



Do Cleaner Fish (*Labroides dimidiatus*) Have General Cognitive Ability? A Reanalysis of Individual Differences Data and Consideration of Phylogenetic Context

Michael A. Woodley of Menie¹ · Mateo Peñaherrera-Aguirre² · Matthew A. Sarraf³

Received: 6 January 2023 / Revised: 13 February 2023 / Accepted: 13 February 2023 / Published online: 17 March 2023
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2023

Abstract

Aellen et al. (2022) recently suggested on the basis of principal component analysis (PCA) that there is no general cognitive ability (GCA) factor in various cognitive ability measures of wild-caught cleaner fish (*Labroides dimidiatus*), making this species an oddity—given the apparent ubiquity of this dimension in many animal taxa. They report the presence of three approximately co-equal factors instead, with the first exhibiting a mixture of positive and negative loadings. Reanalysis of their data employing unit-weighted estimation yielded a GCA factor with all positive loadings accounting for 29.9% of the variance. Adding a fourth ability (feeding against preference) yielded a positive manifold accounting for 19.3% of the variance. As this technique for factor estimation typically yields latent variables exhibiting higher generalisability than those obtained via differentially weighted techniques (such as PCA), it is suggestive of what might be found were sample specificity effects to be reduced via more extensive sampling of individuals. Consistent with this possibility, it is found that the proportion of variance associated with unit-weighted estimated GCA in these data is not significantly different from the proportion of variance associated with this factor in a meta-analysis of 12 other animal taxa. Adaptationist theories of GCA make explicit predictions concerning where in the phylogenetic landscape this factor might be expected to be strongly or weakly present, or even absent altogether. These are discussed in detail.

Keywords Cleaner fish · *Labroides dimidiatus* · General cognitive ability · Unit-weighted factor estimation · Ancestral character reconstruction

Introduction

In a cleverly conceived experiment, Aellen et al. (2022) test for the presence of general cognitive ability (GCA; or the *g* factor) in wild-caught female cleaner fish (*Labroides dimidiatus*), a fish taxon that is frequently studied due to its high sociality. In humans, GCA arises from the tendency for individual differences in performance on distinct measures of cognitive ability (e.g. verbal, spatial, mathematical) to positively covary, indicating that performance differences with respect to these seemingly

narrower measures draw (to a considerable degree) on a common set of cognitive processes (Warne & Burningham, 2019). This tendency has been noted in a variety of non-human animal taxa also, although there is much debate among comparative psychologists concerning the causes and implications of this covariation (for an overview see Burkart et al., 2017).

Aellen et al.'s (2022) evaluation technique involved the measurement of individual differences in performance in four ecologically neutral domains tapping different aspects of cognition. These were selected to overlap with tasks applied to the study of individual differences in cognitive performance in mammalian taxa (so as to ensure comparative nomological breadth), and included flexibility (the ability to efficiently switch between variants of the same task, assessed via reversal learning), self-control (evaluated using a detour task and a feeding against preference task), and numerical competence (evaluated via a simultaneous two-choice task). An object permanence

✉ Michael A. Woodley of Menie
M.A.WoodleyPhD@gmail.com

¹ London, UK

² School of Animal & Comparative Sciences-Research,
University of Arizona, Tucson, USA

³ Boston, USA

task was also administered, but the individuals did not outperform chance—therefore this was not included in their principal components analysis (PCA). The results of Aellen et al.'s PCA involving three of their four measures (feeding against preference was excluded) indicated the presence of three approximately co-equal factors. Moreover, the numerical competence measure exhibited a negative loading onto the first PC. This apparent failure to find a clear single factor with all-positive loadings, is offered as evidence against criticisms of the idea of GCA in animals, specifically that this factor is merely an (unremarkable) by-product of condition dependence (such as the presence of pleiotropic mutations imposing global constraints on neural development and processing efficiency generating potentially spurious performance correlations among otherwise independent cognitive systems), which can effectively be ignored in comparative psychological research (for further discussion of this see Burkart et al., 2017).

