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8-1-2020

Relative size underlies alternative morph development in a salamander

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Recommended Citation

Moore, M.P., Pechmann, J.H.K. & Whiteman, H.H. Relative size underlies alternative morph development in a salamander. *Oecologia* (2020). <https://doi.org/10.1007/s00442-020-04723-8>

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1 **TITLE: Relative size underlies alternative morph development in a salamander**

2

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13 **RUNNING TITLE: Relative size and polyphenism**

14

15 **AUTHOR CONTRIBUTIONS:** HHW and JHK designed the study and collected all data.

16 MPM conducted all analyses and wrote the manuscript. All authors contributed to subsequent
17 revisions.

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23 **ABSTRACT**

24 Size thresholds commonly underlie the induction of alternative morphological states. However,
25 the respective importance of absolute and relative size to such thresholds remains uncertain. If
26 absolute size governs expression, morph frequency should differ among environments that
27 influence absolute sizes (e.g. resources, competition), and individuals of the same morph should
28 have similar average sizes across environments. If relative size determines expression, the
29 frequency of each morph may not differ among environments, but morphs within each
30 environment should differ in size relative to one another. We tested these predictions in a
31 salamander (*Ambystoma talpoideum*) that develops into either a terrestrial metamorph or an
32 aquatic paedomorph. To generate size variation within and among environments, we reared
33 individuals in mesocosm ponds across three conspecific densities. We found that morph
34 frequency did not differ among density treatments, and the morphs were not similarly sized
35 within each density treatment. Instead, within each environment, relatively larger individuals
36 became metamorphs and relatively smaller individuals became paedomorphs. Relative size
37 therefore determined morph development, highlighting the importance of an individual's social
38 context to size-dependent morph induction.

39

40 **Keywords:** facultative paedomorphosis; intraspecific competition; life-history variation;
41 polyphenism; resource polymorphism

42

43

44 INTRODUCTION

45 Discrete, alternative phenotypes are taxonomically widespread and often enable individuals to
46 optimize fitness through differential resource use (Smith and Skúlason 1996). The induction of
47 these morphs commonly depends on a suite of external and internal factors, whereby even
48 genetically identical individuals can express alternative phenotypes based on differing
49 developmental environments (Nijhout 2003; West-Eberhard 2003). Such “polyphenisms”
50 broaden the range of environmental and social circumstances to which a single genotype can
51 produce well-adapted phenotypes (Sultan and Spencer 2002; Nijhout 2003). Polyphenisms also
52 appear to regulate the diversification patterns of many lineages (Pfennig et al. 2010). Identifying
53 the factors underlying polyphenic expression, as well as the ways in which they influence
54 development, therefore can provide insight into the origins and maintenance of alternative
55 phenotypes (Smith and Skúlason 1996; Moczek et al. 2011) and of phenotypic diversity more
56 generally (West-Eberhard 2003; Pfennig et al. 2010).

57 One factor that is commonly associated with alternative morph development is body size
58 (e.g. Wheeler 1991; Tomkins et al. 2011; Phillis et al. 2016), likely because the advantages of
59 each morph usually also depend on an individual’s size (e.g. Michalczyk et al. 2018). Size-
60 dependent morph development can arise via the non-mutually exclusive effects of two features
61 of an individual’s size: its absolute size and its relative size. When a population’s size
62 distribution is temporally constant, morph development should evolve to depend entirely on an
63 individual’s absolute size (Tachiki and Koizumi 2016). Under such conditions, morph induction
64 typically occurs if an individual surpasses energetic thresholds that are themselves correlated
65 with absolute size (Nijhout 2003; Tomkins and Moczek 2009). Alternatively, when a
66 population’s size distribution varies across generations, and negative frequency-dependent

67 selection maintains both morphs in the population, morph development should evolve to rely on
68 an individual's size relative to its competitors (i.e. relative size; Tachiki and Koizumi 2016).
69 Here, the relatively largest individuals express one morph, while the relatively smallest express
70 the other (Tompkins and Hazel 2007). In these cases, relative size often determines the outcome
71 of competition for essential resources (e.g. Ziemba and Collins 1999), which links it to the
72 physiological factors that underlie morph induction (e.g. Lorenzi et al. 2012). Although the
73 effects of absolute and relative size on the expression of behavioral alternatives are well
74 characterized (e.g. alternative mating strategies; Gross 1996; Tomkins and Hazel 2007), their
75 effects on the expression of life-history and/or morphological alternatives remain less well
76 studied (Maret and Collins 1994; Warner et al. 1996; Frankino and Pfennig 2001).

