


COMMENTARY

Confounding social and mating systems predictably lead to biased results when examining the evolution of cooperative breeding in cichlids: A response to Tanaka et al.

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Editor: Dr. Bshary

Abstract

In 2017, we demonstrated that transitions to cooperative breeding in Lamprologine cichlid fishes were not related to a species' social mating system (Dey et al. 2017. *Nature Ecology & Evolution*, **1**, 137). This contrasted previous evidence that monogamy (and a low degree of promiscuity) promoted transitions to cooperative breeding in other taxa. Recently, Tanaka et al. (2018. *Ethology*, **124**, 777–789) critiqued our study and argued that a re-analysis of the data shows transitions to cooperative breeding are promoted by non-monogamous mating systems. Here, we show that Tanaka et al.'s critique contains numerous inaccuracies. In addition, we show that the results put forth by Tanaka et al. emerge only under the extreme scenario in which all cooperative breeding species are classified as non-monogamous, which we argue arises because Tanaka et al. confound social systems and mating systems. While we agree that there is uncertainty regarding the mating system of some Lamprologine species, we argue this uncertainty was sufficiently addressed through the extensive sensitivity analyses conducted in our original study.

1 | INTRODUCTION

Evolutionary transitions to cooperative breeding are thought to be favoured by low degrees of sexual promiscuity (the so-called “monogamy hypothesis”). Monogamous mating generates high levels of within-group relatedness, which increases the potential for kin-selected (i.e., indirect) benefits of cooperating with other group members. Indeed, monogamy (or a low degree of promiscuity) is inferred to be the ancestral state that preceded the transition to eusociality in insects (Boomsma, 2009; Hughes, Oldroyd, Beekman, & Francis, 2014), and has been linked to cooperative breeding

in birds (Cornwallis, West, Davis, & Griffin, 2010) and mammals (Lukas & Clutton-Brock, 2012). However, in a recent study (Dey et al., 2017), we found that the evolution of cooperative breeding in Lamprologine cichlid fishes, the only group of fishes that exhibits cooperative breeding behaviours, was not associated with social monogamy. Instead, we argued that direct fitness benefits are the primary evolutionary driver of cooperative behaviours in this clade.

Tanaka et al. (2018) critiqued our study, suggesting that we (a) used inappropriate proxies of within-group relatedness, (b) conducted our analysis using an inaccurate phylogenetic topology, and (c) misclassified the mating system of 23 species. While Tanaka et

al. (2018) did not challenge our primary inference that direct fitness benefits are more important than indirect fitness benefits in the evolution of Lamprologine cooperative breeding, they claimed – based on a re-analysis of the data – that transitions to cooperative breeding are promoted by non-monogamous (promiscuous) breeding systems. Unfortunately, Tanaka et al.'s (2018) critique contains numerous inaccuracies. Below, we address the specific claims made by Tanaka et al. (2018), and highlight how their concerns were already dealt within our original analyses (Dey et al., 2017). Furthermore, we demonstrate how their re-analysis contains unsupported assumptions which strongly bias their results.

2 | PROXIES OF WITHIN-GROUP RELATEDNESS

Tanaka et al. (2018) criticise the use of mating systems as proxies for within-group relatedness and point out that within-group relatedness may remain high in species where males are promiscuous but females only mate with a single male (e.g., in harems). We fully agree with this statement. In fact, we conducted such an analysis in our original paper to account for the important role of female-mating behaviour on within-group relatedness. Specifically, in Supplementary Table 1 of Dey et al. (2017) we include information on “Female social mating systems”, and describe whether females are socially monogamous or non-monogamous. Moreover, in the “Sensitivity testing” section in Dey et al., (2017), we state:

However, because female monogamy influences within-group relatedness to a greater extent than male monogamy, and increased within-group relatedness is one of the primary arguments for monogamy driving the evolution of cooperation, we also conducted additional analyses considering female-mating system (that is, whether the females are monogamous or promiscuous, regardless of male mating system), rather than using a classical mating system.

