



HAL
open science

Group size, temperature and body size modulate the effects of social hierarchy on basal cortisol levels in fishes

Eduardo Bessa, Bastien Sadoul, David J. Mckenzie, Benjamin Geffroy

► To cite this version:

Eduardo Bessa, Bastien Sadoul, David J. Mckenzie, Benjamin Geffroy. Group size, temperature and body size modulate the effects of social hierarchy on basal cortisol levels in fishes. *Hormones and Behavior*, 2021, 136, pp.105077. 10.1016/j.yhbeh.2021.105077 . hal-03411090

HAL Id: hal-03411090

<https://hal.umontpellier.fr/hal-03411090>

Submitted on 21 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Group size, temperature and body size modulate the effects of social hierarchy on**
2 **basal cortisol levels in fishes**

3 Eduardo Bessa¹, Bastien Sadoul², David J. Mckenzie³ & Benjamin Geffroy^{3*}

4

5 ¹Graduate Program in Ecology, Universidade de Brasília, Distrito Federal, Brazil

6 ²ESE, Ecology and Ecosystem Health, Institut Agro, INRAE, Rennes, France

7 ³MARBEC, Univ Montpellier, Ifremer, CNRS, IRD, Palavas-Les-Flots, France

8

9 *Corresponding author : bgeffroy@ifremer.fr

10

11 **Abstract**

12

13 Social rank in a structured society has been linked to basal levels of glucocorticoids in
14 various species, with dominant individuals generally presenting lower levels than
15 subordinates. The biotic and abiotic factors influencing glucocorticoids levels across
16 social ranks are still, however, unclear in fishes. We investigated the influences of group
17 size, fish size, sex, age, and reproduction type, plus water salinity and temperature, on the
18 basal levels of cortisol, the major stress hormone in fishes. A phylogenetically controlled
19 meta-analysis was performed on data from 72 studies over 22 species of fishes. As
20 expected, dominants generally exhibited lower levels of cortisol than subordinates. More
21 importantly, the strength of the correlation between cortisol and rank was modulated by
22 three main factors, group size, environmental temperature, and fish size. Differences in
23 basal cortisol between dominants and subordinates were significantly greater in small
24 groups (dyadic contexts) when compared to larger groups. Differences between
25 dominants and subordinates were also greater in temperate regions when compared to the
26 tropics, and in species with larger body size. These results help to decipher the links
27 among hierarchy, stress and metabolism in fishes.

28

29

30 **Keywords:** Stress; Aggressiveness; Sociality; Shoal; Meta-Analysis

31

32 1. Introduction

33

34 Many animal societies are organized into hierarchies. First described in the domestic
35 chicken (Schjelderup-Ebbe, 1922), a social hierarchy is a system where individuals
36 organize themselves into a particular, often linear, order of status from dominant to
37 subordinate individuals. Hierarchies are frequently established by aggression or by body
38 size and weight (Rubenstein and Abbot, 2017), and communicated visually (Campderrich
39 et al., 2017; Grosenick et al., 2007) and chemically (Bigiani et al., 2005). Socially
40 dominant individuals gain advantages that can increase their fitness, for instance they
41 have access to more food (Hahn and Bauer, 2008) or have lower risks of predation
42 (Teichroeb et al., 2015). Dominants also secure access to territory and partners for
43 reproduction (Holekamp and Strauss, 2020) and have enhanced access to helpers in
44 species with cooperative breeding (Dawson and Mannan, 1991). This apparently ideal
45 situation also, however, comes with some costs, especially because access to this specific
46 rank involves stressful situations, such as fights for dominance. Hence, gaining and
47 retaining status, but also being a subordinate, may all cause stress. Consequently, social
48 status has been found to be tightly linked to stress levels in various animal species, as
49 measured by tissue glucocorticoid concentrations (Abbott et al., 2003; Ejike and Schreck,
50 1980).

51 Fish represent a very interesting group to investigate the extent to which glucocorticoid
52 levels underscore social status, since they exhibit widely differing degrees of social
53 organization (Wilson, 2000). They vary from isolation with rare social contact (e.g.
54 swordfish *Xiphias gladius* (Palko et al., 1981)), to territorial individuals protecting an area
55 amid conspecifics (Sogawa et al., 2016), to loosely coordinated shoaling (e.g. stickleback
56 *Gasterosteus aculeatus* (Ginnaw et al., 2020)), to highly organized schooling (e.g. a
57 tropical damselfish *Chromis viridis* (Nadler et al., 2018)). Although this myriad of social
58 organization systems might be an advantage in studying links between physiology and
59 behavior, the fact that fish species greatly vary in their life history traits might also
60 obscure any underlying patterns. For example, Baker et al. (Baker et al., 2013) reported
61 higher basal glucocorticoid concentrations for dominant individuals in four tests but the
62 opposite in five other tests. The authors identified confounding factors that were fish
63 density, wild versus captive animals, and level of aggressiveness (Baker et al., 2013).
64 Even within a single species, differences in experimental design may impede the detection

65 of directional patterns. In addition, our understanding of the potential biotic and abiotic
66 factors affecting patterns is limited.

