

1 **Does temperature, light or inter-individual variation explain**
2 **feeding motivation in a tropical freshwater predator?**

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16

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18 **Abstract**

19 Variability in environmental conditions in freshwater ecosystems are increasingly driven by human
20 activity. Increased temperature and light intensity are among the anthropogenic stressors
21 dramatically altering these ecosystems, for example through deforestation that reduces canopy
22 cover of riparian vegetation. Simultaneous exposure to multiple stressors complicates predictions
23 of responses to environmental stressors due to potential interactions, yet the interaction between
24 temperature and light intensity on feeding motivation remains poorly understood. Here, a fully
25 factorial design was employed to investigate the combined effect of increased temperature and
26 light intensity on the feeding motivation of a freshwater predator, the pike cichlid *Saxatilia proteus*.
27 Strikes toward food items were used to quantify the subjects' motivation to feed. We found no
28 effect of temperature or light intensity on feeding motivation, either individually or as an interaction.
29 Our repeated measures design allowed us to test whether the predatory fish showed personality
30 variation, i.e. consistent inter-individual differences, in their motivation to feed. While the time taken
31 to make the first strike was not consistently different between individuals, the number of strikes in 1
32 minute, 3 minutes and the time taken for the 10th strike (which were strongly correlated to one
33 another), was consistently different between individuals. This variation could not be explained by
34 variation in body length, which had no effect as a main effect. Variation between individuals is likely
35 to be magnified in wild predators that are likely to vary more in experience and genetic background
36 than the captive subjects in our study. Thus, we suggest that anthropogenic effects that alter the
37 composition of individuals in a population of predators, for example selective harvesting, will have
38 a greater ecological effect than direct short-term effects of variability in environmental factors.

39

40 **Key words:** individual differences, personality variation, environmental change, multiple stressors,
41 pike cichlid, *Crenicichla*.

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43

44 **Introduction**

45 Temperature and light are fundamental components of ecosystems and play a key role in driving
46 species interactions by influencing foraging, and thus shaping ecological communities (Jägerbrand
47 & Spoelstra, 2023; Kordas et al., 2011). However, as human activities continue to modify
48 ecosystems and impose novel abiotic and biotic conditions, changes to inter-specific interactions
49 may have complex impacts for community function and diversity (Guiden et al., 2019). Particularly
50 in ectotherms, temperature increases energetic demand, which in turn impacts behaviour and
51 physiology (Abram et al., 2017). Behavioural adjustments serve as the initial response to
52 temperature fluctuations (Bailey et al., 2022), primarily manifested in changes to locomotor and
53 feeding behaviours due to changes in the motivation to feed, allowing increased energy
54 requirements to be met (Domenici et al., 2019; Volkoff & Peter, 2006). While the resilience of
55 organisms to environmental stressors is heavily species- and context-dependent, tropical fish are
56 likely to be disproportionately affected by warming because they possess narrow thermal windows
57 and already live close to their thermal tolerance limit (Lapointe et al., 2018; Payne et al., 2016).
58 There is already evidence that increased energy consumption, due to elevated temperatures, is
59 intensifying top-down competition and declining prey populations in the warming Indo-West Pacific
60 Ocean (Johansen et al., 2015). This phenomenon can distort entire food webs and may already be
61 affecting vulnerable freshwater ecosystems.

62 For animals that rely on visual cues, light is crucial for activities including reproduction,
63 predator avoidance and foraging (Marchesan et al., 2005). In a predator-prey context, increased
64 light intensity can aid predators locate prey (Fleming & Bateman, 2018; Richmond et al., 2004);
65 conversely, it can make predators more conspicuous, inducing increased vigilance or fleeing
66 behaviour in prey (Michels et al., 2024). Light in aquatic systems is predominantly influenced by
67 surface illumination, depth and suspended particulates, which can change light intensity, colour
68 composition and polarisation (Jägerbrand & Spoelstra, 2023). Since the development of human
69 civilisation, deforestation has reduced the planet's forests to less than 70% of their original extent
70 (Bologna & Aquino, 2020). This is significant for freshwaters because the shading provided by
71 riparian vegetation regulates both temperature and light conditions in freshwater habitats (Mosisch
72 et al., 1999). In these ecosystems, which possess discrete physical boundaries, inhabitants may
73 not be capable of large-scale movements in response to stressors from human-induced changes in
74 environmental conditions (Morgan et al., 2001).

75 Many studies have researched the isolated effects of either temperature (Alfonso et al.,
76 2021; Barbarossa et al., 2021) or light (Keep et al., 2021) in freshwater systems, controlling for
77 other environmental stressors. To enhance the ecological relevance of research on responses to
78 environmental stressors, there is an increasing focus on the effects of simultaneous exposure to
79 multiple environmental stressors, which are ubiquitous in natural systems (Côté et al., 2016; Orr et
80 al., 2020). Therefore, to form accurate predictions of their impacts it is essential to confirm how
81 they interact as evidence suggests that they can combine in various complex ways (McFarland et

82 al., 2012), which confounds projections of their net ecological impact (Thompson et al., 2018).
83 Effects can be additive when the observed response is the sum of the responses from each
84 stressor (Zanghi et al., 2024). Comparative responses are those dominated by the effect of only
85 one stressor (Folt et al., 1999), whereas a ceiling effect may occur where the effect of an additional
86 stressor is not evident (Ginnaw et al., 2020). An interaction between two stressors can be either
87 synergistic (more than the sum of each response (Zanghi et al., 2023)) or antagonistic (less than
88 the sum of each response (Ferrari et al., 2015)). Given this variability in outcomes, conducting
89 empirical studies to assess the responses to stressors that co-occur is vital.

90 In addition to variation induced by changing environmental conditions, the past few
91 decades have seen widespread interest in consistent variation in behaviour between individuals
92 within populations, also known as animal personality variation, that cannot be explained by other
93 traits such as age, sex and size (Dall et al., 2004; Sih et al., 2015). This research includes growing
94 evidence that this consistent inter-individual variation can have ecological impacts (Brehm et al.,
95 2019; Mittelbach et al., 2014); this is particularly the case regarding variation between individual
96 predators in their motivation to feed, and hence the risk they pose to their prey. Consistent
97 variation between individual predators has been documented particularly in predators in aquatic
98 systems, demonstrating personality variation in direct measures of feeding, including the pike
99 cichlid *Saxatilia frenata* studied *in situ* (Szopa-Comley, Duffield, et al., 2020), and northern pike
100 *Esox lucius* (Nygqvist et al., 2012) and three-spined sticklebacks *Gasterosteus aculeatus* studied in
101 the laboratory (Szopa-Comley, Donald, et al., 2020), although there were no consistent differences
102 between individual blue acara *Andinoacara pulcher* tested under laboratory conditions (Szopa-
103 Comley & Ioannou, 2022). Additionally, other studies have shown predators can vary in other
104 behaviours that are likely to alter the risk they pose to prey, and hence the ecological impact of the
105 predators, including activity (Nakayama et al., 2016), risk-taking tendency, i.e. boldness (Zhao &
106 Feng, 2015), prey search behaviour (Patrick et al., 2014), space use (Villegas-Ríos et al., 2018)
107 and foraging site fidelity (Harris et al., 2020).

