

1 **Predator feeding rates may often be unsaturated under typical prey densities**

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26 <https://github.com/KyleCoblentz/FeedingRateSaturation>. This repository will be permanently archived on

27 Zenodo upon acceptance.

28

29 **Abstract**

30 Predator feeding rates (described by their functional response) must saturate at high prey densities.  
31 Although thousands of manipulative functional response experiments show feeding rate saturation at high  
32 densities under controlled conditions, it is unclear *how* saturated feeding rates are at natural prey  
33 densities. The general degree of feeding rate saturation has important implications for the processes  
34 determining feeding rates and how they respond to changes in prey density. To address this, we linked  
35 two databases – one of functional response parameters and one on mass-abundance scaling – through prey  
36 mass to calculate a feeding rate saturation index. We find that: 1) feeding rates may commonly be  
37 unsaturated and 2) the degree of saturation varies with predator and prey taxonomic identities and body  
38 sizes, habitat, interaction dimension, and temperature. These results reshape our conceptualization of  
39 predator-prey interactions in nature and suggest new research on the ecological and evolutionary  
40 implications of unsaturated feeding rates.

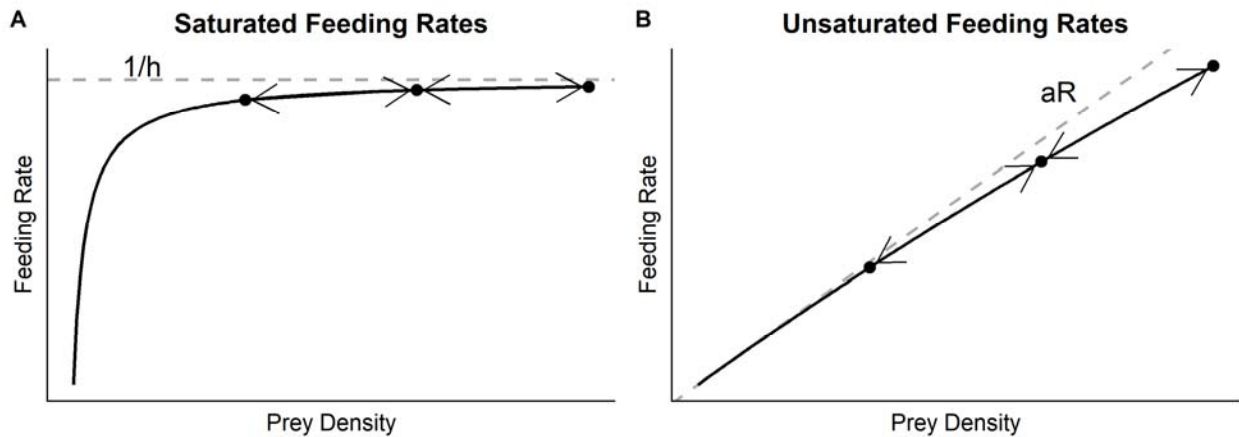
## 41 **Introduction**

42 Predator functional responses describe predator feeding rates as a function of prey density and are a  
43 central component of theory on consumer-resource interactions (Solomon 1949; Holling 1959; Murdoch  
44 *et al.* 2013). As pointed out by Holling (1959), functional responses should saturate with increasing prey  
45 density because the time it takes to process prey items, generally referred to as the handling time, limits  
46 feeding rates at high prey densities. Since its inception, the idea of functional response saturation has  
47 become a canonical component of predator-prey theory, shaping the way we conceptualize predator-  
48 prey interactions and dynamics (Rosenzweig & MacArthur 1963; McCann 2011; Murdoch *et al.* 2013).

49       Logic and thousands of experiments make it clear that feeding rates are saturating functions of  
50 prey densities (Holling 1959; Jeschke *et al.* 2004; Novak & Stouffer 2021; Uiterwaal *et al.* n.d.).  
51 However, it remains unclear *how* saturated feeding rates are under the prey densities that predators  
52 experience in nature. Some models and data suggest that, for carnivores, feeding rates should be saturated  
53 at the prey densities they experience (Jeschke 2007). This is because carnivores appear to be digestion-  
54 limited and satiated, or ‘full and lazy’ (Jeschke 2007). Indeed, some field functional response studies  
55 show saturated feeding rates over large ranges of prey densities (e.g. Messier 1994; Nielsen 1999; Gilg *et*  
56 *al.* 2006; Nilsen *et al.* 2009; Moustahfid *et al.* 2010; Moleón *et al.* 2012). However, other studies show  
57 saturated feeding rates at only one or a few observations at the highest observed prey densities  
58 (Angerbjörn 1989; Korpimäki & Norrdahl 1991; Redpath & Thirgood 1999; Sundell *et al.* 2000; Quinn *et*  
59 *al.* 2017; Coblenz *et al.* n.d.) or little to no evidence of feeding rate saturation (Novak 2010; Novak *et al.*  
60 2017; Preston *et al.* 2018; Beardsell *et al.* 2021, n.d.; Coblenz *et al.* 2021). Therefore, it is currently  
61 unclear how saturated feeding rates are likely to be in general.

62       The saturation level of feeding rates has important implications for predator-prey interactions. On  
63 one extreme, if feeding rates are generally saturated at typical prey densities, then feeding rates are largely  
64 determined by handling times, will be near their maxima (the reciprocal of the handling time), and should  
65 show little response to changes in prey densities (Figure 1A). On the other extreme, if feeding rates are  
66 generally unsaturated, then feeding rates will largely be determined by space clearance rates (aka attack

67 rates), will be lower than their potential maxima, and will dynamically respond to changes in prey  
68 densities (Figure 1B). Knowing whether predator feeding rates generally are saturated or unsaturated  
69 therefore would provide insights into the factors governing the strength of predator-prey interactions and  
70 how dynamic these interaction strengths may be.