67 Plasma cortisol is an established indicator of stress in fishes (Mommsen et al., 1999;
68 Sadoul and Geffroy, 2019), produced by the Hypothalamus-Pituitary-Interrenal (HPI)
69 axis, it plays a key role in energy mobilization to cope with stressful events (Sadoul and
70 Vijayan, 2016) but it may also have multiple other impacts, notably on reproduction
71 (Rousseau et al., 2021) or sex determination (Geffroy and Douhard, 2019). Basal
72 circulating cortisol titer can vary in response to life-history (Ricklefs and Wikelski, 2002),
73 body condition (Breuner and Hahn, 2003) and season (Landys et al., 2006; Love et al.,
74 2005). Since fishes are ectotherms, temperature is a major effector of their general
75 metabolism (Stevens and Fry, 2011), including the production of cortisol (Alfonso et al.,
76 2020). Intra-specific differences in basal cortisol may be genetically driven (Samaras and
77 Pavlidis, 2018) and generally covary with differences in behavior, metabolism and life-
78 history traits, as part of the well described ‘coping style’ (Koolhaas et al., 1999).

79 Consequently, an increase in cortisol production does not necessarily indicate a
80 physiological “stress” *stricto sensu* (Schreck and Tort, 2016), but could be the result of a
81 temperature-driven increase in metabolic rates (Alfonso et al., 2020). Intraspecific
82 differences in cortisol levels could also be the result of genetically-driven differences in
83 species overall metabolic rates. Therefore, distinguishing among stressful situations that
84 actually trigger an increase in cortisol level (Harris, 2020) from those that are a
85 consequence of differences in metabolic rates can be challenging. That is, differences in
86 basal cortisol within a social hierarchy may be caused by the stress imposed by a specific
87 social rank but, inversely, social rank might be the consequence of internal specificities
88 of an individual. For ease of description, we refer to the first situation as the “stress-
89 enhanced hypothesis” and to the second as the “metabolic-enhanced hypothesis”.
90 Providing more information about external and internal effectors that affect relationships
91 between basal cortisol level and social rank could ultimately provide support for these
92 two hypotheses.

93 Here we test whether group size and life history traits can partially explain contrasting
94 results about how social rank influences plasma cortisol. We tested the effect of external
95 and internal factors, and particularly the effect of climate zone (tropical vs. temperate), to
96 assess whether differences in cortisol between social ranks could also be due to the
97 environment. A phylogenetically controlled meta-analysis and meta-regression were
98 conducted to verify these hypotheses, and also to estimate the extent to which life history

99 traits can modulate the relationship. In particular, beyond exploring how group size and
100 temperature would affect the correlation between basal cortisol production and social
101 rank (*i.e.* effect size), we also considered other moderators such as fish size, sex, age,
102 reproduction type and salinity.

103

104 **2. Methods**

105 (a) Literature search and study selection

106 We screened Web of Science for papers published before June 24th 2020 containing the
107 terms “subordinate” OR “dominant” OR “dominance” AND “fish” AND “cortisol” AND
108 “stress”. We obtained 165 studies, from which we retained 73 that measured basal plasma
109 cortisol in groups of fish with established hierarchies, in the Preferred Reporting Items
110 for Systematic Reviews and Meta-Analyses (PRISMA) checklist (Appendix A,
111 supplementary Figure 1).

112

113 (b) Estimating effect sizes

114 Statistical results (r , t , F , χ^2 , z) were extracted directly from text or figures and, when not
115 directly available, results were converted into statistical tests ($n=7$). One study was
116 removed because direction of the effect was not known, leading to a total of 72 studies.
117 In most instances, a Pearson’s product-moment correlation coefficient, r , was provided
118 and used as our measure of effect size, when cortisol values concerned at least three
119 individuals in the study. In all other cases, we followed a recognized methodology by
120 Rosenthal (1991) (Rosenthal, 1991) to estimate r using published statistics. This
121 calculation uses mean and variance of treatments, statistical results (t , F , χ^2 , z), and p -
122 values reported with sample sizes, in respective order of preference. The calculation was
123 performed so that a positive relationship between cortisol values and rank order returned
124 a positive r , meaning that subordinates have higher cortisol than dominants. Generally, r -
125 values above 0.5 are considered to reflect large effect sizes in ecology (Cohen, 1992;
126 Jennions and Møller, 2002). For further analyses, r -values were transformed to Fisher’s
127 z , to improve normality (Koricheva et al., 2013).

