1   **Predation risk and resource abundance mediate foraging behaviour and intraspecific**

2   **resource partitioning among consumers in dominance hierarchies**

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24   analyzed the data and wrote the manuscript with input from all authors.

25
26   ABSTRACT

27   Dominance hierarchies and unequal resource partitioning among individuals are key mechanisms

28   of population regulation. The strength of dominance hierarchies can be influenced by size

29   dependent trade-offs between foraging and predator avoidance whereby competitively inferior

30   subdominants can access a larger proportion of limiting resources by accepting higher predation

31   risk. Foraging-predation risk trade-offs also depend on resource abundance. Yet, few studies

32   have manipulated predation risk and resource abundance simultaneously; consequently, their

33   joint effect on resource partitioning within dominance hierarchies are not well understood. We

34   addressed this gap by measuring behavioural responses of masu salmon to experimental

35   manipulations of predation risk and resource abundance in a natural temperate forest stream.

36   Responses to predation risk depended on body size such that larger dominants exhibited more

37   risk-averse behaviour (e.g., lower foraging and appearance rates) relative to smaller

38   subdominants after exposure to a simulated predator. The magnitude of this effect was lower

39   when resources were elevated, indicating that dominant fish accepted a higher predation risk to

40   forage on abundant resources. However, the influence of resource abundance did not extend to

41   the population level, where predation risk altered the distribution of foraging attempts (a proxy

42   for energy intake) from being skewed towards large individuals to being skewed towards small

43   individuals after predator exposure. Our results imply that size dependent foraging-predation risk

44   trade-offs can mediate the strength of dominance hierarchies by allowing competitively inferior

45   subdominants to access resources that would otherwise be monopolized.

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49   INTRODUCTION

50   Social dominance hierarchies and the maintenance of unequal resource partitioning among

51   individuals are key mechanisms of population regulation and stability (Hassell 1978, Lomnicki

52   1988). The strength and stability of dominance hierarchies depends on the behavioural

53   mechanisms mediating intraspecific competition (Weir and Grant 2004). Predators and resource

54   abundance appear to have particularly important roles in this context given that many animals

55   face a trade-off between maximizing resource intake while minimizing mortality risk (Werner

56   and Gilliam 1984), and that the optimum of this trade-off can vary among individuals as a

57   function of body size and social status (Lima and Dill 1990).

58   Size or status dependent foraging-predation risk trade-offs are often attributed to the asset

59   protection principal (Clark 1994), which posits that larger individuals should be more risk-averse

60   than their smaller conspecifics due to their higher accumulated fitness 'assets' and the

61   diminishing energetic return for a given foraging intake with increasing body size. For

62   consumers in dominance hierarchies, this implies that reduced foraging rates by larger dominants

63   in the presence of predators could allow smaller subdominants to access resources that would

64   otherwise be monopolized (Reinhardt 1999, Catano et al. 2016). As a result, predation risk

65   should shift the distribution of resources from being highly skewed towards a small number of

66   dominant individuals to being more evenly distributed.

67   The shape of foraging-predation risk trade-offs is also influenced by variation in resource

68   abundance, which could further mediate intraspecific competition and subsequent resource

69   partitioning among individuals (Gruber et al. 2016). Theory predicts that with increasing

70   resources, consumers should decrease their foraging activity under predation risk (i.e., be more

71   vigilant) due to the lower marginal benefit of food intake, which should be further reduced with

72   increasing body size (Brown 1988, Olsson et al. 2002). Consequently, elevated resources should

73   exacerbate the effects of predation risk on dominance hierarchies, further widening foraging

74   opportunities for subdominants and reducing resource monopolization. However, an alternative

75   prediction emerges if consumers are conditioned to feast or famine conditions associated with

76   pulsed resources (Armstrong and Schindler 2011). In this case, the marginal value of foraging

77   may be higher when resources are abundant (Higginson et al. 2012), leading to higher foraging

78   rates and agonistic interactions. Consequently, elevated resources would reduce foraging

79   opportunities for subdominants and dampen or even reverse the influence of predation risk on

80   resource monopolization.

81   Despite broad support for foraging-predation risk trade-offs as drivers of intraspecific

82   competition, our ability to predict the specific outcomes of these factors at the population level is

83   currently limited as surprisingly few studies have manipulated both predation risk and resource

84   abundance simultaneously (for exceptions see: Kotler, Brown, & Bouskila, 2004; Matassa &

85   Trussell, 2014; Morosinotto, Villers, Varjonen, & Korpimäki, 2017). Further, these cases are

86   often highly controlled experiments, where resource abundance levels and foraging motivation

87   are tightly regulated. While this is preferable for teasing apart the specific mechanisms

88   underlying behaviour, results may not necessarily translate to resource partitioning in natural

89   populations, where foraging opportunities and among-individual feeding motivation can be

90   highly variable (Yang et al. 2008, 2010). Moreover, inferences into social interactions may be

91   complicated by behavioural artefacts introduced in more controlled settings (Sloman and

92   Armstrong 2002). Therefore, conducting behavioural studies *in situ* is key to thoroughly

93   understand the role that foraging-predation risk trade-offs actually play in natural systems.

94   Here we present the results of a field experiment testing how consumers (red-spotted

95   masu salmon: *Oncorhynchus masou ishikawae*) respond to manipulations of predation risk and

96   resource abundance in a temperate forest stream. Stream salmonids are an ideal taxon to test

97   these ideas given their behaviour is easily observable in the field (Nakano 1995), they often

98   exhibit strong dominance hierarchies where larger dominant individuals exclude smaller

99   subdominants from the most profitable foraging territories (Nielsen 1992, Weir and Grant 2004),

100   and they frequently experience significant predation risk from terrestrial predators (Hoeinghaus

101   and Pelicice 2010, Harvey and Nakamoto 2013)

102   In this study, we first tested whether behavioural responses by masu salmon to predation

103   risk varied with body size and whether this response was mediated by resource abundance.

