

1 **Dominant convict cichlids (*Amatitlania nigrofasciata*) grow faster than subordinates when**
2 **fed an equal ration**

3

4 **Short title: Growth rate of dominant and subordinate cichlids**

5

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11

12 **Summary**

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14 Previous studies indicate that dominant fish grow faster than subordinate fish when fed equal
15 rations. It is unclear, however, whether this growth differential is caused by intrinsic differences
16 related to their propensity to become dominant, or by the extrinsic effect of the social stress
17 experienced by subordinates. We first tested whether dominant convict cichlids (*Amatitlania*
18 *nigrofasciata*) grew faster than subordinates when fed an equal amount of food. Second, we
19 tested whether the growth advantage of dominants occurred when only visual interactions were
20 allowed between pairs of fish. Third, we randomly assigned social status to the fish to rule out
21 the possibility that intrinsic differences between fish were responsible for both the establishment
22 of dominance and the growth differences. In three separate experiments, dominant fish grew
23 faster than size-matched subordinate convict cichlids, but the growth advantage of dominants
24 was higher when there were direct interactions between fish compared to only visual
25 interactions. Our results provide strong support for the hypothesis that the slower growth rate of
26 subordinate fish was due to the physiological costs of stress.

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28

29 *Keywords:* social status, growth rate, stress, convict cichlids, *Amatitlania nigrofasciata*

30 **Introduction**

31

32 The growth rate of individual animals is affected by both extrinsic factors, such as food intake
33 and ambient temperature (Weatherley & Gill, 1987; Scanes, 2003), and intrinsic factors, such as
34 aggressiveness and metabolic rate (Metcalf et al., 1992; Riebli et al., 2011). In cohorts of
35 animals, growth rate differences result in growth depensation, the increase in the variance of
36 body size within a cohort over time (Magnuson, 1962) in a wide variety of taxa (Łomnicki,
37 1988). Growth depensation is of particular interest for the aquaculture industry, in which the goal
38 is to maximize growth rate of fish while minimizing differences in body size between individuals
39 (Thorpe & Huntingford, 1992).

40 Growth depensation in fishes is thought to be primarily related to differences in food
41 intake (Rubenstein, 1981; Koebele, 1985). For example, when food is presented in an
42 economically defensible manner, dominants tend to monopolize a large share of the resource,
43 leading to large growth rate differences within groups (Magnuson, 1962; Noël et al., 2005).
44 However, food intake alone cannot explain growth depensation, because dominant fish grow
45 faster than subordinates, even when fed the same amount of food (Abbott & Dill 1989; Earley et
46 al., 2004). The lower growth rate of subordinate fish may be due to the physiological stress of
47 being forced to interact with a dominant individual (Filby et al., 2010). Indeed, the presence of a
48 conspecific increases the metabolic rate, decreases the food conversion efficiency and decreases
49 the growth rate of a focal fish (Wirtz, 1975; Wirtz & Davenport, 1976; Earley et al., 2004;
50 Millidine et al., 2009a). Hence, dominance status is a potentially important extrinsic factor
51 affecting growth rate.

52 Because previous studies allowed size-matched fish to establish their dominance status at
53 the beginning of feeding trials (Abbott & Dill, 1989; Earley et al., 2004), it is possible that
54 intrinsic differences between fish might have been related to both the probability of becoming
55 dominant and to growing faster. Fish that become dominant in laboratory conditions tend to have
56 higher intrinsic rates of metabolism, the capacity for growth, and the ability to process meals
57 (Metcalfe et al., 1992, 1995; Millidine et al., 2009a,b). Hence, the growth differential observed
58 between dominants and subordinates may have been caused by any of these intrinsic differences
59 rather than dominance status *per se*.