128

129 (c) Meta-analyses using random effects

130 We used hierarchical linear mixed-effects meta-analysis to test for both overall effect
131 sizes and the importance of our moderators (Nakagawa and Santos, 2012) using the
132 package ‘metafor’ v. 2.1-0 (Viechtbauer, 2010) in R v. 3.5.2. The overall effect sizes (i.e.,
133 mean of the effect sizes weighted by the inverse of their variance) were considered
134 significant if their 95% confidence intervals (CI) did not include zero (Koricheva et al.,
135 2013). We used model selection based on the Akaike information criterion to determine
136 which random factors should be included in each meta-analysis (Nakagawa and Santos,
137 2012). Non-independence of effect sizes within and among studies was accounted for by
138 including i) the number of effect sizes collected “id” (which corresponds to the collected
139 values) and ii) the “studies” (which corresponds to the reviewed article itself) as random-
140 factors. Phylogenetic non-independence across studies was handled by including
141 relationships among species (Appendix A, supplementary Figure 2) as a random effect
142 based on the Open Tree of Life database (Hinchliff et al., 2015), and Grafen’s method
143 providing a correlation matrix from branch length (Grafen and Hamilton, 1989). The R
144 package ‘rotl’ v. 3.0.10 was used for this purpose (Michonneau et al., 2016)
145 Group size (dyadic contexts or group>2), reproduction type (monogamous, polygamous
146 and polygynous), habitat temperature (temperate vs tropical), time since grouping (h) and
147 fish weight (g, square-root transformed) were considered as moderators of effect size. We
148 tested for multi-collinearity among moderators and the highest variance inflation factor
149 was 2.26, below the recognized threshold of 3 (Zuur et al., 2010). The factors salinity
150 (freshwater n = 67, sea n = 7 and brackish n =4 water) and sex (male n =23, female= 7,
151 mixed group n=31 and ambisexual n=1) could not be considered owing to discrepancies
152 in the numbers of effect sizes. We used a multi-model inference approach based on
153 Akaike’s criteria corrected for small sample sizes (AICc) (Burnham and Anderson, 2002).
154 We first assessed the relative strengths of each candidate model by calculating its Akaike
155 weight, to identify the most parsimonious model. A constant term (the intercept) was
156 included in all models. We estimated the importance of a predictor by summing the
157 Akaike weights of all models in which that candidate variable appeared, so ranking
158 predictors in order of importance (Burnham and Anderson, 2002). All multi-model
159 analyses were conducted using the *MuMIn* R package v. 1.40.0 (Barton, 2014).

160

161 (d) Heterogeneity

162 We used the I^2 index as a measure of heterogeneity in effect sizes. The index represents
163 the proportion of total variation in the data that is not a consequence of sampling error

164 (Higgins et al., 2003). We used an extended version of I^2 that partitions total heterogeneity
165 between the variation explained by the study identity and by the variation of the residuals.
166 The latter remains to be explained by our moderators (Nakagawa and Santos, 2012). We
167 calculated the degree of phylogenetic signal in our estimates of effect size using the
168 phylogenetic heritability index, H^2 , which is the variance attributable to phylogeny in
169 relation to the total variance in the data (Nakagawa and Santos, 2012). H^2 is equivalent to
170 Pagel's λ (Pagel, 1999), where higher values indicate stronger phylogenetic signals.

171

172 (e) Publication bias

173 We used Egger's regression to highlight any publication bias, because studies with low
174 sample sizes tend to be rejected due to their lower probability of finding significant effects
175 (Egger et al., 1997; Koricheva et al., 2013). The intercept of the regression is considered
176 to demonstrate publication bias when its estimate significantly differs from zero (Egger
177 et al., 1997). To overcome the non-independent nature of our data, we also applied the
178 Egger's regression test on the meta-analytic residuals (Nakagawa and Santos, 2012).

179 **3. Results**

180

181 The final dataset comprised 78 effect sizes, across 22 species, from 72 studies. Of all
182 models tested ($n=11$), the most parsimonious (intercept-only) was the one with both
183 studies and number of effect sizes (categorical) as random factor ($AICc=144.41$), while
184 adding the phylogeny resulted in the second most parsimonious ($AICc=146.57$).
185 Therefore, to retain phylogenetic relatedness in our models, we performed all analyses
186 using this latter model with three random factors. Overall and as predicted, the
187 hierarchical rank (higher for subordinates) was strongly and positively correlated with
188 cortisol (Fisher's $z=0.4546$, $CI=0.26-0.65$, Figure 1). We found considerable variation
189 among studies ($I^2_{total}=88.5\%$, $I^2_{studies}=84.6\%$, $I^2_{residual}=4\%$), which was expected
190 because they were almost as numerous as effect sizes. The phylogenetic signal was weak
191 ($H^2=4.4\%$). We found no evidence of publication bias (Egger's regression of effect sizes:
192 Intercept = 1.1158, $P=0.14$; Egger's regression of meta-analytic residuals: Intercept
193 =0.14, $P=0.85$; Figure 2). Multi-model inference indicated that group size (pair or >2),
194 habitat temperature (temperate or tropical) and body weight were the most important
195 predictors of the magnitude of rank-cortisol relationship (Table 1). When cortisol was
196 evaluated in a dyadic context, there was a stronger and more positive rank-cortisol

197 relationship than when evaluated in groups. For example, dominants in groups sometimes
198 had higher basal cortisol than subordinates (Table 1 and Figure 3A). The difference in
199 basal cortisol between dominant and subordinates was also stronger and more positive in
200 fishes from temperate compared to tropical regions (Table 1 and Figure 3B). Finally,
201 mean fish body weight was positively correlated to Fisher's z (Table 1 and Figure 3C),
202 such that the difference in basal cortisol across hierarchical ranks was highly and
203 positively correlated with fish body weight. Importantly, this was true when testing these
204 moderators alone or in the same model.