77 Facultative paedomorphosis in salamanders—the development of a reproductive aquatic
78 “paedomorphic” phenotype instead of, or sometimes prior to, a terrestrial “metamorphic”
79 phenotype—is well suited for assessing how absolute and relative size influence morph
80 development. Theory extended from the classic models of amphibian metamorphosis (Wilbur
81 and Collins 1973; Werner 1986; Rowe and Ludwig 1991) predicts two size-dependent
82 trajectories of induction (Whiteman 1994). When aquatic conditions promote high survival and
83 rapid growth (e.g. high resources, low predation), the largest individuals within these
84 environments should become paedomorphs while smaller individuals metamorphose to escape
85 competition from their larger counterparts (“Paedomorph Advantage” mechanism). In contrast,
86 when aquatic conditions are less favorable to survival and growth (e.g. low resources, high
87 predation), the largest individuals should escape from the natal habitat via metamorphosis
88 whereas individuals that do not reach minimum thresholds for metamorphosis mature as
89 paedomorphs rather than waiting to attain larger sizes (“Best-of-a-Bad Lot” mechanism). While

90 morphs arising across natural and experimentally manipulated environmental gradients often
91 differ in size (reviewed in Whiteman 1994; Denoël et al. 2005), the respective importance of
92 absolute and relative size to induction is unknown.

93 We evaluated the influence of absolute and relative size on morph development in the
94 polyphenic salamander *Ambystoma talpoideum*. We began by raising larvae in mesocosm ponds
95 across three conspecific densities. We then used the resulting size variation within and across
96 environments to assess how relative and absolute size influence morph development. If relative
97 size affects morph expression, morph frequencies may be similar among density treatments, and
98 one morph will be consistently larger than the other within each mesocosm pond and within each
99 density treatment. If absolute size influences morph development, morph frequencies will differ
100 among density treatments that influence absolute sizes, and the average size of each morph
101 should be similar regardless of the mesocosm pond or density treatment. Finally, the effects of
102 relative size could also depend on absolute size, if, for instance, relative size becomes important
103 only after some minimum absolute size is reached. In such cases, one morph may: 1) only occur
104 above some minimum absolute size; 2) be very rare in high-density treatments, where all
105 individuals are small, but be equally as common as the other morph in medium- and low-density
106 treatments, where individuals are larger; and 3) be consistently larger than the other morph
107 within the subset of tanks and density treatments in which they are both induced.

108

109 **METHODS**

110 *Study System and Collection*

111 *Ambystoma talpoideum* is found in the southeastern United States and northward along the
112 Mississippi River Valley into southern Illinois (Petranka 1998). Individuals typically mature as

113 paedomorphs or undergo metamorphosis before their first winter or prior to maturing in the
114 following spring (Petranka 1998). Paedomorphic *A. talpoideum* remain as mature adults in the
115 aquatic environment or will sometimes subsequently undergo metamorphosis (e.g. Doyle and
116 Whiteman 2008); however, metamorphs cannot become paedomorphs. Relative to other nearby
117 populations, our source population (Ellenton Bay, Savannah River Site, SC) has a longer larval
118 period, higher frequency of paedomorphosis, and greater sensitivity to pond drying (Semlitsch et
119 al. 1990).

120 To generate individuals for this experiment, we bred adults by releasing 9 males and 15
121 females into two 1000 L polyurethane tanks filled with aged water and leaf litter at the Savannah
122 River Ecological Laboratory (SREL). From these tanks, we collected 1008 embryos, which we
123 then mixed and randomly assigned by treatment (see below) into our experimental ponds.

124

125 ***Experimental Design***

126 We reared larvae in 1000 L polyurethane tanks at one of three densities (Low = 10, Medium =
127 24, High = 50 individuals per tank; n = 12 tanks per density), chosen to mimic the range of
128 natural competition and to generate relatively continuous size variation (Semlitsch 1987). After
129 filling the tanks with well water and 1.75 kg of leaf litter, we covered them with mesh lids to
130 prevent colonization by Hylid treefrogs and predatory macroinvertebrates (e.g. *Aeshnidae* and
131 *Dytiscidae* spp.). Standpipes maintained each tank's water depth at 45 cm. Starting at the
132 beginning of the experiment, we also periodically added 1.5 L of concentrated, field-collected
133 plankton to each tank, providing a food source for the larvae. A mesocosm approach was well
134 suited for our study because the focal species can complete its entire life cycle in ponds of this
135 size, and these venues possess features of natural ponds that cannot easily be simulated in lab

136 studies (e.g. self-sustaining food web, natural photoperiod, diurnal temperature changes; Wilbur
137 1997; Semlitsch and Boone 2009).

138 We introduced the salamanders to tanks on 10 March 1997 (Day 1). To gain a fuller
139 picture of morph expression (see also Doyle and Whiteman 2008), the study concluded the
140 following May (after 438 days). In the final week, half of the tanks were accidentally dried much
141 faster than is natural (i.e. overnight). As this drying did not affect the probability of expressing
142 one morph or the other (all $P > 0.223$), or the relationships between morph expression and body
143 size (all $P > 0.253$), it does not bias our results and conclusions (see Electronic Supplementary
144 Materials, ESM; Table S1).