The apparent absence of GCA in this taxon instead suggests that there might be distinct ways in which endotherms and ectotherms apply neuroanatomy to solving cognitive challenges, specifically the smaller brains that are typical of ectotherms may lack sufficient space for the accommodation of the sorts of structures that facilitate integration of distinct cognitive processes (such as executive functions)—thus, among ectotherms, these constraints may prevent the emergence of GCA. The presence of mixed positive and negative loadings onto the first factor might even be suggestive of tradeoffs among different cognitive domains in cleaner fish. Moreover, although Aellen et al. (2022) do not state this, the absence of GCA in at least some taxa is also suggestive of an adaptationist model of GCA, as based on this, the factor emerges only in response to the presence of certain selective challenges, especially those associated with the presence of evolutionarily novel or phylogenetically irregularly occurring fitness challenges, which may require the higher-level coordination of outputs associated with distinct (experience expectant) cognitive systems (modules) in order to yield adaptive solutions. Such a higher-order cognitive system would be slow to yield such solutions (as it would be dependent on domain-general processes such as learning via trial and error and conditioning), but should be characterised by extremely high ecological flexibility, allowing for a very large array of solutions to be generated for any given problem in a way that is unconstrained by the action of dedicated lower-order and context-sensitive forms of cognition (Geary, 2005). The latter by contrast would be expected to dominate cognitive performance in the absence of GCA.

This suggests that when present, GCA should be taken seriously by researchers interested in the study of the adaptive histories of species, as it indicates a significant role for

unpredictable ecological processes in shaping the phylogenesis of cognition.

Statistics and GCA

The primary basis on which Aellen et al. (2022) reject a GCA-factor solution for cleaner fish is the result of their PCA. The PCA structure exhibits the following pattern. The first component accounts for 38.5% of the variance (Eigenvalue = 1.16), the second accounts for 32.8% (Eigenvalue = 0.98), and the third accounts for 28.7% (Eigenvalue = 0.86). The presence of three approximately co-equal factors along with a mixture of positive and negative loadings on the first factor might at first glance challenge the idea of GCA in this taxon—given the expectation that, were this present, the first factor should account for more of the variance than any other factors across tasks, and should exhibit all-positive loadings. Indeed, this is what is typically seen in human populations assessed using psychometric methods (Warne & Burningham, 2019). Obtaining results like those seen in the cleaner fish in human populations is not unheard of, however (where two or three factors emerge instead of one “clean” dominant factor [Warne & Burningham, 2019], and where a first factor emerges exhibiting an anomalous mixture of positive and negative loadings [e.g. Eid et al., 2017]). Indeed, such a situation can result from several different statistical phenomena, including (but not limited to) range restriction, construct reliability and validity limitations, nuisance parameters affecting the measurement model, and other sources of measurement and sampling error. All or some of these can be present, and lead to failure to detect GCA, even though GCA is in fact part of the cognitive architecture of the population considered. In the first instance, GCA-factor covariance can be expected to emerge more clearly once corrections are made for the effects of various sources of sampling and measurement error (Schmidt & Hunter, 2015) and nuisance parameters (such as personality variance influencing cognitive performance independently of the underlying abilities). One technique for dealing with the effects of the latter on designs employing repeated performance measurement involves the use of mixed models to jointly fix these effects in estimating within-individual variance. An example of this approach can be found in Prentice et al. (2022a) who investigated (and found evidence for) the presence of GCA using data from three cognitive tasks (colour association learning, motor learning, and reversal learning) in a sample of 80 Trinidadian guppies (*Poecilia reticulata*) (see also Prentice et al., 2022b).

A secondary basis given by Aellen et al. (2022) for rejecting the presence of a GCA factor in their data is the effectively zero-magnitude mean correlation coefficient estimated on the basis of their correlation matrix. Essentially the same

argument was made by Poirier et al. (2020) in a meta-analysis of the strength of bivariate associations among hundreds of pairs of abilities involving a number of animal taxa, where it was noted that the mean strength of these associations was low. The use of a low- or zero-magnitude average of bivariate phenotypic correlations as a basis for questioning the presence of common factor variance rests on optimistic assumptions regarding the reliability estimates associated with the various correlation coefficients, however. Such associations will necessarily suffer from attenuation due to the potential underlying unreliability inherent in each of two or more measures under statistical examination. According to Cohen and Cohen (1983), this phenomenon is captured by the following equation:

$$\rho_{xy} = r_{xy} / \sqrt{(r_{xx} * r_{yy})}$$

where r_{xy} corresponds to the observed (i.e. raw) correlation coefficient, r_{xx} and r_{yy} represent the reliabilities of x and y , and ρ_{xy} is the disattenuated correlation coefficient.

