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9 Global warming affects foraging efficiency of fish by influencing mutual interference

10

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18

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27 Conflict of Interests

28 The Authors declare no conflict of interest.

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31 Łukasz Jermacz; Methodology: Mateusz Augustyniak, Bálint Preiszner, Jarosław Kobak,  
32 Tomasz Kakareko, Łukasz Jermacz; Investigation: Mateusz Augustyniak, Bálint Preiszner;  
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36 István Czeglédi; Resources: Mateusz Augustyniak, Bálint Preiszner, István Czeglédi, Tibor  
37 Erős; Supervision: Łukasz Jermacz

38 Statement on inclusion

39 Our study brings together researchers from many countries. Researchers from Hungary,  
40 where the study was conducted, are experts in population ecology, working together with  
41 national institutions dealing with conservation biology. The support of an expert in predator-  
42 prey relationships from the United Kingdom provides proper data interpretation and draws  
43 conclusions relevant to a wide range of researchers around the world. The Polish part of the  
44 team has great experience with experimental studies, which allows to plan and conduct the  
45 experiment properly.

46 Data availability statement

47 Data available from the Dryad Digital Repository.

48

49 **Abstract**

- 50 1. Predator-prey interactions underpin ecological dynamics from population to  
51 ecosystem scales, affecting population growth and influencing community stability.  
52 One of the classic methods to study these relationships is the functional response  
53 (FR) approach, measuring resource use across resource densities.
- 54 2. Global warming is known to strongly mediate consumer-resource interactions, but  
55 the relevance of prey and predator densities remains largely unknown. Elevated  
56 temperature could increase consumer energy expenditure, which needs to be  
57 compensated by greater foraging activity. However, such greater activity may  
58 concurrently result in a higher encounter rate with other consumers, which  
59 potentially affects their total pressure on resource population because of synergistic  
60 or antagonistic effects among multiple predators.
- 61 3. We performed a laboratory experiment using three densities of a fish predator  
62 (pumpkinseed, *Lepomis gibbosus*) (one, two, and four specimens), two temperatures  
63 (25 and 28 °C), and six prey densities. Using the FR approach, we investigated the  
64 combined effects of elevated temperature and predator and prey density on  
65 consumer's foraging efficiency.
- 66 4. We observed a reduced maximum feeding rate at the higher temperature for single  
67 predators. However, the foraging efficiency of predators in groups was negatively  
68 affected by antagonistic interactions between individuals and further mediated by  
69 the temperature. Specifically, we observed a general decrease in antagonistic  
70 interactions in elevated compared to the ambient water temperature for multiple

71 predator groupings. Irrespective of temperature, antagonistic multiple predator  
72 effects increased with predator density and peaked unimodally at intermediate prey  
73 densities, indicating multiple dimensions of density-dependence which interact to  
74 supersede the effects of warming.

75 5. This study shows that conspecific presence negatively affects the per capita  
76 performance of predators, but that this effect is dampened with increasing  
77 temperature. Their adaptive response to temperature consists of limited food intake  
78 and further reduced intraspecific interactions. Including intraspecific competition in  
79 study design may thus offer more realistic outcomes compared to widely-used  
80 experiments with only single predator individuals, which could overestimate the  
81 effect of increasing temperature.

82 Keywords: consumer-resource interaction, functional response, intraspecific interaction,  
83 invader effect, prey risk

84

## 85 **Introduction**

86 Predator-prey interactions fundamentally mediate dynamics of populations and influence  
87 community stability (Alebraheem and Abu-Hassan 2023; Schmidt et al. 2014). Prey dynamics  
88 can be affected by both density-mediated and trait-mediated effects from predators, by  
89 reducing recruitment and survival, or through changes in prey behaviour, distribution,  
90 foraging, or growth (Beauchamp et al. 2007). Reciprocally, prey availability can affect  
91 predator population stability, influencing their feeding rates, growth, and reproductive  
92 success (Beauchamp et al. 2007).

93           One classic method to study the role of predator-prey interactions in population  
94 dynamics by investigating foraging efficiency is the functional response (FR) approach. The  
95 FR is defined as the relationship between resource availability and consumption by a living  
96 organism (Holling 1959a, b; Solomon 1949). In the context of predation, the FR is typically  
97 characterised using two parameters: the attack rate, classically interpreted as the search  
98 efficiency, and the handling time, defined as the time spent pursuing, subduing, and  
99 consuming each prey item plus the time spent preparing to search for the next prey item  
100 (Robertson and Hammil 2021). The FR approach allows for rapid, standardised assessments  
101 of per capita interaction strengths. Moreover, the flexibility of FR allows assessment of the  
102 effects of different environmental factors on predation efficiency and its influence on prey  
103 population stability across different contexts (Faria et al. 2023).

104           One pervasive environmental context that governs the strength of trophic  
105 interactions is temperature (Uiterwaal and DeLong 2020). According to the latest IPCC  
106 report, the global air temperature at the end of the 21st century could rise by up to 3 °C  
107 (IPCC, 2023). At the individual level, temperature affects metabolism of ectotherms (Englund  
108 et al. 2011; Kordas et al. 2011; Ohlberger 2013). This increased metabolism needs to be  
109 compensated by higher feeding rates (Volkoff and Rønnestad 2020; Yu et al. 2023), which  
110 can result in changes in interaction strengths between organisms, thereby affecting the top-  
111 down forces regulating whole ecological communities (Hoekman 2010). However, these  
112 trophic outcomes owing to warming can have various forms, mediated by biotic contexts  
113 which are rarely integrated into assessments of warming effects (e.g. predator density, body

114 size, sex, predator and prey behaviour, reproductive cycle) (Coblentz et al. 2022; Landi et al.  
115 2022; Rall et al. 2012; Sheppard et al. 2024; Uiterwaal and DeLong 2020).