108 The feeding behaviour of diurnal, predatory freshwater fishes is likely to be more severely
109 impacted by warming and changes in the light environment than species capable of range shifts or
110 those that are nocturnal which rely less heavily on visual cues (Freitas et al., 2021). Here, we test
111 how the combination of increased water temperature and light intensity affects the feeding
112 motivation of a freshwater fish, *Saxatilia proteus*, a species of pike cichlid (*Crenicichla*). Pike
113 cichlids are piscivorous fish native to South American streams, rivers and lakes, relying mainly on
114 visual cues to ambush prey (Szopa-Comley, Duffield, et al., 2020). In their natural habitat, pike
115 cichlids will often experience elevated temperature and light intensity when changes in land use
116 reduces canopy cover from removing riparian vegetation. Across river sites in the Northern Range
117 mountains of Trinidad where *S. frenata* (which is closely related to *S. proteus* (Varella et al., 2023))
118 are abundant, Zanghi et al. (2024) demonstrated a positive correlation between temperature and
119 light intensity, and declining light intensity with increasing canopy cover, although temperature and

120 canopy cover were not significantly correlated (instead, temperature was negatively associated
121 with flow rate). In our study, strikes on food items were used to measure feeding motivation and
122 assess the subjects' response to altered environmental conditions. Fish were exposed to control or
123 elevated water temperature crossed with control or elevated light intensity in a fully factorial design
124 to determine the individual and combined effects of these stressors. By using a repeated-measures
125 design, i.e. with repeated tests per subject over a four-week period, we were also able to assess
126 consistent inter-individual variation in the feeding response of these fish.

127 The study of Zanghi et al. (2024) also tested for the effects of naturally occurring
128 environmental variation on the presence and predatory behaviour of piscivore fish in their study
129 system. The presence of *S. frenata* was associated with warmer temperatures, and across the
130 predators included in the study, predation pressure such as the number of attacks on the guppy
131 prey presented as a stimulus also increased with temperature. We predicted that as the effects of
132 temperature and light on visual predators are driven by different pathways, i.e. physiological for
133 temperature and visual for light, that their effects would be additive rather than synergistic. Also
134 based on field observations that presented live fish prey to wild pike cichlids (Szopa-Comley,
135 Duffield, et al., 2020), we expected consistent inter-individual differences between the *S. proteus* in
136 our study.

137

138

139 **Methods**

140 Experimental subjects and housing

141 Mixed-sex *S. proteus* (mean standard body length \pm SD = 9.0 cm \pm 1.0 at the time of testing) were
142 reared at the University of Bristol, having been acquired from a commercial aquarium supplier. The
143 30 subadult (2-year-old) fish were housed individually in 45L tanks (L \times W \times H = 70 \times 20 \times 35 cm)
144 enriched with sand and small stone substrate, plastic tube refuges and artificial foliage. Before the
145 experiment, the water temperature was maintained at 25.8°C \pm 0.3 SD, and the light regime
146 followed a 12-hour light-dark cycle. For three weeks before testing started, subjects were
147 exclusively fed 2ml of defrosted BCUK Aquatics Krill Pacifica once a day, which was used
148 throughout the experimental trials because of its consistent sinking behaviour when introduced to
149 the tanks. Opaque white plastic dividers were placed between and behind each tank to eliminate
150 visual cues between subjects, and hence any influence between individuals during the trials.

151 During the trials, each tank had independent filtration provided by a Real Aquatics SF-101 internal
152 sponge filter. The refuges, foliage and sponge filters were placed in the same configuration in each
153 tank at the rear to ensure they would not obscure feeding during the filming of trials. Weekly water
154 testing for nitrite, nitrate, and ammonia was conducted, in addition to 20% water changes on
155 Mondays. Levels of nitrite and ammonia $>$ 0 ppm, or nitrate $>$ 20ppm, prompted water changes.

156

157 Experimental treatments and protocol

158 Trials were conducted in the subjects' housing tanks to minimise handling and stress, and hence
159 facilitate and standardise feeding. Light intensity was manipulated using LEE 211 0.9ND 3-Stop
160 Neutral Density Lighting Gel Filters to reduce lux levels within the tanks by approximately 70%
161 (Table 1). The lighting filter sheets were cut to size (70 x 20 cm), with two slits at the rear to
162 accommodate the air and water inflow tubes, enabling the lighting filters to sit flat on top of the
163 tanks. The elevated light treatment comprised of the LED aquarium lighting without the filter (Table
164 1).

165 AllPondSolutions and HDOM 25W aquarium heaters were positioned uniformly towards the
166 rear of every tank; water temperature was manipulated by switching each of these heaters on (for
167 the elevated temperature) or off (to maintain the initial housing temperature; Table 1). Each heater
168 had a thermostat that was set to 29°C at the start of the experiment to ensure that minimal
169 interference with the tanks would be necessary once the experiment started. 25W heaters were
170 used in preference of greater capacity heaters so that the water temperature increased gradually to
171 allow the fish to acclimate and not induce stress (Figure A1). The maximum temperature was
172 limited to 30°C as this was similar to the highest recorded water temperature in the study of Zanghi
173 et al. (2024). The average water temperature increase of 3.3°C in our study reflects projections for
174 river warming over roughly the next 70 years (Liu et al., 2020).

175

176 Table 1: Mean (\pm SD) temperature and light intensity in tanks during experimental trials measured
177 by HOBO MX2202 loggers. Δ denotes the difference between control and elevated parameters.
178 The values for the control and elevated temperatures is similar to the minimum and maximum
179 temperatures recorded across sites in the Northern Range mountains of Trinidad that is habitat to
180 *S. frenata* (Zanghi et al., 2024). However, light intensity from this study was typically much higher
181 than in our study, with the minimum average light intensity recorded in the field being 111.6 lux.

	Temperature (°C)	Light intensity (lux)
Control	25.8 (\pm 0.3)	45.5 (\pm 1.9)
Elevated	29.1 (\pm 0.7)	151.6 (\pm 38.3)
Δ	3.3 (\pm 0.5)	106.1 (\pm 36.4)

182

183 Three HOBO Pendant MX2202 Waterproof Temperature/Light data loggers were used to
184 record lux level and temperature at 5-minute intervals throughout the experiment, and were moved
185 between tanks at the end of each testing day. In tanks assigned to the elevated temperature
186 treatment and without a HOBO logger, the temperature was measured using an aquarium
187 thermometer to confirm that the water was the correct temperature prior to testing. Experimental
188 trials were conducted between 11 am and 4 pm, Tuesday to Friday over February and March 2024
189 for four weeks. As the fish were not fed on Saturdays and Sundays as part of their routine
190 husbandry, they were fed on Mondays and experimental trials were only conducted Tuesday to
191 Friday to standardise hunger across the testing days.