104   Based on the asset protection principle (Clark 1994), we predicted that riskier behaviour, defined

105   as higher foraging rates after predator exposure, would decline with body size. We further

106   predicted that these effects would be magnified when resources were elevated due to a lower

107   marginal benefit of energy intake for dominant individuals. Although absolute body size may be

108   the ultimate driver of foraging-predation risk trade-offs, behavioural responses may be strongly

109   mediated by social status (dominant vs. subdominant) among directly interacting individuals

110   (Gotceitas and Godin 1991). Thus, we further tested how behavioral responses to predation risk

111   and resource abundance were mediated by social status within a dominance hierarchy, predicting

112   that subdominants should disproportionately benefit from elevated resources under predation

113   risk. The corollary of these individual-level predictions is that predation risk combined with

114   elevated resource abundance should result in reduced resource monopolization, i.e., a more even

115   distribution of resources. Thus, at the population level, we tested whether predation risk and

116   resources modified the distribution of foraging attempts (a surrogate for relative energy intake)

117   among individuals, predicting that subdominants should gain an increasingly greater share of

118   energy with elevated resources under predation risk.

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120   METHODS

121   *Study system and logistics* - Our study was conducted in Hachiman-dani stream, an upper

122   tributary of the Arida River in Kyoto University's Wakayama Forest Research Station in Japan.

123   The study system is a cobble-bottomed stream draining a catchment dominated by planted

124   conifer trees (*Cryptomeria japonica*) and native deciduous vegetation. Masu salmon and low

125   densities of minnows (*Rhynchocypris oxycephalus jouyi*) are the only fish species present in the

126   study area.

127   We conducted our study in conjunction with a large-scale field experiment testing the

128   influence of pulsed resources on the life history of masu salmon (T. Sato unpublished). That

129   experiment involved separating the study stream into six experimental reaches, consisting of

130   three replicates of two resource treatments (control vs. elevated). Reaches were separated by

131   check dams, which constrained movements of fish (< 1% individuals moved across reaches

132   during the two-year experiment; Sato et al. unpublished data). To manipulate resource

133   abundance, live mealworms (*Tenobrio molitor*) were added to the stream at the rate of 100 mg

134   m^{-2} day^{-1}, which corresponds to peak input rates of natural terrestrial invertebrates in temperate

135   forest streams (e.g., Baxter, Fausch, & Saunders, 2005; Nakano & Murakami, 2001). Mealworms

136   were dispensed by automatic fish feeders (W × H × D = 6.8 × 14.9 × 8.7 cm, ~100 mL capacity

137   for food; EHEIM Co. Ltd.) set on wooden stakes ~1.5 m above the stream water surface placed

138   at 10 m intervals throughout the reach. The feeders were deployed in similar habitats (i.e., a riffle

139   upstream of a pool) so that fish had similar access to mealworms. We set each feeder to dispense

140   mealworms four times during daylight (6:00-18:00), which mimicked the slow and haphazard

141   manner by which salmonids encounter natural prey falling from riparian vegetation.

142   We quantified natural variation in ambient prey abundance by sampling aquatic and

143   terrestrial invertebrate drift with 250 μm nets staked to the substrate ($n = 5$ per treatment reach).

144   On two days during the experiment, three 30 minute samples were taken during daylight and

145   pooled for a single estimate at each location. Invertebrates were identified to order, dried, and

146   weighed in the laboratory. Drift concentrations (mg volume filtered^{-1}) was converted to a total

147   flux through each pool following Downes & Lancaster (2010) and biomass was converted to

148   energy (kilojoules) using taxa-specific conversions (Sato et al. 2011). After accounting for drift,

149   ambient terrestrial invertebrate input rates (~20 mg-dry mass m^{-2} day^{-1}; Sato *et al.* unpublished

150   data), and for the added mealworms, we determined that fish in elevated resource reaches had

151   access to 7.5 times more energy on average than those in controls (Figure 1).

152   We took advantage of the infrastructure from the larger experiment to examine

153   behavioural responses to predation risk under ambient (controls) and experimentally elevated

154   resources. Our study began one week after mealworm treatments were initiated, such that fish

155   had sufficient time to adjust to the new prey source. Sampling of stomach contents further

156   confirmed that fish consumed mealworms in elevated treatments (Supplement Fig S1). We first

157   selected pools ($n = 10$ per treatment) with similar abiotic attributes and similar densities of fish

158   (~0.5 m^{-2}). Masu salmon generally forage in pool habitats and maintain strong size-based

159   dominance hierarchies, where larger dominant fish occupy upstream positions that are more

160   energetically profitable to intercept aquatic and terrestrial invertebrates (Fausch 1984, Nakano

161   1995). Social status of fish in the experimental pools was easily identified by body size and

162 corroborated by numerous observations of aggressive interactions where dominant individuals

163 would chase subdominants out of foraging territories (Sato and Watanabe 2014).

164   Observations of fish behaviour were made using underwater videography. We attached

165 underwater video cameras (Seesii 30M 7" LCD, EYOYO Co. Ltd.) to rebar stakes anchored into

166 each pool at locations permitting the widest possible field of view. Two cameras were used for

167 wide or irregularly shaped pools to allow all fish to be visible. Cameras were left overnight after

168 installation and then were connected to viewing monitors, which were positioned out at least 15

169 m away from the pool where fish behaviour could be observed while minimizing any artefacts of

170 human presence.

