1 **Animal or Algal Materials: Food Toughness, Food Concentration and Competitor**

2 **Density Influence Food Choice in an Omnivorous Tadpole**

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4 NOELIKANTO RAMAMONJISOA[1,3], HARISOA RAKOTONOELY[2] AND YOSIHIRO NATUHARA[1]

5

6 [1] Department of Environmental Engineering and Architecture, Nagoya University, Nagoya

7 464-8601, Japan

8 [2] Division of Biosphere Science, Hokkaido University, Hokkaido 060-0808, Japan

9

10 [3] CORRESPONDENCE: e-mail, noelikanto@gmail.com

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ABSTRACT: Little is known about behavioral aspects of tadpole feeding ecology. Resource protein is by far the most studied factor assumed to govern food choice in tadpoles, whereas other factors such as resource toughness and competition have received less attention. Here, we tested the food choice of an omnivorous pond-dwelling tadpole when exposed to animal and algal materials at different toughness and concentrations (1x and 2x amount of food per volume), used as a proxy indicator of energy gain per bite. We subsequently tested how tadpole feeding behavior and food choice change with competitor density (when alone, in pairs or in a group). We found that type, toughness and concentration of the food influenced choice by the tadpoles; however, a three-way interaction among these variables was absent. The tadpoles did not feed randomly and preferred the algal materials when these were softer than, or as tough as, the animal materials. The tadpoles discriminated among foods of different concentrations and readily fed on the high concentration food materials. Tadpole feeding behavior was density-dependent. In a group, the tadpoles nearly doubled their feeding activities and increased their feeding on animal materials, here the less-preferred foods. Food toughness, energy gain per bite, and the presence of competitors influence tadpole feeding behavior, and could be factors used as proximate cues for determining food quality in tadpole foraging strategies.

Key words: Density-dependent food choice; Omnivore; Optimal foraging models; Resource toughness; *Rhacophorus arboreus*; Tadpole feeding behavior

OPTIMAL foraging theory predicts that an organism will maximize its fitness by maximizing its net energy intake per unit time, and will usually choose the resource that yields the most calories for the effort it takes to consume it (Pyke et al. 1977). For many

39 herbivores and omnivores, food protein content has frequently been suggested to govern food

40 choice (Mattson 1980; Sørensen et al. 2008). However, studies have suggested that more than

41 protein content, energy gain (e.g., Le Gall and Behmer 2014), toughness (e.g., Coley 1983)

42 and a social influence (e.g., Giraldeau et al. 2002) can strongly affect food selection. The

43 trade-offs made when deciding among these factors have received less attention.

44   Anuran larvae are model organisms to study the feeding behavior of omnivores.

45 Tadpoles are still some of the least understood in terms of their feeding behavioral ecology,

46 although they can represent the major biomass in freshwater environments (Altig et al. 2007).

47 Information on feeding behaviors is central to understanding the ecological roles of tadpoles

48 because these behaviors are often linked to functional roles (Altig et al. 2007). Tadpoles were

49 previously thought to be indiscriminate feeders, adjusting their feeding rates to food

50 availability (Test and McCann 1976; Wagner 1986). When offered limited choices, however,

51 tadpoles are known to feed selectively (Taylor et al. 1995; Kupferberg 1997). Many tadpoles

52 with general morphology are omnivorous (Whiles and Altig 2010), feeding on both animal

53 and plant materials, but their food preference remains unclear. A long-held hypothesis holds

54 that tadpoles mainly feed on plant materials because of the frequently observed abundance of

55 algal material in their guts and the successful rearing of tadpoles on a plant-based diet (Altig

56 et al. 2007). Observations of opportunistic oophagy, carnivory or necrophagy, and reports of

57 substantial amounts of animal materials found in the gut, however, have suggested a potential

58 affinity for animal materials (Petranka and Kennedy 1999; Altig et al. 2007; Schiesari et al.

59 2009). The preferences of tadpoles, along with the factors regulating resource selection,

60 remain unclear.

61   Previous studies suggested that both the protein content and toughness of a food

62 resource could be important factors in food discrimination in tadpoles. Under limited food

63 choice, tadpoles choose animal-based over plant-based materials, as well as preferred energy-

64   rich and softer materials (Taylor et al. 1995; Petranka and Kennedy 1999; Richter-Boix et al.