192 The four treatments consisted of a control, an elevated light treatment, an elevated
193 temperature treatment and an interaction treatment where both light and temperature were
194 elevated. The fully factorial design allowed for testing the effects of temperature and light intensity
195 both independently and in combination. During testing, each individual experienced each of the
196 four treatments once for one week by manipulating the temperature and light intensity in their
197 home tank. Each tank was part of a block of 6 adjacent tanks; the order of the treatments for each
198 tank was randomised, on the condition that each of the four treatments appeared at least once but
199 not more than twice in that block of 6 tanks in a given week. On each day of testing, the order in
200 which the blocks of 6 tanks were tested was randomised, as was the order of testing of the tanks
201 within each block.

202 On the Friday of the week prior to the start of experimental trials, treatments for the first
203 week were set up, involving the switching on of heaters and installation of light filters depending on
204 which treatment each tank was assigned to, thus allowing the subjects time to acclimate to their
205 respective treatments for three days before testing. Water testing was conducted each Monday
206 morning in addition to water changes, ensuring a full 24-hour period elapsed before testing
207 commenced the following day to allow the water temperature to reach the required temperature
208 after the water change (Figure A1). After testing was completed on Fridays, the next treatment was
209 set up for each tank for the following week.

210 Before the start of trials each day, 60g of BCUK Aquatics Krill Pacifica was defrosted in
211 20ml of filtered water. The trials were filmed using a Logitech C920 HD Pro Webcam mounted to a
212 Manfrotto camera bracket and clamp. The camera was positioned centrally, facing the narrower
213 vertical wall of the tank (i.e. the wall of dimensions 20 cm wide × 35 cm high), approximately 40cm
214 in front of the bottom of the tank, angled at 40° upwards to be able to view the entire water column.
215 Video recording was via QuickTime Player (version 10.5) at 1280×720 resolution and 30 frames
216 per second. Recording was begun and 2ml of krill was injected using a 5 ml plastic syringe into the
217 tank through a circular hole in the plastic lid of each tank (the hole was 2 cm in diameter and its
218 centre 4 cm from the front of the tank, positioned centrally along the tank's width). Feeding was
219 recorded for 5 minutes from the addition of the food. The camera was then moved to the next tank
220 in the testing order and the trial procedure repeated. A total of 480 trials were conducted; of these,
221 data from 10 trials was missing due to malfunctioning of the recording software. In instances where
222 the heaters malfunctioned, these trials were included as additional replicates for the non-elevated
223 temperature treatments; this occurred in 9 trials across the duration of the experiment. After testing
224 on the final day, each fish was caught in a net and their standard body length was measured using
225 callipers.

226

227 Data processing

228 Video recordings were analysed using the event-logging software BORIS (Friard & Gamba, 2016).
229 *Crenicichla* make exaggerated jaw movements during feeding (Martinez et al., 2018), and this

230 strike action was recorded as a point behaviour in BORIS. Strikes were used as a measure of
231 feeding motivation rather than food consumption as the food items were not always visible to the
232 experimenter in the video footage. The time in the video that each strike occurred within the 3
233 minutes after the food was added was recorded. A single experimenter logged the strikes in
234 BORIS to avoid inter-experimenter variability. Four response variables were then calculated: the
235 latency to the first strike (seconds), the latency for the 10th strike (seconds), the number of strikes
236 in 60 seconds, and the number of strikes in 180 seconds. The latency to the first strike was defined
237 as the time from the introduction of the food into the tank until the first strike was made. Similarly,
238 the latency for the 10th strike was measured from when the food was added to when the 10th strike
239 occurred. For the number of strikes within 60 and 180 seconds, the time interval (60 or 180
240 seconds) started from the time of the first strike.

241

242 Statistical analysis

243 R version 4.3.3 was used to conduct the statistical analyses. Using the lmer function in the lme4
244 package (Bates et al., 2015), each response variable (i.e. the latency to first strike, latency for the
245 10th strike, number of strikes in 60s and number of strikes in 180s) was analysed separately in a
246 linear mixed model (LMM). The temperature treatment (control or elevated) and light treatment
247 (control or elevated) were included as fixed factors, as well as the interaction term between them.
248 Testing day within the week (1 to 4), week number (1 to 4), and standard body length were
249 included as main-effect only covariates in the models; these were all transformed using the scale
250 function in R to avoid problems with model fitting. Consistent individual variation between the
251 subjects was modelled using a random effect of subject identity. The DHARMA package (Hartig,
252 2019) was used to check the assumptions of normality of residuals (confirmed using Q-Q plots)
253 and homogeneity of variances (confirmed by plots of the residuals vs. fitted values). As the latency
254 to the first strike and the latency for the 10th strike did not meet these assumptions, they were log-
255 transformed and 1/square root transformed before analysis, respectively; these transformations
256 were determined using Box-Cox transformations (Box & Cox, 1964), and the models met the
257 assumptions after these transformations.

258 To determine whether light intensity, temperature and their interaction were important in
259 predicting feeding motivation, we constructed models that differed in which of these explanatory
260 variables were included, and compared these to one another and a model that lacked these
261 variables (Tables 2, 3, A1 and A2). Model comparisons were carried out with the Akaike
262 information criterion, corrected for small sample sizes (AICc), using the Ictab function from the
263 bbmle package (Bolker & R Development Core Team, 2017). The model with the lowest AICc is
264 considered the most likely model, and a difference of >2 AICc units between models can be
265 considered strong support for the model with the lower AICc. If models are within 2 units of the
266 most likely model, the model with the fewest parameters is favoured as being the most likely
267 (Burnham & Anderson, 2002). The explanatory variables important in explaining variation in the

268 response variable are those included in the most likely model. In these model comparisons, we
269 also included models that tested whether body length and subject ID were important to include in
270 the models. This was done by constructing models that removed body length from the model that
271 lacked light and temperature, removing subject ID as a random effect from the model that lacked
272 light and temperature, then removing both body length and subject ID from this model. Day within
273 week and week were included as scaled covariates in all models. To quantify interindividual
274 differences in feeding motivation, estimates of repeatabilities and their 95% confidence intervals
275 (CIs) were obtained using the rpt function from the rptR package (Stoffel et al., 2017) for each of
276 the four response variables.

277

278 Ethical note

279 The study was approved by the University of Bristol Animal Welfare and Ethical Review Body
280 (UIN/23/074). Elevated temperature treatments were limited to 30°C and increased gradually
281 between treatments (Figure A1) to minimise physiological stress. Water testing and changes were
282 conducted weekly to ensure high water quality. After the experiment, the fish remained housed in
283 the University of Bristol's research facility to be used in future experiments.