116 A pervasive biotic component influencing predator-prey interactions is non-trophic  
117 inter- and intraspecific interactions among multiple predators (Barrios-O'Neill et al. 2014; Sih  
118 et al. 1998). The outcomes of such interactions could be assessed by comparing the  
119 observed total predation rate by multiple predators with the predation rate expected based  
120 on a single predator functional response (i.e. assuming no interactions between hunting  
121 predators). It could be that the observed total rate of predation is greater than expected  
122 (Soluk 1993; Soluk and Collins 1988), which is a result of synergism between predators.  
123 Alternatively, the total prey mortality caused by multiple predators could be additive, i.e.  
124 equivalent to the expected value (Barrios-O'Neill et al. 2014; Cuthbert et al. 2020;  
125 Wasserman et al. 2016). Thirdly, we can observe antagonistic effects, when the total rate of  
126 predation is lower than expected (Kratina et al. 2009; Sitvarin and Rypstra 2014; Skalski and  
127 Gilliam 2001; Vance-Chalcraft and Soluk 2005; Wasserman et al. 2016). The latter could be a  
128 result of negative interactions between predators (Huxel 2007), such as spatial avoidance, or  
129 interference competition (Alebraheem and Abu-Hassan 2023; Schmidt et al. 2014). Due to  
130 identical food preferences and feeding strategies, the highest interference is expected to  
131 occur between individuals of the same species via mutual interference (DeLong and Vasseur  
132 2011). In turn, the strength of predator interference is often greater for higher predator  
133 densities (Griffen, 2008).

134 Freshwater ecosystems are particularly vulnerable to rising temperatures and subject  
135 to multiple predator interactions owing to their high levels of biodiversity, providing habitats

136 for around 30 % of all vertebrate species (Dudgeon et al. 2006). Elevated temperature could  
137 affect water quality, posing a considerable threat to aquatic biodiversity, e.g. through  
138 decreases in oxygen availability (Capon et al. 2021). Furthermore, the presence of invasive  
139 species is considered a major cause of freshwater biodiversity loss by disrupting trophic  
140 networks (Dudgeon et al. 2006; Reid et al. 2019). With over 500 invasive species, fish are  
141 among the most introduced groups of animals worldwide (Bernery et al. 2022; Xu et al.  
142 2024).

143           Thus, to expand understanding about the role of conspecific invasive predator  
144 density on freshwater prey communities in light of global warming, we performed an  
145 experiment using three predator densities, two temperatures, and an FR approach. We  
146 selected the pumpkinseed (*Lepomis gibbosus*) as a predator. This species is known for its  
147 social behaviours (Power and Todd 1976), including intraspecific aggression (Hanson and  
148 Legget 1985; Poulsen 1977) and we expected a high level of mutual interference among  
149 individuals. It originates from North America and was widely introduced as an ornamental  
150 fish and/or unintentionally with carp fry to Europe and Asia (Copp and Fox 2007; Przybylski  
151 and Zięba 2011). Furthermore, future spread due to global warming is predicted for this  
152 species (Britton et al. 2010). We hypothesise that the difference in foraging efficiency  
153 between single and multiple predators caused by mutual interference will be affected by  
154 temperature. One possibility is that mutual interference could increase in elevated  
155 temperatures, as higher energy expenditures will require an individual predator to consume  
156 more prey items. This will intensify the direct competition between multiple predators and  
157 reduce the predator pressure on the prey population. On the other hand, the mutual



158 interference could decrease at an elevated temperature, as predators may not compete for  
159 food with other individuals, to conserve the energy reserves necessary to meet increased  
160 metabolic demands. This system will thus elucidate whether temperature mediates the  
161 emergence of multiple predator effects in a global invader considering both predator and  
162 prey densities.

## 163 Materials and methods

### 164 Animals

165 We collected fish using boat electrofishing (IG200/2B, PDC, 50–100 Hz, 350–650 V, max. 10  
166 kW; Hans Grassl GmbH, Germany) from the rip-rap zones along Lake Balaton (Hungary,  
167 Central Europe) shoreline in July 2023. Tested fish were around 8 cm in standard length (SL;  
168 mean  $\pm$  SD: 8.2  $\pm$  0.6 cm; range: 7.0 – 9.6 cm). We collected 112 individuals of pumpkinseed  
169 in total. The prey individuals (gammarid *Dikerogammarus villosus*, Sovinsky 1894) were  
170 scraped from rip-rap zones of Lake Balaton. This is a common prey item in natural habitats  
171 occupied by the pumpkinseed in Lake Balaton (Rezsű and Specziár 2006). The gammarid  
172 weights were measured by AX224 scale, Sartorius, Göttingen, Germany and were (mean  $\pm$   
173 SD) 33.7  $\pm$  11.7 mg, and head lengths (*sensu* Nahavandi et al. 2011) through pictures in  
174 ImageJ software (Schneider et al. 2012) and were 1.52  $\pm$  0.02 mm.