Reliability attenuation is not an insurmountable methodological problem. For example, Epstein (1986) determined that data aggregation can substantially reduce the extent of measurement error. Moreover, composite scores feature greater stability and generalisability relative to univariate estimates. The reliability estimates of aggregate variables are considerably greater compared with those of individual variables or lower-order indicators. Consequently, the reported small magnitude of the aggregated bivariate correlations noted by Poirier and colleagues (2020), and also Aellen et al. in their study, is most likely merely a product of the individual variables' restricted reliability. Instead, meta-analytic examinations (such as in Poirier et al., 2020) should consider the proportion of variance explained by GCA based on analyses that estimate latent variables. These procedures offer far better insights into the psychometric features of GCA relative to bivariate correlations between individual cognitive tasks featuring low reliabilities and consequently low magnitudes due to statistical attenuation.

Aellen et al.'s suggestion that their apparently "GCA-less" factor structure may reflect the action of phylogenetic constraints on encephalisation is nonetheless a compelling hypothesis. Perhaps the environment of evolutionary adaptiveness of the cleaner fish was characterised by more phylogenetically recurrent problems, which (as was mentioned previously) would tend to favour forms of cognitive modularisation or specialisation over encephalisation of a sort that might accommodate the kinds of executive functions that likely bind discrete cognitive processes, allowing for domain-general problem solving (Burkart et al., 2017). This would potentially yield looser, and possibly even negative, correlations between constituent cognitive processes, allowing them to make independent contributions to problem

solving—especially when the problem encountered is highly matched to its primary functional domain.

A potential theoretical counter to this idea stems from the frequency with which GCA or GCA-like factors have been found across different animal taxa (see Burkart et al.'s 2017 for a multi-species review), including (as previously discussed) very recently in another fish taxon (specifically the Trinidadian guppy [*Poecilia reticulata*] (Prentice et al., 2022a)). The presence of GCA-like factors seems to be the rule rather than the exception across animal taxa. Therefore, the possibility that Aellen et al.'s seemingly anomalous results stem from error associated with sample specificity effects, which can affect the outcome of certain latent variable estimation techniques, must be considered.

Unit-Weighted vs. Differentially Weighted Estimation of Factor Structure

Statistical techniques such as unit-weighted estimation potentially allow for the computation of latent variables (LVs) that are theoretically less constrained by sampling error (Garcia, 2017; Gorsuch, 2015). Conventional factor estimation techniques (such as PCA) employ differential weighting, whereby some criterion is used to differentially weight (w) manifest variables (MVs) of some underlying LV so that additional weight is given to those variables that better represent the underlying LV (where $w \propto \lambda$; Garcia, 2017). This is expressed in the following equation:

$$LV = w_1 zMV_1 + w_2 zMV_2 + w_3 zMV_3 \dots + w_n zMV_n \quad (1)$$

An alternative is to unit-weight the standardised (z) MVs, such that each MV is constrained in terms of weight equivalence ($w = 1$; Garcia, 2017), as follows:

$$LV = \frac{z(MV_1) + z(MV_2) + z(MV_3) \dots + z(MV_n)}{n} \quad (2)$$

This method for LV estimation, while seemingly counterintuitive as it disregards certain sample characteristics, nevertheless yields LVs that correlate typically very highly with ones derived conventionally for the same sample (Schmidt, 1971). Moreover, based on the results of simulations, it has been found that unit-weighted LVs generalise to a much greater degree than conventionally estimated ones across studies exhibiting variation in sample characteristics and conditions (Schmidt, 1971), although the theoretical rationale for why this might be the case has (until recently) been poorly understood.

Garcia (2017) has recently argued that sampling theory might account for the better performance of unit-weighted estimated LVs. He argues as follows:

Now why choose the unit-weighting procedure over the differential-weighting procedure? The latter will better fit the sample data, but the former will generalize better. Unit-weighting generalizes better as it more closely parallels the sampling procedures used in the sampling of individuals (units), which is designed to estimate the population parameters. Whether discussing individuals from a population of potential participants or indicators from a population of potential measures, in both cases some instances will better represent the relevant underlying population (some individuals or indicators will deviate less than others from the true population value). Instances are thus given equal weight in an attempt to correct for systematic differences that cancel out on the aggregate (individual differences in the case of individuals and specific variance components in the case of indicators). What is left is a single point estimate that approximates the true population value. (pp. 29–30)