71 **Figure 1. For saturated feeding rates (A), feeding rates are largely near their maximum as**  
72 **determined by the handling time (gray dashed line;  $1/h$ ) and will change little with changes in prey**  
73 **densities (represented by the dots and arrows). For unsaturated feeding rates (B), feeding rates are**  
74 **near the line determined by the space clearance or attack rate ( $a$ ; gray dashed line) and will change**  
75 **close to proportionally with changes in prey densities (represented by the dots and arrows).**

77 Here we combine two databases to investigate generalizations about how saturated feeding rates  
78 might be under typical prey field densities. The first database, the FoRAGE database (Functional  
79 Responses Across the Globe in all Ecosystems (Uiterwaal *et al.* n.d.)), contains estimates of saturating  
80 Type II functional response parameters from 2,598 functional response experiments, the vast majority of  
81 which are laboratory-based. Most these studies do not include field estimates of prey abundance. We  
82 therefore estimated prey abundances using a database on mass-abundance scaling (aka Damuth's Rule  
83 (Damuth 1981; White *et al.* 2007)) containing 5,985 records of masses and field-estimated abundances  
84 across the major taxa on earth (Hatton *et al.* 2019). Combining the functional response parameters and  
85 prey masses from FoRAGE with estimates of prey field abundances from the mass-abundance scaling  
86 relationships, we estimate an index of feeding rate saturation to address two questions:

- 87 1) How saturated may predator feeding rates be under typical prey densities?  
88 2) What covariates of a predator and prey's biology or environmental context are related to the  
89 degree of feeding rate saturation?

90 Our results suggest that predator feeding rates are commonly unsaturated at prey densities experienced in  
91 the field. We also find that prey and predator taxonomic identity and body sizes, the dimensionality of  
92 their interaction, their habitat, and temperature explain a significant amount of the variation in feeding  
93 rate saturation.

## 94 **Materials and Methods**

95 We first derive an index of feeding rate saturation. We then describe how we calculated the index using  
96 the FoRAGE database (Uiterwaal *et al.* n.d.) and data on mass-abundance scaling relationships (Hatton *et al.*  
97 2019). Last, we describe our statistical analysis to examine how biological covariates influence the  
98 degree of feeding rate saturation.

### 99 *Feeding Rate Saturation Index*

100 Our index of feeding rate saturation gives the proportional reduction in predator feeding rates due to  
101 saturation with increasing prey densities. For a predator with a saturating Type II functional response, we  
102 can derive the saturation index by comparing the feeding rates under the Type II functional response to  
103 the feeding rates under a non-saturating linear functional response. Under a linear (or Type I) functional  
104 response, the predator's feeding rate is proportional to prey density  $R$ :

$$105 \quad f_I = aR, \quad (\text{eqn. 1})$$

106 where  $a$  is the predator's space clearance rate (Fig. 1B). Under a Holling Type II functional response, the  
107 predator's feeding rate is

$$108 \quad f_{II} = \frac{aR}{1+ahR}, \quad (\text{eqn. 2})$$

109 where,  $h$ , is the predator's handling time. Our index of saturation  $I$  gives the proportional reduction in  
110 feeding rates between these two functional responses:

$$111 \quad I = \frac{f_I - f_{II}}{f_I} = \frac{ahR}{1+ahR} \quad (\text{eqn. 3})$$

112 (see Supplemental Information S1 for a derivation). The saturation index can take values between zero  
113 and one. Values near zero indicate the feeding rate is relatively unsaturated and values near one indicate  
114 the feeding rate is close to complete saturation (i.e. maximum feeding rate). This index can also be  
115 generalized to many other common functional response forms (Supplemental Information S7).

### 116 *Estimating the Saturation Index*

117 To estimate the saturation index, we need values for the space clearance rate ( $a$ ), handling time ( $h$ ), and  
118 prey density ( $R$ ). We obtained estimates for the space clearance rates and handling times from the  
119 FoRAGE database (Uiterwaal *et al.* n.d.). The database also contains a suite of biological and contextual  
120 covariates that may influence the functional response parameters including the average mass of the  
121 predator and prey, the dimensionality of their interaction (2D, 3D, or 2.5D i.e. fractional between 2D and  
122 3D), and the size or volume of the arena in which experimental trials were performed (for details see  
123 (Uiterwaal & DeLong 2020; Uiterwaal *et al.* n.d.)).

124 To obtain estimates of typical prey field densities, we used mass-abundance scaling relationships.  
125 Mass-abundance scaling relationships describe the general pattern that a species' abundance is inversely  
126 related to its mass (Damuth 1981; White *et al.* 2007). Using the data from Hatton *et al.* (2019), we fit  
127 separate log-log regressions of abundance on body mass for mammals, birds, ectotherms, protists, and  
128 prokaryotes/algae in a Bayesian framework in Stan through the R package '*brms*' using default priors. We  
129 then used the posterior predictive distributions of these models to estimate abundances for each prey  
130 species in the FoRAGE database whose body mass was available. Specifically, we determined each prey's  
131 density at every decile of its posterior predictive distribution (the 10<sup>th</sup> percentile to 90<sup>th</sup> percentile by  
132 10's), and we used these abundances in our calculation of saturation in order to assess the sensitivity of  
133 the saturation index to the potential mis-estimation of prey abundances (see Supplemental Information S2  
134 for details).

135 Prior to calculating the saturation index, we removed all studies from FoRAGE that used non-  
136 living prey or fungi as prey and studies without associated prey masses. During our analysis, we  
137 identified a small number of functional responses with prey abundance unit conversion issues in the data

138 underlying FoRAGE. We then systematically checked all of the prey abundance unit conversions and  
139 removed those studies with incorrect conversions (74 functional responses from 20 studies; these will be  
140 corrected in future versions of FoRAGE). This reduced the original dataset from 2,598 functional  
141 responses to 2,100 which we refer to as the ‘full dataset’.

#### 142 *Relationships between the Saturation Index and Covariates*

143 To examine the relationships between the saturation index and potential covariates, we used generalized  
144 linear mixed effects models. As fixed effects, we included the major prey and predator taxa (phylum to  
145 class), habitat (terrestrial, aquatic-freshwater, and aquatic-marine), interaction dimension (2D, 2.5D, and  
146 3D), arena size used in the experiment, the natural logarithm of prey mass, the natural logarithm of  
147 predator mass, and a quadratic effect of temperature. We included arena size because prior studies,  
148 including those using FoRAGE, have shown an effect of arena size on space clearance rates (Uiterwaal &  
149 DeLong 2018, 2020). We modeled temperature as a quadratic effect to allow for unimodal relationships  
150 with temperature (Englund *et al.* 2011; Uiterwaal & DeLong 2020). Although the saturation index  
151 includes the prey density that we estimated from prey mass, we included prey mass in our model because  
152 it also influences space clearance rate and handling time and could therefore influence the saturation  
153 index through these parameters as well (Vucic-Pestic *et al.* 2010; Rall *et al.* 2012; Uiterwaal & DeLong  
154 2020). To account for the non-independence of functional response estimates due to multiple estimates  
155 occurring on taxonomically similar species, we included minor prey and predator taxa (class to family) as  
156 random effects (a table of major and minor taxa is in Supplemental Information S3). Because the  
157 saturation index is limited to values between zero and one, we modeled the response as Beta distributed  
158 with a logit link function. We fit the regression model to the data in Stan through R using the package  
159 ‘*brms*’ with default priors.