60 The goal of our study was to test for the extrinsic effect of dominance status on growth
61 rate while controlling for intrinsic factors that might be related to the propensity to become
62 dominant. Because we were unaware of any test of Abbott & Dill's (1989) study, our first
63 objective was to replicate their finding that dominants grow faster than subordinates when fed an
64 equal ration. Convict cichlids (*Amatitlania nigrofasciata*) are an ideal species for this objective
65 because they readily establish dominance relationships in laboratory conditions (Keeley & Grant,
66 1993; Koops & Grant, 1993), and subordinate individuals experience social stress that negatively
67 affects growth (Praw & Grant, 1999; Earley et al., 2004). We then extended their study in two
68 important ways. First, we tested whether the observed growth rate difference between dominants
69 and subordinates persisted when the two fish were only in visual contact. Second, we randomly
70 assigned dominance status by pairing focal fish with larger or smaller conspecifics, respectively,
71 to control for any intrinsic differences that might be correlated with the establishment of
72 dominance. Specifically, we tested the following predictions: dominants grow faster than
73 subordinate convict cichlids when fed equal rations and (1) allowed to interact freely, (2)
74 allowed to interact only visually; and (3) dominance status was randomly assigned. Furthermore,

75 we expected the growth advantage of dominants: (4) to be greater when direct interactions were
76 possible compared to only visual interactions; and (5) to be similar whether or not dominance
77 status was randomly assigned, if the growth advantage was due to the social stress experienced
78 by subordinate fish, but (6) to be greater when dominance status was determined by the animals
79 themselves rather than randomly, if the growth advantage was due to intrinsic differences
80 between fish.

81

82 **Methods**

83 *Subjects*

84

85 The test fish, likely *A. nigrofasciata* (sensu Schmitter-Soto 2007), originated from the laboratory
86 stock at Concordia University. We used juveniles to maximize growth rate and to minimize any
87 reproductive behavior. Fish were held in 110-l stock tanks on a 12:12 light:dark cycle with the
88 lights on at 7am. Experimental tanks, measuring 40.6 x 20.3 x 26cm (l x w x h), were filled with
89 natural-coloured gravel to a depth of 2cm and dechlorinated tap water, which was maintained
90 from 25-27°C. An air stone in each tank provided aeration. Three sides of each experimental
91 tank were covered with opaque plastic to prevent fish from viewing the adjacent experimental
92 tanks; the front was left uncovered to facilitate observations.

93

94 *Experiment 1: physical interactions between fish*

95

96 All 22 fish (mean = 0.339 g; see below) came from a single brood in a single stock tank, so that
97 all fish were of a similar age and social experience. Fish were weighed to the nearest 0.001g on

98 an electronic balance and held individually in a holding tank, identical to the experimental tanks,
99 until a size-matched individual (<8% difference in weight) was found. To facilitate individual
100 recognition, each fish of the 11 pairs was given a caudal fin clip, either the top or bottom corner
101 of the fin, which was determined randomly. By the end of the 7-day trial, the clipped fin had
102 almost entirely regrown in many cases. The pair of fish was transferred to an experimental tank
103 within minutes of each other to avoid any prior-residency effects.

104 Each pair of fish was monitored frequently on the day of introduction to the tank (day 1)
105 for signs of the establishment of dominance. An individual was defined as being dominant
106 following three or more chases within a 3-min period, without retaliation by the other fish. The
107 latency to establish dominance varied widely among pairs, from just a few minutes after
108 introduction to the tank to several hours (see Koops & Grant, 1993). However, dominance status
109 was always established on day 1, and was consistent for the duration of the trial. The dominant
110 fish typically swam freely around the tank, whereas the subordinate fish remained in a corner of
111 the tank near the substrate.

112 Fish were fed once per day beginning on day 2 for seven days, sufficient time to detect
113 growth in juvenile convict cichlids (Praw & Grant 1999; Breau & Grant 2002). A central,
114 removable, opaque divider was inserted in the tank to separate the two fish, and prevent visual
115 contact during feeding. The fish were fed one pellet (Vigor #4, Corey Feed Mills) at a time with
116 a plastic medicine dropper, in an alternating fashion until one fish stopped eating. The uneaten
117 pellets were removed from the tank and the number of pellets eaten by each fish was recorded.
118 The divider was removed after the daily feeding to allow the fish to interact. If one fish ate one
119 fewer pellet on a given day, it would be fed first the next day to ensure that an equal number of
120 pellets were consumed by both members of the pair over the trial. On average, each member of a

121 pair ate 79 pellets, with different pairs eating between 39 and 111 pellets over the 7-day feeding
122 trial. The fish were weighed on day 9, 24 hours after the last feeding, to allow for the digestion of
123 food.