The results from this female-centric mating system classification are consistent with those presented in the main text of our publication (see Dey et al., 2017; Supplementary Table 7).

We were surprised that Tanaka et al. (2018) called for an analysis that we had already conducted in our original publication. More importantly, despite the fact that Tanaka et al. (2018) highlight the importance of considering female-centric mating systems when thinking about within-group relatedness, they chose to employ the classic, male-centric formulation of mating system in their re-analysis of our data (Tanaka et al., 2018; Figure 1). In effect, Tanaka et al. (2018) ignore their own criticisms in their re-analysis of our work, despite the fact that some of their own research demonstrates that polygynous cichlids can have high levels of within-group relatedness (Tanaka et al., 2015).

Tanaka et al. (2018) also point out that within-group relatedness can be affected by a range of factors (e.g., reproductive parasitism or adoption of young). We agree that such factors may influence within-group relatedness in some cichlid species. However, genetic estimates of the mating systems have been performed on only a handful of Tanganyikan cichlid species, and typically within only a few social groups. Importantly, if reproductive parasitism or adoption is frequent within this group of fishes, then these factors would reduce within-group relatedness and further undermine the generality of the monogamy hypothesis – and would therefore further support the main findings of our study.

3 | TREE BUILDING AND PHYLOGENETIC ANALYSES

With respect to our phylogeny, the primary concern raised by Tanaka et al. (2018) is that uncertainty in phylogenetic hypotheses can lead to problematic inferences from subsequent analyses. Specifically, Tanaka et al. (2018) claim that the phylogeny produced in our study produces “an erroneous increase in the number of transitions to cooperative breeding by up to 50%”. However, Tanaka et al. (2018) do not provide any data to directly support this statement.

In their critique, Tanaka et al. (2018) put forward three phylogenetic topologies (their Figures A1, A2, A3), including trees derived from (a) mtDNA, (b) nucDNA, and (c) mtDNA and nucDNA combined. Despite including up to 67% fewer cooperatively breeding species than the phylogeny generated in our study, the distribution of cooperative breeding across Tanaka et al.'s (2018) trees reveals that cooperative breeding evolved: four times in the mtDNA tree, four times in the nucDNA tree, and five times in the mtDNA and nucDNA combined tree. As our study also reported five independent transitions to cooperative breeding, we argue that the trees presented by Tanaka et al. (2018) provide general support for the findings of our study.

Furthermore, Tanaka et al. (2018) claim that the phylogenetic path analysis approach used in our study has “only been assessed in a single simulated dataset” and inflates Type I error rates. However, in the defining publication presenting this method (Hardenberg & Gonzalez-Voyer, 2013), the method examined six datasets and the type I error rates were only slightly anticonservative (range 0.047–0.072). Importantly, the phylogenetic path analysis was not our sole source of inference – it was used to confirm results from a suite of other analyses.

4 | CLASSIFICATION OF TRAITS – WITH AN EMPHASIS ON MATING SYSTEMS

Interspecific variation in data quality is the norm when performing phylogenetic comparative analysis. When there is uncertainty regarding trait classifications, it is important to test whether the results are contingent on equivocal data. In Dey et al. (2017) we conducted a variety of sensitivity analyses and demonstrated that our results were robust to alternative classification of mating systems. Among

our various analyses (Dey et al., 2017: Supplementary Table 7), we included alternative mating system classification for 14 species (20% of our sample size). In all cases, the analyses suggested that there is no relationship between mating system and evolutionary transitions to cooperative breeding.