Garcia (2017) summarises the benefit of unit-weighting as follows:

Until “true” manifest-latent relationships can be derived (e.g. meta-analytic factor loading estimates), unit-weighting is a reasonable and powerful option based in sampling theory. While it is true that unit-weighting results in a loss of sample-level information, the decrease in resolution actually *facilitates* the discovery of more robust effects. (p. 30, italics in original)

This is relevant to Aellen et al. (2022) in that sampling error stemming from sample specificity effects may be the primary cause of their apparent failure to identify a GCA factor in their data. Were this the case, an LV estimated using the unit-weighted procedure would likely yield a coherent positive manifold with respect to the MVs, bringing their data into alignment with the preponderance of findings in other animal (including fish) taxa. The resultant LV ought then to exhibit certain characteristics in common with GCA factors extracted from the preponderance of other animal taxa. For example, it should yield statistically comparable proportions of variance to those found in a meta-analysis of other animal taxa. This prediction can be tested with reference to meta-analytic data on the prevalence of GCA or GCA-like LVs in these other taxa.

Methods

Data

All data, meta-data, and code used in Aellen et al. (2022) have been made publicly available by those authors for full reanalysis (they can be accessed at the following url: <https://doi.org/10.6084/m9.figshare.13215434>).

Unit-Weighted Estimation

Unit-weighted estimation was conducted using ranking data (as was done by Aellen et al., 2022), which obviates the need to reverse-score MVs. The unit-weighted LV was estimated simply as the average of the fish’s rank-scores across each of the four MVs. Factor loadings were estimated by simply correlating each MV with this average, the resultant part-whole correlation functions precisely equivalent to a factor loading (Beauducel & Leue, 2013; Garcia, 2017; Gorsuch, 2015). Proportion of variance associated with the LV can be computed as the average of the squared factor loadings (Garcia, 2017). The Eigenvalue is the sum of the squared factor loadings.

Ancestral Character Reconstruction

Data on 11 taxa were sourced from a supplemental file released as part of a recent meta-analysis of intercorrelation strength among cognitive abilities (Poirier et al., 2020), which also reports proportions of variance associated with the first factor broken out by study (estimated using PCA or principal axis factor [PAF] analysis). In instances of several studies per taxon, a sample-size -weighted average was estimated (such as in the case of mice). Some effect sizes were removed from Poirier et al.’s sample on the basis of repeated measures. For example, the sample of 99 chimpanzees used in Hopkins et al. (2014) is precisely the same as the one used in Woodley of Menie et al. (2015) and in Beran and Hopkins (2018). A similar potential repeated measures problem occurs in the case of the studies of Van Horik et al. (2018, 2019), which are treated as independent in Poirier et al., but which drew their pheasants (31 and 11 individuals, respectively) from the same sample of 200 birds. In this case, the average of 14 GCA factors derived from different ability combinations extracted from the larger of the two samples (Van Horik et al., 2019) is reported. A number of distinct effect sizes are also reported by Poirier et al. for what are in effect subsamples of common samples in various mice studies (Galsworthy et al., 2005; Kolata et al., 2007; Matzel et al., 2017; Sauce et al., 2014). In these cases, the largest subsamples were chosen to represent each study—alternatively, when precisely the same subset of individuals was used in different experimental designs testing different numbers of abilities, the result of factor analyses involving the largest number of abilities was chosen to represent the study. The mouse study of Kolata et al. (2008) was discarded as its data are drawn (for the most part) from previous studies already included. An additional study (Prentice et al., 2022a) is also included in order to broaden out the analysis with respect to fish. The relevant data on the 12 taxa are presented in Table 1.

Ancestral character reconstruction using GCA variance was performed using the phylogenetic package *Phytools*

Table 1 Proportion of variance explained by GCA or a GCA-like latent variable (σ^2) in a sample of 12 nonhuman animal taxa. All effect sizes are estimated via differentially weighted factor estimation (e.g. PCA or PAF). Weighted averages across different samples of the

same taxon are used to generate aggregate estimates. The table also reports total sample size, along with the GCA or GCA-like latent variable variance transformed into Pearson’s r estimates as well as their respective 95% confidence intervals