145 We captured individuals with minnow traps on days 76-77 (May 1997), 226-228
146 (October 1997), 297-303 (January 1998), 363-366 (March 1998), and 437-438 (May 1998). We
147 also set out and regularly checked floating plastic boxes with mesh ramps, which allowed
148 metamorphs to climb out of the water. We measured each captured individual's snout-vent
149 length (SVL) to the nearest 0.5 mm using a ruler and then returned all gilled individuals to tanks.
150 We focused on SVL, rather than mass, because it changes less across metamorphosis and is not
151 confounded with egg production by paedomorphic females (Dodd 2010). Once the larvae were
152 large enough to handle without injuring them (day 226), we uniquely toe clipped each captured
153 individual with microdissecting scissors. Individuals were considered metamorphs if they had
154 resorbed their gills and tail fin, and we removed them from their tanks upon observation. To
155 avoid destructive sampling and decreasing tank densities, we differentiated paedomorphs from
156 larvae prior to the final sample by visually inspecting their cloacae for swelling and pigmentation
157 and by "candling" with a fiber optic light to observe eggs. On day 438, we emptied all tanks and
158 recovered and measured all remaining survivors. We sacrificed animals with MS-222, fixed them

159 in 10% formalin, and preserved them in 70% ethanol. We dissected aquatic individuals to
160 differentiate paedomorphs from larvae. Paedomorphic males have enlarged, pigmented vasa
161 deferentia and testes, while paedomorphic females have pigmented ova (Semlitsch 1987).

162

163 **STATISTICAL ANALYSES**

164 We conducted analyses with R v.3.6.0 (R Core Team 2019). For analyses of morph and size, we
165 used an individual's traits at the final capture except where noted (see below for further
166 rationale). Mixed-effects models were fit using 'lme4' (Bates et al. 2015). When used,
167 significance tests were conducted with likelihood ratio tests in which we compared a model with
168 all of the effects to one without the effect of interest. Post-hoc tests were conducted using the
169 *lsmeans* package (Lenth 2016). We report parameter estimates \pm SE from the fitted models.

170 We began by comparing survival among density treatments using a generalized linear
171 model with a quasibinomial error distribution. We also verified the presence of size differences
172 among density treatments using a linear mixed-effects model with each individual's SVL as the
173 response, density as a fixed effect, and tank as a random effect.

174 To first determine if morphs differed in average body size across the entire study (e.g.
175 Semlitsch 1987; Doyle & Whiteman 2008), we assessed overall size differences between
176 metamorphs and paedomorphs using a linear mixed-effects model with each individual's final
177 SVL as the response, its morph as a fixed effect, and its tank as a random intercept. Next,
178 because our study design did not experimentally manipulate each individual's position in the size
179 hierarchy within its tank, and there was not a single best analysis to conduct, we used several
180 approaches to examine the effects of absolute and relative size on morph induction.

181 If morph expression depends on absolute size variation, then the frequency of each morph
182 within a tank should be related to the average size of individuals in that tank. We used two
183 analyses to test this. We first used a generalized linear model with a quasibinomial error
184 distribution to examine if the proportion of individuals expressing each morph (arbitrarily scored
185 as 1=metamorph, 0=paedomorph) within a tank varied with the average size of the individuals
186 within that tank. We also used a similar model to test for differences in morph expression among
187 density treatments, which explained the vast majority of variation in tank-mean size ($R^2=0.900$;
188 $F_{2,33}=149.0$, $P<0.001$). Because of their strong association, and because we were interested in the
189 overall effect of tank-mean size and of density treatment, rather than the effect of either one after
190 controlling for the other, we report the results from separate models. However, results were
191 qualitatively similar even when fitting a model with both terms simultaneously.

192 Next, for individuals within those tanks where both morphs developed, we used a multi-
193 model inference approach to examine the effects of absolute and relative size on morph
194 expression. First, we fit a generalized linear mixed-effects model that included an individual's
195 morph as the response (scored as above); its relative size, absolute size, and their interaction as
196 fixed effects; and tank as a random effect. Here, relative size was calculated as the mean SVL of
197 an individual's tankmates subtracted from the individual's SVL. To improve model convergence,
198 we also "centered" an individual's absolute size by subtracting the mean SVL of all individuals
199 in the experiment from the individual's SVL (Schielzeth 2010). Using AIC_c, which is less
200 sensitive to issues of correlated predictors than likelihood ratio tests (Freckleton et al. 2011;
201 Grueber et al. 2011), we compared models with all possible combinations of relative and
202 absolute size via the 'dredge' function in *MuMIn* (Bartoń 2019). Models were considered
203 equivalent if they had the same number of parameters and were separated by less than 2

204 (Burnham and Anderson 2002). Despite the relationship between relative size and absolute size,
205 simulations indicated that this multi-model inference approach rarely excludes an important term
206 from the best-supported model (see ESM for full details). To evaluate the magnitude and
207 direction of any effects that absolute and relative size have on morph expression, we used either
208 the parameter estimates of the best-supported model or model-averaged estimates for sets of
209 equally supported models ($\Delta AIC_c < 2$). We also compared another set of models beginning with
210 all of the terms described above, except an individual's density treatment was included instead of
211 its absolute size. If an individual's relative size controls morph expression, then relative size will
212 be included in the best-supported models. If an individual's absolute size determines morph
213 expression, then the best-supported model will include an individual's absolute size or its density
214 treatment, which controls the vast majority of variation in absolute size. If, for example, relative
215 size only affects morph expression after some minimum absolute size has been reached or only
216 in some densities, then the interaction between relative size and absolute size or between relative
217 size and density should be in the best-supported model. Because of the very strong association
218 between an individual's size and its tank's density treatment, a single global model
219 simultaneously including fixed effects of density, absolute size, and relative size did not
220 converge. However, we present several other analyses using this approach, including models of
221 absolute size and density, in the Electronic Supplementary Materials. In all cases, the results
222 from these analyses align with the those presented in the main text (ESM Table S3).