65   2007). These patterns should not be surprising for at least two reasons: (1) proteins are often

66   limited in the plant materials commonly consumed by tadpoles (Mattson 1980; Bowen et al.

67   1995; Kupferberg 1997); and (2) animal materials are excellent sources of the protein

68   necessary for growth (Crump 1990), are generally softer (e.g., decaying animal materials),

69   and thus, should be readily selected upon availability. In particular, toughness (the ability to

70   resist mechanical abrasion and penetration; sensu Watson and Norton 1985) can strongly

71   influence resource edibility and feeding niche in herbivores and omnivores (Deraison et al.

72   2015). Indeed, increasing food toughness reduces food ingestion rate and assimilation, thus

73   energy gain with adverse consequences on development and fitness (Simpson et al. 2004;

74   Clissold et al. 2009). In tadpoles, resource toughness is expected to influence food choice but

75   in general, the effects of the biomechanical properties of the food on tadpole choice remain

76   poorly understood (but see Taylor et al. 1995). In contrast to terrestrial herbivores that cut

77   and shear plant materials, tadpole feeding is generally accomplished by anchoring the

78   keratinized mouth to a substrate and raking materials off of it (Venesky et al. 2010; de Sousa

79   et al. 2014). As such, strength limitation of their mouthparts might result in the avoidance of

80   hard materials by tadpoles.

81   In addition to the food properties, the presence or absence of competitors is suggested

82   to influence food choice and fitness (Galef and Giraldeau 2001; Giraldeau et al. 2002).

83   Optimal foraging models predict that individuals should feed on the preferred resource when

84   competition is low but should consider moving to lower quality patches with increasing

85   competition (Pyke et al. 1977). Density-dependent food selection has been documented in

86   mammals (Kausrud et al. 2006), arthropods (Sherratt and Harvey 1993), fishes (Schindler et

87   al. 1997) and birds (Weale et al. 2000), but has received less attention among amphibian

88   species. Previous studies suggested that density-dependent feeding behavior could be a

89   pervasive mechanism in tadpoles, yet these studies did not specifically test the influence of

90   conspecific density on food choice. For example, Griffiths and Foster (1998) and Altig and

91   Christensen (1981) reported that tadpoles frequently exhibit higher levels of activity in

92   groups compared to when alone; but whether or not higher activity levels produce higher

93   feeding rates remains unclear. Eterovick (2000) reported that, when grouped together,

94   *Rhinella crucifer* tadpoles tend to consume greater amounts of low-ranked foods than solitary

95   tadpoles.

96   In this study, we investigated the food choice of an omnivorous pond-dwelling

97   tadpole when offered the choice between animal and high-protein algal materials at different

98   toughness and concentrations, which was used as a proxy indicator of energy gain per bite.

99   We subsequently analyzed how tadpole feeding behavior and food choice change as a

100   function of competitor density. We predicted that tadpoles prefer animal materials, and those

101   foods that are softer and of higher nutrient concentration. Following the predictions of

102   optimal foraging models, we also predicted that foraging activities, and preference for low-

103   ranked foods, would increase with increasing conspecific density.

104

105   MATERIALS AND METHODS

106   Forest Green Tree Frogs, *Rhacophorus arboreus*, are relatively large frogs found in

107   Honshu, Japan, and the island of Sado, off the eastern coast of Honshu. The species occurs

108   from sea level to mountainous regions at altitudes > 2000 m (Wilkinson 2003). After mating,

109   females deposit eggs in foam nests (300–800 eggs per nest) on vegetation near standing water

110   (Uchiyama et al. 2002). The tadpoles have generalized morphology (Wilkinson 2003), and

111   the labial tooth row formula is 4–5/3. An earlier experiment indicated that the tadpoles are

112   omnivores and can feed both on algal and animal materials (Iwai and Kagaya 2005).

113   On 16 June 2014, we collected four egg masses from a pond located in Shiga

114   prefecture, Japan (35.147368°N, 135.87881°E; datum = WGS84). Upon hatching (after 2–3

115   d), we kept the tadpoles in 3-L aquaria filled with 2 L aged water, maintained within an

116   incubator (18°C) at a density of 15 tadpoles/L. We fed the tadpoles with one pellet of rabbit

117   food per day (~150 mg), which was nearly ad libitum, as food still remained until the next

118   day. The experiments occurred when the tadpoles were at Gosner stage 26–28 (Gosner 1960).