<i>Binomial</i>	Vernacular name	<i>n</i>	$g(\sigma^2)$	$g(r)$	95% CI $g(r)$
<i>Canis lupus</i>	Domestic dog	65	0.170	0.412	0.187, 0.596
<i>Chlamydera maculata</i>	Spotted bowerbird	11	0.441	0.664	0.107, 0.903
<i>Gymnorhina tibicen</i>	Australian magpie	46	0.646	0.804	0.671, 0.887
<i>Melospiza georgiana</i>	Swamp sparrow	20	0.314	0.560	0.157, 0.803
<i>Melospiza melodia</i>	Song sparrow	41	0.385	0.621	0.388, 0.779
<i>Mus musculus</i>	Domestic mouse	1144	0.270	0.520	0.477, 0.561
<i>Pan troglodytes</i>	Chimpanzee	99	0.192	0.438	0.264, 0.584
<i>Petroica longipes</i>	New Zealand robin	16	0.345	0.587	0.129, 0.838
<i>Phasianus colchicus</i>	Pheasant	31	0.325	0.570	0.271, 0.769
<i>Poecilia reticulata</i>	Trinidadian guppy	80	0.570	0.755	0.642, 0.836
<i>Ptilonorhynchus violaceus</i>	Satin bowerbird	20	0.275	0.524	0.107, 0.784
<i>Rattus norvegicus</i>	Norwegian rat	22	0.323	0.568	0.193, 0.798

(Revell, 2012) in R version 4.0.1. As the spotted bowerbird was not included in the most recent version of the *TimeTree* online data repository (Kumar et al., 2017), this taxon was excluded from the ancestral character reconstruction.

An additional step involved the use of Fisher’s r -to- z test in order to determine the significance of the difference between the proportion of variance accounted for by the (unit-weighted) LV in the cleaner fish and the meta-analytically weighted GCA variance across the 12 taxa listed in Table 1.

Results

Unit-Weighted Estimation Involving Three and Four MVs

Two separate unit-weighted estimations were performed. The first involved the use of the three MVs from Aellen et al. (2022). The second involved the use of all four MVs (including feeding against preference). The results of the first unit-weighted estimation yielded indications of a GCA-like factor with all-positive loadings. This LV explained 29.9% of the performance variance (Eigenvalue = 0.897).

The second estimation yielded a single GCA-like LV that explained 19.3% of the variance (Eigenvalue = 0.772). The results of these analyses are presented in Table 2.

Ancestral Character Reconstruction

The ancestral character reconstruction, as displayed in Fig. 1, suggests that although the proportion of variance explained by GCA in cleaner fish is relatively small in magnitude relative to other taxa, it falls within the range of values associated with other nonhuman animals.

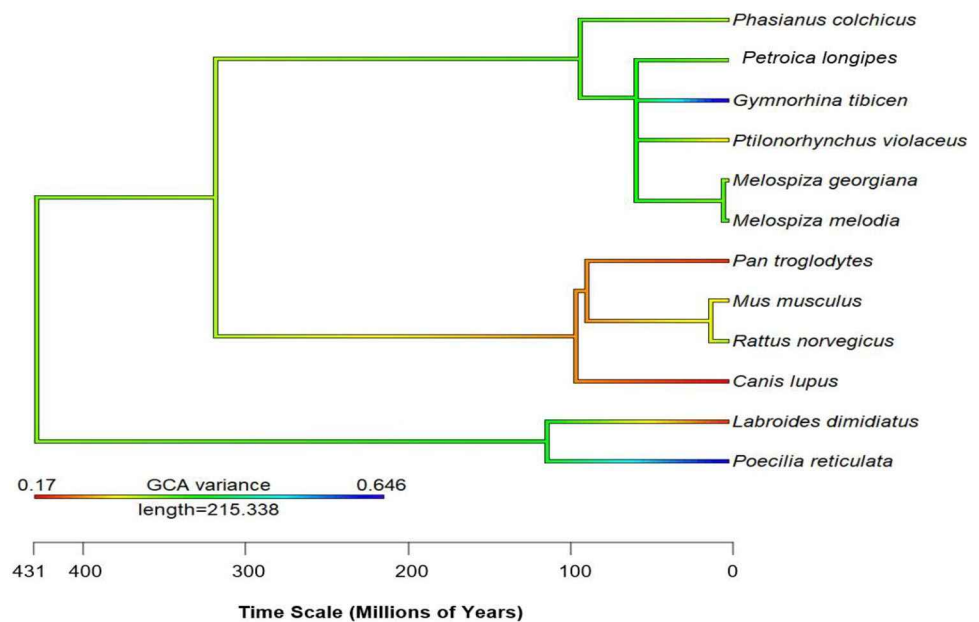
There was no significant difference between the sample-size-weighted proportion of LV variance (expressed as a correlation coefficient) across all species in the dataset and the equivalent parameter derived from the reanalysis of the cleaner fish data involving all four ability measures (ρ 12 species = 0.544, n = 1595; r cleaner fish = 0.439, n = 69; z = 1.11; p = 0.267). Consequently, the unit-weighted GCA-like LV estimated for the cleaner fish does not appear to be anomalously small when considered in the broader context of similar findings involving other animal (including fish) taxa.