160 We fit the model to a subset of the full dataset. We excluded studies that were missing any values  
161 for the covariates included in the analysis and those for which the fitted handling time value was less than  
162  $1 \times 10^{-6}$  days to exclude functional responses with unidentifiable handling times (Uiterwaal & DeLong  
163 2020). We also limited the number of major predator and prey taxa considered by dropping all predator

164 taxa with less than 15 functional response studies and then dropping all prey taxa with less than 15  
165 functional response studies. We limited the number of major predator and prey taxa to ensure enough  
166 functional response studies within each major taxa to include minor taxa as a random effect and prevent  
167 estimating major taxa effects based on only a few observations. Last, we also excluded mammals and  
168 birds for several reasons. First, the functional response studies on mammals and birds were performed in  
169 the field whereas all remaining studies were performed in laboratory conditions, confounding the effects  
170 of these taxa with the effects of measuring functional responses in the field. Second, the mammal and bird  
171 studies had no area boundaries, preventing our inclusion of arena size in the analysis. Third, unlike for all  
172 other taxa, which are ectotherms, the bird and mammal temperatures listed in FoRAGE represent the  
173 predator's endothermic average body temperature rather than the environmental temperature at which the  
174 study was conducted. After applying these criteria to the 2,100 functional response studies in the full  
175 dataset, 1,468 studies remained. We used this 'reduced dataset' in our generalized linear mixed model  
176 analysis. We performed the analysis using the saturation index calculated at the 10<sup>th</sup> percentile, median,  
177 and 90<sup>th</sup> percentile of estimated prey densities.

### 178 *Explaining Relationships between the Saturation Index and Covariates*

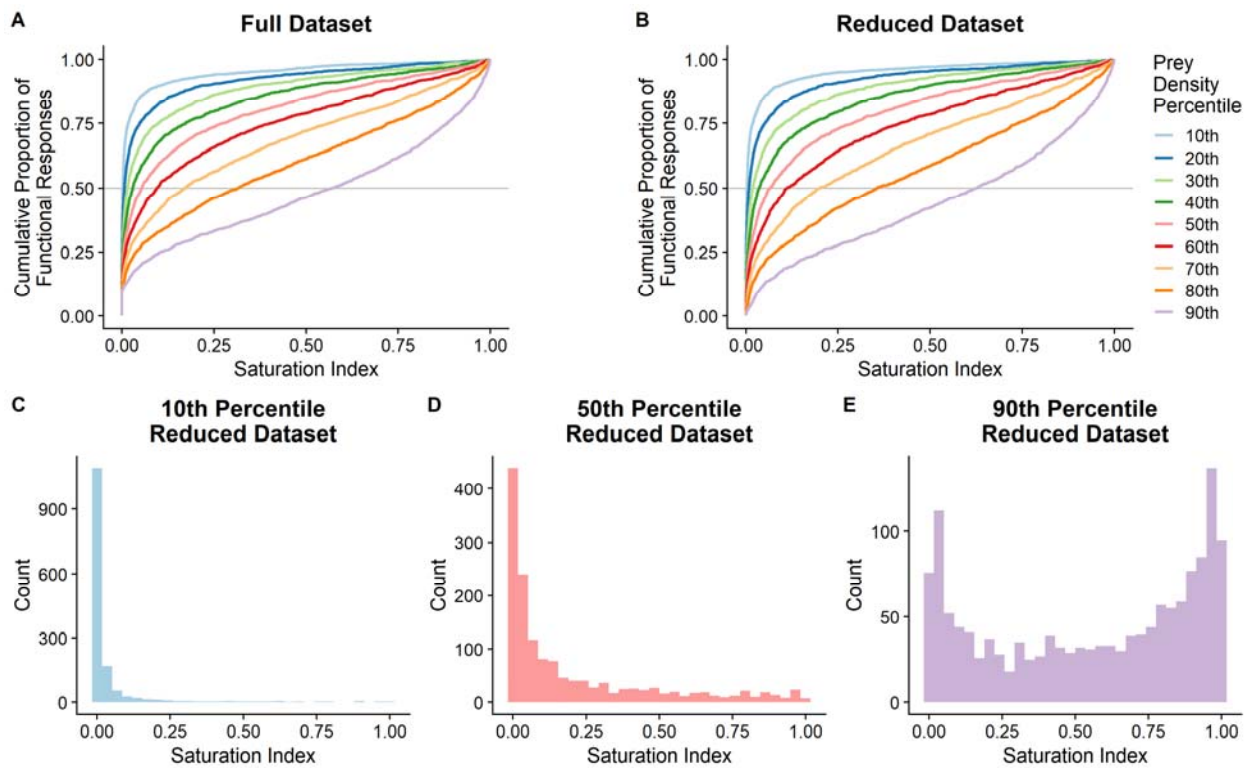
179 The analysis of the relationship between the saturation index and covariates gives the net relationship  
180 between saturation and the covariates but does not explain *why* these covariates have the relationships  
181 with saturation they do. As the saturation index is a function of the functional response parameters (space  
182 clearance rate and handling time) and the density of prey (Equation 3), the effects of the covariates on the  
183 saturation index are dependent on their effects on these three factors. We therefore performed two  
184 additional analyses on the reduced dataset using the same model as for estimating the effects of covariates  
185 on the saturation index to determine the partial effects of each of the covariates on the natural log of the  
186 space clearance rates and handling times. We again used Stan through R using the package '*brms*' with  
187 default priors assuming a normal distribution of residuals and an identity link. We did not perform an  
188 analysis for prey densities as the response variable because these were determined completely by prey  
189 mass and classification as algae, ectotherm, or protist (see Methods: Estimating the Saturation Index).