119   The mean (± 1 SD) body mass of the tadpoles at this stage was 0.291 ± 0.061 g ($n = 20$). The

120   tadpoles were not fed for 24 h before the start of each experiment. We did not measure the

121   water temperature of the test aquaria, but the room in which we conducted the experiments

122   was maintained at 25°C with a natural photoperiod regime.

123   Experiment 1: Effects of Type, Toughness and Concentration of Food

124   We first tested for the influence of food concentration and toughness on tadpoles'

125   preference for algal and animal materials. We used food materials of nearly the same protein

126   content: green-blue algae (Sun Nutrition Kabushikugaisha, Japan; protein = 57%, lipid = 7%,

127   C/N = $5.25 \pm 0.85\%$; CN Corder MT 700, Yanaco) and dry sludge worm (Itomimizu

128   Kamihata Fish Industry Group, Japan; protein = 52%, lipid = 12%, C/N = $5.41 \pm 0.95\%$; CN

129   Corder MT 700, Yanaco). We report food nutritional information as indicated on the food

130   packages.

131   The general experimental design follows Taylor et al. (1995). We manipulated food

132   concentrations (1x and 2x amount of food per unit volume) and food toughness (low and

133   high) by mixing 2.5 g or 5 g of the respective food in 100 mL of either 0.5% or 1% agar

134   solutions. We molded the food solutions into bricks of 2.5 mL each. The toughness of each

135   food brick was 0.23 ± 0.04 N and 1.01 ± 0.08 N ($n = 25$; measured with a tension gauge,

136   Ouba Instrument, Ltd.), for the 0.5% and 1% agar solution, respectively.

137   In 1-L containers filled with 0.5 L of aged tap water, we introduced groups of eight

138   tadpoles with two food bricks of animal materials of each concentration and two food bricks

139   of algal materials of each concentration. Our experimental design employed three different

140   treatments of food toughness: In treatment A, the four food bricks were of the same

141   toughness (agar concentration 0.5%); in treatment B, the algal materials were tougher than

142   the animal ones (agar concentration 1% vs. 0.5%) and in treatment C, the animal materials

143   were tougher (agar concentration 1% vs. 0.5%). Each treatment was replicated 11 times,

144   making a total of 33 experimental units. Controls consisted of containers with food bricks but

145   with no tadpoles and were replicated six times. The controls were used to estimate the

146   amount of food that was potentially dissolved in water. We left the tadpoles to feed for 48 h,

147   and the foods remaining after that time were dried at 55°C for 36 h. The percentage of

148   removed food was estimated by dividing the dry weight of remaining food brick in question

149   by the mean dry weight of food bricks from the associated control (Taylor et al. 1995).

150   Experiment 2: Effects of Individual Density

151   In this experiment, we tested how the feeding activities of individual tadpoles

152   changed with increasing competitor density. We observed the food choice and feeding

153   duration of individual tadpoles under three different group sizes (one, two, or five individuals

154   per container; hereafter, Density 1, Density 2, and Density 5). Punzo (1992) applied similar

155   densities when testing social facilitation in tadpoles. As in Experiment 1, the replicates

156   consisted of 1-L containers filled with 0.5 L aged tap water and four food bricks of animal

157   and algal materials of different concentrations (1x and 2x) but of the same toughness (0.5%

158   agar solution). We introduced the respective number of tadpoles into each container, allowed

159   them to acclimate for a period of 5 min, and then recorded tadpole feeding behavior for 15

160   min with a digital camera at 24 frames/s. The foods were tagged with small pins to

161   differentiate between high and low concentration foods. Within each group, individual

162 tadpoles were identified by stopping the recording at the onset of each filming period. From

163 each recording, a single focal tadpole was randomly selected. Feeding was defined as when

164 the tail is raised and undulated to keep the mouth next to the food (Altig and Christensen

165 1981). In contrast to the first experiment, we used feeding duration as an indicator of food

166 preference because the manner by which we manipulated the food materials did not allow us

167 to measure individual food intake, especially at Density 1. Each density treatment was

168 replicated 32 times.

169   Data Analysis

170   In Experiment 1, we analysed the effect of food properties on tadpole preference

171 using conventional linear models, as this is more appropriate for our percentage data

172 (Crawley 2013). We combined the results from the three treatments and performed a linear

173 mixed-effects model with the package "lme4" (Bates et al. 2012) using the function "lmer."