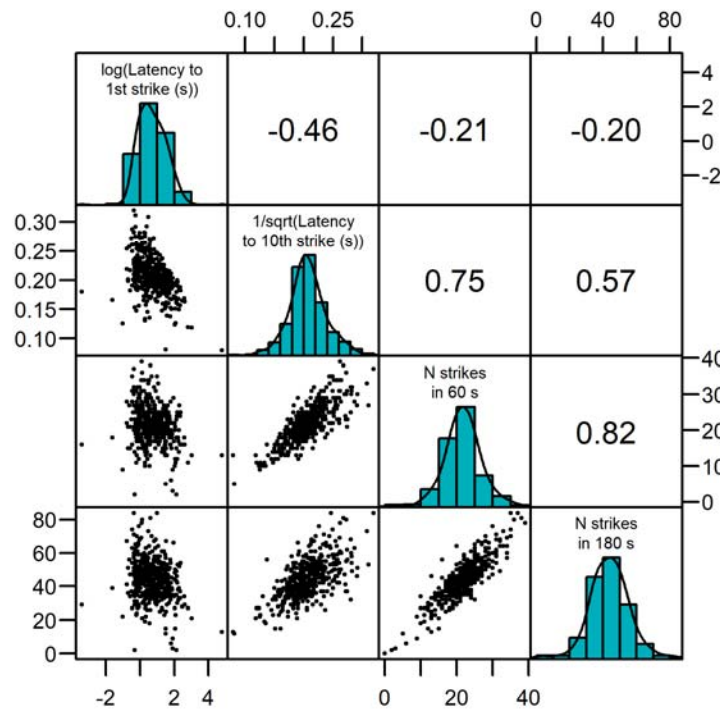
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286 **Results**

287 The four measures of feeding motivation varied in the extent that they were correlated with one
288 another (Figure 1). The latency to the 10th strike and the number of strikes in both 60 seconds and
289 180 seconds were more strongly correlated than any of these were correlated with the latency to
290 the first strike, although there was a moderate correlation between the latency to the first and 10th
291 strikes. For all four measures, there was no evidence that differences in light levels and
292 temperature affected the feeding motivation of the fish, as models with these variables (either as
293 the single main effect, both as main effects or as an interaction term) were less likely (or were only
294 marginally more likely) than simpler models that lacked these terms (Tables 2, 3, A1 and A2,
295 Figures 2a, 3a, A2a and A3a).

296



297

298 Figure 1: Correlations between the measures of feeding motivation (i.e., latency to the first strike,
 299 latency for the 10th strike, number of strikes in 60s, and number of strikes in 180s). The values in
 300 the top right section of the plot are Spearman's rank correlation coefficients. Note that with the
 301 1/square root transformation for the latency to the 10th strike, larger values indicate shorter
 302 latencies.

303

304 Table 2: Δ AICc (difference in the Akaike information criterion, corrected for small sample sizes,
 305 between the model and the most likely model) model comparisons to determine which explanatory
 306 variables and the random effect of subject ID affected the latency to the first strike (natural
 307 logarithm transformed). The df is the number of parameters that are estimated in each model. All
 308 models include day of the week (1-4) and week (1-4) as main effects, and the random effect of
 309 individual identity unless otherwise stated. SBL is standard body length. N = 469 trials.

Response variable: log(Latency to 1st strike (s))	Δ AICc	df
Subject ID random effect only	0	5
No random effect	0.1	4
SBL	1.9	6
SBL, no random effect	1.9	5
Temperature + SBL	3.4	7
Light + SBL	3.9	7
Temperature + Light + SBL	5.4	8
Temperature \times Light + SBL	7.4	9

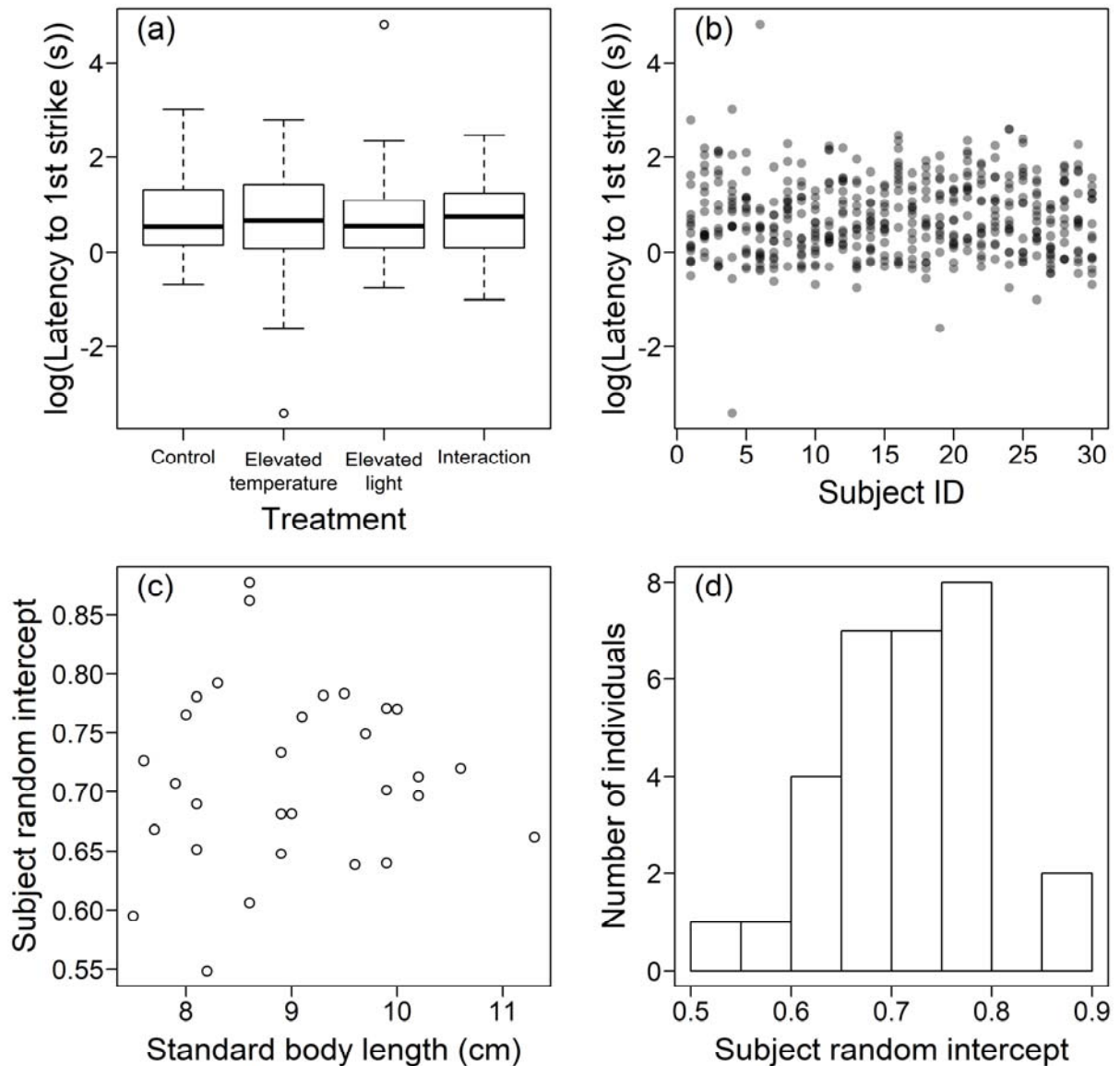
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311 Table 3: Δ AICc model comparisons to determine which explanatory variables and the random
312 effect of subject ID affected the number of strikes in the 60 seconds after the first strike. See Table
313 2's legend for further details. N = 470 trials.

