices to have strongly affected our main

488     conclusions.

489         Overall our results indicate that, while the complexity and dynamics of food webs can

490     appear intractable (Polis 1991), at least some interaction attributes are more consistent than often

491     recognized. As a result, the dynamics of trophic interactions may be predictable over space and

492     time based on characteristics of the interacting species and their environment. Species

493     interactions can thus be highly dynamic while still generating empirical patterns that prove

494     ubiquitous across unique food webs (Wootton and Emmerson 2005). Promising next steps in

495     efforts to understand and predict species interactions will require developing and testing

496     mechanistic models that incorporate species densities, species traits beyond body size, and

497     environmental covariates in shaping the strength and functional form of species interactions in

498     species-rich communities. Achieving this aim will benefit from future empirical work that

499     bridges across scales of interactions in space and time, ranging from species pairs to whole food

500     webs.

505    Scharfstein, Johnny Schwartz, Leah Segui, Isaac Shepard, Samantha Sturman, Ernesto Vaca Jr,

506    and Beatriz Werber. Richard Van Driesche and Michael Bogan provided input on identifying

507    aquatic invertebrates and Stan Gregory provided background information on our field sites. We

508    thank the Oregon State University College of Forestry for providing access to field sites in the

509    McDonald-Dunn Research Forest. Funding was provided by the National Science Foundation

510    Grant DEB-1353827, Oregon State University, and the University of Wisconsin-Madison. Data

511    are available from the Dryad Digital Repository: http://(upon publication).

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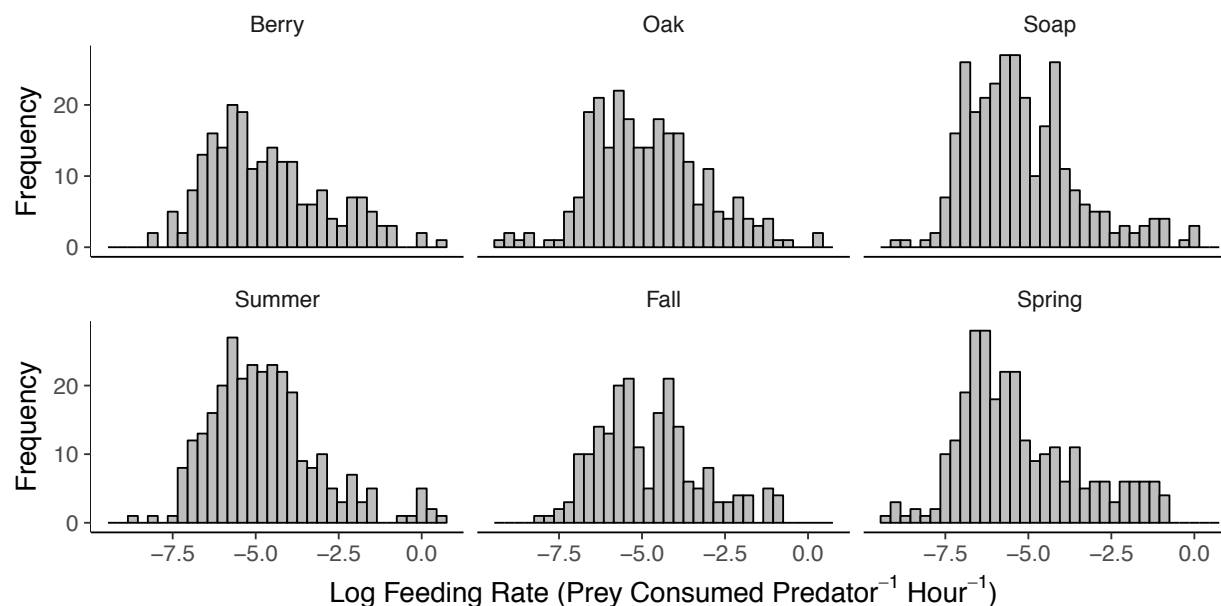
**Figure 1.** Log-transformed sculpin feeding rate distributions across three streams (top) and three