171   Predator simulations consisted of a decoy of a crow, which was fashioned to a fishing

172 line that we tied across each pool 3 weeks prior. Lines were tied at a sufficient distance from the

173 pool such that the investigator would not disturb fish when releasing them. There were no

174 noticeable effects of moving the overhead line on fish behaviour. Before initiating predator

175 simulations, we ensured fish were present in the pools then began recording video for at least 30

176 minutes. Then, one investigator stealthily attached the bird decoy to the line and released it while

177 a second observed fish behaviour through the monitor to ensure no artefacts were present. The

178 bird was rigged to fly over the pool from upstream to downstream at roughly 15-degree angle at

179 a speed of 0.5 body lengths sec^{-1}, making brief contact with the water. We marked the time of the

180 exact moment that fish reacted to the predator simulation, then proceeded to record footage for at

181 least one hour. Technical difficulties with cameras resulted in recording times differing slightly,

182 thus subsequent calculations are standardized by recording time. All predator simulations

183 occurred between 10:00 and 14:00 to minimize effects of diel variation in fish activity.

184   The predator simulation was designed to replicate the behaviour of several avian

185   predators in the study area, including two kingfishers (*Halcyon coromanda* and *Megaceryle*

186   *lugubris)* and brown dippers (*Cinclus pallasii*). Several opportunistic observations suggested fish

187   responses to the decoy were qualitatively similar to their responses to these predators (S. Naman

188   and T. Sato personal observation). While there is some evidence for size-biased avian predation

189   on salmonids (Miyamoto et al. 2018), previous observations of visible injury to captured fish

190   suggest that predation risk is not strongly size biased within the range of fish sizes in our

191   experiment (55-162 mm; T. Sato unpublished data).

192   *Behaviour observations* - We quantified changes in foraging behaviour for each observed

193   fish in response to predation risk and resource abundance several different ways following

194   Nakano (1995). First, we defined the appearance rate (AR) as the proportion of time a fish was

195   visible in the pool relative to the total footage recorded. Second, we define the frequency of

196   foraging attempts (FFA) as the number of foraging attempts per minute that a given fish was

197   visible. Third, we define the actual foraging rate (AFR) as the product of AR and FFA. We also

198   quantified the number of aggressive interactions across all fish in a given pool during each

199   observation period. While we did not explicitly quantify their direction of initiation or outcome,

200   nearly all interactions involved dominants chasing or charging subdominants.

201   We visually estimated fish size using ceramic tiles with known dimensions placed in the

202   pool during camera installation. This technique was validated by capturing fish by backpack

203   electrofishing in a subset of pools immediately after observations, which indicated we were able

204   to correctly estimate size within 5 mm on average ($n = 9$, $r = 0.70$). Individual fish within each

205   pool were generally identifiable by their relative size and an ongoing mark-recapture experiment

206   has demonstrated an extremely high site fidelity of fish to individual pools in the study site (Sato

207   and Watanabe 2014). Thus, we were confident that fish returning to a given pool after predator

208   exposure were the same fish that were originally there. In several cases there was uncertainty in

209   this regard and these observations were not incorporated in subsequent analysis. Altogether,

210   behavioural observations of 34 fish were analyzed.

211   *Statistical Analysis* - We used generalized linear mixed effects models (GLMM) to test

212   whether body size influenced behavioural responses to predation risk and resource abundance.

213   For these analyses, the response variable was the change in a given foraging metric (AR, FFA,

214   AFR) from before to after exposure to the predator decoy. The predictors were body size,

215   resource abundance (ambient control or elevated), and their interaction. Each pool was treated as

216   a random factor. We fit models using the R package *glmer* (Bates et al. 2015) with a Gaussian

217   error distribution and tested the significance of each predictor using sequential likelihood ratio

218   tests. For significant predictors ($P < 0.05$) we computed 95% confidence intervals using a

219   parametric bootstrap ($n = 10,000$ iterations).

220   We tested the difference in foraging rates between subdominants and dominants in each

221   pool using a similar GLMM approach, but in this case resource abundance, time (before-after

222   predator exposure) and their interaction were predictors. Fish ID was used as a random factor to

223   account for repeated measures on the same fish. We initially included pool as another random

224   factor (where fish ID is nested within pool) but this did not improve model fits and resulted in

225   poor parameter convergence so only fish ID was retained; moreover, only two pools had more

226   than two fish. We tested for main treatment effects as previously described and also examined

227   whether 95% confidence intervals in each group (e.g., control-before, elevated-after etc.)

228   overlapped zero, which would indicate that foraging rates of subdominants did not differ from

229   dominants on average. We tested treatment effects on the frequency of aggressive interactions

230   using a GLMM with a quasi-Poisson distribution. All data were analyzed in R v. 3.2.0 (R Core

231   Development Team). Model diagnostics for *glmer* were evaluated with residual simulations

232   using the package DhArma (Hartig 2016).

233   To determine the effects of predation risk and resource abundance on energy distribution

234   among individuals and the extent of resource monopolization, we compared the frequency

235   distributions of the total foraging attempts observed across body lengths (mm) before versus

236   after predator exposure and among resource treatment combinations. While foraging attempts as

237   a metric of absolute energy intake is inappropriate given many attempts are likely unsuccessful

238   (Neuswanger et al. 2014), we assume it is a reasonable proxy for the *relative* energy intake

239   among individuals. We specifically tested the prediction that predation risk and resource

240   abundance should lead to more positively skewed foraging attempt-body size distributions,

241   indicating a higher relative energy intake by smaller individuals. Skewness was determined by

242   fitting Gamma probability functions to scaled frequency distributions by maximum likelihood

243   using the R package *fitdistplus* (Delignette-Muller and Dutang 2015), deriving estimates and

244   95% bootstrapped confidence intervals of shape parameters (α), then computing skewness using

245   the formula: $2/\sqrt{\alpha}$

246   We inferred if skewness differed between two distributions if 95% confidence intervals did not

247   overlap. Higher skewness values indicate a longer right tail; thus, an increase in skewness

248   following predator exposure would indicate a shift in energy distribution to smaller individuals.