175 Fish were transported to the HUN-REN Balaton Limnological Research Institute in 80-l  
176 barrels filled with constantly aerated water from the sampling site, with a maximum density  
177 of 30 fish per barrel. In the laboratory, they were placed in holding tanks (100 x 50 x 50 cm,  
178 length x width x height) filled with aerated and filtered water from their natural habitat,  
179 which was gradually replaced with conditioned (aerated for 24 hours in 600-l tanks) tap

180 water with a maximum density of 25 fish per tank. Gammarids were placed in the holding  
181 tanks of the same dimensions with a density of ca. 500 individuals per tank. Each tank was  
182 equipped with an aeration stone, an external filter, and rocks on the bottom to imitate  
183 natural habitats for animals. The holding tanks were randomly divided into two groups  
184 according to the temperature used later on in the experiment. The holding tanks were  
185 illuminated using an ambient light, with a 13:11 L:D cycle. The fish were acclimated for two  
186 weeks before transfer to the experimental tanks. The test fish were fed daily *ad libitum* with  
187 frozen Chironomidae larvae. Gammarids were acclimated for 4 days before use and they  
188 were also fed daily with frozen Chironomidae larvae and decomposing leaves.

189 Water parameters in holding tanks, measured between each consecutive  
190 experimental trial with a multiparameter probe HI98194/10 (HANNA Instruments,  
191 Smithfield, USA), were as follows (mean  $\pm$  SD): (1) ambient temperature  $25.3 \pm 1.1^\circ\text{C}$   
192 (ambient), oxygen levels  $7.3 \pm 0.9$  mg/l and  $89.3 \pm 10.3$  %, conductivity  $816.8 \pm 130.5$   $\mu\text{S/cm}$ ,  
193 pH  $8.2 \pm 0.1$ ; (2) elevated temperature  $27.3 \pm 1.1^\circ\text{C}$ , oxygen levels  $7.0 \pm 0.5$  mg/l and  $86.3 \pm$   
194  $6.6$  %, conductivity  $965.8 \pm 46.0$   $\mu\text{S/cm}$ , pH  $8.2 \pm 0.1$ .

#### 195 Ethical statement

196 The present study adheres to the ASAB/ABS (2023) guidelines for the use of animals in  
197 research. All procedures involving the handling and treatment of the animals followed  
198 Hungarian law and the permit for the delivery and use of aquatic animals for scientific  
199 purposes in the HUN-REN Balaton Limnological Research Institute (permit reg. no.: VE-I-  
200 001/01890-3/2013, valid between 22 August 2013 and 21 August 2023, issued by the Food-  
201 Security and Animal Health Directorate, Governmental Office of Veszprém County, Hungary).

## 202 Experimental design

203 To test for the effects of temperature and predator density on fish foraging efficiency, we  
204 used live *D. villosus* as a prey at multiple densities. We tested *L. gibbosus* in single, two, and  
205 four individual treatments in two water temperatures: ambient (25°C) and elevated (28°C).  
206 The ambient temperature represents the mean summer water temperature of Lake Balaton  
207 in the last 10 years (HUN-REN Balaton Limnological Research Institute researchers' data),  
208 while the elevated temperature reflected an increase in the global water temperature by 1-  
209 4°C up to the end of the 21<sup>st</sup> century, as predicted by global change scenarios (IPCC, 2023).  
210 We provided six prey densities (for a single predator: 5, 10, 15, 20, 30 and 60 gammarids; for  
211 2 predators: 10, 20, 30, 40, 60, 120 gammarids; for 4 predators: 10, 20, 40, 60, 80, 120  
212 gammarids) for fish in each of the 6 treatments (3 predator densities x 2 temperatures).  
213 Higher densities of prey were needed for the multiple predator groups to reach feeding  
214 saturation, but did not affect the later analyses because FR models and multiple predator  
215 predictions were fit separately per treatment.

## 216 Experimental setup

217 We placed test fish inside 40-l white, opaque tanks (51 x 38 x 30 cm, length x width x height,  
218 hereafter: experimental tank). Each experimental tank bottom was covered with a 1 cm  
219 layer of sand and had constant aeration and water filtering (Supplementary Figure 1a).  
220 Experimental tanks were filled with conditioned (aged for 24 hours and aerated) water from  
221 the fish's natural environment to the level of 20 cm. The water temperature in the ambient  
222 temperature treatment (25°C) was maintained using air conditioning. For the elevated  
223 temperature treatment (28°C), we placed the opaque experimental tanks in larger 60-l ones

224 (58 x 39 x 35 cm, length x width x height, hereafter: baths) with a heater placed at the  
225 bottom. Baths were filled with water to the level of 20 cm (Supplementary Figure 1b). Each  
226 fish or set of fish (for groups of predators) were assigned to the particular experimental tank  
227 and stayed in it until the end of the experiment. Thus, each fish or set of fish were tested six  
228 times, with six prey densities offered in random order in 48h intervals. The 48 experimental  
229 tanks were set up at the same time (eight replicates per treatment), with tanks assigned to  
230 different water temperatures and predator densities were randomly distributed in the  
231 laboratory.

