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

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Abstract :

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

Highlights

► This meta-analysis investigates whether dominants or subordinates are more stressed. ► We covered 72 studies and evaluated 22 fish species from 13 families. ► Subordinate individuals have higher basal cortisol than dominant fish. ► Differences in cortisol are higher in small compared to large group. ► These results link social hierarchy, stress and metabolism in fishes.

Keywords : Stress, Aggressiveness, Sociality, Shoal, Meta-analysis

1. Introduction

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

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

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

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

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

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

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

2. Methods

(a) Literature search and study selection

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

(b) Estimating effect sizes

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

(c) Meta-analyses using random effects

We used hierarchical linear mixed-effects meta-analysis to test for both overall effect sizes and the importance of our moderators (Nakagawa and Santos, 2012) using the package 'metafor' v. 2.1-0 (Viechtbauer, 2010) in R v. 3.5.2. The overall effect sizes (i.e., mean of the effect sizes weighted by the inverse of their variance) were considered significant if their 95% confidence intervals (CI) did not include zero (Koricheva et al., 2013). We used model selection based on the Akaike information criterion to determine which random factors should be included in each meta-analysis (Nakagawa and Santos, 2012). Non-independence of effect sizes within and among studies was accounted for by including i) the number of effect sizes collected and ii) studies, as random-factors. Phylogenetic non-independence across studies was handled by including relationships among species (Appendix A, supplementary Figure 2) as a random effect based on the Open Tree of Life database (Hinchliff et al., 2015), and Grafen's method providing a correlation matrix from branch length (Grafen and Hamilton, 1989). The R package 'rotl' v. 3.0.10 was used for this purpose (Michonneau et al., 2016)

Group size (dyadic contexts or group>2), reproduction type (monogamous, polygamous and polygynous), habitat temperature (temperate vs tropical), time since grouping (h) and fish weight (g, square-root transformed) were considered as moderators of effect size. We tested for multi-collinearity among moderators and the highest variance inflation factor was 2.26, below the recognized threshold of 3 (Zuur et al., 2010). The factors salinity (freshwater n = 67, sea n = 7 and brackish n =4 water) and sex (male n =23, female= 7, mixed group n=31 and ambisexual n=1) could not be considered owing to discrepancies in the numbers of effect sizes. We used a multi-model inference approach based on Akaike's criteria corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). We first assessed the relative strengths of each candidate model by calculating its Akaike weight, to identify the most parsimonious model. A constant term (the intercept) was included in all models. We estimated the importance of a predictor by summing the Akaike weights of all models in which that candidate variable appeared, so ranking predictors in order of importance (Burnham and Anderson, 2002). All multi-model analyses were conducted using the *MuMIn* R package v. 1.40.0 (Barton, 2014).

(d) Heterogeneity

We used the I^2 index as a measure of heterogeneity in effect sizes. The index represents the proportion of total variation in the data that is not a consequence of sampling error (Higgins et al., 2003). We used an extended version of I^2 that partitions total heterogeneity

between the variation explained by the study identity and by the variation of the residuals. The latter remains to be explained by our moderators (Nakagawa and Santos, 2012). We calculated the degree of phylogenetic signal in our estimates of effect size using the phylogenetic heritability index, H^2, which is the variance attributable to phylogeny in relation to the total variance in the data (Nakagawa and Santos, 2012). H^2 is equivalent to Pagel's λ (Pagel, 1999), where higher values indicate stronger phylogenetic signals.

(e) Publication bias

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

3. Results

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

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

4. Discussion

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

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

amongst multiple subordinates. Altogether, these results support the "stress-enhanced hypothesis": holding a particular status drives your stress levels, indicated by cortisol values. The metabolism of dominant individuals is often, however, higher than that of subordinates (Geffroy et al., 2016; Metcalfe et al., 1995). Basal cortisol levels are also positively correlated with metabolism (Mommsen et al., 1999), and we might therefore expect that dominants would have higher cortisol values. The opposite was observed in our study, further supporting the "stress-enhanced hypothesis".