249

250   RESULTS

251   Fish reacted strongly to predator simulations, generally by burst swimming out of the pool or

252   moving close to the substrate. As predicted, individual-level foraging rates following predator

253   exposure were inversely related to body size (Figure 2), with all foraging metrics declining for

254   the largest fish while increasing for smaller fish. However, this relationship was not mediated by

255   resource abundance as the interaction between resource abundance and fish size was not

256   significant for any of the foraging metrics we examined (Supporting Information, Table S1).

257   When foraging behaviour was examined in the context of dominant-subdominant

258   interactions within individual pools, effects of both predation risk and resources were evident,

259   albeit contrary to our predictions. Before predator exposure, appearance rates of subdominants

260   were equal to dominants in pools with elevated resources but lower than dominants in control

261   pools with ambient resources (Figure 3). This pattern changed after predator exposure such that

262   appearance rates were still equal with elevated resources but subdominants exceeded dominants

263   in controls, i.e., there was a significant resource-time interaction (Table S1). Foraging attempt

264   frequency was lower for subdominants in both resource treatments before predator exposure but

265   changed after exposure such that subdominants foraged more frequently than dominants in

266   controls but not in elevated resource treatments where foraging frequency was equivalent (Figure

267   3). Actual foraging rate (i.e., appearance rate × foraging attempt) followed a similar pattern as

268   the frequency of foraging attempts, which had larger effect sizes than appearance rate (Table 1).

269   These changes in foraging metrics appeared to be primarily driven by changes in the absolute

270   foraging rates of dominant fish, whereas subdominant foraging rates were relatively constant

271   (Figure 3)

272   The frequency of aggressive interactions among masu salmon in each pool responded to

273   both predation risk and resource abundance, but there was no evidence for an interaction [Time

274   (before/after-predation risk): $\chi^2 = 19.2$, $P < 0.001$; Resources: $\chi^2 = 5.3$, $P = 0.02$; interaction: P =

275   0.7]. Aggressive interactions decreased by 9-fold on average from before to after predator

276   exposure and were 15 and 6-fold higher in elevated resource treatments relative to controls

277   before and after predator exposure respectively.

278   Examining the frequency distribution of total foraging attempts across body size largely

279   supported our prediction that predation risk should redistribute resources to smaller individuals

280   (Figure 4). Specifically, skewness was higher after relative to before predator exposure when

281   resource treatments were pooled together, indicating a shift toward smaller individuals [before:

282   0.53 (95% CIs, 0.50-0.57); after: 0.63 (95% CIs 0.58-0.69)]. Distributions appeared to differ

283   when resource treatments were separated, with foraging attempts being more skewed towards

284   larger individuals before predator exposure, and more evenly distributed after predator exposure

285   when resources were elevated (Figure 4). However, confidence intervals around skewness

286   estimates overlapped between all resource-time treatment combinations.

287

288   DISCUSSION

289   Dominance hierarchies and unequal partitioning of resources are well known to be key

290   mechanisms of population regulation (Lomnicki 1980, Keeley 2001) and size-dependent

291   foraging-predation risk trade-offs have been observed over a wide range of taxa including

292   salmonids (Reinhardt 2002, Kotler et al. 2004, Morosinotto et al. 2017). Our experiment is

293   relatively unique in its integration of these concepts insofar as it incorporated simultaneous

294   manipulations of predation risk and resource abundance, and explicitly tests the consequences of

295   individual-level behaviour on intraspecific resource partitioning at the population level.

296   Together, our results suggest that body size and social status drive responses to predation risk

297   and resource abundance among individuals, which in turn influences the extent of resource

298   monopolization, and ultimately the distribution of energy within populations. While we are

299   limited in our ability to disentangle the specific mechanisms underlying these findings, the

300   patterns we observed are arguably strengthened when viewed against the background variation

301   associated with wild populations in natural conditions.

302   Consistent with the asset protection principle, behavioural responses to predation risk

303   varied with absolute body size, with larger individuals more risk averse relative to their smaller

304   conspecifics. The effects of resource abundance on these responses were more nuanced and

305   appeared to be mediated by social status among fish within each pool; they were also contrary to

306   predictions. In particular, dominant fish decreased their foraging rates in both treatments

307   following predator exposure but less so when resources were elevated. This contradicts our

308   expectation that consumers should be more vigilant due to a lower marginal benefit of foraging

309   on abundant resources (McNamara and Houston 1986, Kotler et al. 2004). Instead, this result

310   may support the alternative hypothesis, where feast-or-famine conditions lead consumers to

311   accept higher predation risk when resources are abundant in order to meet their energetic

312   demands (Higginson et al. 2012). In our system, masu salmon experience long periods of

313   resource limitation due to large-scale deforestation followed by a monotonic conifer plantation,

314   leading to depressed growth (Sato unpublished data). Thus, we speculate that mealworm

315   additions may have represented a crucial foraging opportunity where increased foraging under

316   risky conditions was necessary to meet energetic demands over longer timescales (e.g., seasonal

317   growing periods).