223 Given the variation in size and morph frequencies among tanks (see Results), we next
224 tested if one morph was consistently larger than tankmates of the other morph. For each tank
225 where both were produced, we first averaged the sizes of its metamorphs and pedomorphs.
226 Next, we counted the tanks where the average size of each morph was larger than that of the

227 other, and then we used a χ^2 test to evaluate if one morph was the larger of the two within each
228 tank more often than would be expected by chance. Importantly, if the body-size distribution
229 within every tank was similar, this approach would not clarify the role of relative size. However,
230 this was not the case (see Results), and one morph being consistently larger than the other within
231 each tank would support a role for relative size.

232 Finally, we compared the morphs' sizes using a linear mixed-effects model with density
233 and morph as fixed effects. Tank was fitted as a random effect, and metamorphs and
234 paedomorphs across all tanks were included. This approach compares the two morphs' sizes after
235 accounting for the variation in size associated with the individual's density treatment. It therefore
236 tests if morphs are different sizes *within* each density. As density explained the vast majority of
237 variation in tank-mean size, size differences between the morphs within each density should
238 emerge if there are effects of relative-size variation within the tanks. One additional benefit of
239 this approach is that it allowed us to test if the smaller morph in one density was larger than the
240 larger morph in a higher density—a pattern indicative of relative-size effects. If relative size
241 underlies morph development, then, after accounting for the effects of density, morph should be
242 associated with SVL. Moreover, if the effect of relative size on morph expression differs among
243 density treatments (Whiteman 1994), we could find a significant morph by density interaction,
244 whereby one morph is larger in low-density treatments but smaller in high-density treatments.

245 Although only one individual underwent metamorphosis prior to the final month of the
246 experiment (April 1998), following individuals across ontogeny would yield insight into how
247 absolute and relative size affect development. However, several supplemental analyses indicate
248 that using traits at the end of the experiment is unlikely to bias our conclusions (see ESM for full
249 details). First, among the small subset of marked individuals that were recovered and identified

250 at the end of the experiment (63 out of 163 total metamorphs and paedomorphs, 38.7%), those
251 that became paedomorphs and then metamorphosed did not differ in absolute ($t=1.4$, $P=0.17$) or
252 relative SVL ($t=0.9$, $P=0.38$) from those that metamorphosed directly from the larval state
253 (ESM, Table S2). Similarly, among the smaller subset of individuals who were marked in
254 October 1997 and recaptured as metamorphs or paedomorphs, their size at this time was strongly
255 related to their size in May 1998 ($R^2=0.755$, $F_{1,31}=95.5$, $P<0.001$). Growth between these time
256 points also did not differ substantially among the developmental trajectories ($\chi^2_2=5.0$, $P=0.08$).
257 Thus, final size reasonably reflects size when morph development typically begins.

258

259 RESULTS

260 Survival did not differ significantly among density treatments ($F_{2,33}=2.7$, $P=0.08$), but body size
261 did ($\chi^2_2=53.8$, $P<0.001$; all pairwise linear contrasts $P<0.001$). Additionally, across the study,
262 metamorphs were 3.29 ± 0.61 mm larger than paedomorphs ($\chi^2_1=27.2$, $P<0.001$; Fig. 1).

263 The frequency of metamorphs and paedomorphs within each tank was not related to the
264 mean body size within the tank ($\chi^2_1=1.4$, $P=0.25$) or to the tank's density treatment ($\chi^2_2=1.9$,
265 $P=0.39$).

266 Among those individuals that were reared within the 15 tanks where both morphs
267 developed, we next used a multi-model inference approach to assess the effects of an
268 individual's absolute and relative size on morph expression. A model including only relative size
269 had the most support, though a more complex model that included both relative size and absolute
270 size had a similar, but slightly worse, AIC_c score (Table 1). Model-averaged parameter estimates
271 indicated that, for a given absolute size, the log-odds of metamorphosis increased by $0.384 \pm$
272 0.142 for every 1 mm increase in relative size (95% CIs: 0.103-0.665; Fig 1A). In contrast, for a

273 given relative size, the log-odds of metamorphosis only increased by 0.045 ± 0.081 for a 1 mm
274 increase in absolute size (95% CIs: -0.115-0.205). We also compared candidate models starting
275 from one that included an individual's relative size, its density treatment, and the interaction
276 between relative size and density treatment (Table 1). Among these candidate models, only the
277 model including relative size was well supported (Table 1), with the log-odds of an individual
278 undergoing metamorphosis increasing by 0.421 ± 0.130 for every 1 mm in relative size (95%
279 CIs: 0.196-0.719). Collectively, these two comparisons indicate that the relatively largest
280 individuals within tanks and within density treatments underwent metamorphosis. Alternative
281 approaches for examining the effects of absolute and relative size were also consistent with a
282 strong effect of relative size (ESM, Table S3). Likewise, a multi-model inference approach
283 revealed a strong effect of relative size when calculating relative size as an individual's size
284 divided by the mean size of its tankmates (ESM, Table S3).