190 **Results**

191 *Estimates of Functional Response Saturation*

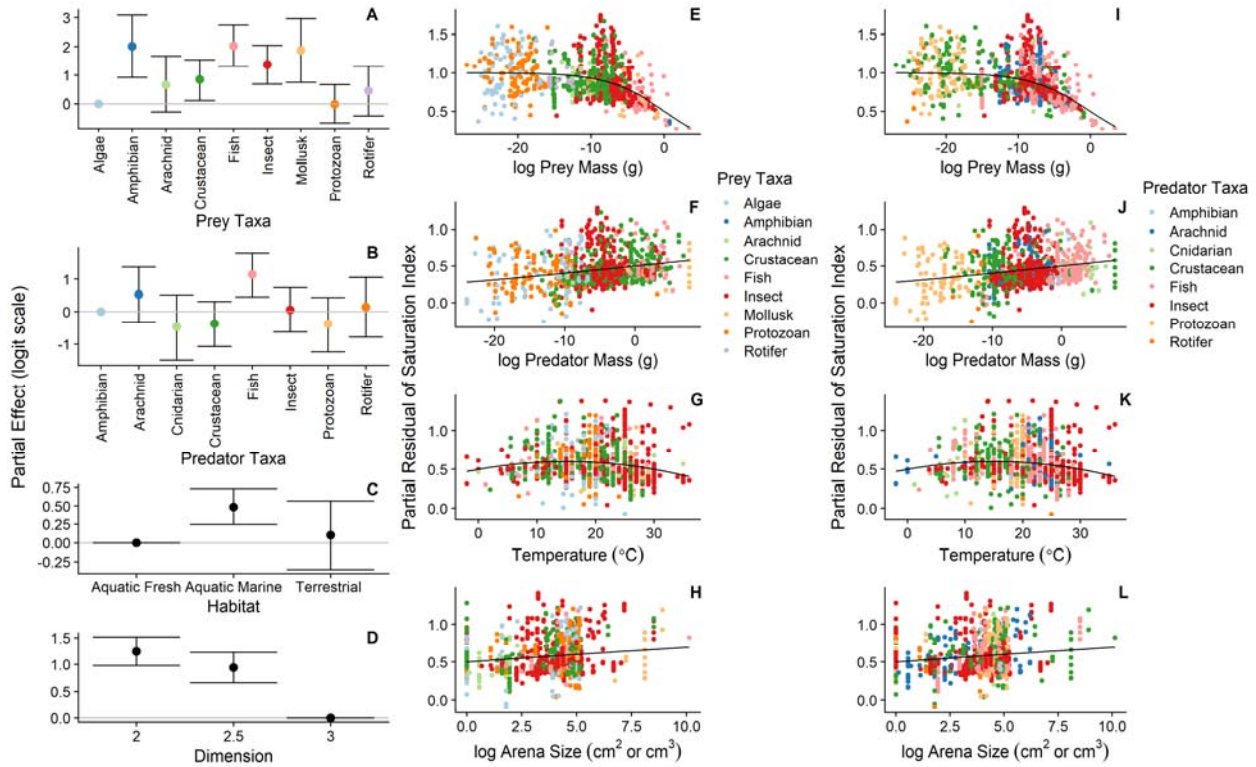
192 The feeding rate saturation index showed a right-skewed distribution with a mode near zero for most  
193 deciles of prey densities (10<sup>th</sup> through 70<sup>th</sup> percentiles; Figure 2). At the two highest deciles of prey  
194 densities (80<sup>th</sup> and 90<sup>th</sup> percentiles; Figure 2), the saturation index showed a bimodal distribution with  
195 modes near zero and one. For the full dataset, half of the studies were below a saturation index of 0.002 at  
196 the 10<sup>th</sup> percentile of prey densities, below 0.05 at the 50<sup>th</sup> percentile, and below 0.57 at the 90<sup>th</sup> percentile  
197 (Figure 2A). For the reduced dataset, half of the studies were below a saturation index value of 0.003 at  
198 the 10<sup>th</sup> percentile, below 0.06 at the 50<sup>th</sup> percentile, and below 0.62 at the 90<sup>th</sup> percentile (Figure 2B-E).



199  
200 **Figure 2. For both the full (A) and reduced (B) datasets, the index of predator feeding rate**  
201 **saturation showed right-skewed distributions with a mode near zero for the 10<sup>th</sup> to 70<sup>th</sup> percentiles**  
202 **of mass-estimated prey densities, and bimodal distributions with modes near zero and one for the**  
203 **80<sup>th</sup> and 90<sup>th</sup> percentiles of prey densities. Histograms of the index distributions at the 10<sup>th</sup>, 50<sup>th</sup>, and**  
204 **90<sup>th</sup> percentiles of prey densities for the reduced dataset are given in C, D, and E, respectively.**

205 *Analysis of Functional Response Saturation Covariates*

206 Here we present only the results for the saturation index calculated at the median estimate of prey density.  
207 Similar results occurred at the 10<sup>th</sup> and 90<sup>th</sup> percentiles of estimated prey densities except for estimates of  
208 prey taxa partial effects (Supplementary Information S4 and Discussion). Our model, the intercept of  
209 which represents an amphibian feeding on algae in freshwater in three dimensions (-6.07; 90% Credible  
210 Interval (CrI) (-7.36,-4.82)), suggests that all considered covariates influence the feeding rate saturation  
211 (Figure 3; for a summary table of the regression results see Supplementary Information S3). As prey,  
212 amphibians (median posterior partial effect = 2.03; (0.95,3.1)), crustaceans (0.87; (0.22, 1.57)), fish (2.04;  
213 (1.38,2.78)), insects (1.38; (0.74,2.09)), and mollusks (1.89;(0.83,3.01)) showed positive partial effects on  
214 saturation with all other prey taxa showing no apparent partial effects (Figure 3A). As predators, only fish  
215 showed a positive partial effect on the saturation index (1.14;(0.47,1.8)) with all other predator taxa  
216 showing no apparent partial effects (Figure 3B). Marine habitats showed a positive partial effect on the  
217 saturation index (0.49; (0.25,0.73)) as did the interaction dimension being 2 (1.24; (0.97,1.52)) or 2.5D  
218 (0.94; (1.66,1.22); Figures 3C, 3D). For the continuous factors, the saturation index decreased with prey  
219 mass (-0.26; (-0.29,0.34); Figures 3E, 3I), increased with predator mass (0.04; (0.01,0.07); Figures 3F,  
220 3J), showed a unimodal, concave relationship with temperature (median posterior linear effect = 0.05;  
221 (0.07,0.09); median posterior quadratic effect = -0.0018; (-0.003,-0.0008); Figures 3G, 3K), and  
222 increased with arena size (0.08; (0.04,0.12); Figures 3H, 3L).