#### 232 Experimental procedure

233 One week before the start of the experiment, fish were measured (with a ruler to the  
234 nearest 1 mm), weighed (to the nearest 0.1 g using CB 1001 scale, ADAM, UK), and placed  
235 inside experimental tanks to acclimatize. The fish in the groups of two and four were  
236 matched based on their SL to make sure that all tested fish inside one experimental tank  
237 were of similar sizes (i.e. the difference between the biggest and the smallest one was less  
238 than 2 cm in SL) and thus able to effectively compete with each other. Fish were fed daily  
239 with 15 gammarids per individual and starved for 48 h before the first trial.

240 On the test days, gammarids were collected from holding tanks and a specific  
241 number of individuals were placed into 0.5-l containers filled with conditioned tap water of a  
242 given temperature (according to the experimental treatment). After containers with  
243 gammarids were prepared, the aeration in experimental tanks was turned off, but the  
244 sponge filters were left inside to provide gammarids with shelter. Each trial started between  
245 9 and 10 AM. The gammarids were added to the experimental tank by flushing them into the

246 water and spreading them evenly over the tank, and each test fish had one hour to forage.  
247 After that, gammarids that remained alive were removed and counted. After counting, fish  
248 were fed *ad libitum* with gammarids for one hour, and then starved for ~46 h before the  
249 next trial.

250 We performed two trials without predators for the three highest prey densities in  
251 each treatment to control for natural prey mortality. The reported prey mortality was < 0.1  
252 %, thus we did not consider it in the statistical analyses.

### 253 Statistical analysis

254 We used independent two-sample T-tests (with Levene's and Shapiro-Wilk's tests to check  
255 assumptions of homogeneity of variances and normal distribution of data, respectively) to  
256 compare general fish size and differences in the size of fish placed in the same experimental  
257 tank between temperature treatments.

258 Observed functional responses were identified using logistic regression of the  
259 proportion of prey eaten as a function of prey density for each pumpkinseed density and  
260 temperature using the "frair" package (Pritchard et al. 2017) in R. We applied the Type II  
261 Rogers' random predator equation (Rogers 1972) to account for prey depletion during the  
262 experiments:

$$263 \quad N_e = N_0(1 - \exp(a(N_e h - T)))$$

264 (1)

265 where  $N_e$  is the number of prey eaten,  $N_0$  the initial prey density,  $a$  the predator attack rate,  
266  $h$  the predator handling time, and  $T$  the duration of the experiment. The difference ( $\Delta$ )

267 method was used to compare functional response attack rates and handling times between  
268 temperatures (Juliano 2001; Pritchard et al. 2017).

269 The attack rate ( $a$ ) and handling time ( $h$ ) estimates from the single predator (i.e. in  
270 the absence of conspecifics) functional responses (equation 1) were used to predict the  
271 multiple predator feeding rates assuming no non-trophic interactions. These predictions  
272 were calculated following McCoy et al. (2012) and Sentis & Boukal (2018):

$$\frac{dN}{dt} = -\sum_{i=1}^n f_i(N)P_i$$

274 (2)

275 where  $N$  is the prey population density,  $P$  is the predator population density of predators  $i$ ,  
276 and  $f_i(N)$  is the functional response of predator  $i$  (i.e., equation 1). Initial values of  $N$  and  $P$   
277 were set at the experimental initial prey and predator densities corresponding to the  
278 experimental treatment. For each predator treatment and prey density, equation 2 was  
279 integrated over the full experimental time to get the expected number of surviving prey.  
280 These predicted FR curves were then compared with observed ones (calculated from  
281 equation 1) within each predator density and temperature treatment.

282 To estimate variances around predictions for each FR curve, a global sensitivity  
283 analysis was employed (Soetaert and Petzoldt 2010). It uses the 95 % confidence intervals of  
284 each FR parameter estimate and their variance-covariance matrix (covariance is assumed to  
285 be zero when unknown) to generate 100 random parameter sets using a Latin hypercube  
286 sampling algorithm. For each parameter set ( $n = 100$ ), equation 2 was then integrated over  
287 time, and expected prey survival was calculated using the 'sensRange' function in the R

288 package 'FME' (Soetaert and Petzoldt 2010). Confidence intervals between predicted and  
289 observed functional responses were compared to report differences (i.e. mutual  
290 interference effects) across prey densities.

291 We then quantified interaction strength (IS) as the proportion of prey killed at each  
292 predator density, temperature, and prey density by dividing the number of observed prey  
293 consumed by the initial prey density (Veselý et al. 2019):

$$294 \quad IS(P, Z) = \frac{N_P - N_{P,Z}}{N_P}$$

295 (3)

296 where  $N_P$  and  $N_{P,Z}$  are the numbers of live prey at the beginning and end of the experiment,  
297 respectively. The proportion of prey killed (IS) includes both trophic ( $IS_T$ ) (i.e., feeding on  
298 prey) as well as non-trophic ( $IS_{NT}$ ) interactions. To disentangle these,  $IS_{NT}$  was quantified as  
299 the difference between the observed IS and the IS predicted from the population dynamic  
300 approach (equation 2) model (Sentis et al. 2017). We then used linear mixed models (Brooks  
301 et al. 2017) to analyse  $IS_{NT}$  as a function of predator density, temperature, and prey density,  
302 as well as all of their interactions, with tank identity as a random effect. Backward step  
303 deletion of non-significant terms was used to obtain the most parsimonious model.