124

125 *Experiment 2: visual interactions only*

126

127 The protocol for this experiment was identical to Experiment 1, except for the following
128 changes. After the establishment of dominance on day 1, a central, clear divider was used to
129 separate the two fish for the remainder of the trial. The fish could see each other and often
130 interacted through the divider. To ensure that both halves of the tank were identical, we placed a
131 heater and an airstone in each half. We also switched the type of food used from trout pellets to
132 frozen brine shrimp, after noticing that the fish occasionally took up to 1 minute to handle a
133 pellet in Experiment 1. An opaque divider was placed beside the clear divider to prevent visual
134 interactions during the daily feeding, as in Experiment 1. On average, each member of a pair ate
135 52 shrimp (range = 30-82) over the 7-day trial. Ten pairs of fish were tested (mean = 0.261 g; see
136 below).

137

138 *Experiment 3: dominance status randomly assigned*

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140 The protocol was identical to Experiment 1 with one major difference. Instead of allowing the
141 fish in a size-matched pair to establish dominance, the dominant role was randomly assigned to
142 one fish by placing it in a tank with a fish 25-50% smaller in weight. The other fish in the size-
143 matched pair was assigned the subordinate role by placing it in a separate tank with a fish 25-

144 50% larger. As in Experiment 1, the two fish in the same tank established their social status on
145 day 1, typically within 1 hour of being placed in the tank. Opaque barriers were used to ensure
146 that each fish in the same tank ate approximately the same amount of food; the smaller fish
147 typically ate less than the dominant because of size constraints. The size-matched dominant and
148 subordinate fish were in separate tanks and did not see each other during the trial, but were fed
149 the same number of food items over the 7-day trial. Because the two fish within a tank differed
150 considerably in size, we added an artificial plant to each tank to provide a hiding place for the
151 smaller fish. On average each member of the size-matched pair ate 69 shrimp (range = 55-95)
152 during the 7-day trial. Ten pairs of fish were tested (mean = 0.487 g; see below).

153

154 **Results**

155

156 In Experiment 1, with physical interactions between fish, the dominant (mean \pm SD = 0.343 \pm
157 0.078) was initially larger than the subordinate fish (0.335 \pm 0.068) in 9 of 11 pairs (0.011 g \pm
158 0.010; paired *t*-test, $t_{10} = 1.83$, $p = 0.099$; all tests are 2-tailed). After 7 days of feeding ,
159 dominants gained more weight than subordinate fish in 10 of 11 pairs (Figure 1; paired *t*-test, t_{10}
160 = 4.51, $p = 0.002$).

161 In Experiment 2, with only visual interactions between fish, dominants (0.263 \pm 0.048)
162 were initially larger than subordinate fish (0.259 \pm 0.047) in 6 of 10 pairs (0.004 \pm 0.011; paired
163 *t*-test, $t_9 = 1.278$, $p = 0.234$). After 7 days of feeding, dominants gained more weight than
164 subordinate fish in 9 of 10 trials (Figure 1; paired *t*-test, $t_9 = 2.912$, $p = 0.020$).

165 In Experiment 3, with no interactions between the size-matched fish, all focal fish
166 adopted the social status to which they were assigned. Because status was randomly assigned,

167 dominants ($0.482\text{g} \pm 0.077$) were initially larger than subordinate fish ($0.491\text{g} \pm 0.082$) in only 4
168 of 10 pairs (-0.009 ± 0.027 ; paired t -test, $t_9 = -1.117$, $p = 0.294$). After 7 days of feeding while
169 interacting with either a larger or smaller fish, dominants gained more weight than subordinate
170 fish in 9 of 10 trials (Figure 1; paired t -test, $t_9 = 3.708$, $p = 0.0066$).