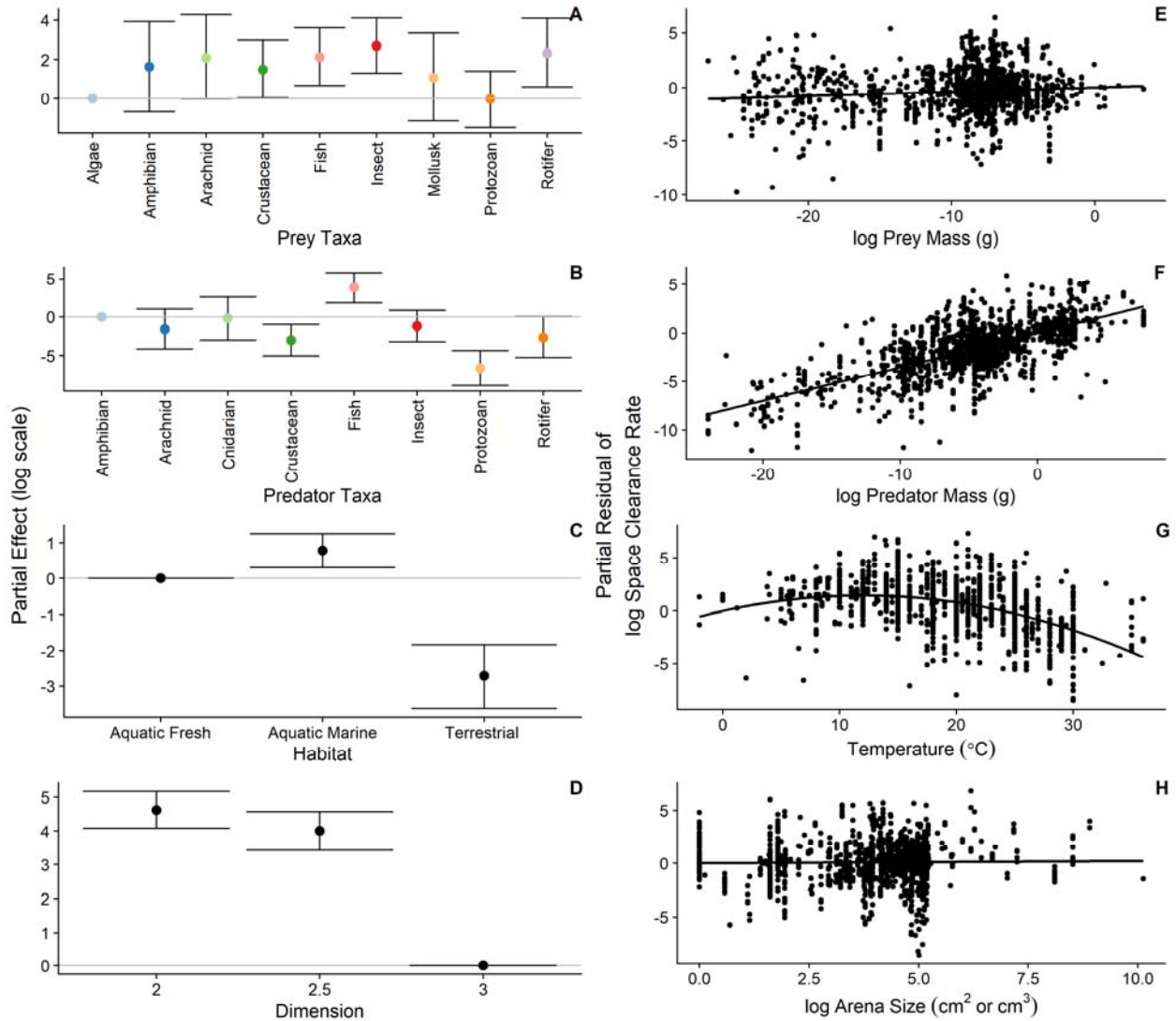
223  
 224 **Figure 3. Prey taxa (A), predator taxa (B), habitat (C), and dimension (D) exhibited partial effects**  
 225 **on the saturation index on the logit scale (error bars represent 90% credible intervals). The**  
 226 **saturation index decreased with prey mass (E,I), increased with predator mass (F,J), showed a**  
 227 **unimodal, concave relationship with temperature (G,K), and increased with arena size (H,L). Note**  
 228 **that E-H and I-L include the same data, but E-H are color-coded by prey taxa and I-L are color-**  
 229 **coded by predator taxa. Colors in E-H correspond to the same colors in A and the colors in I-L**  
 230 **correspond to the same colors in B.**

231 *Covariate Effects on Space Clearance Rates and Handling Times*

232 With the intercept (-8.5; (-10.9,-6.2)) again representing an amphibian feeding on algae in freshwater in  
 233 three dimensions, the model explaining variation in space clearance rates (Figure 4; See Supplemental  
 234 Information S6 for a summary table of the regression results) suggested that arachnids (2.13; (0.02,4.29)),  
 235 fish (2.15; (0.71,3.64)), insects (2.71, (1.24, 4.12)), and rotifers (2.37; (0.59, 4.09)) had partial positive  
 236 effects on space clearance rates when they were the prey with all other prey showing no apparent partial  
 237 effect(Figure 4A) and that fish had a partial positive effect on space clearance rate when they were

238 predator (3.87, (1.86,5.9)) with all other predator taxa showing no apparent partial effect (Figure 4B).  
239 Marine habitats had a positive partial effect (0.78; (0.29,1.25)) while terrestrial habitats had a negative  
240 partial effect on space clearance rates (-2.71; (-3.63,-1.82); Figure 4C). Two- and 2.5-dimension studies  
241 showed positive partial effects on space clearance rates (2D: 4.61; (4.08,5.15), 2.5D: 3.99; (3.43,4.55);  
242 Figure 4D). Whereas predator mass was positively associated with space clearance rates and temperature  
243 showed a unimodal, concave relationship with space clearance rates, prey mass and arena size did not  
244 have statistically clear relationships with space clearance rates (Figures 4E-H).