seasons (bottom). Each distribution includes feeding rates from nine replicate surveys and all
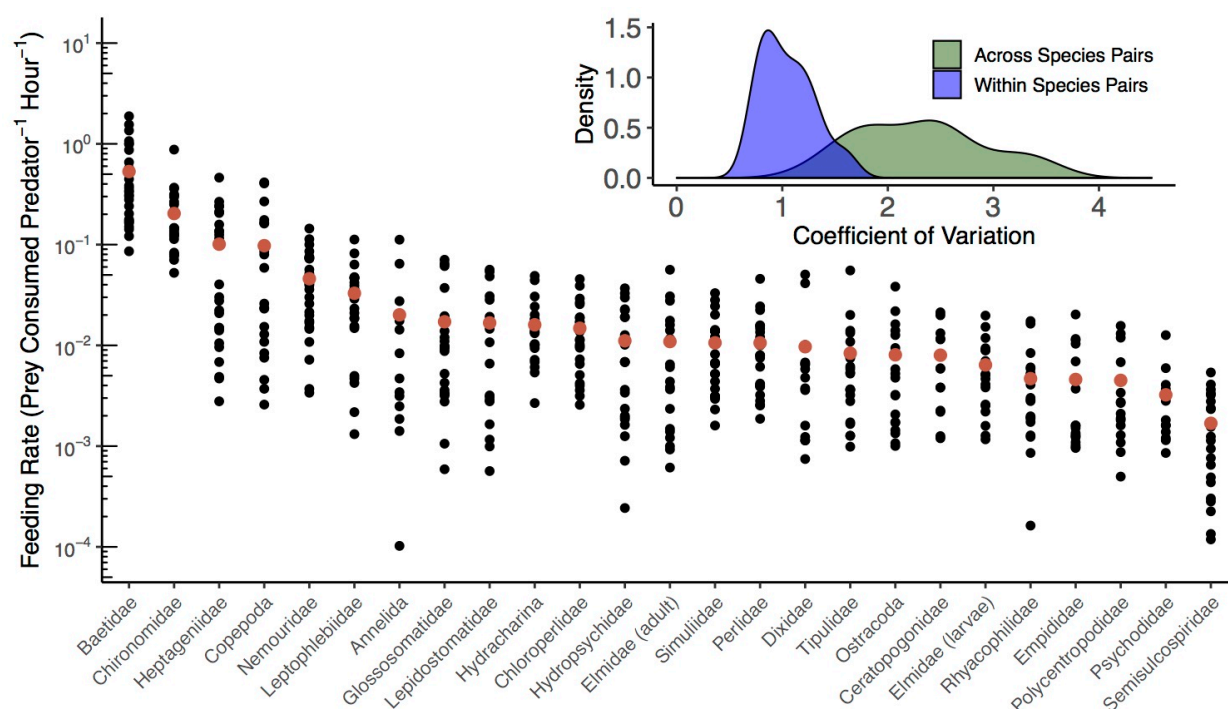
observed prey.