318   Foraging metrics for subdominant fish were largely consistent across all treatments.

319   Consequently, the foraging rates of subdominants *relative* to dominants increased following

320   predator exposure, especially in control treatments where dominants were more vigilant. This

321   suggests that subdominants accepted a greater predation risk relative to dominants in controls,

322   which may have been due to subdominants having lower energetic status such that avoiding

323   starvation necessitated riskier behaviour (Lima and Bednekoff 1999). However, subdominant

324   foraging rates were unchanged in elevated resource treatments suggesting they did not accept a

325   proportionally higher level of risk with a higher energetic return. One explanation could be that

326   subdominants were sufficiently satiated such that their energetic demands could be met without

327   increasing their foraging rates. We cannot rule out this possibility; however, it appears unlikely

328   in light of the strong resource limitation these fish experienced prior to mealworm additions

329   (Sato Unpublished data). Alternatively, this inconsistency could potentially be explained by

330   aggressive interactions, which were significantly higher when resources were elevated. Agonistic

331   interactions are energetically costly and reduce foraging time (Puckett and Dill 1985, Metcalfe

332   1986, Mathot and Dingemanse 2015), thus may have mediated these responses.

333   Inferences into the mechanisms underlying individual-level behaviour should be

334   tempered by several caveats inherent in our design. First, body size and social status likely

335   covary with energetic state, which we did not explicitly account for and may be the ultimate

336   driver of short-term behavioural responses (Gotceitas and Godin 1991). Second, we cannot

337   completely rule out the possibility that perceived predation risk varied with body size (Miyamoto

338   et al. 2018). While these uncertainties cannot be resolved with the data at hand, they do not

339   change any of the conclusions of our study so much as offer alternative mechanisms for them.

340   Ultimately, predation risk and resource abundance still altered foraging behaviour and

341   intraspecific interactions, leading to a shift in population-level resource distribution toward

342   smaller individuals. Thus, our study as a whole provides an important *in situ* demonstration of

343   state-dependent behavioural responses to predation risk and resource abundance, and its potential

344   consequences for populations.

345   While our inferences are constrained by the short duration of our study, the redistribution

346   of resources we observed may further affect population dynamics over longer time scales.

347   Theory of density-dependent population regulation predicts that more equal partitioning of

348   resources should result in unstable population dynamics relative to skewed distributions where

349   resources are monopolized by a small number of competitively superior individuals (Lomnicki

350   1980, Johst et al. 2008). The extent that population dynamics are related to short term

351   behavioural changes that modify dominance structure is an important question, especially with

352   regards to territorial taxa like salmonids. To further bridge the gaps between short-term

353   behaviour and long-term population processes, the following issues should be addressed: (1) the

354   frequency that consumers experience predation risk over short and long time scales in natural

355   systems; (2) whether consumers can adaptively respond to temporal variability in predation risk

356   and resource abundance via memory and behavioral adjustment (Lima and Dill 1990, Armstrong

357   and Bond 2013); and (3) whether these adaptive responses (if any) shape the foraging-predation

358   risk trade-offs and consequent resource partitioning.

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368   PERMITS

369   The experiment was conducted in accordance with the regulations for animal experiments at

370   Kobe University. Electrofishing was conducted according to regulations of Inland Fisheries

371   Adjustment of Wakayama Prefecture with the permission of the Department of Agriculture,

372   Forestry and Fisheries, Wakayama Prefecture.

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374   CONFLICTS OF INTEREST

375   The authors have no conflicts of interest to declare.

376

377   SUPPORTING INFORMATION

378   Figure S1: Stomach contents of masu salmon in each resource abundance treatment.

379   Table S1: Summary statistics for GLMM analysis of the effects of body size and social status on

380   foraging rates.

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483   TABLES AND FIGURES

484

485   **Table 1.** GLMM parameter estimates and 95% confidence intervals for the difference between

486   subdominant and dominant foraging rates. Cases where confidence intervals did not overlap zero

487   are highlighted in bold.

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| Treatment	Estimate	5% CI	95% CI
Appearance Rate			
Control-Before	**-0.23**	**-0.46**	**-0.02**
Elevated-Before	0.03	-0.20	0.26
Control-After	**0.37**	**0.15**	**0.60**
Elevated-After	0.13	-0.09	0.36
Foraging Frequency			
Control-Before	**-0.78**	**-1.40**	**-0.17**
Elevated-Before	**-1.76**	**-2.38**	**-1.13**
Control-After	0.61	0.00	1.23
Elevated-After	-0.01	-0.63	0.60
Actual Foraging Rate			
Control-Before	**-0.76**	**-1.34**	**-0.18**
Elevated-Before	**-0.83**	**-1.40**	**-0.25**
Control-After	**0.67**	**0.08**	**1.24**
Elevated-After	0.26	-0.31	0.83

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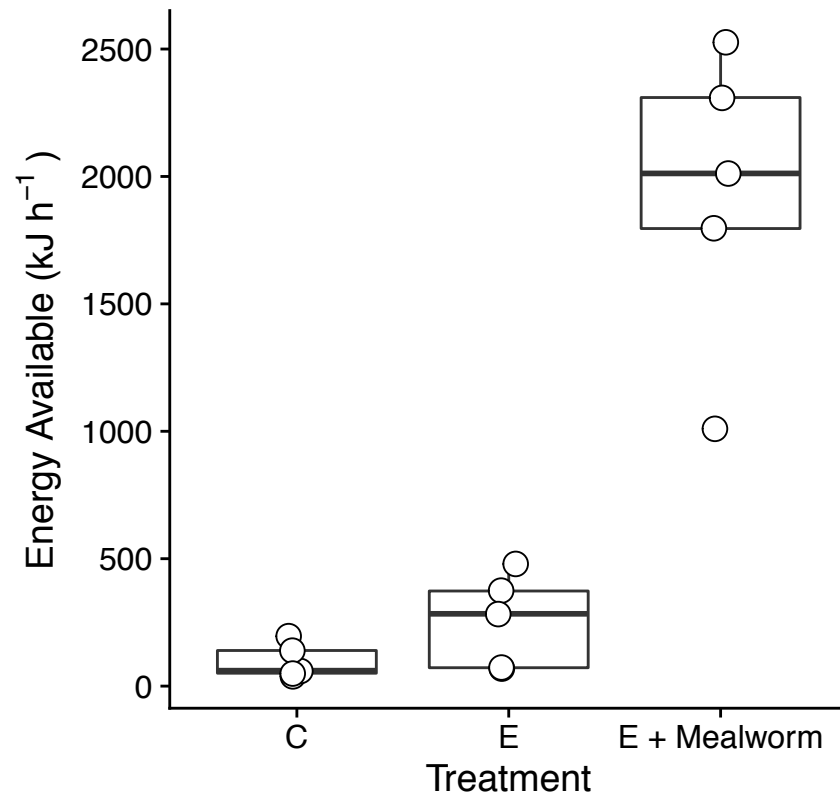
Figure 1. Boxplots showing the total invertebrate energy available to fish (kJ hour^{-1}) in control