174 Our response variable, the "proportion of removed food," was arcsine square-root-

175 transformed prior to analysis. Our predictors were "food type" (animal or algal material),

176 "food concentration" (high and low) and "food toughness" (high and low). We had two

177 random effects with "container" (11 replicates per treatment) nested within "treatments" (the

178 three combinations of food block toughness).

179   In Experiment 2, we used Generalized Linear Mixed Model fitted by maximum

180 likelihood assuming a Laplace approximation to the likelihood function (package "lme4")

181 using the function "glmer." We fitted our data to a negative binomial distribution (following

182 a comparison between a Poisson, a binomial and a negative binomial distribution using

183 Akaike Information Criterion). Our response variable was the duration that an individual

184 tadpole feeds on a specific food type (measured in seconds). Our predictors were "tadpole

185 density" (Density 1, 2 and 5), "food type" (algal or animal materials) and "food concentration"

186 (1x and 2x). We set "container" (32 replicates per treatment) as a random effect.

187   For the analyses of both experiments, *P*-values were obtained by likelihood ratio tests

188   of the full model with the effect in question against the model without the effect of

189   explanatory variables using the function "anova." We considered a fixed effect as significant

190   when the difference between the likelihood of two models (with and without the effect in

191   question) was significant. To test for food preference, we ran pairwise differences with the

192   function "lsmeans" (Lenth 2013) with Tukey adjustment after bootstrapping method using

193   the package "pbkrtest" (Halekoh and Højsgaard 2013). In Experiment 1, post-hoc tests were

194   conducted across treatments. In Experiment 2, we first analyzed how foraging activities

195   changed with the number of competitors, and subsequently compared food preference in the

196   individual tadpole at Density 1, 2 and 5. All statistical analyses were performed with R

197   (v3.2.3, R Core Development Core Team) with a significance level held at $\alpha = 0.05$.

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199   Rᴇsᴜʟᴛs

200   Experiment 1: Effects of Type, Toughness and Concentration of Food

201   Food type, concentration and toughness influenced tadpole food preference. The

202   tadpoles preferred algal to animal materials when the foods were similar in toughness or the

203   animal materials were tougher (Fig. 1). A two-way interaction between food type and food

204   toughness was significant, likely because food preference was reversed when the algal

205   materials were tougher than the animal ones (Table 1, Fig. 1). The other two-way interactions

206   (food concentration by food toughness and food concentration by food type), and the three-

207   way interaction, were not significant. Food toughness and food type had relatively little effect

208   on tadpoles' preference for foods available at high concentrations (Fig. 1). The ability of

209   tadpoles to discriminate food concentration, however, diminished when food toughness

210   increases (Fig. 1). Although the tadpoles reversed their food choice when the animal

211   materials were tougher, they still tended to prefer the high concentration to the low

212   concentration foods (Table 1, Fig. 1).

213   Experiment 2: Effects of Individual Density

214   Tadpole feeding duration did not change in the presence of one competitor ($Z = -1.30$,

215    $P = 0.39$) but increased in groups (Density 1 vs. Density 5, $Z = 4.24$, $P < 0.001$; Density 2 vs.

216   Density 5, $Z = 2.99$, $P = 0.007$). Competitor density, food type and food concentration

217   influenced feeding activity in the tadpoles (Table 2). In line with the first experiment, there

218   was no interaction between food type and concentration that affected tadpole food choice

219   (Table 2). The number of competitors tended to influence food preference ($\chi^2 = 5.44$, $P =$

220   0.06). When alone or in pairs, the tadpoles preferentially fed on the high concentration algal

221   material. In a group of 5 individuals, however, the tadpoles still exhibited a preference for the

222   high concentration algal material but increased their feeding on food items that contained

223   animal materials (Fig. 2).

224

225   DISCUSSION

226   Similar to previous research (Taylor et al. 1995; Kupferberg 1997), the tadpoles fed

227   selectively in these experiments. Our results indicate that food type, food toughness, food

228   concentration, and competitor density influence food choice in *Rhacophorus arboreus*

229   tadpoles. Generally, subjects preferred food that contained algal materials, in higher

230   concentration, and that was soft. Food preference was reversed when the algal materials were

231   tougher, and consequently feeding on the animal materials increased. In the second

232   experiment, we observed that the duration of feeding behavior in the tadpoles did not change

233   in the presence of one competitor, but almost doubled in the presence of a group. Those food

234   items that were less preferred in the absence of competitor became more preferred at a higher

235   density of tadpoles. Although aggressive individuals pushing others into adjacent food

236   patches might be responsible for a portion of the difference, the fact that all food bricks were

237   fed upon indicates that samplings were made but feeding was not random (otherwise the

238   amounts of food removed from the food bricks would have been similar).