## 304 **Results**

305 The mean fish size did not differ between temperatures ( $t_{110} = 0.414$ ,  $p = 0.679$ ) and was 82.5  
306 mm (70-96 mm, range) for the ambient and 82.0 mm (71-95 mm) for the warming  
307 treatments. The mean differences between the smallest and the biggest fish in the same

308 experimental tank were 5.4 mm (0-19 mm) for ambient and 8.1 mm (2-15 mm) for warming  
309 treatments, and did not differ ( $t_{30} = -1.670$ ,  $p = 0.105$ ) between temperatures.

310 Type II functional responses were exhibited by pumpkinseeds under both  
311 temperatures, as indicated by significantly negative linear coefficients (Juliano 2001) (Table  
312 1). Attack rates and handling times for the single predator both tended to increase with  
313 warming, with handling times significantly different between temperatures ( $z = 4.222$ ,  $p <$   
314  $0.001$ ), but attack rate differences were marginally not statistically clear ( $z = 1.814$ ,  $p =$   
315  $0.070$ ).

316 Confidence intervals were divergent at higher prey densities in single predators,  
317 suggesting significant differences in maximum feeding rates, whereby warming reduced  
318 feeding magnitudes (Figure 1a). For multiple predator functional responses, however,  
319 confidence intervals mostly overlapped, except for at maximal prey densities for two fish  
320 (Figure 1b, c).

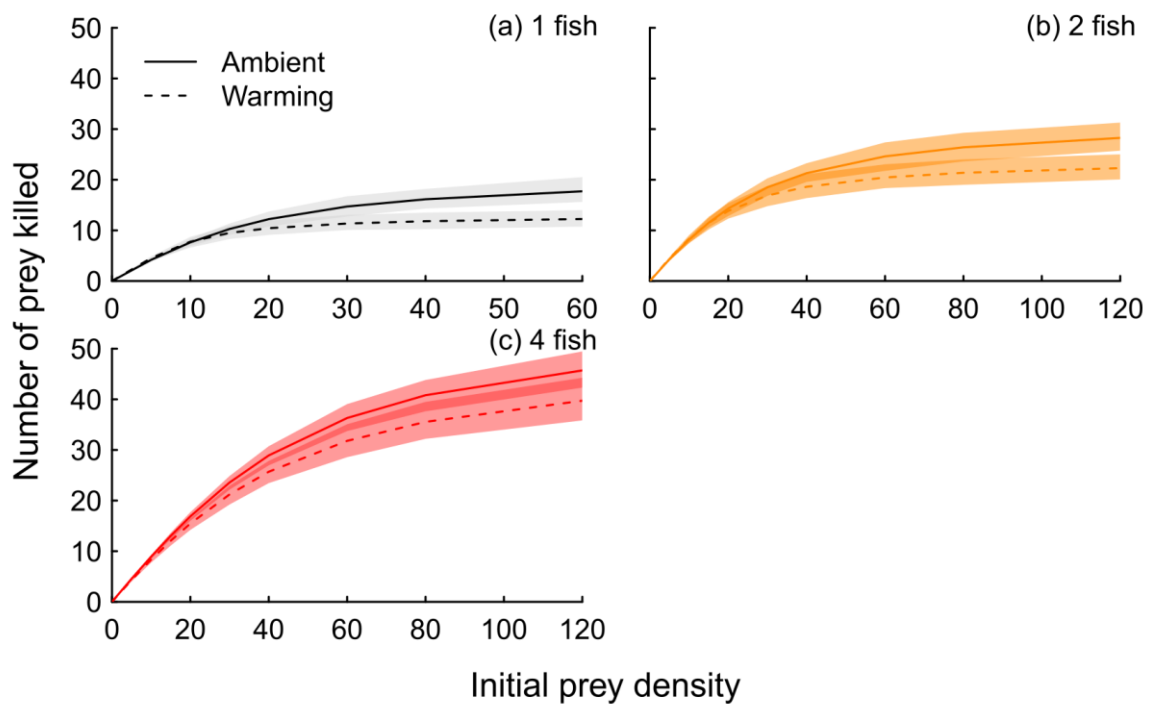
321 **Table 1.** Functional response linear coefficient estimates (types), attack rates, handling  
322 times, and maximum feeding rates among temperature treatment groups for single  
323 pumpkinseeds. Estimates were determined using logistic regression and parameters were  
324 returned from Rogers' random predator equation. P-values correspond to the difference of  
325 the estimate from zero.