245         With the intercept (-10.9; (-13.0,-8.9)) still representing an amphibian feeding on algae in  
246 freshwater in three dimensions, the model explaining variation in handling times (Figure 5; See  
247 Supplemental Information S6 for a summary table of the regression results) suggested that all prey taxa  
248 other than algae showed positive partial effects on handling times (Amphibian: 9.3; (7.31,11.2), Arachnid:  
249 6.4; (4.44,8.3), Crustacean: 7.0; (5.7,10.2), Fish: 8.93; (7.7,10.2), Insect: 6.7; (5.5,8.0), Mollusk: 9.8;  
250 (7.9,11.7), Protist: 2.26; (1.0,3.6); Rotifer: 5.98; (4.5,7.6); Figure 5A). As predators, fish showed a  
251 negative partial effect (-1.86; (-3.6,-0.12)) and protists showed a positive partial effect on handling times  
252 (6.0; (3.7,7.7)) with all other predator taxa showing no apparent partial effects (Figure 5B). Marine and  
253 terrestrial habitats showed positive partial effects (Marine: 0.4; (0.04,0.8), Terrestrial: 2.5; (1.8,3.2);  
254 Figure 5C) while 2- and 2.5-dimension interactions had negative partial effects on handling times (2D: -  
255 1.1; (-1.5,-0.7), 2.5D: -1.3; (-1.7,-0.9); Figure 5D). For the continuous variables, handling times increased  
256 with prey mass, decreased with predator mass, increased with arena size, and decreased linearly with  
257 temperature (Figures 5E-H).



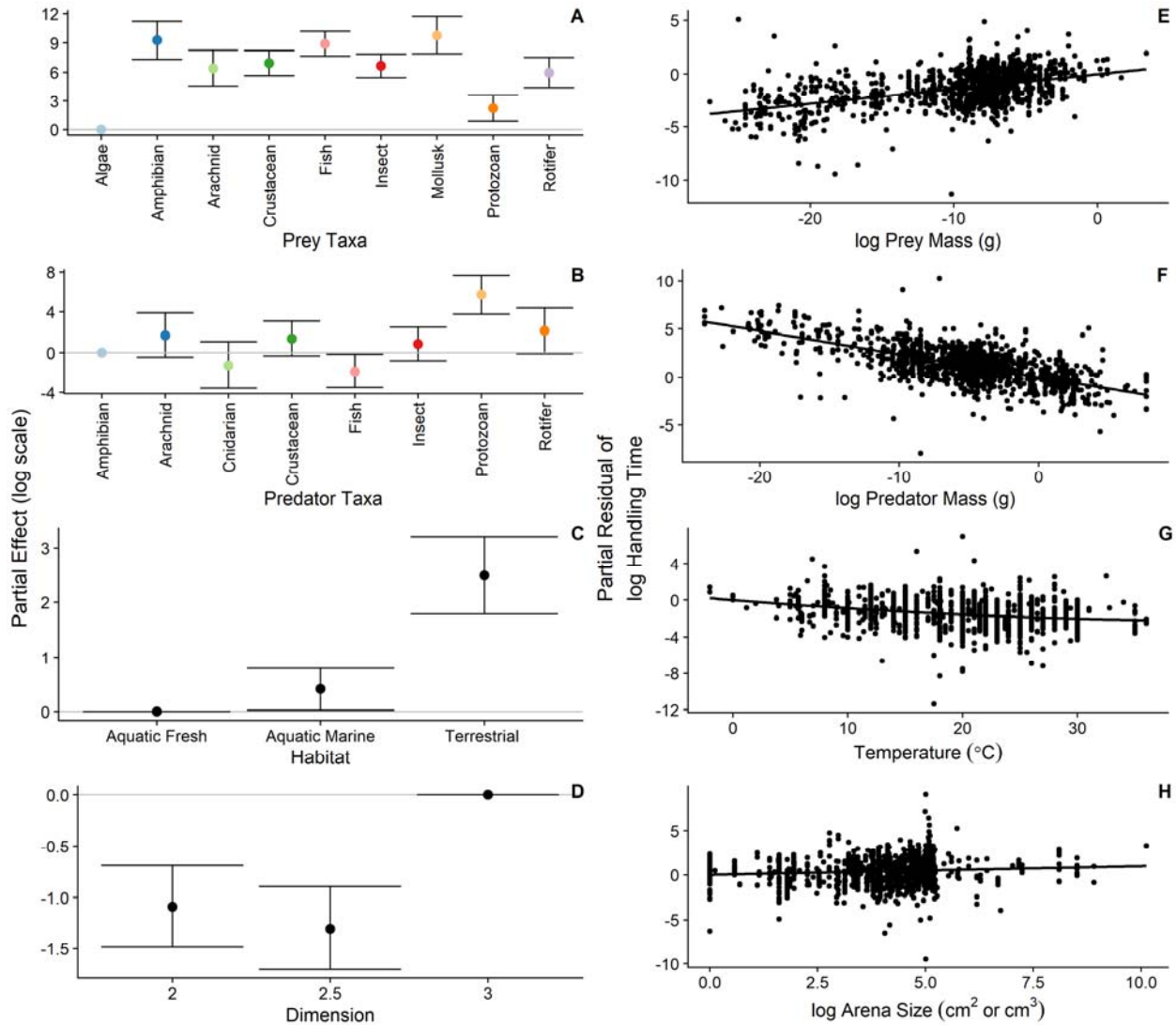
258

259 **Figure 4. Prey taxa (A), predator taxa (B), habitat (C), and dimension (D) exhibited partial effects**

260 **on log-transformed space clearance rates (error bars represent 90% credible intervals). Space**

261 **clearance rates increased with predator mass (E), showed a unimodal, concave relationship with**

262 **temperature (G), and had no apparent relationship with prey mass and arena size (D, H).**



263  
 264 **Figure 5. Prey taxa (A), predator taxa (B), habitat (C), and dimension (D) exhibited partial effects**  
 265 **on log-transformed handling times (error bars represent 90% credible intervals). Handling times**  
 266 **increased with prey mass (D), decreased with predator mass (E), decreased with temperature (G),**  
 267 **and increased with arena size (H).**

268 **Discussion**

269 Combining functional response parameter estimates from laboratory-controlled experiments with field-  
 270 relevant estimates of prey density obtained from mass-abundance scaling relationships, our results  
 271 suggest that predator feeding rates may often be unsaturated under typical field conditions. Indeed, our  
 272 analysis identified several predator functional responses that remained unsaturated even at high prey