treatments (C), elevated resource treatments before mealworm additions (E), and elevated

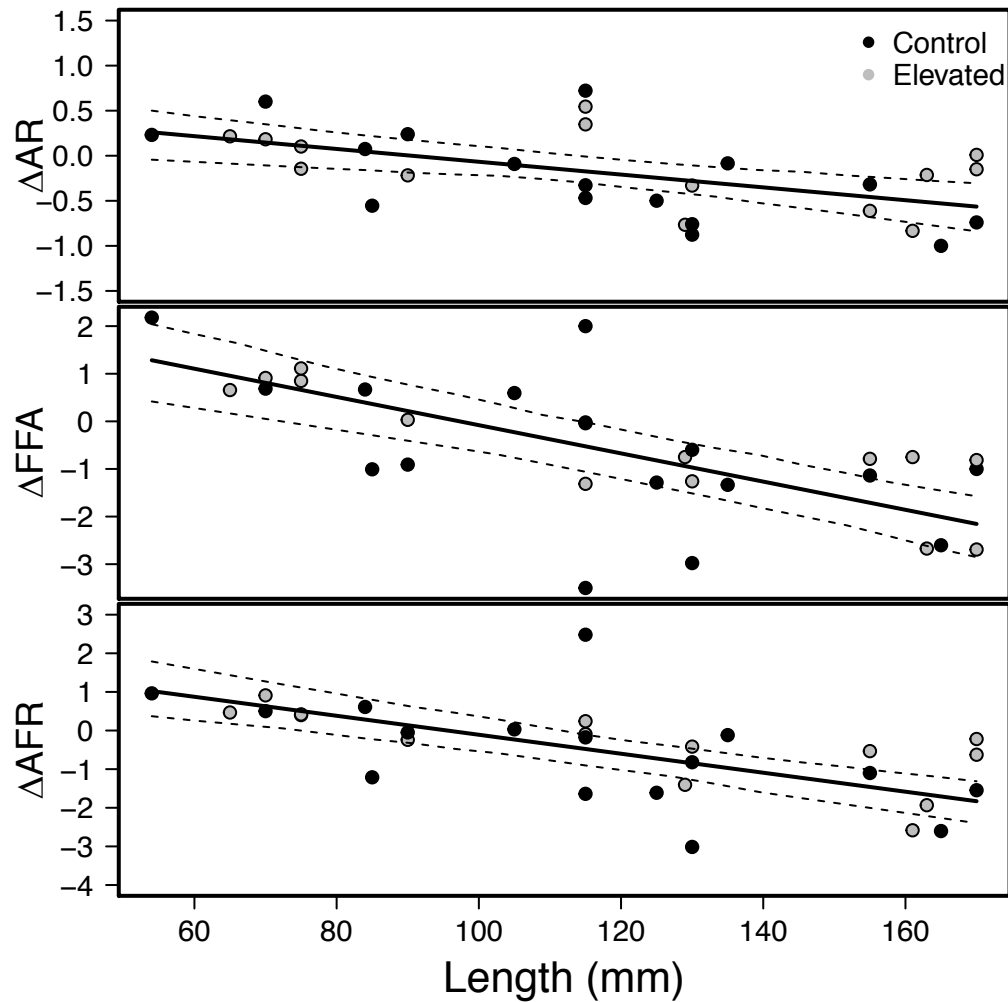resource treatments after mealworm additions (E + Mealworm).

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Figure 2. The change in appearance rate (AR), frequency of foraging attempts (FFA), and actual

foraging rate (AFR) for fish in elevated and control resource treatments from before to after

predator exposure. Solid lines indicate predictions from GLMM models and dashed lines