239   As with many omnivores, feeding on both plant and animal foods might ensure that

240   tadpoles meet the necessary nutrients they cannot acquire from one food type alone. When

241   the foods were of the same toughness, the tadpoles preferred the algal to the animal materials.

242   It was not clear whether food choice was driven by calorie gain, nutrient content or

243   palatability in our experiment. A previous study indicated that even when comprising a small

244   component of the diet, animal materials can greatly contribute to growth in freshwater

245   omnivores (Evans-White et al. 2003). Schiesari et al. (2009) revealed that carnivory could be

246   ubiquitous in many pond dwelling tadpoles. Nevertheless, compared to filamentous algae and

247   other plant materials, animal materials represent a relatively smaller proportion of the diet. It

248   is not known whether food choice is mediated by preference or food availability but in a

249   parallel experiment, we found that animal materials were toxic if their concentration was too

250   high in the diet of tadpoles (Ramamonjisoa, personal observation). This might explain why

251   animal materials were consumed at a relatively lower rate compared to algal materials when

252   the two resources were of the same toughness in our experiment.

253   Food toughness influenced food selection. Recent studies suggested that

254   biomechanical traits (e.g., bite strength) predict feeding niche and food choice in herbivores

255   (Ibanez et al. 2013; Deraison et al. 2015). Indeed, increased toughness reduces the rate of

256   nutrient supply by reducing food ingestion and assimilation (Clissold et al. 2009), with direct

257   consequences on development. In contrast to terrestrial omnivores that use shearing and

258   tearing to break down and process food resources, tadpoles feed via scraping or filter-feeding,

259   collecting and vacuuming the surface of substrates (Alford 1999). Feeding occurs by

260   anchoring the oral disc onto a substrate and raking material from it (Venesky et al. 2010). A

261 tadpole's keratinized labial teeth might not be strong enough to penetrate tough materials;

262 thus, strength limitations might obscure food preferences by tadpoles that are based on food

263 hardness. This might explain why the tadpoles could not differentiate food concentrations at a

264 higher level of food toughness. Similarly, limitation in bite strength might explain the

265 opposite pattern in food choice when the algal materials were tougher than the animal ones.

266 This situation might be more common in nature because plants usually show the greatest

267 variation of toughness, and most animal tissues are relatively soft and decompose more

268 quickly. Resource protein content has often been suggested to be the prime factor of food

269 choice in tadpoles (Taylor et al. 1995; Kupferberg 1997; Richter-Boix et al. 2007). However,

270 previous laboratory work established that, as in some herbivores, resource toughness could

271 exert a larger effect on food choice than food protein content (Ramamonjisoa, personal

272 observation).

273   Tadpoles in our study were able to distinguish resources having a different

274 concentration of food. In the treatment of 2x amount of food per volume, the tadpoles

275 removed the same food volume but gained twice the actual nutrients per bite. This is in line

276 with the predictions of foraging models in that animals should choose the resource that yields

277 the most calories for the effort it takes to consume it (Pyke et al. 1977). The ability to

278 discriminate foods of different concentrations might not be pervasive among tadpoles. For

279 example, the larvae of *Lithobates sphenocephalus* and *Anaxyrus woodhousii* have the same

280 labial structure, but only *Anaxyrus woodhousii* tadpoles could distinguish materials with

281 different food concentration (Taylor et al. 1995). The ability of tadpoles to discriminate foods

282 of different concentrations is intriguing, and future tests should attempt to control for taste

283 and cue intensity emanating from the foods.

284   Our second key finding was consistent with the prediction that a common arousal

285 mechanism modulates feeding duration (Altig and Christensen 1981; Ziv et al. 1991).

286   Interestingly, feeding duration only increased in groups; the presence of one conspecific did

287   not trigger a competitive behavior that we predicted would have increased the feeding

288   activity in the individual tadpole (Altig and Christensen 1981). This pattern is not in line with

289   the common observations reported in some other taxa such as rodents (Harlow 1932),

290   molluscs (Ziv et al. 1991) and birds (Plowright and Redmond 1996) where the mere presence

291   of one conspecific causes the individual to increase its rate of feeding activity. The size of our

292   experimental unit, which could be relatively large at a tadpole scale, might be one of the

293   explanations. The exact cues responsible for the arousal are still unclear, but tadpoles are

294   thought to be sensitive to undulating tails (Michimae et al. 2005), and the stimuli from a

295   larger group could be more detectable than that from one individual.