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**Figure 2.** Feeding rates of reticulate sculpin on 25 taxa of invertebrate prey. In the main panel, the red points indicate the mean feeding rates across all surveys within a prey taxon and the black points represent individual surveys. Note the log-scale on the y-axis and that the prey-specific feeding rates are ordered by their means. The inset panel shows the replicate coefficients of variation for sculpin feeding rates within a species pair across surveys in space and time (n = 25 taxa shown in blue) and across species pairs within a survey at a specific site (n = 27 surveys shown in green). The mean CV within species pairs is 1.1 and the mean CV across species pairs is 2.3. In the larger panel, within pair variation corresponds to variation in the vertical direction for each prey taxon, while across pair variation corresponds to variation in the horizontal direction across prey taxa in a survey.
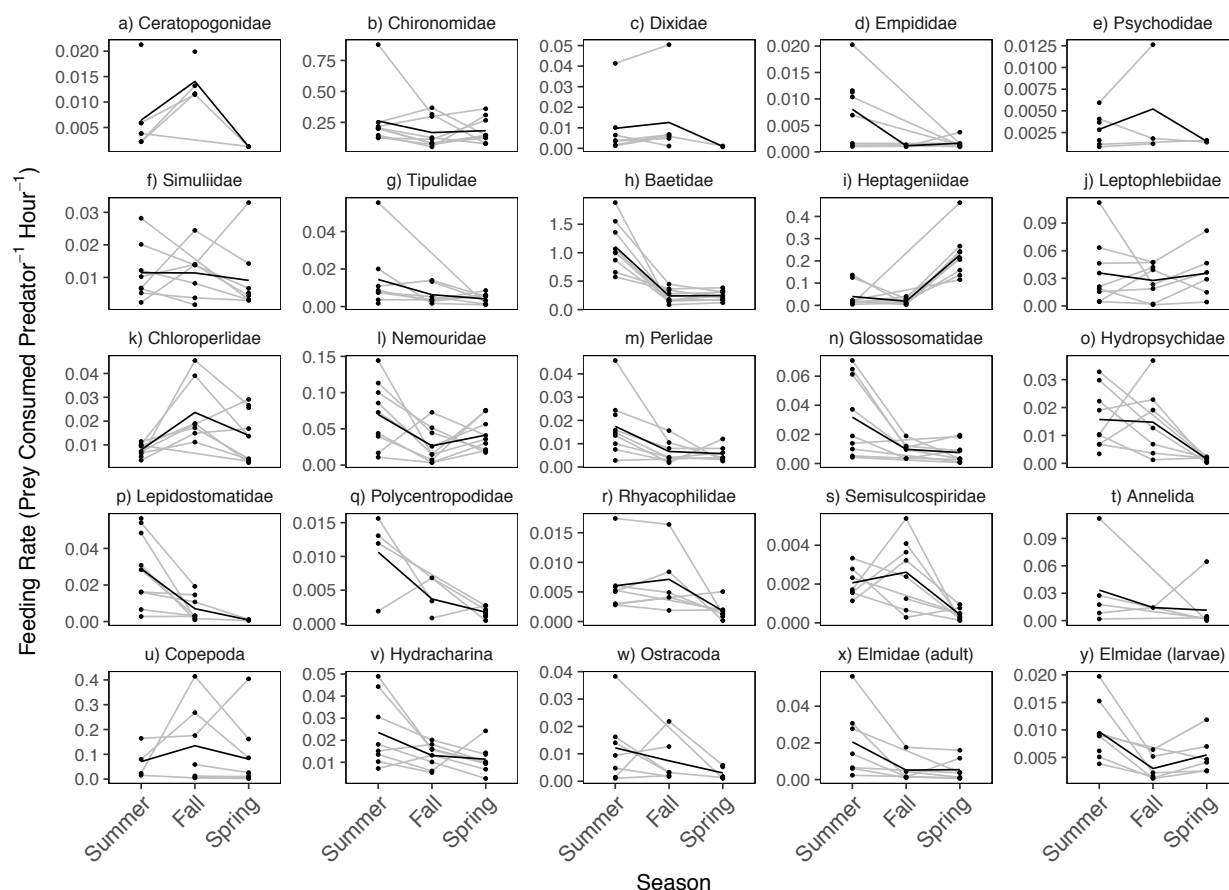
**Figure 3.** Spatial and temporal variation in reticulate sculpin feeding rates on 25 invertebrate prey taxa. The black lines show the seasonal mean feeding rates and the grey lines connect the same sites over time. Note the differences in the y-axis scale across panels.
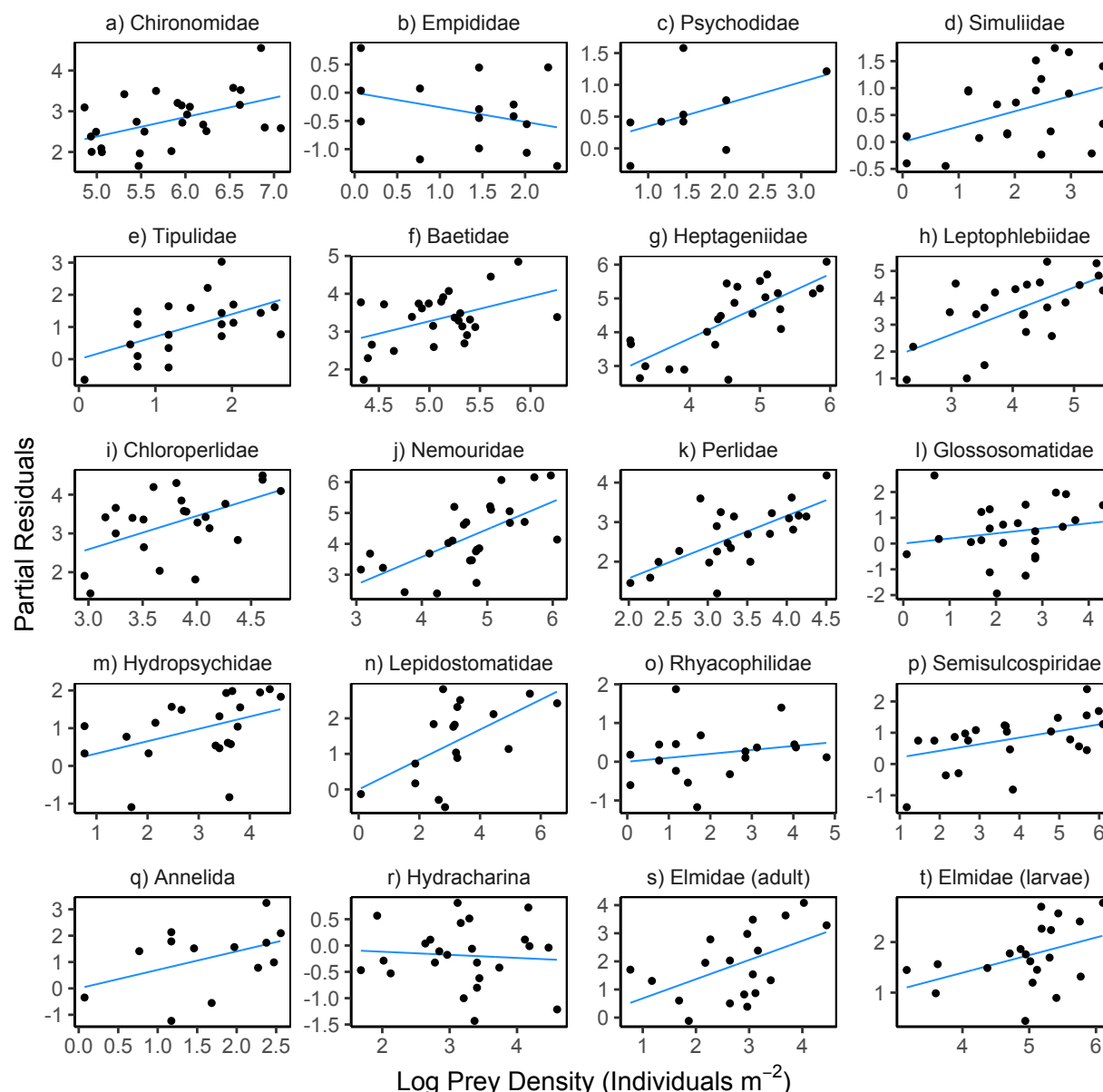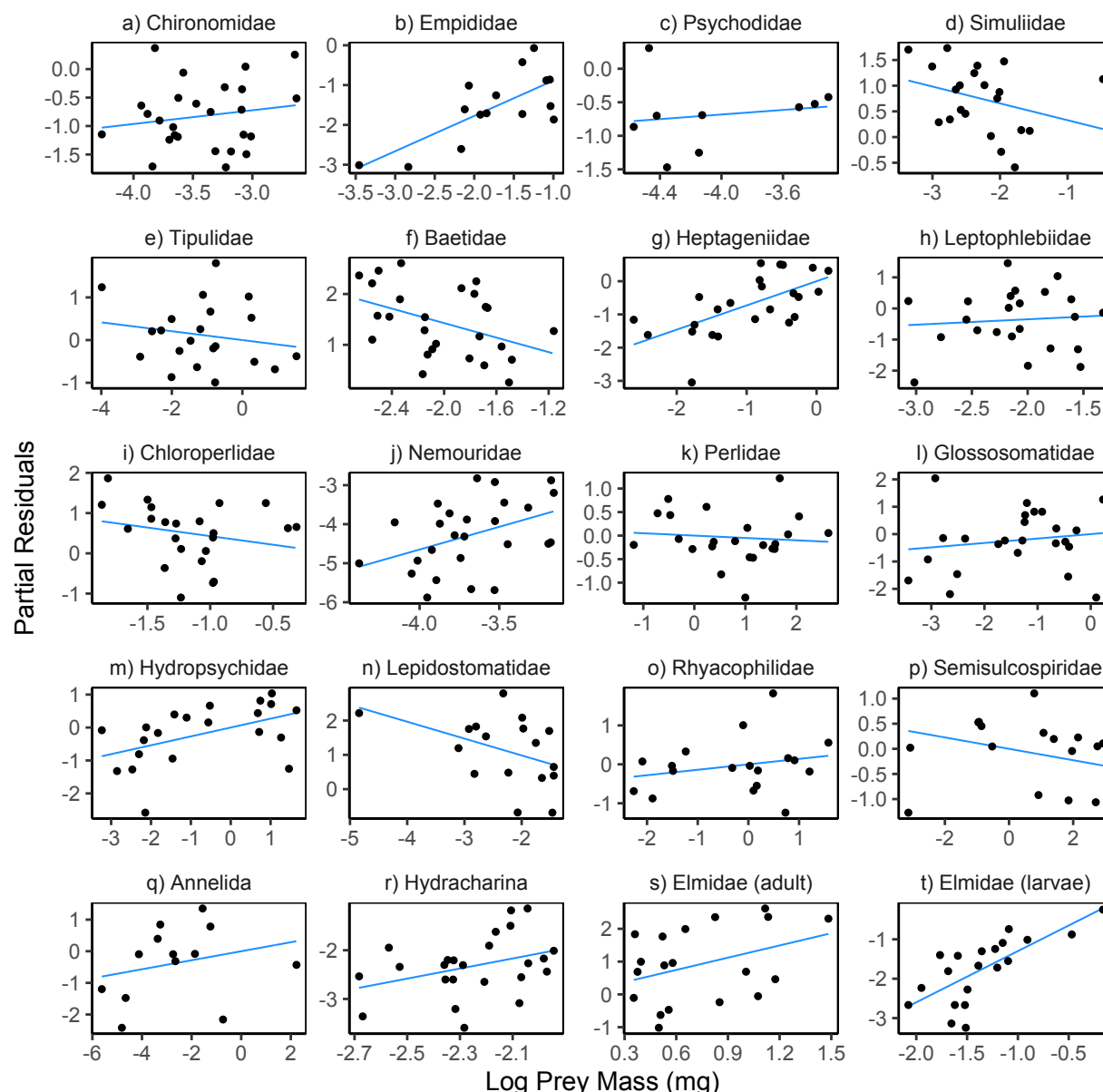
34