Response variable: Number of strikes in 60 s	Δ AICc	df
Subject ID random effect only	0	5
Light + SBL	0.9	7
SBL	1.8	6
Temperature + Light + SBL	3	8
Temperature + SBL	3.9	7
Temperature \times Light + SBL	5.1	9
No random effect	149	4
SBL, no random effect	149.5	5

314
315 For the latency to the first strike, the model that lacked temperature, light and standard
316 body length as explanatory variables, and the individual identity of the fish as a random effect, was
317 0.1 AICc units from the most likely model, suggesting none of these variables explained variance in
318 the latency to the first strike (Table 2, Figure 2). The individual identity of the fish was, however,
319 important to include in the models predicting the number of strikes within the first 60 seconds; the
320 model with this as the random effect was the most likely model (Table 3). Figure 3b demonstrates
321 the inter-individual variation in the number of strikes within the first 60 seconds. As the models with
322 standard body length were less likely than the model with just the random effect, the consistent
323 inter-individual variation was not due to differences in body size; Figure 3c demonstrates no
324 association between body length and the individual-level intercepts fitted from the most likely
325 model in Table 3. The distribution of the individual-level intercepts for the most likely model is
326 unimodal (Figure 3d), suggesting that the consistent inter-individual variation was not driven by
327 differences between sexes, as strong sex differences would be expected to generate a bimodal
328 distribution (i.e. a mode for each sex). Consistent with the correlations between the measures of
329 feeding motivation, these results were replicated with the number of strikes within 180 seconds and
330 the latency to the 10th strike (Tables A1 and A2, Figures A2 and A3).

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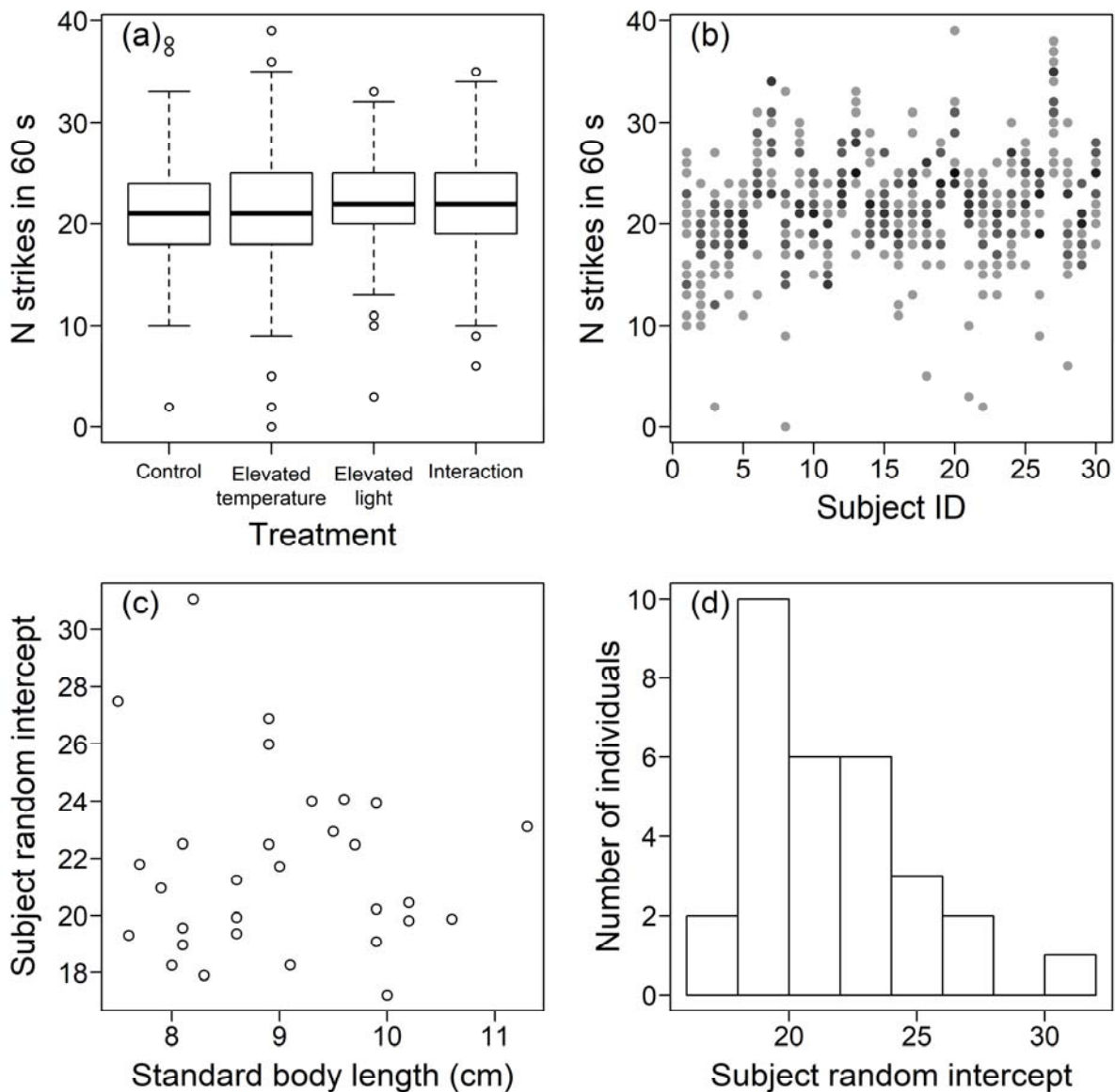
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Figure 2: The latency to the first strike as a measure of feeding motivation. (a) shows how the latency to the first strike was affected by the manipulated environmental variables, and (b) how it varied between the different individual fish. Using the intercept fitted for the random effect of subject ID, (c) shows how differences between the fish in the latency to first strike varied with body size, and (d) shows the distribution of these random intercepts. In (a), the box length denotes the interquartile range, and the median value is represented by the horizontal black lines inside the boxes. The vertical black dashed lines indicate data points within 1.5 times the interquartile range above and below the upper (75%) and lower quartiles (25%). The circles represent outliers.



341

342 Figure 3: The number of strikes in the first minute as a measure of feeding motivation. Plotting as
343 in figure 2.

344

345 As the AICc model comparisons demonstrated strong consistent variation between the
346 individual fish that could not be accounted for by differences in body size, and which are unlikely
347 have been due to sex differences, we calculated repeatability estimates for the measures of
348 feeding motivation. Consistent with the model comparisons, the repeatability estimate was low and
349 the 95% confidence intervals included zero for the latency to the first strike ($R = 0.03$, 95% CIs: 0 -
350 0.082). However, the other three measures of feeding motivation demonstrated moderate
351 repeatability estimates with confidence intervals that did not include zero (the number of strikes in
352 60 seconds: $R = 0.38$, 95% CIs: 0.234 - 0.505; the number of strikes in 180 seconds: $R = 0.478$,
353 95% CIs: 0.33 - 0.602; the latency to the 10th strike: $R = 0.26$, 95% CIs: 0.147 - 0.382).