285 We next assessed if one morph was usually the larger of the two within the tanks where
286 both developed (2 high-density tanks, 5 medium-density tanks, and 8 low-density tanks). Despite
287 the density treatment causing large differences in the average size of individuals among these
288 tanks, metamorphs were larger, on average, than their paedomorph tankmates within 93% of
289 tanks ($\chi^2_1=11.3$, $P<0.001$).

290 After accounting for overall density-dependent reductions in size ($\chi^2_2=63.2$, $P<0.001$),
291 metamorphs were consistently larger than paedomorphs within each density (morph: $\chi^2_1=36.7$,
292 $P<0.001$; interaction: $\chi^2_2=4.1$, $P=0.13$, Fig. 1B). Notably, paedomorphs from low-density
293 treatments were larger than metamorphs from medium-density treatments (linear contrast: $t=2.8$,
294 $P=0.008$; Fig. 1B), though medium-density paedomorphs were not different from high-density
295 metamorphs ($t=1.4$, $P=0.54$). Results were similar when focusing only on the tanks where both

296 morphs developed (ESM, Table S4). Individuals that were marked and re-captured also showed
297 this pattern ($\chi^2=27.2$, $P<0.001$). Within density treatments, paedomorphs were smaller than
298 metamorphs that transitioned directly from the larval state ($t=-4.6$, $P<0.001$) and metamorphs
299 that became paedomorphs first ($t=-3.2$, $P=0.006$; ESM, Fig. S1).

300

301 **DISCUSSION**

302 We evaluated the effects of relative and absolute size on morph development in a salamander,
303 *Ambystoma talpoideum*. Metamorphs tended to be larger than paedomorphs across the study, and
304 multiple lines of evidence indicate that relative size strongly influenced this pattern. First, several
305 multi-model inference approaches found that the relatively largest individuals within each tank
306 and within each density treatment were more likely to undergo metamorphosis while relatively
307 smaller individuals were more likely to become paedomorphs. Second, even though the size
308 distribution differed among tanks and density treatments, metamorphs averaged larger sizes than
309 paedomorphs within nearly all tanks. Third, metamorphs were also consistently larger than
310 paedomorphs within each density treatment. Finally, despite being smaller than metamorphs
311 from low-density treatments, paedomorphs from low-density treatments were larger than
312 metamorphs from medium- and high-density treatments. In contrast, we found little support for
313 an effect of absolute size on morph expression. First, the proportion of morphs within each tank
314 was not related to either the average size of individuals in the tank or to the tank's density
315 treatment. Second, although absolute size was included in a well-supported model that also
316 included relative size, this model had a worse AIC_c score and was less parsimonious than the
317 best-supported model, which only included relative size. The effect of absolute size on morph
318 expression also had confidence intervals that overlapped 0. Third, rather than individuals from

319 the same morph being similarly sized across density treatments, morphs were consistently
320 different sizes within each density treatment. While manipulations that place absolutely large
321 individuals at the smaller end of a population size distribution, and vice versa, could empirically
322 disentangle the effects of absolute and relative size (*sensu* Maret and Collins 1994; Van Buskirk
323 et al. 2017), our correlative findings indicate that relative size regulates morph development.

324 Size-dependent models of morph development often assume absolute-size thresholds
325 (e.g. Wheeler 1991; Emlen and Nijhout 2000; Chapman et al. 2011). Among the size-dependent
326 models of facultative paedomorphosis, our results are largely consistent with the “Best-of-a-Bad
327 Lot” trajectory, whereby individuals become paedomorphs when they cannot reach the minimum
328 threshold for metamorphosis (Whiteman 1994). However, we did not find much evidence for
329 these absolute-size thresholds, nor did we find that the effect of relative size changed with the
330 favorability of the aquatic environment for growth (cf. Whiteman 1994). Other natural and
331 mesocosm studies that have considered competition have also found patterns of morph
332 expression and size differences that are consistent with the “Best-of-a-Bad Lot” trajectory (e.g.
333 Doyle and Whiteman 2008; Whiteman et al. 2012; Lackey et al. 2019), but this is the first to
334 show that relative size is largely responsible. Given these findings, it may be valuable to expand
335 size-dependent models of this polyphenism to include a larger role for relative size.

336 Because relative size influences morph expression, understanding the factors that
337 generate variation in relative size should be an emphasis for future research. Previous work has
338 shown that size variation often stems from many factors (Ziembra and Collins 1999), including
339 additive genetic effects on growth or resource acquisition (Mousseau and Roff 1987; Watkins
340 and McPeck 2006), maternal effects on hatching size or hatching date (Moore et al. 2015; Moore
341 et al. 2019), and fortuitous consumption of high-value resources early in life (Wilbur and Collins

342 1973; Álvarez and Nicieza 2002; Whiteman et al. 2003). Once such variation arises, however,
343 interference competition will reinforce it: relatively larger individuals will subsequently
344 outcompete smaller individuals and maintain their status in the hierarchy (Ziembra and Collins
345 1999; Johnson et al. 2003; Buston 2003). Although we do not know what caused relative size to
346 vary in our study, the strong correlation between size in October 1997 and size in May 1998 is
347 consistent with variation arising early in life and being maintained via such reinforcement. In
348 light of its importance to morph expression, examining the sources of relative size variation in
349 natural settings could provide insight into the origins and maintenance of facultative
350 paedomorphosis and, perhaps, other polyphenisms (Whiteman et al. 2012).