171 The relative growth rate of the dominant compared to the subordinate fish differed
172 between the three experiments (Figure 1; one-way ANOVA: $F_{2,28} = 3.67$, $p = 0.038$). As
173 predicted, dominants gained relatively more weight than subordinates in Experiment 1 and 3,
174 when the two fish could interact throughout the 7-day trial, than in Experiment 2, where the two
175 fish were separated by a clear divider (planned contrast for unequal variances: $t_{28} = 3.406$, DF
176 adjusted for unequal variances = 24, $p = 0.002$). However, the growth advantage experienced by
177 the dominant fish did not differ between experiment 1 and 3 (planned contrast for equal
178 variances: $t_{28} = 0.61$, $p = 0.545$).

179

180 **Discussion**

181

182 Our results provided strong support for Abbott & Dill's (1989) findings for juvenile steelhead
183 trout (*Oncorhynchus mykiss*). Dominants gained 107, 57, and 105% more weight than
184 subordinate convict cichlids in the three experiments, respectively, compared to an 11.5%
185 difference for steelhead trout. The greater growth differential in our study was even more
186 striking, considering that our trials lasted only 7 days, compared to the 34 days of Abbott & Dill
187 (1989). If physiological stress is responsible for the slower growth of the subordinate fish, then
188 these results suggest that the dominance relationships in cichlids were more intense than in
189 steelhead (e.g. Sloman et al., 2000). A potential method to quantify differences in stress levels of

190 our pairs of fish would be to measure the cortisol levels released by individual fish when held in
191 small aquaria (Wong et al., 2008).

192 Experiment 2 indicated that the lingering effects of the establishment of dominance plus
193 the continuing visual interactions between fish were sufficient to cause dominants to grow faster
194 than subordinates. These findings are consistent with previous findings indicating that the mere
195 sight of a larger or dominant conspecific is sufficient to increase the metabolic rate of the smaller
196 fish (Wirtz & Davenport, 1976; Millidine et al., 2000a; Sloman et al., 2000). Not surprisingly,
197 the growth differential was greater when direct interactions between fish occurred compared to
198 when only visual interactions were permitted. The results of Experiment 3 were consistent with
199 the hypothesis that the lower growth rate of subordinate individuals was due to the extrinsic
200 effect of social status (e.g. Earley et al. 2004; Filby et al., 2010), rather than intrinsic differences
201 between the fish (e.g. McGhee & Travis, 2010). Comparisons of the growth differential between
202 experiments need to be interpreted with caution, however, because of the different food types
203 used in our three Experiments.

204 Our results may have implications for the animal husbandry and aquaculture industries. If
205 direct interactions with, or the sight of, dominants causes stress in subordinates, then adding
206 structure to the rearing environment might reduce the frequency of aggressive interactions
207 (Carfagnini et al., 2009; Barley & Coleman, 2010). Furthermore, the addition of structure tends
208 to make aggressive behaviour less economical as a competitive strategy (Höjesjö et al., 2004),
209 and reduces the variance in food intake within groups (Basquill & Grant, 1998). The negative
210 effects of the dominant individual on subordinates in the group can also be diluted by increasing
211 the group size or density (e.g. Kim & Grant, 2007).

212 The convict cichlid is an interesting model species for studying the interactions between
213 body size, dominance status and growth rate. As in previous studies (Keeley & Grant, 1993;
214 Earley et al. 2004), dominance status was related to body size, even within size-matched pairs;
215 dominant fish were larger in 16 of 21 pairs in Experiments 1 and 2 (Sign Test, $p = 0.027$). In
216 competitive feeding experiments, food intake is the best predictor of growth rate (Praw & Grant,
217 1999), which leads to growth depensation, particularly when food is economically defensible
218 (Noël et al., 2005). In addition to our findings, which indicate a stress cost to being subordinate,
219 circumstantial evidence suggests a cost of aggression and of being dominant. Mean growth rate
220 in groups of convict cichlids decreases with increasing rates of aggression (Noël et al., 2005),
221 and the growth rate of dominants decreases with the number of intruders on its territory (Praw &
222 Grant, 1999).