354

355

356 Discussion

357 Interactions between multiple human-induced environmental stressors have been found to impose
358 significant impacts across a range of behavioural contexts (Côté et al., 2016; Schmitz & Trussell,
359 2016). Although temperature and light intensity have been confirmed to impact feeding in other
360 species (Domenici et al., 2019; Fleming & Bateman, 2018; Richmond et al., 2004; Volkoff & Peter,
361 2006), within the ranges tested in our study we found no effect of these stressors on the feeding
362 motivation of *S. proteus*. There was, however, evidence of consistent inter-individual differences,
363 i.e. personality variation, in this population of *S. proteus* in their motivation to feed. Thus, the
364 composition of a predator population is more likely to impact prey, with potentially knock-on effects
365 for the ecosystem via lethal and non-lethal effects (Binckley & Resetarits Jr., 2003; Resetarits Jr. &
366 Pintar, 2016; Rudolf, 2012), than changes in temperature and light intensity that would be expected
367 to occur through habitat change such as the removal of canopy cover over freshwater streams
368 from deforestation.

369 The composition of a predator population with respect to their feeding motivation will vary
370 depending on both natural and anthropogenic factors. For mesopredators such as pike cichlids,
371 populations can become more risk-averse with an increased perception of predation risk, including
372 a decreased feeding rate due to the trade-off between predation risk and foraging (Verdolin, 2006).
373 In addition to this non-lethal effect, predation can selectively remove less risk-averse individuals
374 from a population through direct consumption (Bell & Sih, 2007), although this is not always the
375 case (Balaban-Feld et al., 2019). Harvesting by humans, either for recreation or commercially, is
376 frequently non-random with respect to the risk-taking tendency of the individuals harvested, thus
377 shifting the average risk-taking tendency in the population, usually toward shyer, more timid
378 behavioural types (Arlinghaus et al., 2017; Biro & Post, 2008). Thus, harvesting of wild populations
379 can act as an anthropogenic stressor indirectly impacting prey consumption by altering the
380 behavioural composition of predator populations.

381 Increased temperature and light intensity are not the only effects of deforestation around
382 freshwaters, which includes alteration of hydrological and water chemistry parameters (Castello et
383 al., 2013; Ríos-Villamizar et al., 2017). Increased run-off and sedimentation caused by
384 deforestation contributes to increased water turbidity, which declines the rate of predation by visual
385 predators (Ehlman et al., 2020; Lunt & Smee, 2015). However, Zanghi *et al.* (2023) found that in
386 turbid, warm water, guppies *Poecilia reticulata* (prey of the pike cichlid *S. frenata*) reduced shoaling
387 and increased proximity to another predatory fish, the blue acara (*A. pulcher*), suggesting that
388 these conditions could be advantageous to predators by reducing prey anti-predator behaviour.
389 Increased light penetration from reduced canopy cover from deforestation could be counteracted
390 by more frequent and severe incidences of elevated turbidity, while the elevated temperature could
391 increase the energetic demand of predators. Habitat change, driven by the single human activity of

392 deforestation, can thus alter multiple environmental parameters that can potentially impact
393 predator-prey interactions in freshwater ecosystems.

394 By conducting the trials before the fish were fed that day, our study was designed to infer
395 feeding rates when motivation to feed would be high. However, over longer time scales, piscivore
396 fish become satiated when prey are abundant, which is a likely driver for type II and type III
397 functional responses being common in piscivores under natural conditions (Moustahfid et al.,
398 2010). When prey are abundant, individuals with a greater motivation to feed will satiate earlier,
399 reducing their consumption of prey, and reducing the difference in feeding rates compared to less
400 motivated predators that are less sated. Such a state-behaviour feedback (Sih et al., 2015) will
401 reduce inter-individual variation in feeding. Research on three-spined sticklebacks (*G. aculeatus*)
402 has demonstrated consistency in individual differences was reduced in a foraging context but
403 maintained in control trials where no food was present (MacGregor et al., 2021), although the
404 opportunity to forage tended to make individuals less predictable rather than reduce variation
405 between individuals. Further research in this area is needed to determine the extent of consistent
406 inter-individual variation between predators at different prey densities. Another factor which may
407 suppress consistent differences between individuals is conformity, where individuals become more
408 similar in their behaviour due to signals or cues from one another (Ioannou & Laskowski, 2023).
409 Although adult pike cichlids are not found in social groups other than reproductive pairs, multiple
410 individuals can occupy the same pools and be within visual range of one another (Szopa-Comley,
411 Duffield, et al., 2020; Zanghi et al., 2024), and social information can be used in a foraging context
412 even in fish species that do not live in groups (Webster & Laland, 2017). The extent to which
413 consistent inter-individual variation within a predator population is suppressed by social information
414 leading to conformity deserves further study.

415 The latency to the first strike was not consistently different between individual *S. proteus*,
416 and this variable was not strongly correlated with the other three variables used to quantify feeding
417 motivation (the latency to the 10th strike, and the food consumed in the first minute and first three
418 minutes), which were all correlated with one another. While the latency to the first strike has been
419 used as an indicator of feeding motivation in fish previously (Volpato et al., 2013), in our study this
420 variable may have been sensitive to the location and orientation of subjects within the tank when
421 the food was introduced, contributing unaccounted variation in the statistical models predicting the
422 latency to the first strike. The feeding trials in our study were conducted in the fish's home tanks to
423 reduce stress by being a familiar environment and to avoid handling before the trials, and hence
424 facilitate feeding. With a different tank arrangement that would allow filming from multiple
425 perspectives, the fish's location and orientation within the tank could be quantified and included as
426 covariates in the statistical models (as in MacGregor et al., 2020). The use of pose tracking
427 software (e.g. Pereira et al., 2022) would also allow kinematic measurements of the strikes.
428 Alternatively, when investigating the effect of temperature on feeding motivation in Pacific halibut
429 *Hippoglossus stenolepis*, Stoner et al. (2006) arranged multiple vertical feeding tubes in each tank

430 for food introduction. This setup allowed food to emerge at the greatest distance from the test
431 subject, standardising subject positioning within tanks and minimising potential confounding effects
432 on latency measurements. In our study, the variable location and orientation of the subjects within
433 the test tank when the food was first introduced is likely to have had a reduced contribution to the
434 variability in strikes after the first strike, explaining why we were able to detect consistent inter-
435 individual variation in the latency to the 10th strike, and the food consumed in the first minute and
436 first three minutes.

437 Overall, our study suggests that feeding motivation in pike cichlids is robust to relatively
438 short-term exposure to changes in temperature and light intensity that is likely to be associated
439 with removal of canopy cover from deforestation adjacent to freshwater streams. Instead,
440 individuals of *S. proteus* show consistent differences in their feeding motivation, and these
441 differences were unrelated to the body size of the individuals. A similar trend of consistent inter-
442 individual variation in feeding that was independent of body size has been also demonstrated in
443 another pike cichlid, *S. frenata*, under field conditions (Szopa-Comley, Duffield, et al., 2020), and in
444 northern pike *E. lucius* (Nyqvist et al., 2012). Despite the prevalence of consistent inter-individual
445 differences in predator populations, the ecological impacts of these differences have yet to be
446 extensively explored, which are likely to be varied. For example, individual predators posing a
447 greater risk to prey are likely to have different spatial distributions to less dangerous individuals,
448 creating risk landscapes for their prey (Dammhahn et al., 2022; Steinhoff et al., 2020). Predator-
449 prey interactions in freshwater aquatic systems, which can be studied under both laboratory and
450 field conditions and are amenable to experimental manipulation as well as observation, are
451 particularly promising for future studies in this area.