205

206 **4. Discussion**

207

208 Our data support the main hypothesis, that dominants generally exhibit lower basal
209 cortisol level than subordinates. This effect is, however, modulated by group size, habitat
210 temperature and fish size. We identified two main possible explanations for why cortisol
211 varies in such cases, the 'stress-enhanced hypothesis' where this would be due to stress
212 itself, or the 'metabolic-enhanced hypothesis' where this would be due to variation in
213 metabolic rates.

214 Since cortisol is recognized as the main stress hormone in fishes, the fact that dominants
215 generally produce less cortisol than subordinates was expected, as a consequence of the
216 "stress-enhanced hypothesis". Dominants are aggressive towards subordinates in order to
217 keep their status. All these aggressive acts are perceived as stressful events explaining the
218 difference in cortisol levels. Interestingly, we found that the cortisol differences between
219 dominant and subordinates were more prominent when groups are small. This is because
220 in most tests performed in dyadic contexts, dominants presented lower cortisol levels than
221 subordinates whereas, in tests performed in larger groups, dominants could actually
222 exhibited slightly higher cortisol levels than subordinates. This reveals the complexity
223 with which social hierarchies can elicit stress. Individuals in large groups may face more
224 intense food competition (Borcherding et al., 2019), cannibalism (Naumowicz et al.,
225 2017), susceptibility to capture (Thambithurai et al., 2018) and sex competition (Wacker
226 et al., 2017), for example. All of these processes may stress fishes, but dominants can use
227 their status to monopolise opportunities to improve fitness. In larger groups, such valuable
228 status could also result in more frequent challenges by conspecifics, increasing the costs
229 of retaining dominant status and resulting in higher relative stress levels. In addition, our
230 results could also indicate that subordinates are relatively less stressed in groups. This

231 would be the consequence of having the aggressive behavior of the dominant fish shared
232 amongst multiple subordinates. Altogether, these results support the “stress-enhanced
233 hypothesis”: holding a particular status drives your stress levels, indicated by cortisol
234 values. The metabolism of dominant individuals is often, however, higher than that of
235 subordinates (Geffroy et al., 2016; Metcalfe et al., 1995). Basal cortisol levels are also
236 positively correlated with metabolism (Mommsen et al., 1999), and we might therefore
237 expect that dominants would have higher cortisol values. The opposite was observed in
238 our study, further supporting the “stress-enhanced hypothesis”.

239 Our findings relative to group-size also provide a plausible hypothesis to explain why
240 cortisol would show opposite results depending on the reproductive strategy of a species
241 (protandry or protogyny). In such species, cortisol has a key role in sex determination
242 (Geffroy and Douhard, 2019), notably in many hermaphroditic reef fishes where social
243 interactions shape the dynamics of sex-change (Goikoetxea et al., 2017). Indeed, a
244 contribution of cortisol was demonstrated in two protogynous species where big males
245 monopolize harems (large groups of females), and an increase in cortisol is necessary for
246 dominant females to change into the male (Nozu and Nakamura, 2015; Todd et al., 2019).
247 On the other hand, the female dominant of small groups of protandrous fish (e.g.
248 clownfish) may be less stressed, and subordinate males would then remain males because
249 of the stress imposed by the female, although this remains to be fully demonstrated
250 (Olivotto and Geffroy, 2017). The fact that mating system (monogamous, polygamous
251 and polygynous) was not included in the most parsimonious model does not permit us to
252 extrapolate our results, since most protandrous fish are monogamous and most
253 protogynous fish are polygynous. More studies focusing on hermaphroditic fishes are,
254 clearly, required.

255 In any case, the fact that the difference between basal cortisol in dominants and
256 subordinates of large groups was lesser than in small groups argues for the ‘stress-
257 enhanced hypothesis’, where basal cortisol levels in dominants (and subordinates) is a
258 consequence of a physiological stress, not merely of metabolic rate.

259 We found that habitat temperature (temperate versus tropical) also shapes the relationship
260 between basal cortisol and social status. This would advocate for the “metabolic-
261 enhanced” hypothesis. In warmer habitats, fishes will generally have higher metabolic
262 rates (Killen et al., 2016), reflecting direct thermodynamic effects on all biochemical and
263 physiological processes (Cossins and Bowler, 1987). Rates of basal cortisol production
264 are known to be stimulated by increased temperature within fish species (Goikoetxea et

265 al., 2021). High background rates of basal cortisol production in all individuals at high
266 temperatures may tend to obscure differences in production that reflect stress due to social
267 rank, especially if these are relatively subtle. The higher metabolism of fishes in warm
268 environments may also lead to higher overall activity levels and general aggressiveness
269 (Biro et al., 2010; Colchen et al., 2017), and reduce the stability of hierarchies (Kochhann
270 et al., 2015), which could also obscure inter-individual differences in basal cortisol
271 production due to social rank. That is, subtle differences in the level of stress due to social
272 rank might be easier to observe in fish with overall lower metabolic rates in cooler
273 temperate habitats (Alfonso et al., 2020), especially if differences in rank are associated
274 with greater relative differences in activity level or behavioral tendencies such as
275 boldness.