351 Whereas relative size strongly affected morph expression in this study, we found little
352 evidence that absolute size was particularly impactful. However, absolute size could be more
353 influential under other conditions. Our study generated a wide range of body sizes but still might
354 not have created small enough average sizes to observe effects of absolute size on morph
355 frequency or to identify some minimum threshold for metamorphosis (Wilbur and Collins 1973).
356 Likewise, our low-density treatments were higher than in some studies (cf. Semlitsch 1987;
357 Anderson and Whiteman 2015) and were higher than the very lowest densities observed in
358 natural populations (Anderson et al. 2018). Although it seems unlikely that using even more
359 extreme densities would have changed the frequency of metamorphosis or importance of
360 absolute size, other studies have produced a higher frequency of metamorphs than our study (e.g.
361 Semlitsch 1987; Doyle and Whiteman 2008; Anderson and Whiteman 2015). We therefore
362 cannot rule out the possibility that using even more extreme density treatments would have
363 increased the importance of absolute size. Beyond intra-cohort competition, absolute size could
364 also be influential in the context of other environmental factors. For instance, in natural

365 permanent or semi-permanent ponds, aquatic ambystomatids from previous cohorts compete
366 with and consume young-of-the-year (Wissinger et al. 2010; Whiteman et al. 2012; Anderson et
367 al. 2013). Size asymmetries of these inter-cohort interactions could render the aquatic
368 environment so unsuitable that only the very smallest individuals become paedomorphs
369 (Whiteman et al. 2012). Absolute-size thresholds could also differ among populations. In
370 organisms with environmental sex determination, for example, sex expression often occurs after
371 achieving some fraction of an individual's maximum possible body size, but the exact threshold
372 varies among populations and species (Munday et al. 2006). This subsequently alters the
373 likelihood of reaching the absolute-size threshold and, therefore, also whether or not relative size
374 can play any role at all (e.g. Collin 2006). Thus, although our results show that relative size can
375 determine morph expression over a range of ecologically relevant conditions, disentangling the
376 effects of absolute and relative size across a wider array of experimental and natural
377 environments remains necessary.

378 We tested here if morph expression depends on relative size, yet exploring the ecological
379 and physiological consequences of relative size variation will inform why morph expression has
380 evolved to rely on it in the first place. Relative size often affects an individual's competitive
381 outcomes more than absolute size (e.g. Warner et al. 1996; Ziemba and Collins 1999). Provided
382 that relative size remains reliably linked to competitive outcomes, this has at least two
383 consequences. First, because relative size determines the outcome of interference competition
384 (Ziemba and Collins 1999), relatively larger individuals could be better at acquiring resources
385 necessary for morph induction (Frankino and Pfennig 2001; Johnson et al. 2003). In this way,
386 relative size controls induction via acquisition differences of essential resources. However, under
387 such a scenario, absolute size seems like it should also have strong effects, which it did not in

388 this study. Alternatively, because of that same relationship between relative size and competitive
389 outcomes, individuals of the same relative size may experience their respective environments
390 similarly, and as a result, have similar physiological responses (Lorenzi et al. 2012). While the
391 neural and hormonal underpinnings of facultative paedomorphosis are poorly understood,
392 previous work has implicated the thyroxine hormone cascade (Voss et al. 2012), which interacts
393 with stress hormone concentrations (Denver 2009). These pathways require more research, and
394 experiments that manipulate circulating hormones and relate them to morph expression in
395 mesocosm and natural settings could illuminate the proximate mechanisms driving morph
396 expression.

397 As with the proximate factors linking relative size to morph expression, exploring the
398 selective pressures that have favored this relationship will provide insight into the evolution of
399 resource polyphenisms. For any cue to adaptively induce a resource polyphenism, it must predict
400 the future competitive outcomes for that individual (Nijhout 2003). Small relative size, and its
401 associated eco-physiological factors, may be a reliable cue if individuals retain their position in
402 the size hierarchy across life stages. Such a pattern is likely in *A. talpoideum* because: 1) growth
403 between metamorphosis and maturity is small (Semlitsch et al. 1988); 2) metamorphs typically
404 do not emigrate far into the terrestrial environment (Scott et al. 2013); and 3) paedomorphs
405 remain in their natal ponds. Additionally, for morph induction to be adaptively cued by small
406 relative size in any organism, those individuals must have higher fitness as one morph than they
407 would have had as the other (Roff 1996; West-Eberhard 2003). Paedomorphosis could be
408 favored for these individuals if relatively small metamorphs are outcompeted for the best
409 burrows and foraging opportunities by larger terrestrial counterparts (Searcy et al. 2014). With
410 larger individuals leaving the pond, reduced competition may also offset other unfavorable

411 conditions for relatively small individuals that remain in the pond as paedomorphs. Earlier
412 maturity and/or increased breeding frequency of paedomorphs (Whiteman 1997; Ryan and
413 Plague 2004; Lackey et al. 2019) could further compensate for any costs of being relatively
414 smaller than metamorphs during reproduction (e.g. mate attraction, Whiteman et al. 2006;
415 relative fecundity, Lackey et al. 2019). Because intense interactions with competitors frequently
416 persist across the life cycle, being relatively smaller than competitors in an earlier stage may
417 often predict lifetime competitive outcomes and, therefore, could be a cue for many resource
418 polyphenisms (Pfennig and Pfennig 2009).