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- 700
- 701

702 **Appendix**

703

704 Table A1: Δ AICc model comparisons to determine which explanatory variables and the random
705 effect of subject ID affected the latency to the 10th strike. See Table 2's legend for further details.
706 N = 464 trials.

Response variable: 1/sqrt(Latency to 10th strike (s))	Δ AICc	df
Subject ID random effect only	0	5
Temperature + SBL	1.8	7
SBL	2	6
Temperature + Light + SBL	2.2	8
Light + SBL	2.4	7
Temperature \times Light + SBL	3.6	9
No random effect	81.3	4
SBL, no random effect	83	5

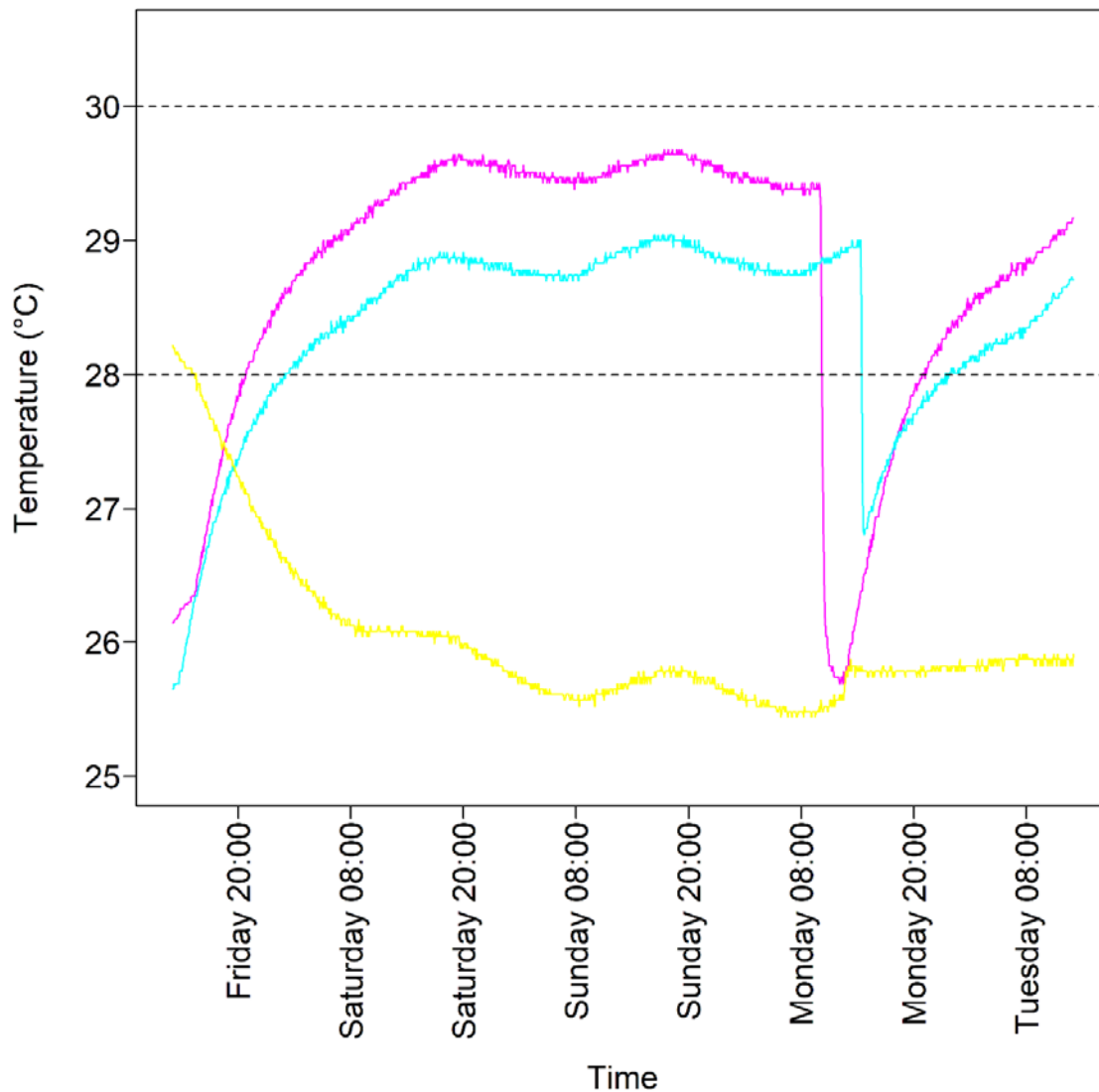
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709 Table A2: Δ AICc model comparisons to determine which explanatory variables and the random
710 effect of subject ID affected the number of strikes in the 180 seconds after the first strike. See
711 Table 2's legend for further details. N = 470 trials.