Temperature (25, 28 °C)	Estimate, p (type)	Attack rate, p	Handling time, p
----------------------------	-----------------------	----------------	---------------------



Ambient	-0.040, < 0.001 (II)	2.306, < 0.001	0.048, < 0.001
Warming	-0.045, < 0.001 (II)	3.883, < 0.001	0.077, < 0.001

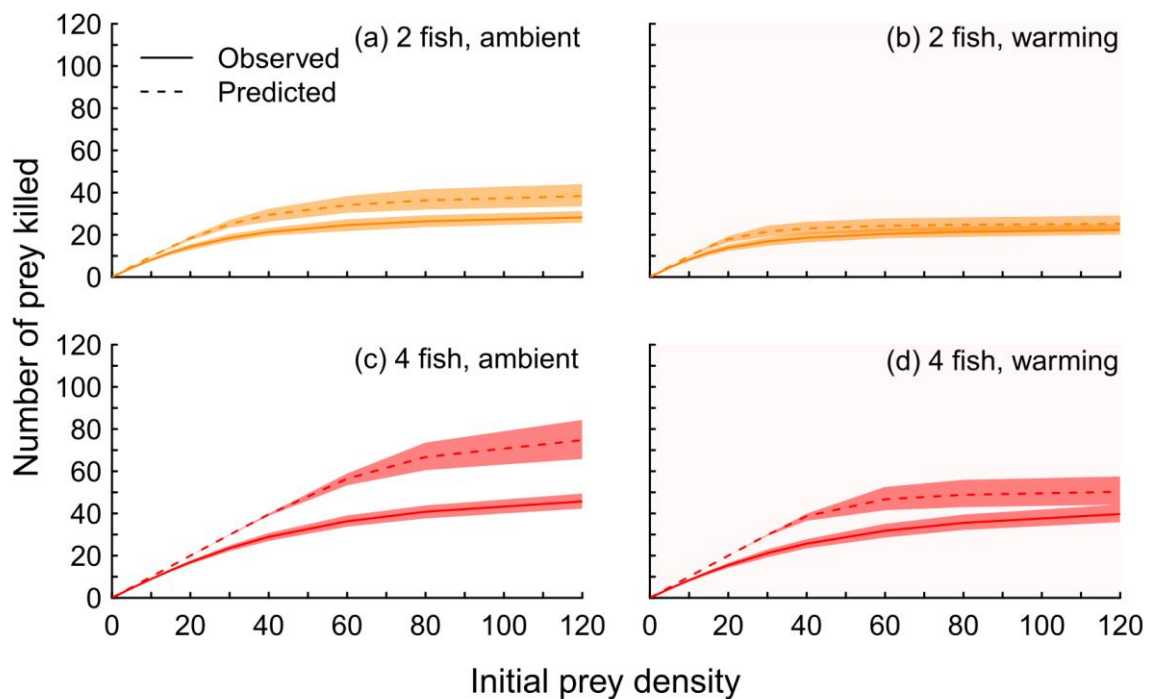
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327

328 **Figure 1.** Functional responses of (a) single, (b) double, and (c) quadruple pumpkinseeds  
 329 under different temperature scenarios (ambient 25 °C, warming 28 °C). Lines represent fits  
 330 from Rogers' random predator equation and shaded areas are 95% confidence intervals.  
 331 Note that maximal prey densities differed for the single versus multiple pumpkinseed  
 332 groups.

333 Antagonistic multiple predator effects were generally shown across all fish densities  
334 and temperatures because observed feeding rates were below the additive predictions,  
335 however, the magnitude of the difference varied. Significant divergence in functional  
336 responses was shown for both two and four fish treatments under ambient conditions, but  
337 the extent of antagonistic interactions was amplified at higher predator densities (Figure 2).  
338 Contrastingly, warming tended to dampen the influence of multiple predator effects as  
339 observed and predicted curves became closer, especially in the two fish treatment.



340

341 **Figure 2.** Functional responses of two and four pumpkinseeds under different temperature  
342 scenarios (ambient 25 °C, warming 28 °C). Observed results were actually recorded from  
343 feeding trials, whereas predicted functional responses were based on a population dynamic  
344 model from single predator functional responses per temperature, assuming an absence of

345 non-trophic interactions. Lines represent fits from Rogers' random predator equation and  
 346 shaded areas are 95% confidence intervals.

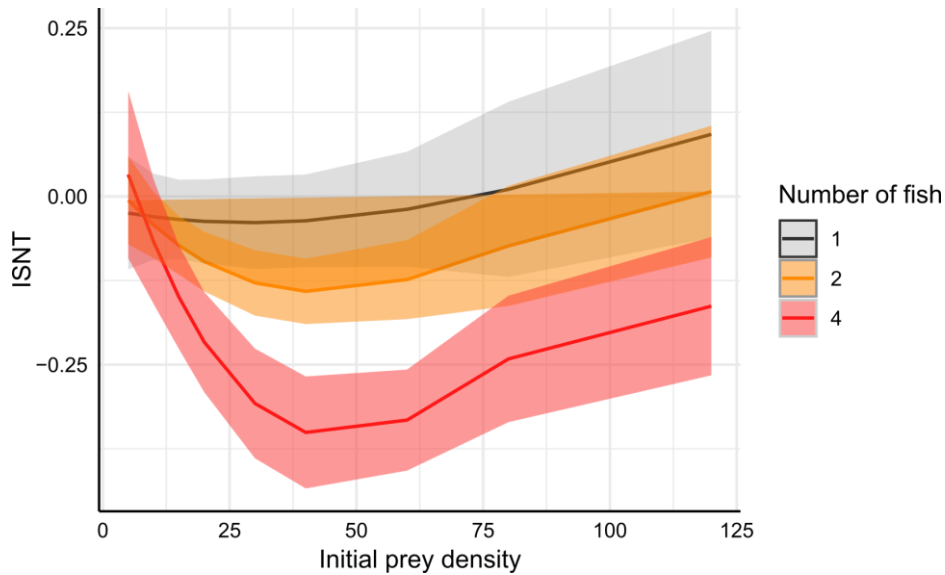
347 Non-trophic interaction strength was not significantly affected by temperature (Table  
 348 2). Including a cubic or quadratic term with the prey density effect significantly improved the  
 349 fit compared to the linear term ( $dAICc \geq 16.9$ ), while cubic and quadratic terms were  
 350 competitive ( $dAICc = 0.3$ ). A significant interaction between predator density and prey  
 351 density (cubic) significantly influenced  $IS_{NT}$  (Table 2). Generally, the intensity of antagonistic  
 352 interactions increased with greater predator numbers (Figure 3). Negative  $IS_{NT}$  peaked at  
 353 intermediate prey densities, and the interaction reflected that this effect was especially  
 354 pronounced at highest predator densities.