276 The finding that mean weight of fish was positively correlated to the Fisher's z might
277 simply indicate that a difference in size between dominant and subordinates becomes
278 more pronounced as mean size increases. Hence, cortisol differences between dominants
279 and subordinates also increase with this size difference. This could be due to the fact that
280 bigger dominant fish impose higher stress on subordinates. Size difference may also
281 reflect differences in life-history stage, another factor known to influence basal cortisol
282 (Love et al., 2005). Unfortunately, the exact size of fish at social ranks was rarely reported
283 in the articles reviewed, so this remains an interesting topic for future study.

284 After a dominance hierarchy is initiated by the formation of a group, cortisol should
285 increase in all individuals. Cortisol levels are expected to stabilize and diverge once ranks
286 are established. That led us to expect 'time since grouping' to be an important variable in
287 our model but we did not observe this. This suggests that the hierarchy is established very
288 readily in most instances and that differences in basal cortisol among social ranks are
289 relatively consistent over time, or at least that the studies we used only began measuring
290 cortisol once the hierarchy had been settled.

291 Overall, our phylogenetic meta-analysis provided strong support for the hypothesis that
292 dominant fish generally display lower baseline cortisol than subordinates, where high
293 cortisol likely represents physiological stress. Nonetheless, it remains difficult to assess
294 whether social status is a cause (due to stress) or a consequence (due to metabolic rate)
295 of differences in basal cortisol levels among individuals. Our results seem to provide
296 support for both stress-enhanced and metabolism-enhanced hypotheses, indicating that
297 multiple contributing factors are probably at play. That is, there can be a contribution of
298 both biotic (sociality and fish size) and abiotic (habitat temperature) factors. The

299 establishment of a hierarchy triggers physiological stress but the degree of cortisol release
300 is accentuated or diminished by habitat temperature and its effects on metabolism. These
301 findings have major implications for our understanding of the ecology and sociality of
302 fishes.

303

304 **Acknowledgements**

305 We are grateful to Diogo S. Samia for advice on meta-analysis.

306 **Funding**

307

308 The study is supported by the project 3S (Seabass, Sex & Stress, grant number
309 4320175237) and by FAP-DF (Process 24052018).

310

311 **Bibliography**

312

313 Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman,
314 W., Snowdon, C.T., Ziegler, T.E., Banjevic, M., Garland, T., Sapolsky, R.M., 2003. Are
315 subordinates always stressed? A comparative analysis of rank differences in cortisol
316 levels among primates. *Horm. Behav.* 43, 67–82.

317 Alfonso, S., Gesto, M., Sadoul, B., 2020. Temperature increase and its effects on fish
318 stress physiology in the context of global warming. *J. Fish Biol.*

319 <https://doi.org/10.1111/jfb.14599>

320 Baker, M.R., Gobush, K.S., Vynne, C.H., 2013. Review of factors influencing stress
321 hormones in fish and wildlife. *J. Nat. Conserv.* 21, 309–318.

322 <https://doi.org/10.1016/j.jnc.2013.03.003>

323 Barton, K., 2014. MuMIn: Multi-model inference. R package version 1.40.0.

324 Bigiani, A., Mucignat-Caretta, C., Montani, G., Tirindelli, R., 2005. Pheromone
325 reception in mammals, in: *Reviews of Physiology, Biochemistry and Pharmacology,*
326 *Reviews of Physiology, Biochemistry and Pharmacology.* Springer, Berlin, Heidelberg,
327 pp. 1–35. <https://doi.org/10.1007/s10254-004-0038-0>

328 Biro, P.A., Beckmann, C., Stamps, J.A., 2010. Small within-day increases in
329 temperature affects boldness and alters personality in coral reef fish. *Proc. R. Soc. B*
330 *Biol. Sci.* 277, 71–77. <https://doi.org/10.1098/rspb.2009.1346>

331 Borcharding, J., Heubel, K., Storm, S., 2019. Competition fluctuates across years and
332 seasons in a 6-species-fish community: empirical evidence from the field. *Rev. Fish*
333 *Biol. Fish.* 29, 589–604. <https://doi.org/10.1007/s11160-019-09567-x>

334 Breuner, C.W., Hahn, T.P., 2003. Integrating stress physiology, environmental change,
335 and behavior in free-living sparrows. *Horm. Behav.* 43, 115–123.

336 [https://doi.org/10.1016/S0018-506X\(02\)00020-X](https://doi.org/10.1016/S0018-506X(02)00020-X)

337 Burnham, K.P., Anderson, D.R., 2002. *Model selection and multimodel inference: a*
338 *practical information-theoretic approach*, 2nd edn. ed. Springer, New York, NY.