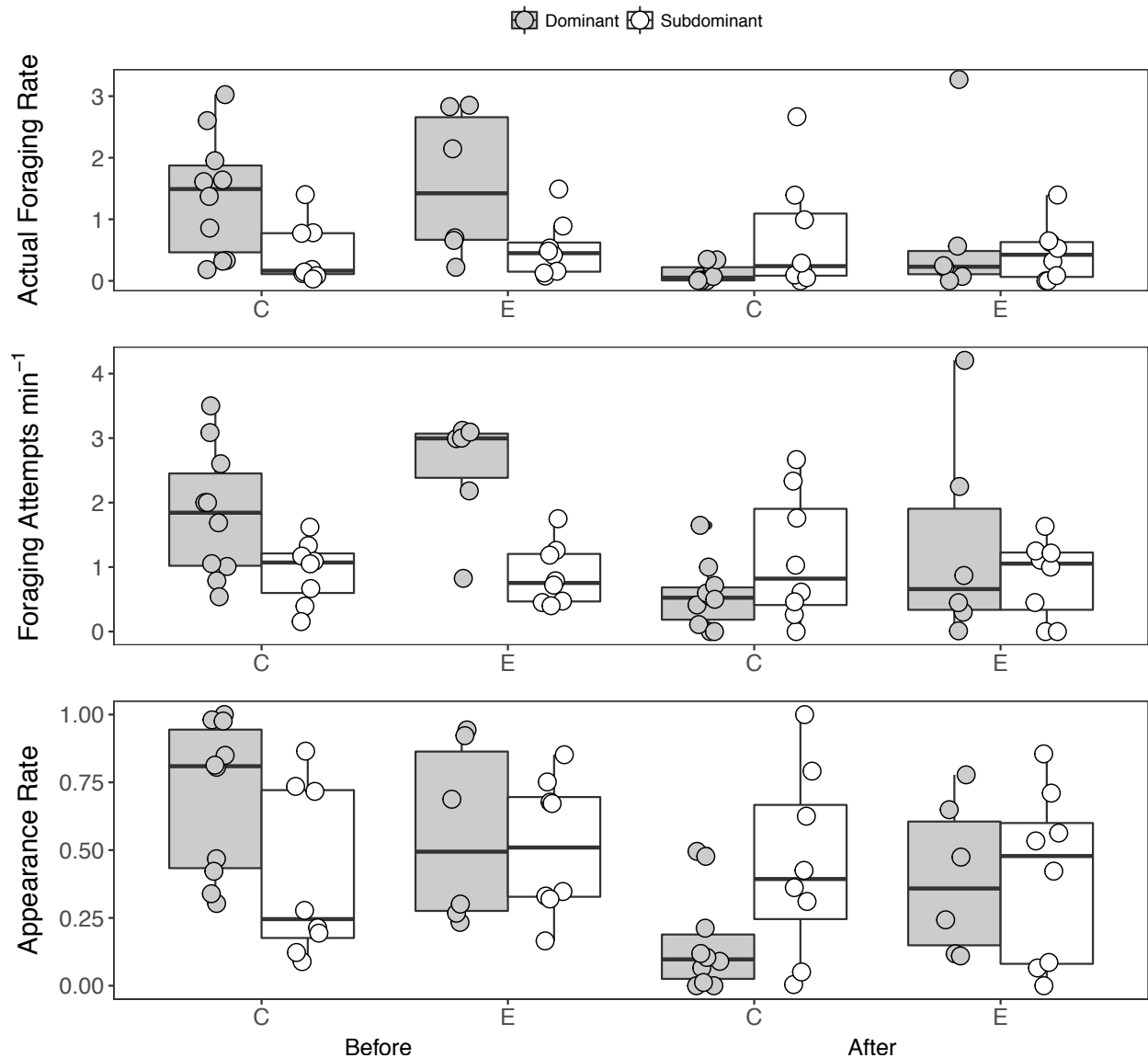indicate 95% confidence intervals. Note the differing scales of y-axes.

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Figure 3. Foraging metrics of subdominants and dominants in control (C) and elevated resource

(E) treatments, before and after predator exposure. Boxes are 25% and 75% quantiles and

overlaid points are raw values. Note that y-axis values are on different scales.
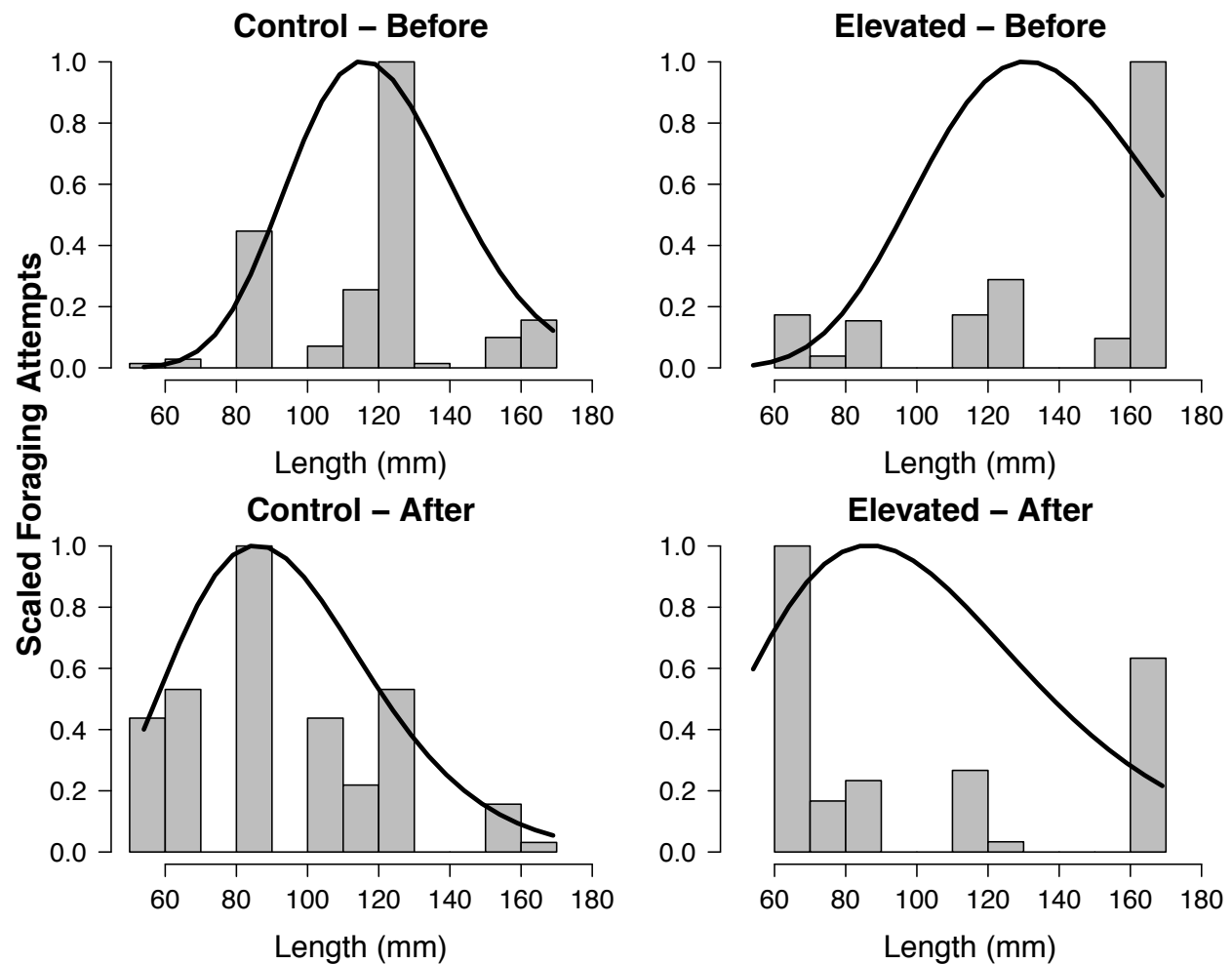
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Figure 4. The distribution of relative foraging attempts among different body sizes in each