223 While numerous studies on fishes focus on the physiological costs of being subordinate
224 (see Gilmour et al., 2005), fewer studies have investigated the costs of being dominant (but see
225 Noakes & Leatherland, 1977; Riebli et al. 2011). By contrast, the physiological costs of being
226 both dominant and subordinate have been investigated more in the mammalian literature (e.g.
227 Sands & Creel, 2004). Future studies should focus on the costs of dominance in fishes, and on
228 the differential costs of social status in more natural circumstances (e.g. Sloman et al., 2008).

229

230

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232

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237

238 **References**

239

240 Abbott, J.C. & Dill, L.M. (1989). The relative growth rate of dominant and subordinate juvenile
241 steelhead trout (*Salmo gairdneri*) fed equal rations. – Behaviour 108: 104-113.

242 Barley, A.J. & Coleman, R.M. (2010). Habitat structure directly affects aggression in convict
243 cichlids *Archocentrus nigrofasciatus*. – Curr. Zool. 56: 52-56

244 Basquill, S.P. & Grant, J.W.A. (1998). An increase in habitat complexity reduces aggression and
245 monopolization of food by zebra fish (*Danio rerio*). - Can. J. Zool. 76: 770-772.

246 Breau, C. & Grant, J.W.A. (2002). Manipulating territory size via vegetation structure: optimal
247 size of area guarded by the convict cichlid (Pisces, Cichlidae).- Can. J. Zool. 80: 376-380.

248 Carfagnini, A.G., Rodd, F.H., Jeffers, K.B. & Bruce A.E.E. (2009). The effects of habitat
249 complexity on aggression and fecundity in zebrafish (*Danio rerio*). - Environ. Biol. Fish.
250 86: 403-409.

251 Earley, R.L., Blumer, L.S. & Grober, M.S. 2004. The gall of subordination: changes in gall
252 bladder function associated with social stress. Proc. R. Soc. Lond. B 271: 7-13.

253 Filby, A.L., Paull, G.C., Bartlett, E.J., Van Look, K.J.W. & Tyler, C.R. (2010). Physiological
254 and health consequences of social status in zebrafish (*Danio rerio*). - *Physiol. Behav.*
255 101: 576-587.

256 Gilmour, K.M., DiBattista, J.D. & Thomas, J.B. (2005). Physiological causes and consequences
257 of social status in salmonid fish. - *Integr. Comp. Biol.* 45: 263-273.

258 Höjesjö J, Johnsson J, Bohlin T. 2004. Habitat complexity reduces the growth of aggressive and
259 dominant brown trout (*Salmo trutta*) relative to subordinates. *Behav. Ecol. Sociobiol.* 56:
260 286-289.

261 Keeley, E.R. & Grant, J.W.A. (1993). Asymmetries in the expected value of food do not predict
262 the outcome of contests between convict cichlids. - *Anim. Behav.* 45: 1035-1037.

263 Kim, J-W. & Grant, J.W.A. (2007). Effect of patch shape and group size on the effectiveness of
264 defence by juvenile convict cichlids. - *Anim. Behav.* 73: 275-280.

265 Koebele, B.P. 1985. Growth and the size-hierarchy effect: an experimental assessment of three
266 proposed mechanisms; activity differences, disproportional food acquisition,
267 physiological stress. - *Environ. Biol. Fish.* 12: 181-188.

268 Koops, M.A. & Grant, J.W.A. (1993). Weight asymmetry and sequential assessment in convict
269 cichlid contests. - *Can. J. Zool.* 71: 475-479.

270 Łomnicki, A. (1988). Population ecology of individuals. - Princeton University Press, Princeton.

271 Magnuson, J.J. (1962). An analysis of aggressive behaviour and competition for food and space
272 in medaka (*Oryzias latipes*), Pisces, Cyprinodontidae. - *Can. J. Zool.* 40: 313-363.

273 McGhee, K.E. & Travis, J. (2010). Repeatable behavioural type and stable dominance rank in the
274 bluefin killifish. - *Anim. Behav.* 79: 497-507.

275 Metcalfe, N.B., Wright, P.J. & Thorpe, J.E. (1992). Relationships between social-status, otolith
276 size at 1st feeding and subsequent growth in Atlantic salmon (*Salmo salar*). - J. Anim.
277 Ecol. 61: 585-589.