273 densities (i.e. 25% of the functional responses were below a saturation index value of 0.2 with prey  
274 densities at the 90<sup>th</sup> percentile). For these functional responses, variation in feeding rates should be  
275 determined largely by variation in space clearance rates and prey densities. Space clearance rates are the  
276 product of predator and prey velocities, the distance over which predators can detect prey, the probability  
277 of a predator attacking a prey individual given its detection, and the probability that the attack is  
278 successful (Jeschke *et al.* 2002; DeLong 2021; Wootton *et al.* n.d.). For unsaturated feeding rates, these  
279 processes are central to determining the magnitude of feeding rates. A lack of saturation also means that  
280 predator feeding rates are lower than their potential maxima. This result is congruent with a previous  
281 study on fishes suggesting that fish digestive capacities are often larger than what would be necessary for  
282 the average amount of food they encounter (Armstrong & Schindler 2011). Feeding rates occurring below  
283 their potential maxima may also be indicative of the evolution of prudent predation (Gutiérrez Al-  
284 Khudhairy & Rossberg 2022) or constraints on predator feeding rates from other sources (Vuorinen *et al.*  
285 2021). Last, unsaturated feeding rates should dynamically respond to changes in prey densities leading to  
286 density-dependent prey mortality that is close to proportional to prey densities. Our results suggest that  
287 for the species that remained unsaturated at the highest prey abundance decile, the use of linear functional  
288 responses to describe variation in feeding rates may be a sufficient approximation (Wootton & Emmerson  
289 2005; Novak 2010; Jonsson 2017).

290         Many of the functional responses showed a gradient in feeding rate saturation with unsaturated  
291 feeding rates under most deciles of prey abundance and saturated feeding rates at the very highest deciles  
292 of prey abundance. In the full dataset, less than half of the functional responses show a reduction in  
293 feeding rates of more than 20% (relative their hypothetical linear functional response) when prey were  
294 assumed to be at their 70<sup>th</sup> abundance percentile. Yet, with the prey at the 90<sup>th</sup> abundance percentile, half  
295 of the functional responses have feeding rates that show a reduction of over 60%. This result suggests two  
296 nonexclusive scenarios for feeding rate saturation. One is that the extent of saturation may be dependent  
297 on whether a prey species is relatively abundant or not given its mass. For prey that are very abundant for  
298 their mass, predator feeding rates are likely to be saturated. Yet, for prey with abundances more typical of

299 their size, predator feeding rates are likely to be unsaturated. For example, invasive and pest species can  
300 reach extremely high abundances relative to other species of their size (Hall Jr. *et al.* 2006). Predators  
301 feeding on these species may exhibit saturated feeding rates even though they might exhibit unsaturated  
302 feeding rates on prey of a similar size with more typical abundances. Another view of the result that  
303 feeding rate saturation occurs generally at the highest predicted prey abundances is that the predator's  
304 feeding rate may be typically unsaturated but become saturated in times or areas where prey are  
305 particularly abundant. For example, extreme abundance events like oak masts and periodical cicada  
306 emergences are known to saturate predators and are thought to have evolved for that purpose (Karban  
307 1982; Kelly 1994). Indeed, many field functional response studies show feeding rate saturation at only a  
308 few high prey abundance observations (Angerbjörn 1989; Korpimäki & Norrdahl 1991; Redpath &  
309 Thirgood 1999; Sundell *et al.* 2000; Quinn *et al.* 2017; Coblenz *et al.* n.d.). Thus, it may be that  
310 unsaturated predator feeding rates are typical except when prey exhibit high abundances.

311 We found that the extent of feeding rate saturation depended on prey and predator taxonomic  
312 identities and masses, habitat, interaction dimension, and temperature after accounting for experimental  
313 arena size. Our results suggest that, at the median prey abundances, amphibians, crustaceans, fish, insects,  
314 and mollusks showed a greater degree of saturation as prey than algae. These same five prey taxa also  
315 show positive partial effects on space clearance rates and handling times. However, our results suggest  
316 that the differences among prey taxa in there are effects on saturation are dependent on how abundant  
317 they are. For example, protists and rotifers showed negative partial effects at the 10<sup>th</sup> percentile of  
318 estimated prey densities with all other taxa having no apparent effect and all prey taxa other than the  
319 reference taxa, algae, showed positive partial effects at the 90<sup>th</sup> percentile of estimated prey densities  
320 (Supplemental Information S4). For the predator taxa, only fish showed a positive partial effect on the  
321 degree of saturation. This likely reflects the generally higher space clearance rates of fish relative to the  
322 other predator taxa, which has been attributed to their relatively higher velocities in moving through their  
323 environment after accounting for body size (Pawar *et al.* 2012; Buba *et al.* 2022; Wootton *et al.* n.d.).  
324 This conclusion is partially supported by a similarly positive partial effect for mammals and birds which



325 also are likely to have higher velocities in their environments for their body sizes in an analysis including  
326 these predator taxa but not accounting for arena size (Supplementary Information S5).

327 Habitat and interaction dimension also had effects on the degree of feeding rate saturation, with  
328 2- and 2.5-dimensional interactions having higher levels of feeding rate saturation compared to 3-  
329 dimensional interactions. This result is driven by the higher values of space clearance rates in the 2- and  
330 2.5-dimensional studies that outweighed the generally lower handling times in 2- and 2.5-dimensional  
331 studies. In general, although the magnitudes of space clearance rates are not comparable across  
332 dimensions due to differences in spatial units (e.g.  $\text{m}^2\text{predator}^{-1}\text{time}^{-1}$  versus  $\text{m}^3\text{predator}^{-1}\text{time}^{-1}$ , Uiterwaal  
333 & DeLong 2020), the saturation index is unitless. Therefore, the higher absolute values of space clearance  
334 rates in 2 and 2.5 dimensions lead to greater saturation. However, it remains unclear why 2- and 2.5-  
335 dimensional space clearance rates are generally greater than 3-dimensional space clearance rates. Marine  
336 studies also showed higher feeding rate saturation as a result of higher space clearance rates and handling  
337 times. Although terrestrial studies also showed higher space clearance rates compared to freshwater  
338 studies, they also showed lower handling times that counteracted the effects of higher space clearance  
339 rates. It is unclear whether this pattern of greater saturation in marine studies is general or whether it is the  
340 product of the species on which functional response studies have been conducted across different habitats.  
341 Confirming whether marine species show generally greater feeding rate saturation could be important for  
342 understanding how predation operates differently in different ecosystems (Shurin *et al.* 2002, 2006).