339 <https://doi.org/10.1016/j.ecolmodel.2003.11.004>

340 Campderrich, I., Liste, G., Estevez, I., 2017. The looks matter; aggression escalation
341 from changes on phenotypic appearance in the domestic fowl. PLOS ONE 12,
342 e0188931. <https://doi.org/10.1371/journal.pone.0188931>
343 Cohen, J., 1992. A power primer. Psychol. Bull. 112, 155–159.
344 Colchen, T., Teletchea, F., Fontaine, P., Pasquet, A., 2017. Temperature modifies
345 activity, inter-individual relationships and group structure in a fish. Curr. Zool. 63, 175–
346 183. <https://doi.org/10.1093/cz/zow048>
347 Cossins, A.R., Bowler, K., 1987. The direct effects of temperature changes, in: Cossins,
348 A.R., Bowler, K. (Eds.), Temperature Biology of Animals. Springer Netherlands,
349 Dordrecht, pp. 23–60. https://doi.org/10.1007/978-94-009-3127-5_2
350 Dawson, J.W., Mannan, R.W., 1991. Dominance Hierarchies and Helper Contributions
351 in Harris' Hawks. The Auk 108, 649–660. <https://doi.org/10.2307/4088105>
352 Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta-analysis
353 detected by a simple, graphical test. BMJ 315, 629–634.
354 Ejike, C., Schreck, C.B., 1980. Stress and Social Hierarchy Rank in Coho Salmon.
355 Trans. Am. Fish. Soc. 109, 423–426. [https://doi.org/10.1577/1548-
356 8659\(1980\)109<423:SASHRI>2.0.CO;2](https://doi.org/10.1577/1548-8659(1980)109<423:SASHRI>2.0.CO;2)
357 Geffroy, B., Bolliet, V., Bardonnet, A., 2016. Kleptoparasitism and aggressiveness are
358 influenced by standard metabolic rate in eels. Physiol. Behav. 157, 165–169.
359 Geffroy, B., Douhard, M., 2019. The Adaptive Sex in Stressful Environments. Trends
360 Ecol. Evol. 34, 628–640. <https://doi.org/10.1016/j.tree.2019.02.012>
361 Ginnaw, G.M., Davidson, I.K., Harding, H.R., Simpson, S.D., Roberts, N.W., Radford,
362 A.N., Ioannou, C.C., 2020. Effects of multiple stressors on fish shoal collective motion
363 are independent and vary with shoaling metric. Anim. Behav. 168, 7–17.
364 <https://doi.org/10.1016/j.anbehav.2020.07.024>
365 Goikoetxea, A., Sadoul, B., Blondeau-Bidet, E., Aerts, J., Blanc, M.-O., Parrinello, H.,
366 Barrachina, C., Pratlong, M., Geffroy, B., 2021. Genetic pathways underpinning
367 hormonal stress responses in fish exposed to short- and long-term warm ocean
368 temperatures. Ecol. Indic. 120, 106937. <https://doi.org/10.1016/j.ecolind.2020.106937>
369 Goikoetxea, A., Todd, E.V., Gemmill, N.J., 2017. Stress and sex: does cortisol mediate
370 sex change in fish? Reproduction 154, R149–R160. [https://doi.org/10.1530/REP-17-
371 0408](https://doi.org/10.1530/REP-17-0408)
372 Grafen, A., Hamilton, W.D., 1989. The phylogenetic regression. Philos. Trans. R. Soc.
373 Lond. B Biol. Sci. 326, 119–157. <https://doi.org/10.1098/rstb.1989.0106>
374 Grosenick, L., Clement, T.S., Fernald, R.D., 2007. Fish can infer social rank by
375 observation alone. Nature 445, 429–432. <https://doi.org/10.1038/nature05511>
376 Hahn, S., Bauer, S., 2008. Dominance in feeding territories relates to foraging success
377 and offspring growth in brown skuas *Catharacta antarctica lonnbergi*. Behav. Ecol.
378 Sociobiol. 62, 1149–1157. <https://doi.org/10.1007/s00265-007-0543-7>
379 Harris, B.N., 2020. Stress hypothesis overload: 131 hypotheses exploring the role of
380 stress in tradeoffs, transitions, and health. Gen. Comp. Endocrinol. 288, 113355.
381 <https://doi.org/10.1016/j.yggen.2019.113355>
382 Higgins, J.P.T., Thompson, S.G., Deeks, J.J., Altman, D.G., 2003. Measuring
383 inconsistency in meta-analyses. BMJ 327, 557–560.
384 <https://doi.org/10.1136/bmj.327.7414.557>
385 Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M.,
386 Crandall, K.A., Deng, J., Drew, B.T., Gazis, R., Gude, K., Hibbett, D.S., Katz, L.A.,
387 Laughinghouse, H.D., McTavish, E.J., Midford, P.E., Owen, C.L., Ree, R.H., Rees,
388 J.A., Soltis, D.E., Williams, T., Cranston, K.A., 2015. Synthesis of phylogeny and
389 taxonomy into a comprehensive tree of life. Proc. Natl. Acad. Sci. 112, 12764–12769.