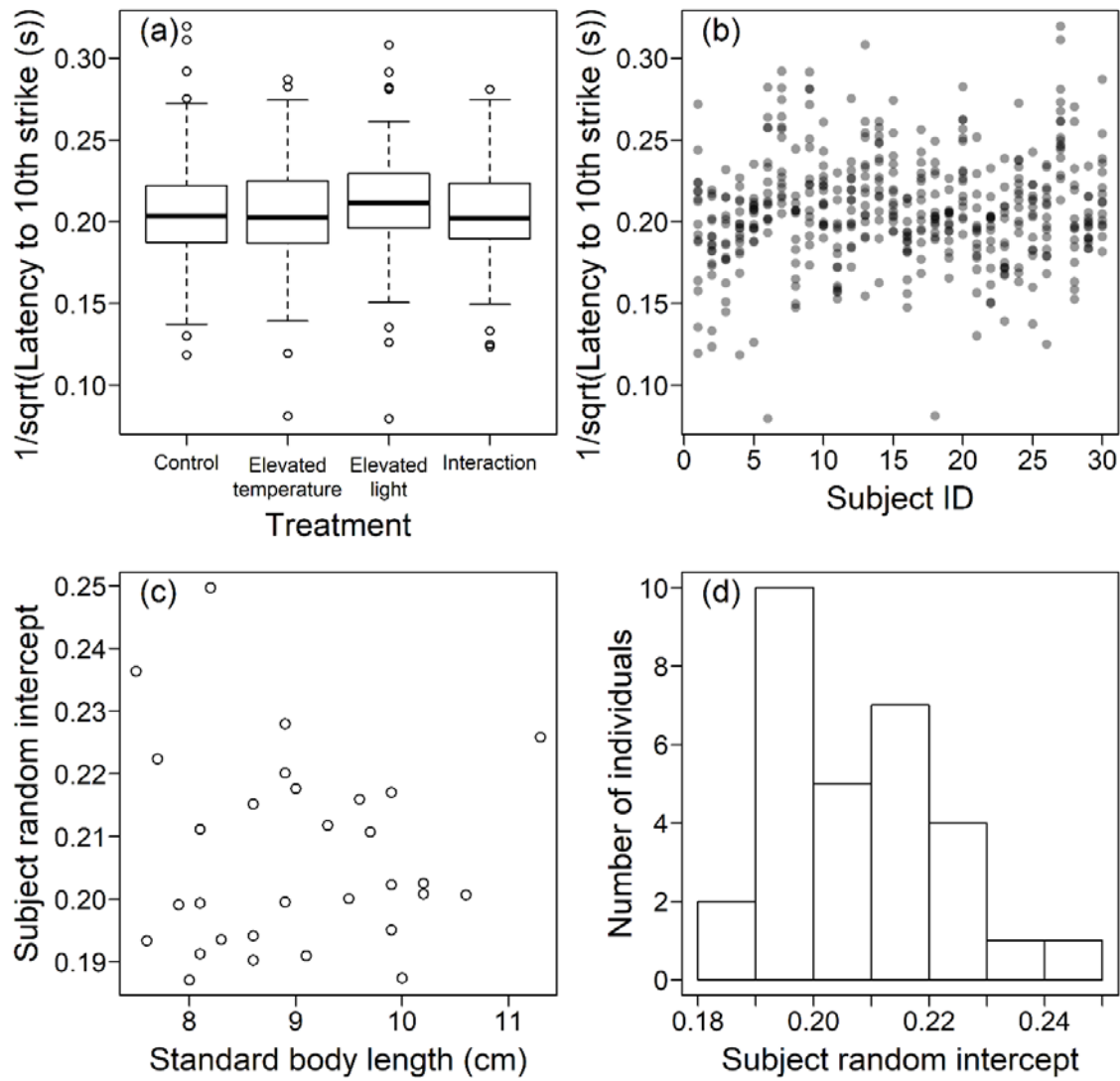
Response variable: Number of strikes in 180 s	Δ AICc	df
Subject ID random effect only	0	5
SBL	1.4	6
Light + SBL	1.7	7
Temperature + SBL	3.4	7
Temperature + Light + SBL	3.6	8
Temperature \times Light + SBL	4.6	9
SBL, no random effect	217	5
No random effect	220	4

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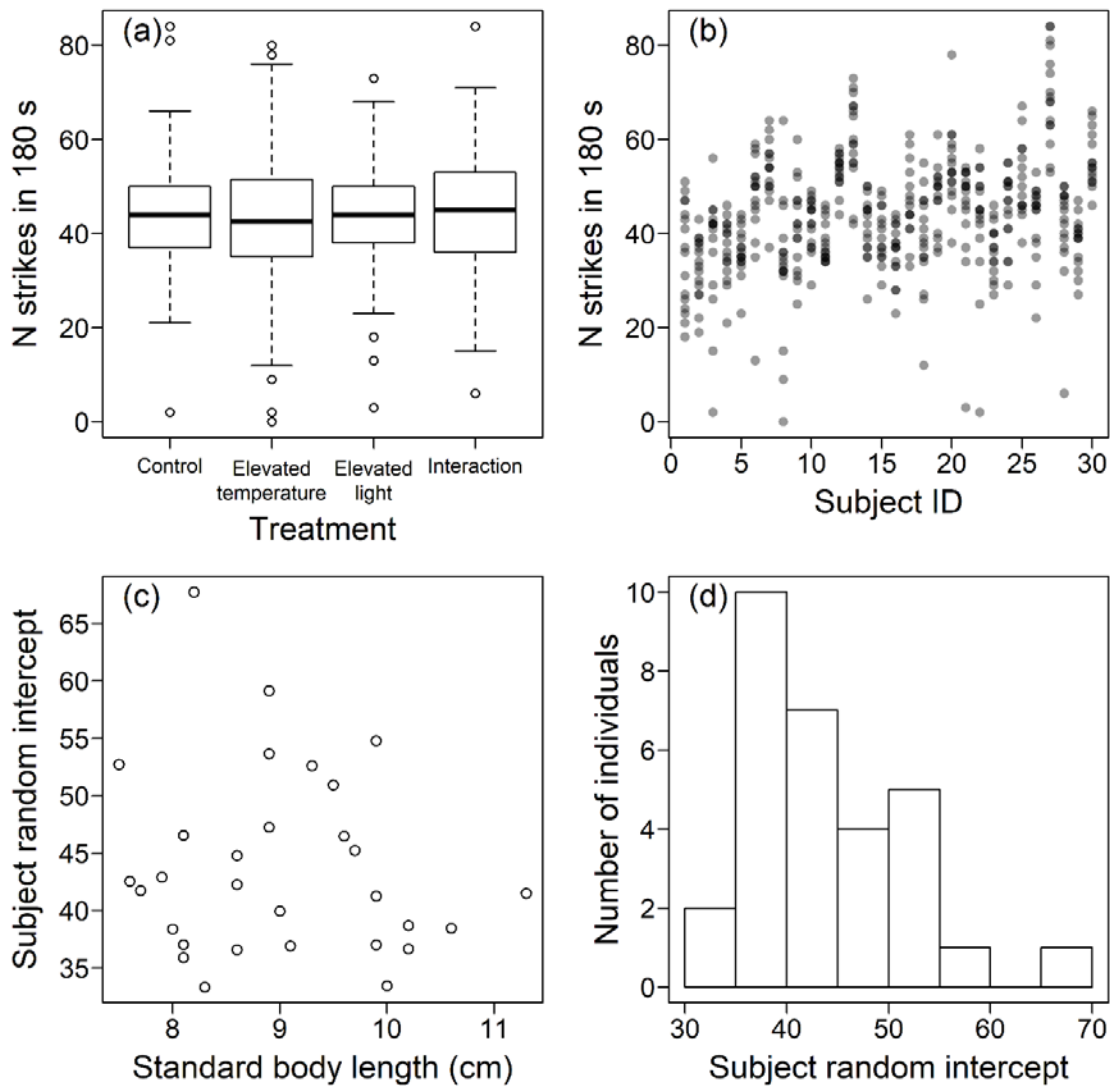
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714 Figure A1: Water heating and cooling profiles for tanks 9 (magenta), 22 (cyan) and 28 (yellow)
715 during the transition from week 1 to week 2 of trials. Temperature readings were captured by
716 HOBO MX2202 loggers at 5-minute intervals. The black dashed lines at 28°C and 30°C represent
717 the lower and upper thresholds for elevated temperature treatments. The transition from week 1 to
718 week 2 treatments occurs on Friday, with trials commencing on Tuesday. The sharp temperature
719 decline on Monday was due to the activation of the inflow system for water changes. Within 24
720 hours, the heaters in tanks 9 and 22 reached the elevated temperature range in preparation for the
721 trials, while tank 28 remained at the control temperature.



722
723

Figure A2: The latency to the 10th strike as a measure of feeding motivation. Plotting as in figure 2.



724

725 Figure A3: The number of strikes in the first three minutes as a measure of feeding motivation.

726 Plotting as in figure 2.

727

728