278 Metcalfe, N.B., Taylor, A.C. & Thorpe, J.E. (1995). Metabolic-rate, social-status and life-history
279 strategies in Atlantic salmon. - Anim. Behav. 49: 431-436.

280 Millidine, K.J., Armstrong, J.D. & Metcalfe, N.B. (2009a). Juvenile salmon with high standard
281 metabolic rates have higher energy costs but can process meals faster. - Proc. Roy. Soc.
282 Lond. B: Biol. 276: 2103-2108.

283 Millidine, K.J., Metcalfe, N.B. & Armstrong, J.D. (2009b). Presence of a conspecific causes
284 divergent changes in resting metabolism, depending on its relative size. - Proc. Roy. Soc.
285 Lond. B: Biol. 276: 3989-3993.

286 Noakes, D.L.G. & Leatherland, J.F. (1977). Social dominance and interrenal cell activity in
287 rainbow trout, *Salmo gairdneri* (Pisces: Salmonidae). - Environ. Biol. Fish. 2: 131-136.

288 Noël, M.V., Grant, J.W.A. & Carrigan, J.G. (2005). Effects of competitor-to-resource ratio on
289 aggression and size variation within groups of convict cichlids. - Anim. Behav. 69: 1157-
290 1163.

291 Praw, J.C. & Grant, J.W.A. (1999). Optimal territory size in the convict cichlid. - Behaviour
292 136: 1347-1363.

293 Riebli, T., Batur, A., Bottini, A-M., Duc, C., Taborsky, M. & Heg, D. (2011). Behavioural types
294 affect dominance and growth in staged encounters of cooperatively breeding cichlids. -
295 Anim. Behav. 81: 313-323.

296 Rubenstein, D.I. (1981). Combat and communication in the Everglades pygmy sunfish. - Anim.
297 Behav. 29: 249-258.

298 Sands, J. & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a
299 wild population of wolves, *Canis lupus*. *Anim. Behav.* 67: 387-396.

300 Scanes, C.G., ed (2003). *Biology of growth of domestic animals*. Iowa State Press, Ames.

301 Schmitter-Soto, J.J. (2007). A systematic revision of the genus *Archocentrus* (Perciformes:
302 Cichlidae), with the description of two new genera and six new species. – *Zootaxa* 1603:
303 1-78.

304 Sloman, K.A., Motherwell, G., O'Connor, K.I. & Taylor, AC. (2000). The effect of social stress
305 on the Standard Metabolic Rate (SMR) of brown trout, *Salmo trutta*. - *Fish Physiol.*
306 *Biochem.* 23: 49-53.

307 Sloman, K.A., Baker, D., Winberg, S. & Wilson RW. 2008. Are there physiological correlates of
308 dominance in natural trout populations? – *Anim. Behav.* 76: 1279-1287.

309 Thorpe, J.E. & Huntingford, F.A., eds (1992). *The importance of feeding behavior for the*
310 *efficient culture of salmonid fishes*. World Aquaculture Society, Baton Rouge.

311 Weatherley, A.H. & Gill, H.S. (1987). *The biology of fish growth*. Academic Press, London.

312 Wirtz, P. (1975). Physiological effects of visual contact to a conspecific in *Blennius pholis*
313 (Pisces, Teleostei). - *J. Comp. Physiol.* 101: 237-242.

314 Wirtz, P. & Davenport, J. (1976). Increased oxygen consumption in blennies (*Blennius pholis* L.)
315 exposed to their mirror images. - *J. Fish Biol.* 9: 67-74.

316 Wong, S.C., Dykstra, M., Campbell, J.M. & Earley, R.L. – 2008. Measuring water-borne cortisol
317 in convict cichlids (*Amatitlania nigrofasciata*): is the procedure a stressor? *Behaviour*
318 145: 1283-1305.