**Figure 4.** Partial residual plots for models predicting reticulate sculpin feeding rates on 20 prey taxa. The regression lines show partial fits from the prey-specific full models (Table S6) which included prey density, prey body mass, predator density, and abiotic factors. The points show the full model residuals $+ \beta_i X_i$, where $\beta_i$ is the regression coefficient for prey density from the full model and $X_i$ is the observed prey density shown on the x-axis. Note the varying scales for log prey density across panels.

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**Figure 5.** Partial residual plots for models predicting reticulate sculpin feeding rates on 20 prey

taxa. The regression lines show partial fits from the prey-specific full models (Table S6) which

included prey density, prey body mass, predator density, and abiotic factors. The points show the

full model residuals $+ \beta_i X_i$, where $\beta_i$ is the regression coefficient for prey mass from the full

model and $X_i$ is the observed prey mass shown on the x-axis. Note the varying scales for log prey
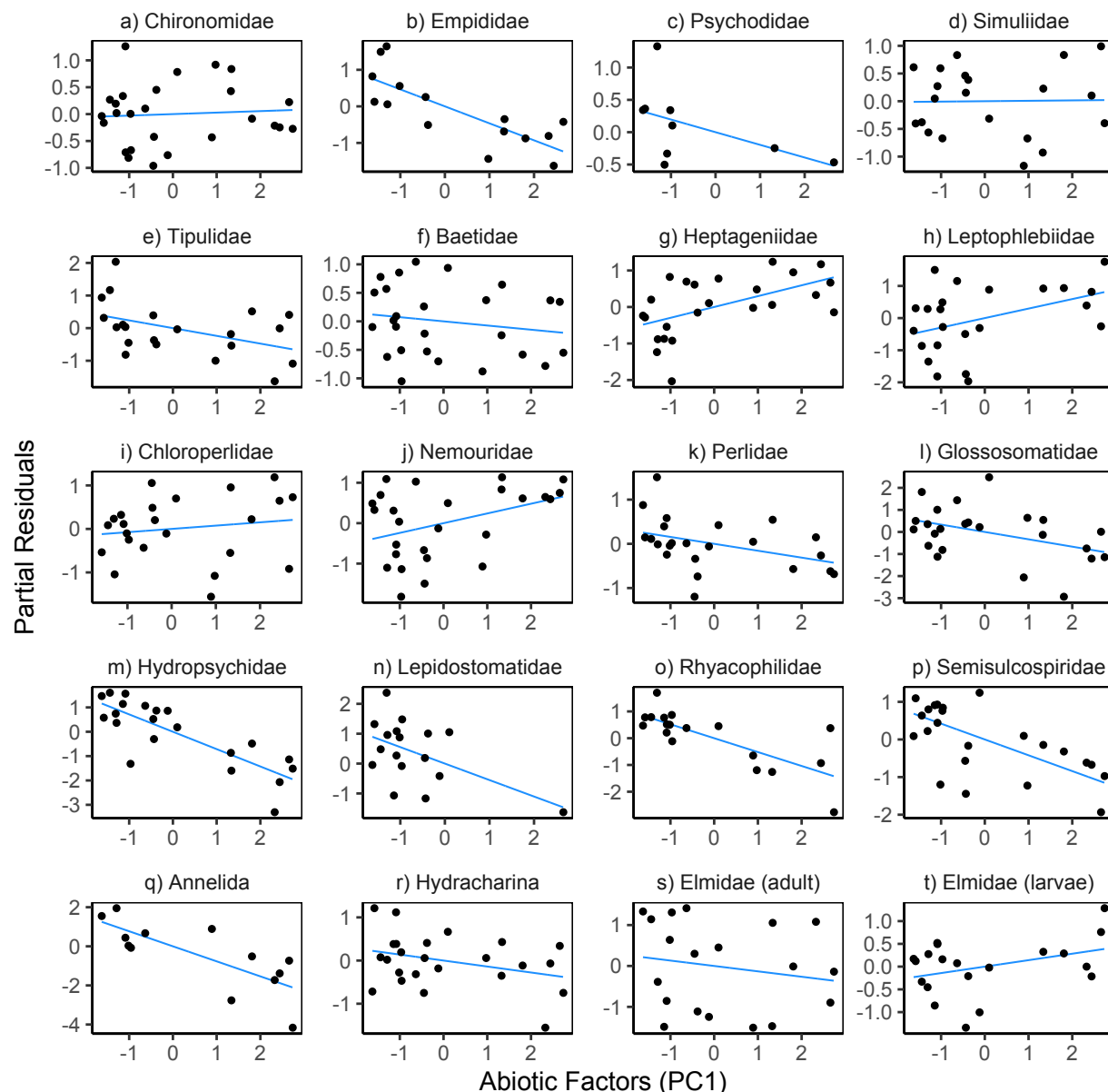
mass across panels.

**Figure 6.** Partial residual plots for models predicting reticulate sculpin feeding rates on 20 prey

taxa. The regression lines show partial fits from the prey-specific full models (Table S6) which

included prey density, prey body mass, predator density, and abiotic factors. The points show the

full model residuals $+ \beta_i X_i$, where $\beta_i$ is the regression coefficient for the abiotic factors from the