control and elevated resource treatments, before and after predator exposure. Distributions are

scaled to a maximum of 1. Black lines represent gamma probability density functions fit to the

data in each group.

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535 <div align="center">Supporting Information</div>

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537 **Table S1:** GLMM results for the change in foraging rates from before to after predator exposure

538 and the difference in foraging rates between subdominant and dominant individuals. χ^2 and P

539 values are from sequential likelihood ratio tests. $R^2_{Marginal}$ indicates the proportion of variation

540 explained by only fixed effects; $R^2_{Conditional}$ indicates the variance explained by fixed and random

541 effects.

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| Model Term	χ^2	P	$R^2_{Marginal}$	$R^2_{Conditional}$
Change in Foraging Rates After Predator Exposure				
Actual Foraging Rate			0.37	0.62
Body Size	15.69	0		
Resources	0.41	0.52		
Body Size x Resources	0.14	0.7		
Foraging Frequency			0.36	0.60
Body Size	16.85	0		
Resources	0.11	0.73		
Body Size x Resources	0.18	0.75		
Appearance Rate			0.36	0.49
Body Size	11.26	0		
Resources	1.2	0.28		
Body Size x Resources	1.5	0.21		
Subdominant-Dominant Foraging Differences				
Actual Foraging Rate			0.38	0.39
Resources	0.00	0.95		
Time	18.61	0.00		
Resources x Time	3.06	0.08		
Foraging Frequency			0.50	0.56
Resources	2.77	0.10		
Time	23.87	0.00		
Resources x Time	0.29	0.59		
Appearance Rate			0.31	0.31
Resources	0.31	0.58		
Time	10.20	0.00		
Resources x Time	10.11	0.00		

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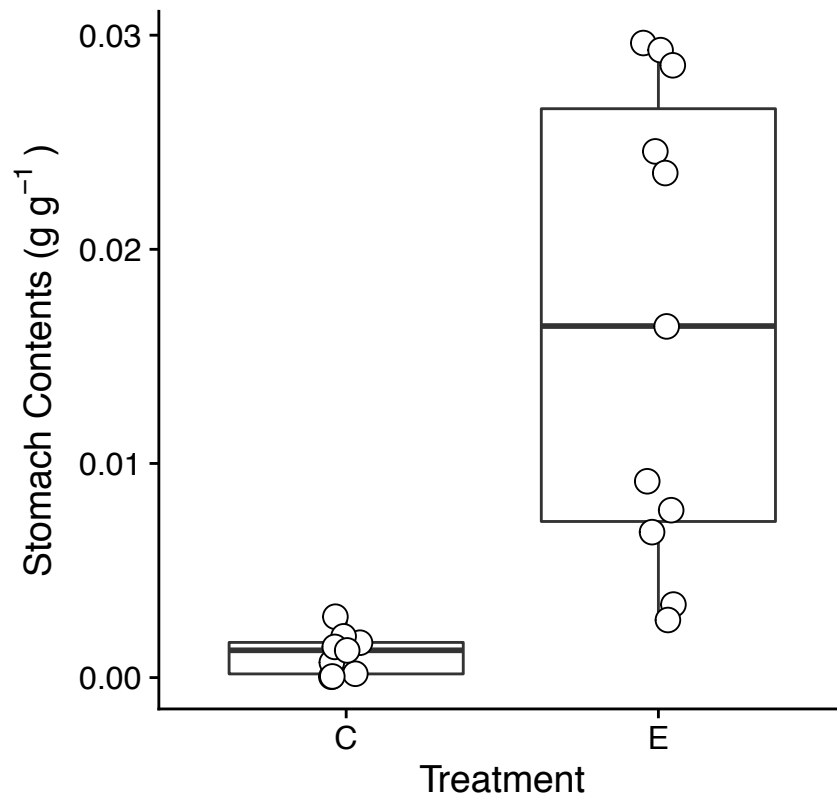
548 **Figure S1**. Mass specific stomach content biomass (g dry mass invertebrates · g wet mass fish[-1])

549 of masu salmon in control (C) and elevated resource (E) treatments. Stomach contents were

550 collected with gastric lavage two weeks prior to the experiment. Contents were stored in 75%

551 ethanol, identified to order, oven dried at 60° C, and weighed in the laboratory. Mealworms

552 constituted ~70% of the stomach content biomass in elevated treatments on average.