Table 2 Unit-weighted factor estimate of GCA employing three and four ability measures respectively in a sample of 69 cleaner fish

Ability	UWF 1 λ	95% CI	UWF 2 λ	95% CI
<i>Z</i> -reverse learning	0.543	0.352, 0.690	0.420	0.204, 0.597
<i>Z</i> -detour task	0.596	0.419, 0.729	0.397	0.177, 0.579
<i>Z</i> -numerical competency	0.496	0.294, 0.655	0.535	0.342, 0.684
<i>Z</i> -feeding against preference	–	–	0.390	0.169, 0.573

λ = factor loading; p < 0.0001 in all cases

Fig. 1 Ancestral character reconstruction examining the magnitude of change in the proportion of variance explained by a GCA or GCA-like latent variable across a sample of 12 nonhuman animal taxa (including cleaner fish and excluding spotted bowerbirds). The proportion of variance explained by GCA in cleaner fish was computed using a unit-weighted factor estimation employing all four ability measures. All other estimates are derived using differentially weighted latent variables (estimated via PCA or PAF)



Discussion

Unit-weighted estimation is suggestive of the presence of a GCA or GCA-like factor in Aellen et al.'s (2022) data. When employing all four ability measures, an LV with all-positive loadings is identified, accounting for 19.3% of the variance. When restricted to the three measures employed by Aellen et al., the resultant LV explained 29.9% of the variance, and once again all-positive loadings are observed. Neither LV exhibits an Eigenvalue >1 , which indicates that caution needs to be exercised when interpreting these findings, as the LVs exhibit less variance than their constituent MVs.

A very useful way to consider LVs derived via unit-weighted estimation is, in a sense, as hypotheses concerning the way in which the factor structure may appear if sampling error were minimised. In other words, they can suggest models that should be tested in future research (Beauducel & Leue, 2013). As Garcia (2017) notes, the higher generalisability of unit-weighted LVs with respect to different samples characterised by different conditions suggests that such LVs may serve as adequate approximations of the “true” manifest-latent relationships among variables in the absence of meta-analytic estimates of these relationships. The case for this possibility is strengthened in the context of the matter at hand, since, when considered in relation to the proportion of variance associated with the differentially weighted LVs in other animal taxa, the estimate does not appear to have significantly different magnitude from the meta-analytic aggregate of those LVs. Moreover, the presence of GCA or GCA-like factors in this fish taxon might not be entirely unexpected. This is because, as mentioned previously, a compelling GCA factor has also now been found

in one other fish species, specifically Trinidadian guppies, where it was observed to account for a somewhat larger proportion of performance variance, relative to the current finding, 57% among various learning tasks (Prentice et al., 2022a).

Unit-weighted estimation is agnostic concerning the precise source of sampling error in a given sampling design, but it is notable that the MV onto which the first PC loads anomalously in Aellen et al.'s analysis (numerical competency) is associated with the lowest coefficient of variance (CV), which is suggestive of range restriction with respect to this measure. At the level of the raw performance data, the CV associated with this measure was 7.121, compared with values ranging from 33.848 for feeding against preference to 69.567 for detour task. It might therefore be that fish collected from this specific site exhibited non-representatively low phenotypic variability with respect to this specific MV. It is also possible that the experimental design inadvertently attenuated variance for this ability—perhaps via the unintended introduction of selection effects associated with the use of only female specimens and selection for certain personality types (see Carere & Locurto, 2011 for further discussion of this). Generally, smaller samples are more likely to be confounded with sampling error (Schmidt & Hunter, 2015). The sample size employed in Aellen et al. falls below the average across studies sourced from Poirier et al. (2020) grouped by species, with the mean sample size being 133. However, it will be noted that the values vary enormously, with mice being the most intensively studied of all taxa ($n = 1144$) and spotted bowerbirds being the least well studied in this regard ($n = 11$), despite exhibiting an apparently adequate GCA-factor (it accounted for 44% of

the performance variance in this taxon). In any event, larger samples of cleaner fish would be desirable for future research.