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

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

We found that habitat temperature (temperate versus tropical) also shapes the relationship between basal cortisol and social status. This would advocate for the "metabolic-enhanced" hypothesis. In warmer habitats, fishes will generally have higher metabolic rates (Killen et al., 2016), reflecting direct thermodynamic effects on all biochemical and physiological processes (Cossins and Bowler, 1987). Rates of basal cortisol production are known to be stimulated by increased temperature within fish species (Goikoetxea et al., 2021). High background rates of basal cortisol production in all individuals at high

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

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

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

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

is accentuated or diminished by habitat temperature and its effects on metabolism. These findings have major implications for our understanding of the ecology and sociality of fishes.

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Figure 1. Forest plot of the social rank-cortisol effect sizes. Effect sizes are shown in ascending order. Filled circles with horizontal lines represent effect size ± 95% confidence intervals. The overall and significant effect size is represented by a diamond.
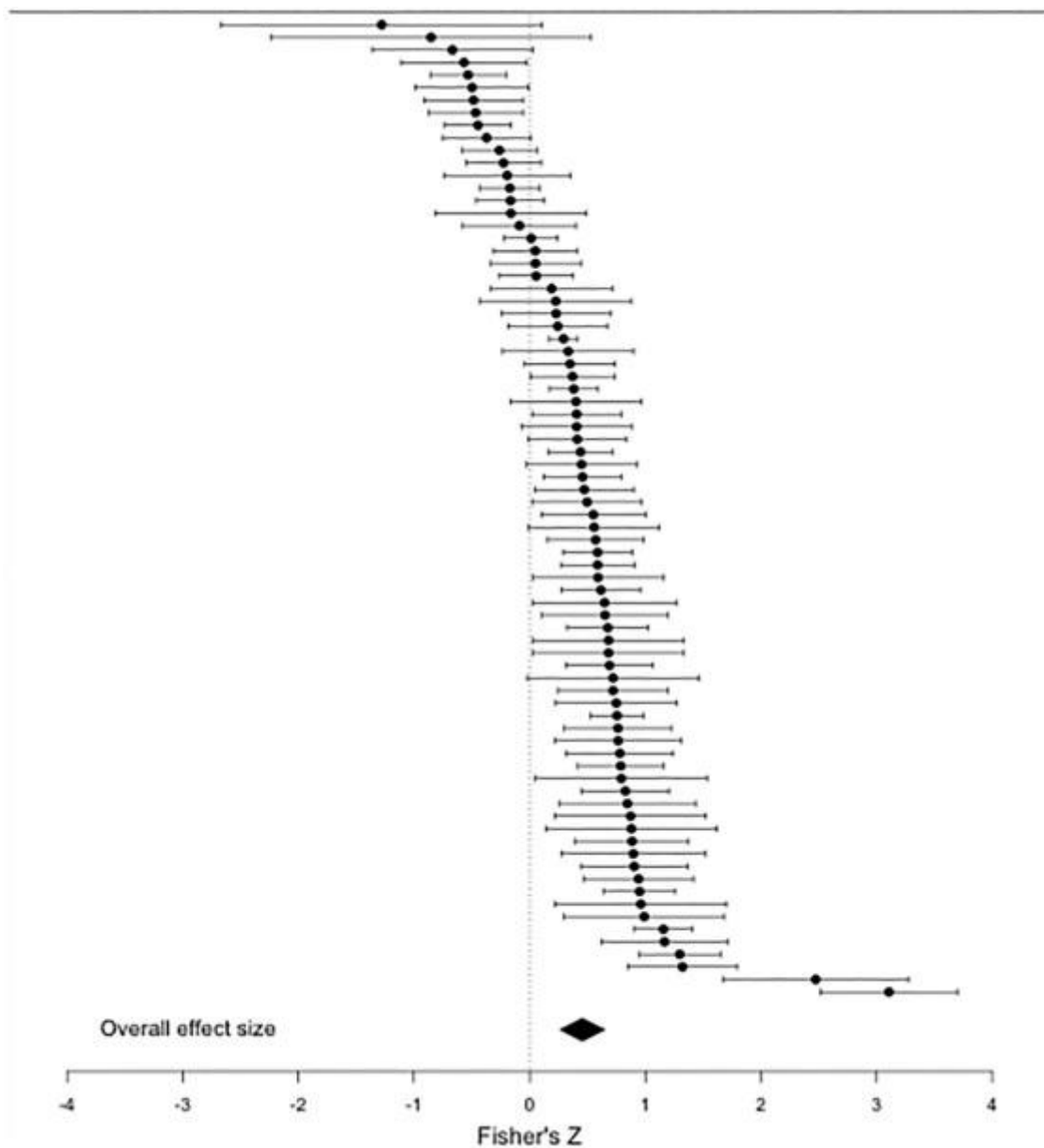
Figure 2. Funnel plots of the meta-analyse using both the effect sizes and the meta-analytic residuals of the best model.
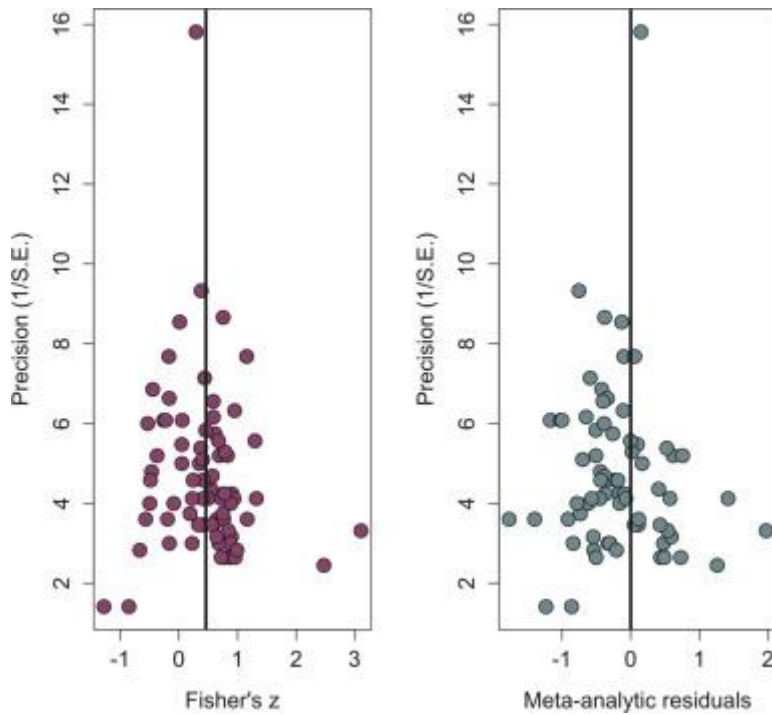
Figure 3. Effects of (A) group size, (B) temperature and (C) mean fish size on the social rank-cortisol relationship (Fisher's *z*). Plots (A) and (B) show mean ± 95% confidence intervals. The number of species tested at each factor level is shown in the bottom of plots.
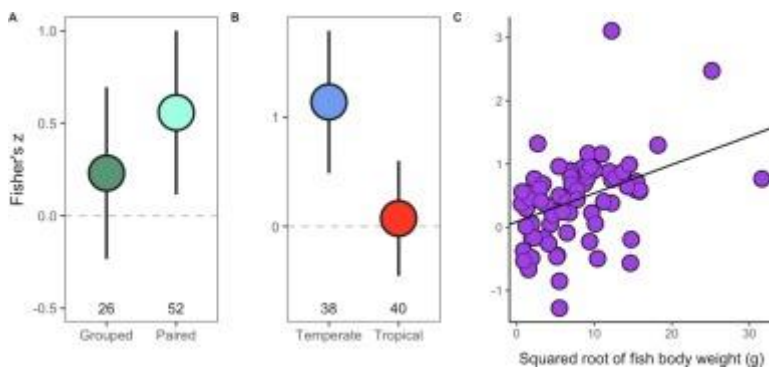
Table 1. Summary of the multi-model inference conducted to explain variation in the social rank-cortisol in fish

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*

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