296   The tadpoles used in our study were able to discriminate foods on a small

297   spatiotemporal scale and exhibited a preference for high concentration algal food. We

298   observed that subjects generally browsed briefly on each food brick before foraging longer on

299   a typical food, so physical contact with the food might be required to assess its quality. The

300   tadpoles exhibited density-dependent feeding behavior and food choice. Interestingly, food

301   preference did not change at low competitor density but did at the highest density of tadpoles

302   that we tested (Fig. 2), following the pattern observed in some fish and mammal taxa

303   (Schindler et al. 1997; Weale et al. 2000; Kausrud et al. 2006). The tadpoles remained

304   selective, but the presence of a group increased the preference for low-quality food following

305   the predictions of foraging models. In fact, the tadpoles did not decrease their preference for

306   high protein algal food but increased their preference for the other food items. Eterovick

307   (2000) reported similar results where single and aggregated *Rhinella crucifer* tadpoles

308   exhibited similar diets, but aggregated tadpoles incorporated more of the less-preferred food

309   in their diet. Our experiment could not answer whether the increasing preference for the less-

310   preferred food was driven by competition (aggressive tadpoles may displace others onto

311   adjacent food bricks), by social facilitation (Sontag et al. 2006), or by individual

312   specialization (Bolnick et al. 2011). In any case, the presence of conspecifics induced higher

313   activity, allowed the tadpoles to explore more food choices, and opened the opportunity to

314   feed on "not priority" foods.

315   In conclusion, food type, food concentration (as a proxy for resource profitability),

316   resource toughness and competitor density all appear to be important factors of resource

317   discrimination in tadpoles. Researchers have increasingly appreciated the feeding kinematics

318   available for study within this life-history stage (Venesky et al. 2010; de Sousa et al. 2014),

319   and there is still a relative lack of data about bite strength in relation to labial structure in

320   tadpoles. For example, understanding the bite strength might address the question of why

321   tadpoles having similar mouthpart configurations exhibit different feeding strategies (Taylor

322   et al. 1995). Perhaps the question to ask is: Would tadpoles maintain the same pattern of food

323   choice if they were presented the same foods along ontogeny, given that tadpole nutritional

324   needs may vary with body size and the state of the environment? Another research direction

325   would be providing a better understanding of the functional significance of a sole resource

326   diet, or switching between plant and prey, and in turn, how such behavior affects tadpole

327   fitness.

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458

459   TABLE 1.—Interactive effects of food type (animal or algal materials), toughness (0.5% or

460   1% agar) and concentration (1x and 2x amounts of food per unit volume) on food choice in

461   tadpoles of *Rhacophorus arboreus*. *P*-values were obtained by likelihood ratio tests following

462   a linear mixed-effects model (statistically significant values indicated in bold).

463

Predictor	χ^2	df	*P*
Food concentration (Concentration)	11.09	1	**< 0.001**
Food toughness (Toughness)	104.41	1	**< 0.001**
Food type	96.89	1	**< 0.001**
Food type × Toughness	18.76	1	**< 0.001**
Food type × Concentration	0.43	1	0.51
Concentration × Toughness	0.79	1	0.37
Food type × Concentration × Toughness	0.21	1	0.64

464

465

466   TABLE 2.—Interactive effects of competitor density (one, two or five tadpoles in a container),

467   food type (animal or algal materials) and food concentration (1x or 2x of food amount per

468   unit volume) on the feeding preferences of *Rhacophorus arboreus* tadpoles. *P*-values were

469   obtained by likelihood ratio tests following a generalized linear mixed-effects model with

470   negative binomial distribution (statistically significant values indicated in bold).