full model and $X_i$ is the first principal component from a PCA analysis of the abiotic factors.
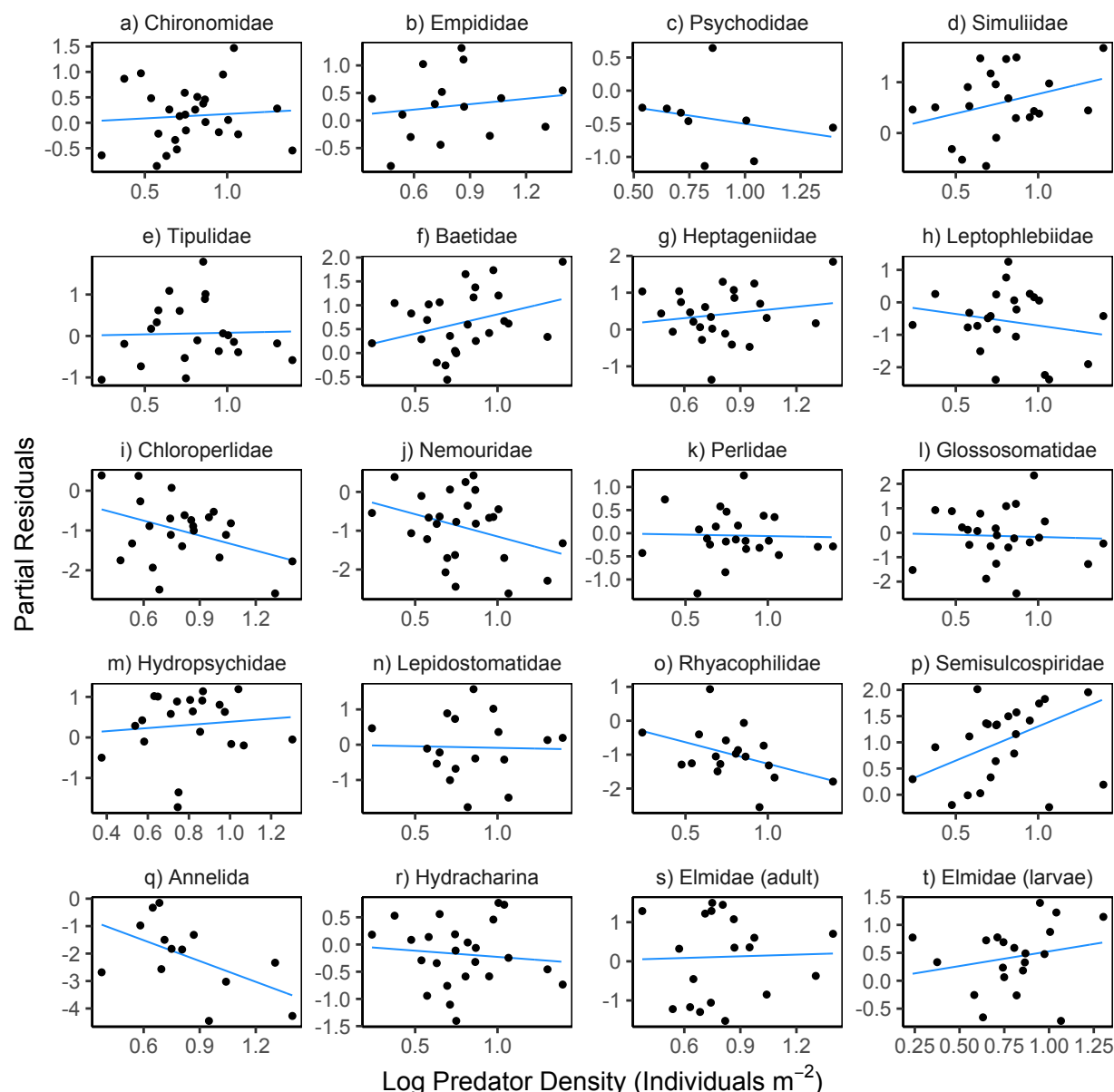
**Figure 7.** Partial residual plots for models predicting reticulate sculpin feeding rates on 20 prey

taxa. The regression lines show partial fits from the prey-specific full models (Table S6) which

included prey density, prey body mass, predator density, and abiotic factors. The points show the

full model residuals $+ \beta_i X_i$, where $\beta_i$ is the regression coefficient for predator (sculpin) density

from the full model and $X_i$ is the observed predator density shown on the x-axis.