It is also entirely possible that the unit-weighted structures recovered from these data may not generalise to a larger sample if its absence based on the use of differential-weighting techniques such as PCA is contingent in any way upon systematic sample specificity effects. One finding that is potentially consistent with this possibility is the lack of a correlation between the unit-weighted GCAs and their PCA-derived counterparts in Aellen et al.'s data. Generally, there are correlations between these, even in cases where the unit-weighted LVs better approximate the meta-analytic value (Schmidt, 1971).

If in the process of collecting larger and prospectively more representative samples of this taxon, or if in the course of meta-analysing the results of various studies on this taxon involving smaller samples, it becomes clear that the factor structure identified by Aellen et al. is robust and replicable, then there will be evidence against the GCA hypothesis applied to this taxon, which is a prospectively extremely important finding, as it would be consistent with an adaptationist model of GCA.

Adaptationist models of GCA should yield predictions concerning where in the phylogenetic landscape GCA is likely to be present and where it is more likely to be only weakly present, or even absent altogether. Environments characterised by highly predictable ecologies in which an organism's phylogenetic history is strongly correlated with its ontogenetic experiential history are expected to favour weaker correlations among cognitive abilities and higher (experience-expectant) modularisation. Environments, where these phylogenetic-ontogenetic correlations are absent or are relatively weak are predicted to promote tighter correlations among cognitive processes perhaps mediated by the presence of executive systems that allow for domain -widening “bundling” of representations arising from modular systems, coupled with selective retention of these potential “solution sets” based on the outcomes of (e.g.) trial-and-error learning. This would be expected to greatly enhance cognitive flexibility in the face of ecological unpredictability (see further discussion in Burkart et al., 2017). Environmental fluctuations have been posited to select for species' levels of ecological generalism more broadly; thus, it is feasible that these contingencies also promote the evolution of tighter integration among cognitive abilities, allowing for greater cognitive flexibility (Fernandes, 2020). Some hints of this have been found in research on primates using species-level *G* data, where it has been observed that species exhibiting lower levels of *G* also exhibit lower levels of integration among cognitive abilities (Fernandes, 2020). Future studies should (a) revisit in an intensified manner the cleaner fish with a view to compellingly replicating the GCA-less factor structure in this taxon, and (b) expand the scope of species considered so as to explicitly target those known to live in highly ecologically

stable environments, where it is predicted that GCA-factor covariance will be only weakly present, or even absent. Such efforts must, however, take great care when interpreting the results of said studies which might, due to reasons of sampling error, nuisance parameters, (limited) construct reliability and validity, etc., be unable to confidently rule out the presence of the construct in a given taxon.

Acknowledgements We would like to thank Alastair Wilson and Redouan Bshary for their constructive comments on earlier drafts of this manuscript.

Author Contribution MAW devised the analysis and contributed to drafting the text. MPA conducted all analyses. MAS contributed to drafting of the text.

Data Availability All data are publicly available from the following url: <https://doi.org/10.6084/m9.figshare.13215434>.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest The authors declare no competing interests.

References

- Aellen, M., Burkart, J. M., & Bshary, R. (2022). No evidence for general intelligence in a fish. *Ethology*, *128*, 424–436.
- Beauducel, A. & Leue, A. (2013). Unit-weighted scales imply models that should be tested! *Practical Assessment, Research, & Evaluation*, *18*, Article 1.
- Beran, M. J., & Hopkins, W. D. (2018). Self-control in chimpanzees relates to general intelligence. *Current Biology*, *28*, 574–579.
- Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral & Brain Sciences*, *40*, e192.
- Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*, 491–498.
- Cohen, J., & Cohen, P. (1983). *Applied multiple regression/correlation analysis for the behavioral sciences*. Erlbaum.
- Eid, M., Geiser, C., Koch, T., & Heene, M. (2017). Anomalous results in G-factor models: Explanations and alternatives. *Psychological Methods*, *22*, 541–562.
- Epstein, S. (1986). Does aggregation produce spuriously high estimates of behavior stability? *Journal of Personality & Social Psychology*, *50*, 1199–1210.
- Fernandes, H. B. F. (2020). *Evolutionary trajectories of cognitive abilities and of their putative neuroanatomical and allometric correlates: Testing novel hypotheses of cognitive evolution and cognitive integration with phylogenetic comparative methods* (Unpublished doctoral dissertation) The University of Arizona, Tucson, AZ.
- Galsworthy, M. J., Paya-Cano, J. L., Liu, L., Monleón, S., Gregoryan, G., Fernandes, C., & Plomin, R. (2005). Assessing reliability,

- heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behavior Genetics*, 35, 675–692.
- Garcia, R. (2017). *I'd give my right kidney to be altruistic: The social biogeography of altruism in the United States of America* (Unpublished doctoral dissertation). The University of Arizona, Tucson, AZ.
- Geary, D. C. (2005). *The origin of mind: Evolution of brain, cognition, and general intelligence*. American Psychological Association.
- Gorsuch, R.L. (2015). *Factor analysis: Classic edition*. Routledge.
- Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, 24, 1649–1652.
- Kolata, S., Light, K., & Matzel, L. D. (2008). Domain-specific and domain-general learning factors are expressed in genetically heterogeneous CD-1 mice. *Intelligence*, 36, 619–629.
- Kolata, S., Light, K., Grossman, H. C., Hale, G., & Matzel, L. D. (2007). Selective attention is a primary determinant of the relationship between working memory and general learning ability in outbred mice. *Learning & Memory*, 14, 22–28.
- Kumar, S., Stecher, G., Suleski, M., & Hedges, S. B. (2017). TimeTree: A resource for timelines, timetrees, and divergence times. *Molecular Biology Evolution*, 34, 1812–1819.
- Matzel, L. D., Kolata, S., Light, K., & Sauce, B. (2017). The tendency for social submission predicts superior cognitive performance in previously isolated male mice. *Behavioural Processes*, 134, 12–21.
- Poirier, A.-A., Kozlovsky, D. Y., Morand-Ferron, J., & Careau, V. (2020). How general is cognitive ability in nonhuman animals? A meta-analytical multi-level reanalysis approach. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201853.
- Prentice, P., Mnatzaganian, C., Houslay, T. M., Thorton, A., & Wilson, A. J. (2022b). Individual differences in spatial learning are correlated across tasks but not with stress response behaviour in guppies. *Animal Behaviour*, 188, 133–146.
- Prentice, P. M., Thorton, A., & Wilson, A. J. (2022a). A multivariate view of cognitive performance reveals positive correlation in the Trinidadian guppy (*Poecilia reticulata*). *bioRxiv*. <https://doi.org/10.1101/2021.11.04.467320>.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology & Evolution*, 2, 217–223.
- Sauce, B., Wass, C., Smith, A., Kwan, S., & Matzel, L. D. (2014). The external–internal loop of interference: Two types of attention and their influence on the learning abilities of mice. *Neurobiology of Learning & Memory*, 116, 181–192.
- Schmidt, F. L. (1971). The relative efficiency of regression and simple unit predictor weights in applied differential psychology. *Educational & Psychological Measurement*, 31, 699–714.
- Schmidt, F. L., & Hunter, J. E. (2015). *Methods of meta-analysis: Correcting error and bias in research findings (3rd ed.)*. Thousand Oaks.
- Van Horik, J. O., Langley, E. J., Whiteside, M. A., & Madden, J. R. (2019). A single factor explanation for associative learning performance on colour discrimination problems in common pheasants (*Phasianus colchicus*). *Intelligence*, 74, 53–61.
- Van Horik, J. O., Langley, E. J., Whiteside, M. A., Laker, P. R., & Madden, J. R. (2018). Intra-individual variation in performance on novel variants of similar tasks influences single factor explanations of general cognitive processes. *Royal Society Open Science*, 5, 171919.
- Warne, R. T., & Burningham, C. (2019). Spearman's *g* found in 31 non-Western nations: Strong evidence that *g* is a universal phenomenon. *Psychological Bulletin*, 145, 237–272.
- Woodley of Menie, M.A., Fernandes, H.B.F., & Hopkins, W.D. (2015). The more *g* loaded, the more heritable, variable and evolvable: Homology with humans in chimpanzee cognitive abilities. *Intelligence*, 50, 159–163.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.