471

| Predictor	χ^2	df	*P*
Food type	29.42	1	**< 0.001**
Tadpole density (Density)	11.72	2	**0.002**
Food concentration (Concentration)	47.55	1	**< 0.001**
Food type × Density	3.42	2	0.18
Food type × Concentration	0.68	1	0.41
Density × Concentration	2.26	2	0.32
Density × Food type × Concentration	5.44	2	0.06

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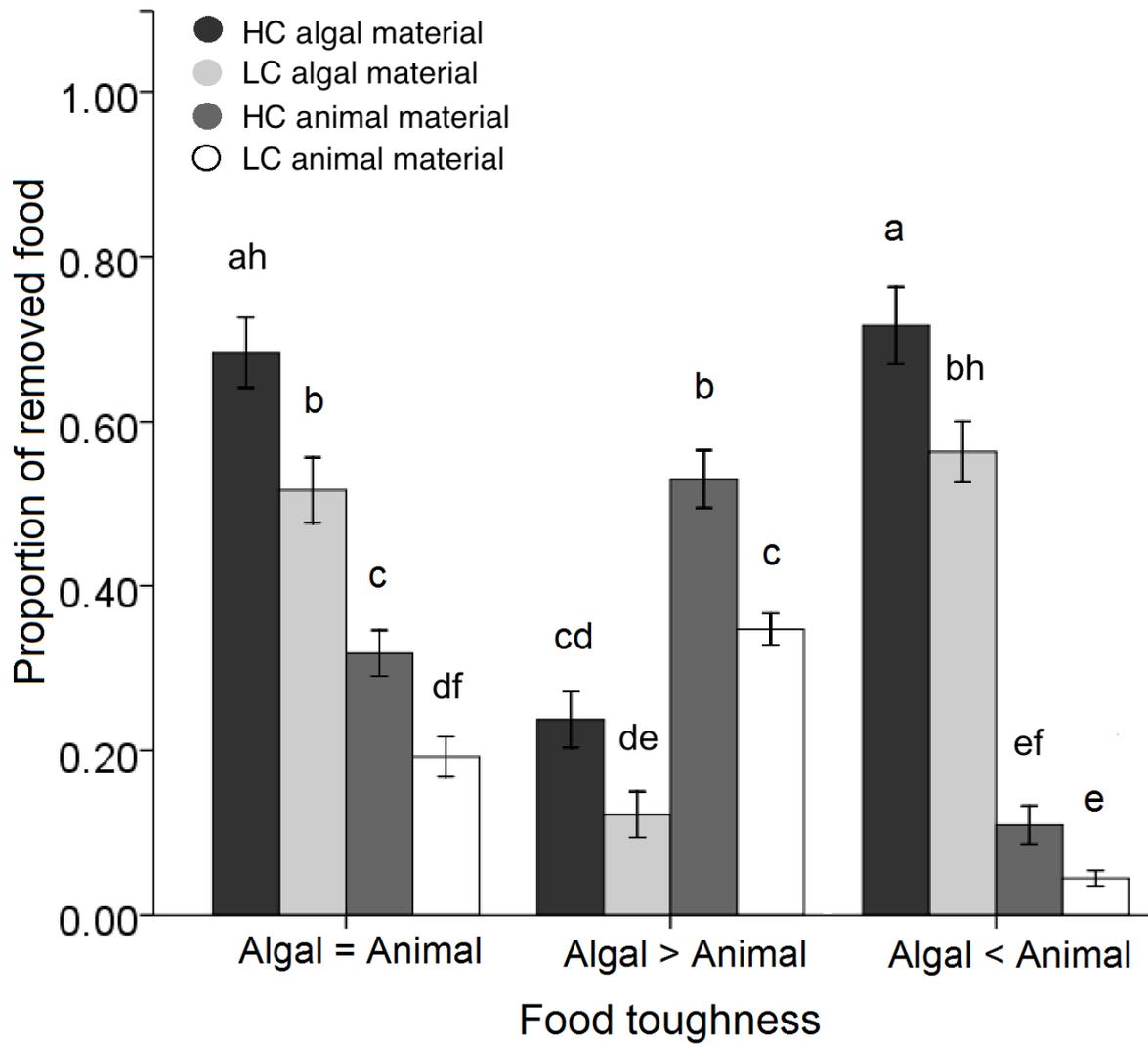
476   FIG. 1.—Proportion of food consumed by *Rhacophorus arboreus* tadpoles when

477   presented with animal and algal materials of different concentrations (LC and HC denote 1x

478   and 2x amounts of food per unit volume, respectively). Resource toughness was manipulated

479   over three treatments: same toughness (agar 0.5%) or one food (algal or animal materials)

480   being tougher than the other (agar 1% vs. 0.5%). Different lowercase letters indicate

481   differences among response means ($\pm$ 1 SE. $n = 11$ in each treatment) based on a linear

482   mixed-effects model with Tukey post-hoc adjustments.