390 <https://doi.org/10.1073/pnas.1423041112>
391 Holekamp, K.E., Strauss, E.D., 2020. Reproduction Within a Hierarchical Society from
392 a Female's Perspective. *Integr. Comp. Biol.* 60, 753–764.
393 <https://doi.org/10.1093/icb/icaa068>
394 Jennions, M., Møller, A.P., 2002. How much variance can be explained by ecologists
395 and evolutionary biologists? *Oecologia* 132, 492–500. [https://doi.org/10.1007/s00442-](https://doi.org/10.1007/s00442-002-0952-2)
396 [002-0952-2](https://doi.org/10.1007/s00442-002-0952-2)
397 Killen, S.S., Glazier, D.S., Rezende, E.L., Clark, T.D., Atkinson, D., Willener, A.S.T.,
398 Halsey, L.G., 2016. Ecological Influences and Morphological Correlates of Resting and
399 Maximal Metabolic Rates across Teleost Fish Species. *Am. Nat.* 187, 592–606.
400 <https://doi.org/10.1086/685893>
401 Kochhann, D., Campos, D.F., Val, A.L., 2015. Experimentally increased temperature
402 and hypoxia affect stability of social hierarchy and metabolism of the Amazonian
403 cichlid *Apistogramma agassizii*. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 190,
404 54–60. <https://doi.org/10.1016/j.cbpa.2015.09.006>
405 Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G.,
406 Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in
407 animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* 23,
408 925–935. [https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)
409 Koricheva, J., Gurevitch, J., Mengersen, K., 2013. Handbook of meta-analysis in
410 ecology and evolution. Princeton University Press, Princeton, New Jersey.
411 Landys, M.M., Ramenofsky, M., Wingfield, J.C., 2006. Actions of glucocorticoids at a
412 seasonal baseline as compared to stress-related levels in the regulation of periodic life
413 processes. *Gen. Comp. Endocrinol.* 148, 132–149.
414 <https://doi.org/10.1016/j.ygcen.2006.02.013>
415 Love, O.P., Chin, E.H., Wynne-Edwards, K.E., Williams, T.D., 2005. Stress Hormones:
416 A Link between Maternal Condition and Sex-Biased Reproductive Investment. *Am.*
417 *Nat.* 166, 751–766. <https://doi.org/10.1086/497440>
418 Metcalfe, N.B., Taylor, A.C., Thorpe, J.E., 1995. Metabolic rate, social status and life-
419 history strategies in Atlantic salmon. *Anim. Behav.* 49, 431–436.
420 <https://doi.org/10.1006/anbe.1995.0056>
421 Michonneau, F., Brown, J.W., Winter, D.J., 2016. rotl: an R package to interact with the
422 Open Tree of Life data. *Methods Ecol. Evol.* 7, 1476–1481.
423 <https://doi.org/10.1111/2041-210X.12593>
424 Mommsen, T.P., Vijayan, M.M., Moon, T.W., 1999. Cortisol in teleosts: dynamics,
425 mechanisms of action, and metabolic regulation. *Rev. Fish Biol. Fish.* 9, 211–268.
426 <https://doi.org/10.1023/A:1008924418720>
427 Nadler, L.E., Killen, S.S., Domenici, P., McCormick, M.I., 2018. Role of water flow
428 regime in the swimming behaviour and escape performance of a schooling fish. *Biol.*
429 *Open* 7. <https://doi.org/10.1242/bio.031997>
430 Nakagawa, S., Santos, E.S.A., 2012. Methodological issues and advances in biological
431 meta-analysis. *Evol. Ecol.* 26, 1253–1274. <https://doi.org/10.1007/s10682-012-9555-5>
432 Naumowicz, K., Pajdak, J., Terech-Majewska, E., Szarek, J., 2017. Intra-cohort
433 cannibalism and methods for its mitigation in cultured freshwater fish. *Rev. Fish Biol.*
434 *Fish.* 1, 193–208. <https://doi.org/10.1007/s11160-017-9465-2>
435 Nozu, R., Nakamura, M., 2015. Cortisol Administration Induces Sex Change from
436 Ovary to Testis in the Protogynous Wrasse, <i>Halichoeres
437 trimaculatus</i>; *Sex. Dev.* 9, 118–124.
438 <https://doi.org/10.1159/000373902>
439 Olivotto, I., Geffroy, B., 2017. Clownfish, in: Calado, R., Olivotto, I., Oliver, M.P.,