355 **Table 2.** Linear mixed model with Type III analysis of deviance considering non-trophic  
 356 interaction strength as a function of predator density, temperature, and prey density (cubic  
 357 term), as well as their interactions. Tank identity was included as a random effect to control  
 358 for repeated measures of fish. Significant terms are reported from the reduced model and  
 359 are in bold.

Term	Chisq (df)	p-value
<b>Predator density</b>	<b>17.666 (1)</b>	<b>&lt; 0.001</b>
Temperature	0.077 (1)	0.781
Prey density	4.784 (3)	0.188
Predator density:Temperature	0.002 (1)	0.989
<b>Predator density:Prey density</b>	<b>16.765 (3)</b>	<b>&lt; 0.001</b>

Temperature:Prey density	1.294 (3)	0.730
Predator density:Temperature:Prey density	2.436 (3)	0.487

360



361

362 **Figure 3.** Linear mixed model considering non-trophic interaction strength ( $IS_{NT}$ ) as a  
 363 function of initial prey density (cubic term) and predator density, with shaded areas  
 364 representing 95% confidence intervals. Negative  $IS_{NT}$  indicates antagonism, whereas positive  
 365 values indicate synergies among predators.

366

### 367 Discussion

368 The results supported our hypothesis that elevated temperature affects the mutual  
 369 interference between foraging predators, with the effects of temperature being eroded by  
 370 greater predator densities. This study presents novel insights into the interplay between  
 371 temperature, density-dependence and non-trophic interactions to shape the foraging  
 372 efficiency of an aquatic predator.

373           The foraging efficiency of a single predator was lower at elevated compared to the  
374 ambient temperature, unlike past studies (e.g. Bergman 1987; Hoekman 2010; Oyugi et al.  
375 2012; South et al. 2017). Invasive species are often favoured by elevated temperatures and  
376 increase their foraging efficiency (see reviews by Dick et al. 2017 and Faria et al. 2023) up to  
377 the point where the temperature exceeds their optimum (Volkoff and Rønnestad 2020). The  
378 pumpkinseed is a warm-water fish, thriving in temperatures between 24 and 32 °C (Holtan  
379 1998), and summer water temperatures exceeding 20 °C are common in the study region  
380 (Padisak 1992; Livingstone and Padisak 2007). Therefore, we assume that different  
381 mechanisms, rather than exceeded thermal optimum, played a role here, including predator  
382 behaviour, prey antipredatory response, or the interaction of both. It is known that the  
383 elevated temperature affects the metabolic rate of ectotherms (Dillon et al. 2010), usually  
384 decreasing their aerobic scope, which is a proxy for an animal's physical capacity, i.e. the  
385 ability to increase its aerobic metabolic rate above the maintenance level (Halsey et al.  
386 2018). Thus, ectotherms need to provide more energy (e.g. by increasing the food intake) or  
387 save the existing energy reserves (e.g. by decreasing activity) when the temperature  
388 increases. In the current study, a single predator decreased its maximum feeding rate at  
389 elevated compared to ambient temperature, which could be the result of a decrease in its  
390 general activity. However, the attack rates did not differ between temperatures, which may  
391 indicate similar activity levels of the single predator in both temperatures used. Instead, we  
392 may assume that we observed an example of “aerobic scope protection” (Sandblom et al.  
393 2014; Jutfelt et al. 2021). In that context, the digestive processes in ectotherms cause an  
394 increase in animals’ metabolic rate, which leaves less residual aerobic scope for other  
395 functions, e.g. activity, growth, or reproduction. To save this energy, ectotherms limit the

396 amount of food intake in elevated temperatures to reduce the amount of energy used for  
397 the digestion processes, and this may be especially pertinent in the short-term and at high  
398 prey densities, per the nature of our experiments.

399         It is also critical to consider potential changes in prey antipredatory behaviour with  
400 temperature. Specifically, *D. villosus* is known for its low activity level and shelter association  
401 (Maazouzi et al. 2011; Platvoet et al. 2009; Kobak et al. 2016). When outside the shelter, it  
402 forms aggregations in response to predator danger (Jermacz et al. 2017). Although in our  
403 study shelter for gammarids was provided, we observed a portion of prey individuals outside  
404 the shelter at the end of experiments. Additionally, the study by Jermacz et al. (2020)  
405 showed that *D. villosus* reduced its activity when the water temperature increased up to  
406 24°C compared to 17°C. Combining these results, it is possible that in the current study, the  
407 gammarids decreased their activity and increased their aggregation with conspecifics in the  
408 elevated temperature. Forming aggregations is a well-known antipredatory behaviour  
409 resulting in a greater prey handling time (Elner et al. 1978; Krebs et al. 1977). Taken  
410 together, we cannot exclude that because of the lower AS in the elevated temperature, and  
411 the greater energy expenditures needed to effectively forage on aggregated prey, the *D.*  
412 *villosus* in such a scenario became unprofitable prey for the predator.