483

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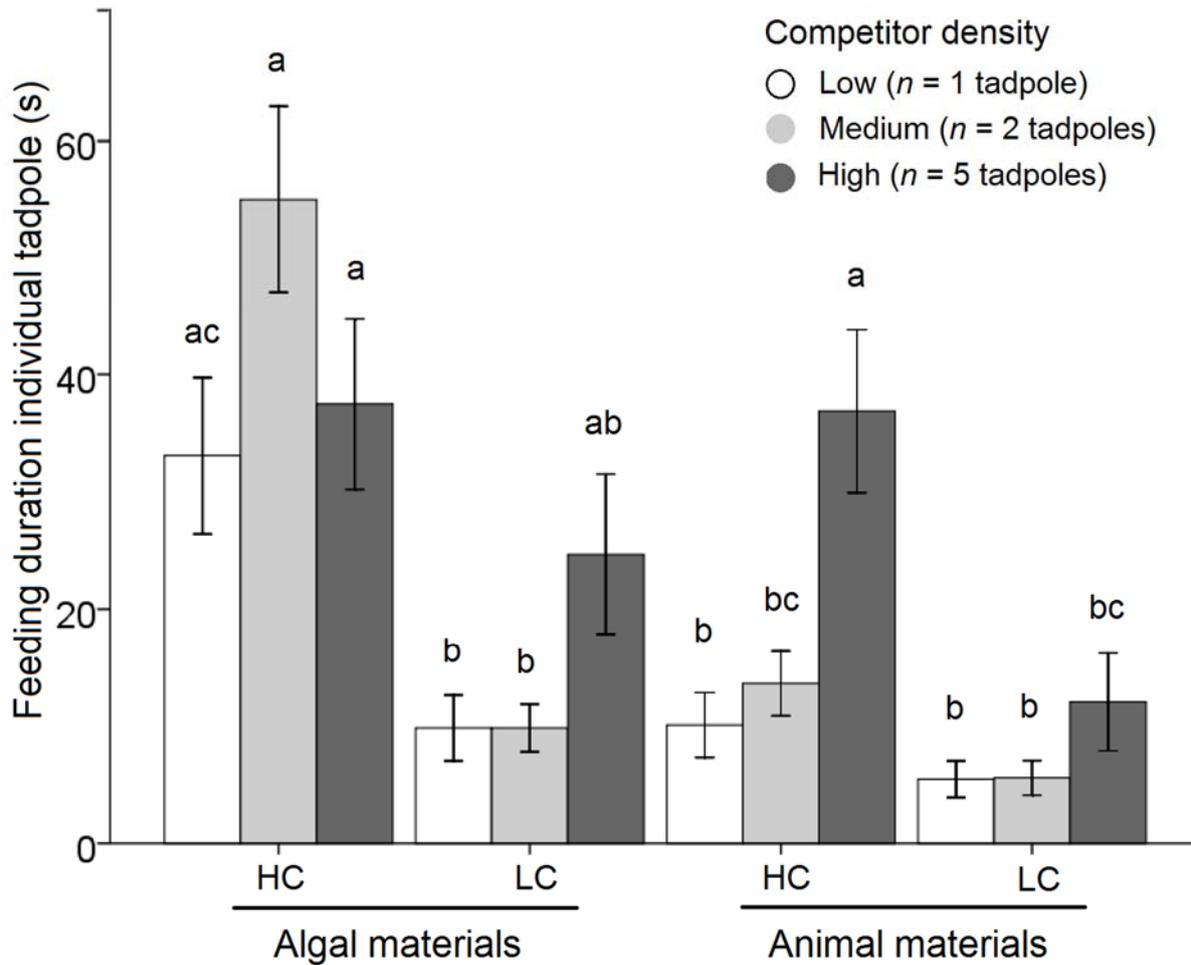
FIG. 2.—Duration of feeding by individual *Rhacophorus arboreus* tadpoles when presented with animal and algal materials of different concentrations (LC and HC denote 1x and 2x amounts of food per unit volume, respectively), but of the same toughness. Feeding behaviors were recorded when tadpoles were alone, in pairs, or in the presence of a group. Different lowercase letters indicate differences among response means ($\pm$ 1 SE. $n = 32$ in each level of density) based on a general linearized mixed-model with negative binomial distribution with Tukey post-hoc adjustments.