440 Holt, G.J. (Eds.), *Marine Ornamental Species Aquaculture*. John Wiley & Sons, Ltd, pp.
441 177–199. <https://doi.org/10.1002/9781119169147.ch12>
442 Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401,
443 877–884. <https://doi.org/10.1038/44766>
444 Palko, B.J., Beardsley, G.L., Richards, W.J., 1981. Synopsis of the biology of the
445 swordfish, *Xiphias gladius* Linnaeus. NOAA Tech. Rep.
446 Ricklefs, R.E., Wikelski, M., 2002. The physiology/life-history nexus. *Trends Ecol.*
447 *Evol.* 17, 462–468. [https://doi.org/10.1016/S0169-5347\(02\)02578-8](https://doi.org/10.1016/S0169-5347(02)02578-8)
448 Rosenthal, R., 1991. *Meta-analytic procedures for social research*, Rev. ed, Meta-
449 *analytic procedures for social research*, Rev. ed. Sage Publications, Inc, Thousand Oaks,
450 CA, US. <https://doi.org/10.4135/9781412984997>
451 Rousseau, K., Prunet, P., Dufour, S., 2021. Special features of neuroendocrine
452 interactions between stress and reproduction in teleosts. *Gen. Comp. Endocrinol.* 300,
453 113634. <https://doi.org/10.1016/j.ygcen.2020.113634>
454 Rubenstein, D.R., Abbot, P., 2017. *Comparative Social Evolution*. Cambridge
455 University Press.
456 Sadoul, B., Geffroy, B., 2019. Measuring cortisol, the major stress hormone in fishes. *J.*
457 *Fish Biol.* 94, 540–555. <https://doi.org/10.1111/jfb.13904>
458 Sadoul, B., Vijayan, M.M., 2016. 5 - Stress and Growth, in: Carl B. Schreck, L.T.,
459 Anthony P. Farrell and Colin J. Brauner (Eds.), *Fish Physiology, Biology of Stress in*
460 *Fish*. Academic Press, pp. 167–205.
461 Samaras, A., Pavlidis, M., 2018. Regulation of divergent cortisol responsiveness in
462 European sea bass, *Dicentrarchus labrax* L. *PLOS ONE* 13, e0202195.
463 <https://doi.org/10.1371/journal.pone.0202195>
464 Schjelderup-Ebbe, T., 1922. Contributions to the social psychology of the domestic
465 chicken. *Repr. Z. Fuer Psychol.* 88, 225–252.
466 Schreck, C.B., Tort, L., 2016. 1 - The Concept of Stress in Fish, in: Schreck, C.B., Tort,
467 L., Farrell, A.P., Brauner, C.J. (Eds.), *Fish Physiology, Biology of Stress in Fish*.
468 Academic Press, pp. 1–34. <https://doi.org/10.1016/B978-0-12-802728-8.00001-1>
469 Sogawa, S., Ota, K., Kohda, M., 2016. A dear enemy relationship in a territorial cichlid:
470 evidence for the threat-level hypothesis. *Behaviour* 153, 387–400.
471 <https://doi.org/10.1163/1568539X-00003351>
472 Stevens, E.D., Fry, F.E.J., 2011. Heat transfer and body temperatures in non-
473 thermoregulatory teleosts. *Can. J. Zool.* <https://doi.org/10.1139/z74-152>
474 Teichroeb, J.A., White, M.M.J., Chapman, C.A., 2015. Vervet (*Chlorocebus*
475 *pygerythrus*) Intragroup Spatial Positioning: Dominants Trade-Off Predation Risk for
476 Increased Food Acquisition. *Int. J. Primatol.* 36, 154–176.
477 <https://doi.org/10.1007/s10764-015-9818-4>
478 Thambithurai, D., Hollins, J., Leeuwen, T.V., Rácz, A., Lindström, J., Parsons, K.,
479 Killen, S.S., 2018. Shoal size as a key determinant of vulnerability to capture under a
480 simulated fishery scenario. *Ecol. Evol.* 8, 6505–6514. <https://doi.org/10.1002/ece3.4107>
481 Todd, E.V., Ortega-Recalde, O., Liu, H., Lamm, M.S., Rutherford, K.M., Cross, H.,
482 Black, M.A., Kardailsky, O., Graves, J.A.M., Hore, T.A., Godwin, J.R., Gemmell, N.J.,
483 2019. Stress, novel sex genes, and epigenetic reprogramming orchestrate socially
484 controlled sex change. *Sci. Adv.* 5, eaaw7006. <https://doi.org/10.1126/sciadv.aaw7006>
485 Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. *J.*
486 *Stat. Softw.* 36, 1–48.
487 Wacker, S., Ness, M.H., Östlund-Nilsson, S., Amundsen, T., 2017. Social structure
488 affects mating competition in a damselfish. *Coral Reefs* 36, 1279–1289.
489 <https://doi.org/10.1007/s00338-017-1623-4>

490 Wilson, E.O., 2000. Sociobiology: The New Synthesis, Twenty-Fifth Anniversary
491 Edition. Harvard University Press.
492 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid
493 common statistical problems. *Methods Ecol. Evol.* 1, 3–14.
494 <https://doi.org/10.1111/j.2041-210X.2009.00001.x>
495

496

497

498

499

500

501

502

503

504

505 **Figure Captions**

506

507 **Figure 1.** Forest plot of the social rank-cortisol effect sizes. Effect sizes are shown in
508 ascending order. Filled circles with horizontal lines represent effect size \pm 95%
509 confidence intervals. The overall and significant effect size is represented by a diamond.

510

511 **Figure 2.** Funnel plots of the meta-analyse using both the effect sizes and the meta-
512 analytic residuals of the best model.

513

514 **Figure 3.** Effects of (A) group size, (B) temperature and (C) mean fish size on the social
515 rank-cortisol relationship (Fisher's z). Plots (A) and (B) show mean \pm 95% confidence
516 intervals. The number of species tested at each factor level is shown in the bottom of
517 plots.

518

519

520

521

522

523

524

525

526

527

528

529

530

531

532

533

534 **Table 1.** Summary of the multi-model inference conducted to explain variation in the
535 social rank-cortisol in fish

Predictor	Levels	Estimate	S.E.	z-value
Intercept		0.5	0.34	1.49
Group size	Paired	0.28	0.14	1.98*
Species body size		0.028	0.014	2.12*
Environment	Tropical	-0.67	0.32	-2.08*

536 Estimates are average coefficients of the model, their associated standard error (S.E). *
537 indicates a p-value < 0.05.

538