413         While temperature warming dampened the maximum feeding rate on a *per capita*  
414 level, conspecifics further mediated prey risk over and above the effect of temperature. The  
415 foraging efficiency of predators in groups was associated with consistent antagonistic  
416 interactions, such as mutual interference. This potential mutual interference was greater for  
417 higher predator densities, as more individuals were competing for the same limited food  
418 source. The pumpkinseed is known for its aggressiveness towards conspecifics (Poulsen

419 1977; Hanson and Legget 1985), and the elevated temperature has been seen to cause an  
420 increase in the level of aggression in ectotherms (Kua et al. 2020; Bissell and Cecala 2019;  
421 Almeida et al. 2014). However, we observed a general decrease in mutual interference level  
422 in elevated compared to ambient temperature for both (i.e. two and four) multiple predator  
423 densities. The energy saving strategy by the pumpkinseed may be its adaptive response to  
424 elevated temperature. Specifically, when foraging in groups, the pumpkinseed individuals  
425 limited the amount of food intake and reduced their interactions with conspecifics. For the  
426 group of two pumpkinseeds, this resulted in a lack of mutual interference at the elevated  
427 temperature and lower general foraging efficiency compared to the ambient water  
428 temperature. For the group of four predators, antagonistic interactions could be present  
429 because, for this particular predator density, individuals were not able to completely avoid  
430 each other in the provided tank volume. Moreover, the foraging efficiency of the group of  
431 four predator individuals did not differ significantly between temperatures. In the ambient  
432 water temperature, the maximum food intake was probably limited by antagonistic  
433 interactions between actively foraging and aggressive conspecifics. In the elevated  
434 temperature, in turn, the level of aggression could decrease, but the limited *per capita*  
435 consumption rate could have resulted in a similar total amount of food consumed by the  
436 whole group of predators and less competition. Thus, we can say that, at least for some  
437 predator densities, the total predator pressure on prey population may not change with  
438 global warming. Further behavioural assays would be needed to elucidate these potentially  
439 countervailing behavioural mechanisms. Nevertheless, this finding provides new insights into  
440 the density-dependence of consumer responses under environmental change.

441           The strength of the antagonistic non-trophic interactions between foraging predators  
442 was greater at higher predator densities. In turn, the effect of multiple conspecifics and prey  
443 density was over and above effects of warming. The general effect of increasing predator  
444 density is in line with the study by Griffen (2008), which showed that the interference  
445 between conspecifics is stronger for higher predator densities. Furthermore, the relationship  
446 between prey density offered and non-trophic interaction strength was not linear. A peak  
447 was observed in the intermediate prey densities, where antagonisms are highest (Sentis et  
448 al. 2017; Cuthbert et al. 2021). According to optimal foraging theory (Werner and Hall 1974;  
449 Pyke and Starr 2021), an individual is expected to select a food item that is abundant, easy to  
450 capture, and provides the greatest net energy gain. Thus, if the prey density is low, there are  
451 not enough prey individuals that could compensate for the predator energy losses for  
452 potential competition with other individuals. It is thereby more profitable for an individual to  
453 avoid intensive competition with others and to save energy to search for more profitable  
454 food patches. Alternatively, at low prey densities, a lack of prey replacement experimentally  
455 could drive high rates of prey depletion, which reduce capacities to detect multiple predator  
456 effects. On the other hand, at high prey densities, the amount of food is sufficiently high and  
457 each predator individual can meet its energy demands without the need for direct  
458 interaction with other foraging predators. Between these two extremes, there is an  
459 intermediate prey density where the competition between predator individuals is highest, as  
460 the potential energy loss for aggressive interactions with others can be compensated by the  
461 amount of food available, and where potential experimental artefacts associated with non-  
462 replacement of prey do not dampen effects.



463 To summarise, the results demonstrate that the effects of elevated water  
464 temperature on predators' foraging efficiency are strongly mediated by consumer's group  
465 size. Specifically, increasing temperature limits the food intake by individual predators,  
466 which results in reduced trophic effects of single predators on prey populations. Yet, this  
467 effect became less clear at higher predator densities. We postulate that a decrease in the  
468 level of intraspecific interactions leaves more time for foraging, but reduced food intake with  
469 thermal stress limits the total amount of food consumed. In the long-term, this could affect  
470 growth, activity, and reproduction, which could influence the overall fitness of predators.  
471 Future research should provide more environmentally relevant conditions to study the  
472 foraging efficiency of social predators, i.e. include conspecifics as food competitors. As  
473 proven by the current study, this may affect the outcome and the interpretation of the  
474 results compared to those with only single predator individuals, because such experiments  
475 may overestimate the effect of increasing temperature. Thus, we strongly encourage  
476 including predator density as an additional factor for studies considering the foraging  
477 efficiency of social predators in different biotic and abiotic contexts in the future.

478

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