419 It is also intriguing why selection would favor metamorphosis for relatively large
420 individuals that had likely been performing successfully in the aquatic habitat (Asquith and
421 Vonesh 2013; Michalczyk et al. 2018). One plausible explanation is that metamorphosis is
422 simply the default trajectory, and being relatively large provides no new information to shift
423 individuals from this path. Paedomorphosis, not metamorphosis, would then be sensitive to
424 relative size, which would mirror situations where the default morph is developed unless some
425 external factor induces the alternative (e.g. heterophyllic leaves, Cook 1968; carnivore-morph
426 tadpoles, Pfennig 1990). Being relatively large could also provide less reliable information than,
427 and be overridden by, extrinsic cues that indicated metamorphosis was their best option overall
428 (Whiteman 1994; Denoël et al. 2005). For example, under high desiccation or predation risk, the
429 cues associated with being larger than one's competitors may not be very predictive of one's
430 fitness prospects and could be ignored in favor of more informative cues (Werner 1986; Rowe
431 and Ludwig 1991). The fitness benefits of metamorphosis for relatively large individuals would
432 be clarified by experimentally inducing the expression of each morph in individuals across the

433 full range of relative sizes and then measuring their lifetime reproductive success (*sensu* Warner
434 and Shine 2008).

435 Overall, our results indicate that relative size underlies facultative paedomorphosis in
436 salamanders. Given the historical emphasis on absolute size, it would be useful to expand some
437 of the models of size-dependent morph expression to include a greater role for relative size.
438 Furthermore, habitat differences may favor varying degrees of reliance on relative size. The
439 specific thresholds for induction could therefore differ greatly, as has occurred in some
440 alternative mating tactics (Gerhardt et al. 1987) and environmental sex determination (Warner et
441 al. 1996). For instance, relative size as an aquatic larva may predict competitive outcomes in
442 later terrestrial stages less reliably in populations sourced by multiple natal ponds (Moore and
443 Whiteman 2016; Lackey et al. 2019). In such cases, selection could reduce reliance on relative
444 size and/or could increase the relative-size threshold such that the only individuals that
445 metamorphose are those that are certain to compete successfully in the terrestrial environment
446 (Tachiki and Koizumi 2016). Many other taxa with resource polymorphisms have life cycles
447 where the environment of just one stage varies widely among populations (e.g Moczek and
448 Nijhout 2003; Tomkins and Brown 2004), and such stage-dependent environmental variation
449 could commonly promote diversification in how individuals integrate the information conveyed
450 by relative size during development (Tomkins et al. 2011; Moore and Martin 2019). Thus,
451 beyond identifying how frequently relative size influences morph expression, insight into the
452 origins and maintenance of many size-dependent morphs will emerge from investigating how
453 ecological factors shape the strength of this reliance.

454

455 **ACKNOWLEDGEMENTS**

456 We thank the many mentors who have patiently awaited this work, especially J.W. Gibbons. T.
457 Ryan provided assistance in experimental monitoring. Feedback from T. Anderson, A. Lackey,
458 M. Dugas, and members of the CWRU Ecology and Evolution reading group improved the
459 presentation of the study. At various times throughout this long-gestating project, funding for
460 MPM was provided by the Watershed Studies Institute (WSI), an MSU Graduate Innovation
461 Assistantship, a GAANN Fellowship, the CWRU Department of Biology, as well as G.
462 Kornblum and the Living Earth Collaborative. JHKP was funded by the Savannah River Ecology
463 Laboratory (SREL), Florida International University, and Western Carolina University. HHW
464 was funded by the SREL, WSI, the MSU Department of Biological Sciences, an MSU CISR
465 award, and the NSF (DEB-1354787). Financial assistance was also provided by the Department
466 of Energy Office of Environmental Management under award number DE-EM0004391. This
467 report was prepared as an account of work sponsored by an agency of the United States
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476 States Government or any agency thereof.

477

478 **ETHICAL APPROVAL**

479 All applicable institutional and/or national guidelines for the care and use of animals were
480 followed.

481

482 **DATA AVAILABILITY**

483 Data used in these analyses available at Dryad Digital Repository
484 (doi:10.5061/dryad.sf7m0cg3p)

485

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- 650

651 **TABLES**

652 Table 1. Results from a multi-model inference approach that explicitly compared two sets of
653 candidate models of morph expression. All models included the stated fixed effects as well as a
654 random intercept that accounted for non-independence of individuals from the same tank.
655 Pseudo-R² statistics were estimated using the approach advocated by Nakagawa & Schielzeth
656 (2013). Although all analyses were conducted using the same responses from the same set of
657 individuals, convergence issues prevented us from fitting a single global model with all the of the
658 terms simultaneously. We therefore present results from approaches beginning with two separate
659 “full” models, even though some terms are shared between the two sets.