343 Overall, our results suggest that predator and prey masses are likely to have opposite net effects  
344 on the degree of feeding rate saturation. We found that prey mass was negatively associated with the  
345 degree of feeding rate saturation. However, previous research has shown that increasing prey mass is  
346 associated with higher space clearance rates and higher handling times, which would lead us to expect  
347 prey mass to be positively associated with feeding rate saturation (Vucic-Pestic *et al.* 2010; Rall *et al.*  
348 2012; Uiterwaal & DeLong 2020). This difference in expectation can be explained by the fact that prey  
349 density decreases with prey mass (Damuth 1981; White *et al.* 2007; Hatton *et al.* 2019) and that the net  
350 effect of prey mass on feeding rate saturation is the product of all three of these relationships. That is, the

351 negative scaling of prey densities with prey mass is stronger than the positive relationships between prey  
352 mass and space clearance rates and handling times, resulting in a positive effect of mass on saturation. In  
353 contrast to prey mass, predator mass was positively associated with feeding rate saturation. Previous  
354 results suggest that predator mass is typically positively associated with space clearance rates and  
355 negatively related to handling times (Vucic-Pestic *et al.* 2010; Rall *et al.* 2012; Uiterwaal & DeLong  
356 2020). In our dataset, predator mass exhibits a slightly stronger positive relationship with space clearance  
357 rates than a negative relationship with handling times, thereby producing a net positive relationship  
358 between feeding rate saturation and predator mass.

359         Temperature has strong effects on functional response parameters in laboratory studies  
360 (Thompson 1978; Englund *et al.* 2011; Rall *et al.* 2012; Uiterwaal & DeLong 2020), with studies  
361 typically documenting positive or unimodal, concave relationships between temperature and space  
362 clearance rates and negative or unimodal, convex relationships between temperature and handling times  
363 (Englund *et al.* 2011; Rall *et al.* 2012; Uiterwaal & DeLong 2020). This suggests that the net effect of  
364 temperature on feeding rate saturation should be dependent on the relative strengths of the relationships  
365 between temperature and space clearance rates and handling times. Our results show a stronger unimodal,  
366 concave relationship between space clearance rates and temperature than the negative relationship  
367 between handling times and temperature, and this leads to a net unimodal, concave relationship between  
368 temperature and saturation. These results lead to the prediction of a mid-latitudinal peak in feeding rate  
369 saturation and that the degree of feeding rate saturation will be sensitive to continued climate change,  
370 with potentially profound consequences for predator-prey interactions on a global scale.

371         Although our results suggest that predator feeding rates are unsaturated across a range of typical  
372 prey densities, many of our estimates are likely to be overestimates. First, the mass-abundance scaling  
373 relationships we used to predict prey densities may overestimate prey densities because the abundances  
374 are typically reported in aerial square meters. Thus, for aquatic organisms, abundances are integrated over  
375 some depth often greater than a meter and therefore are likely overestimates of the abundances in a cubic  
376 meter, the relevant metric for three dimensional studies (Hatton *et al.* 2019). Mass-abundance scaling

377 relationships also may reflect maximum abundances rather than typical abundances because researchers  
378 often measure abundances of organisms where they are abundant (Lawton *et al.* 1990; Marquet *et al.*  
379 1995; White *et al.* 2007). Second, because functional response experiments are typically performed in  
380 spatially and structurally simplified arenas, the estimates of functional response parameters may be biased  
381 toward values that lead to higher feeding rates than those that are likely to be observed in nature (Novak  
382 *et al.* 2017; Griffen 2021).

383         In our analysis, we assumed that predator feeding rates within predator-prey pairs were described  
384 by a saturating Type II functional response. However, predators can exhibit other functional response  
385 types and typically incorporate more than one prey type into their diets. For example, predators might  
386 exhibit sigmoidal Type III functional responses or predator feeding rates could be dependent on predator  
387 densities (Holling 1959; DeLong & Vasseur 2011; Novak & Stouffer 2021). In general, considering these  
388 additional aspects of predator functional responses shows that our estimates of saturation will be  
389 conservative or show little change with these alternative functional response scenarios (See Supplemental  
390 Information S7 for a general derivation of the saturation index and specific examples). In the case of a  
391 Type III functional response, the saturation index becomes a sigmoidal function of prey densities and  
392 should give similar results as the Type II functional response except with lower saturation values at low  
393 prey densities (Supplemental Information S7). In the case of functional responses with predator  
394 dependence or the inclusion of multiple prey in the predator's diet, the degree of feeding rate saturation  
395 should be lower than that estimated for the Type II functional response and our results here will be  
396 conservative (Supplemental Information S7). However, one caveat with respect to the multi-prey case is  
397 that, although feeding rate saturation with respect to the focal prey should decrease with the addition of  
398 alternative prey, the saturation of the predator's total feeding rate across all prey can increase with the  
399 addition of alternative prey. Whether saturation of the predator's total feeding rate increases with  
400 additional prey in the diet will depend on whether and how the parameters of the functional response  
401 change with the addition of prey species to the diet. In general, we know little about how functional

402 response parameters are likely to change with diet richness and understanding how total feeding rate  
403 saturation in the predator is likely to change with diet richness will require studies measuring functional  
404 responses and their saturation under field conditions.

## 405 **Conclusion**

406 The degree to which predator feeding rates are saturated has important consequences for what factors  
407 predominantly determine predator feeding rates, whether predator feeding rates are near their maxima or  
408 not, and how predator-prey interaction strengths respond to changes in prey densities. Our results suggest  
409 that it may be the case that predator feeding rates are often far from saturated over large ranges of typical  
410 prey densities. Furthermore, our results suggest that the degree of feeding rate saturation is shaped by  
411 predator and prey traits and the environment. We suggest that future work on feeding rate saturation focus  
412 on 1) measuring saturation under field conditions, 2) understanding the proximate and ultimate causes of  
413 feeding rates being unsaturated over a range of typical prey densities, and 3) determining the ecological  
414 and evolutionary consequences of unsaturated feeding rates for predator-prey systems.

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