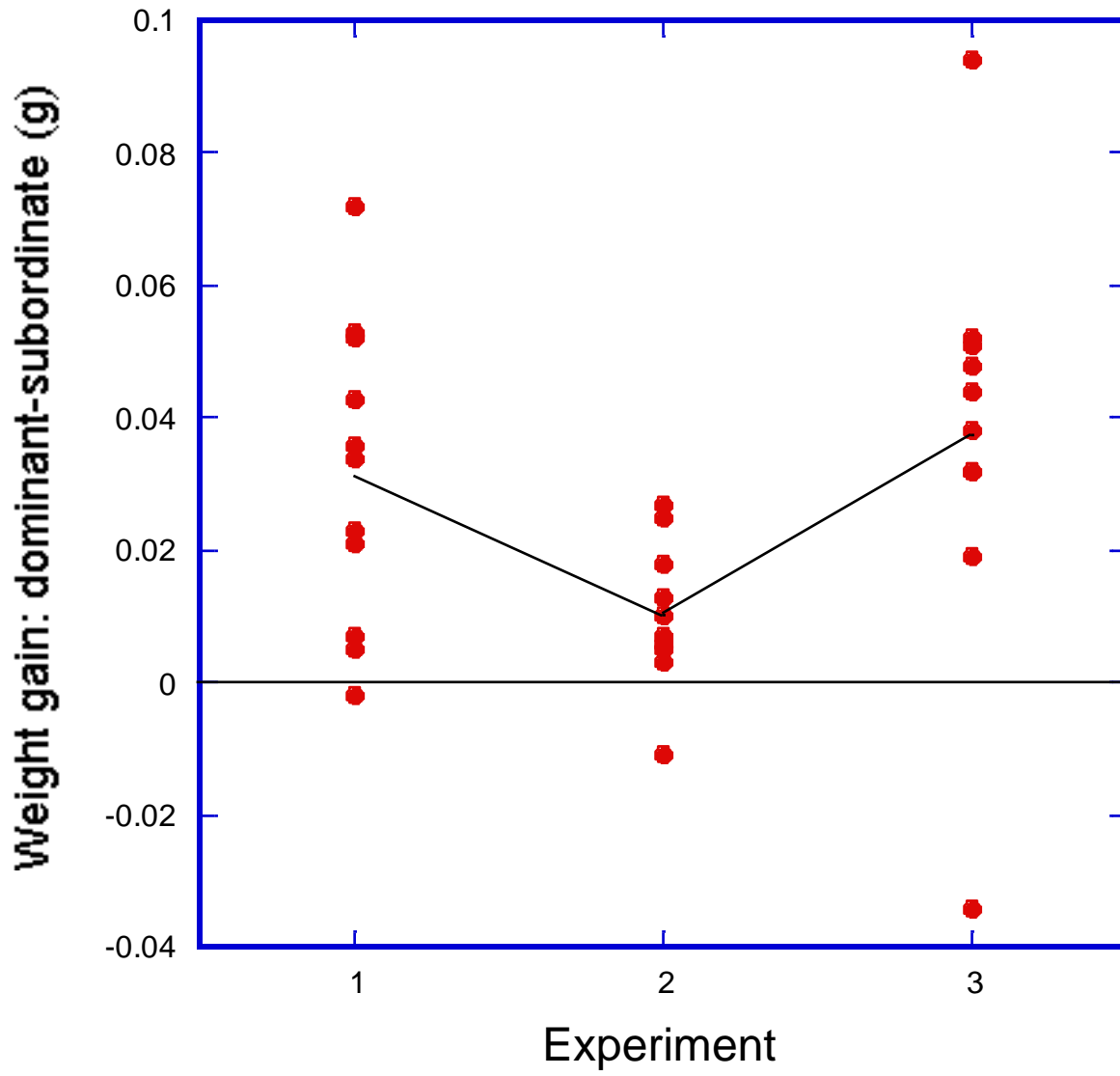
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320 **Legend for figure**

321

322 Figure 1. Difference in weight gain between pairs of dominant and subordinate convict cichlids
323 when fed equal rations in three experiments: (1) when allowed to interact freely ($n = 11$); (2)
324 when allowed to interact only visually ($n = 10$); and (3) when the dominant and subordinate
325 status were randomly assigned ($n = 10$).

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328