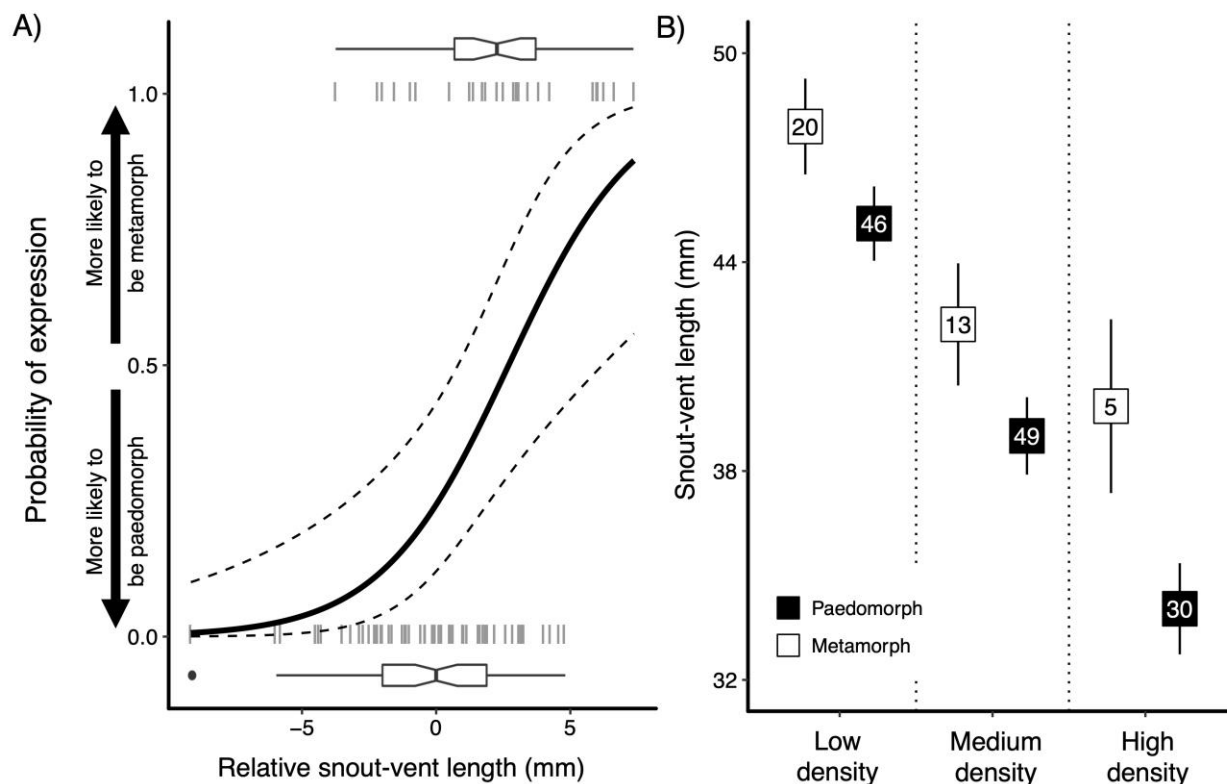
660

661 **Table 1.**

Approach	Rank	Fixed Effects	k	logLik	AIC _c	Δ	Weight	Pseudo-R ²
Relative Size (RS) vs SVL ¹	1	RS	3	-48.13	102.5	0.0	0.510	0.468
	2	RS + SVL	4	-47.44	103.3	0.8	0.343	0.462
	3	RS + SVL + RS:SVL	5	-47.39	105.5	3.0	0.118	0.473
	4	SVL	3	-51.00	108.3	5.8	0.029	0.387
	5	Int.	2	-56.41	117.0	14.5	0.000	0.130
Relative Size (RS) vs Density	1	RS	3	-48.13	102.5	0.0	0.863	0.468
	2	RS + Density	5	-47.96	106.6	4.1	0.112	0.464
	3	RS + SVL + RS:Density	7	-47.17	107.7	7.2	0.024	0.497
	4	Int.	2	-56.41	117.0	14.5	0.001	0.130
	5	Density	4	-56.41	121.3	18.8	0.000	0.129

662

663 1- As described in the main text, SVL was centered to improve model convergence.

664 **FIGURES**

665

666

667 Figure 1. The effects of relative size on morph expression. Metamorphic *A. talpoideum* tended to

668 be (A) the relatively largest individuals within a tank and (B) the largest individuals within a

669 density treatment. A) Each tick mark represents an individual that either became a metamorph

670 (1) or a paedomorph (0), and box plots are provided to aid visualization of the relative-size

671 distributions. The line is fitted from the best-supported mixed-effects model reported in the main

672 text, and it illustrates the predicted probability of an individual of a given relative size within a

673 tank becoming either a paedomorph or a metamorph (\pm 95% CIs). B) Squares represent the least-674 squares-mean SVL (\pm 95% CIs) for individuals expressing that morph. Numbers inside points

675 are the sample sizes.

676