Nonetheless, Tanaka et al. (2018) contend that we misclassified the mating systems of some species by misreading a table heading in Heg and Bachar (2006), and that a re-analysis is therefore warranted. Tanaka et al. (2018) claim that we mistook "M" to mean "monogamy" rather than "multi-male or multi-female groups". However, this claim is inaccurate. We correctly interpreted this table and used this reference as one of several sources for our mating system classifications. In fact, in our analysis we classified five species differently than we would have if (as Tanaka et al. (2018) claim) we had incorrectly interpreted Heg & Bachar's table, 2006, demonstrating that Tanaka et al.'s (2018) claim is false.

Of particular interest are seven cooperatively breeding species which Tanaka et al. (2018) assigned as "non-monogamous" based on evidence that they live in "multi-male or multi-female groups" (citing Heg & Bachar, 2006). Since by definition all cooperative breeding species live in social groups, Tanaka et al.'s (2018) approach clearly confounds their classification of social and mating system. Social living does not necessitate a polygamous mating system (Townsend, Bowman, Fitzpatrick, Dent, & Lovette, 2011), and there is no genetic evidence that these seven cooperative species are polygamous. In fact, in Tanaka et al.'s (2018) classification scheme, all 21 cooperatively breeding species are classified as monogamous (including the 13 cooperatively breeding species in their Table 1, and the eight additional cooperatively breeding species for which we agree on the mating system classification).

The assumption that all cooperatively breeding species are polygamous introduces a strong bias into Tanaka et al.'s (2018) re-analysis of our work. Using this confounded approach, Tanaka et al. (2018) produce the (unsurprising) conclusion that transitions to cooperative breeding are more likely to occur in polygamous species. Imagine if the first comparative study examining evolutionary transitions to cooperative breeding in birds or mammals assumed that all cooperative species were polygamous because they lived in social groups. As is the case with Tanaka et al.'s (2018) re-analysis, such an approach clearly fails to offer an impartial test of the monogamy hypothesis.

In the Appendix to this paper (Table A1), we show that Tanaka et al.'s (2018) findings emerge only under the extreme scenario in which all cooperative breeders are classified as non-monogamous. All other mating system classifications (including a focus on female-centric mating systems as championed, but not employed, by Tanaka et al., 2018), yield results consistent with our original analysis, which reports *no relationship* between mating system and evolutionary transitions to cooperative breeding (Dey et al., 2017). Thus, we argue that the available data do not support Tanaka et al.'s (2018) claim that transitions to cooperative breeding are associated with non-monogamous mating systems in Lamprologine cichlids.

Yet, one helpful outcome of Tanaka et al.'s (2018) critique is that during our re-examination of our mating system classifications, we discovered that some of our references for mating system classification were accidentally deleted from the final version of Dey et al. (2017; Supplementary Table 1). This omission likely contributed to some confusion between the mating system classification we report and those suggested by Tanaka et al. (2018). This error has now been corrected on the *Nature Ecology & Evolution* website (see Dey et al. (2017), revised Supplementary Table 1).

In the Appendix to this paper, we provide a detailed, species-by-species, account of the disagreement in mating system classification for which Tanaka et al. (2018) claim our mating system assignment is incorrect. This species-by-species description demonstrates that, in contrast to Tanaka et al. (2018), we classified species based on species-typical behaviours available from the literature. When there were conflicting data to consider, we performed extensive sensitivity analyses to evaluate the impact of trait uncertainty on our results (Dey et al., 2017).

5 | CONCLUSION

To conclude, Tanaka et al.'s (2018) critique of our recent study ignores analyses that we had already conducted, and presents a flawed re-analysis of our results. When these issues are considered, Tanaka et al.'s (2018) commentary offers little insight beyond our main findings. The past decade has witnessed an enlightening debate about the possible evolutionary drivers of cooperative behaviours. Given the alternative path to cooperative breeding reported in our study, it is clear that Tanganyikan cichlids have an important role to play in this debate. Further insights into the genetic mating systems and evolutionary relationships among Tanganyikan cichlids are certainly welcomed and will undoubtedly help refine our understanding of social evolution in these remarkable fishes. In the meantime, our recent study provides a much-needed platform from which to move forward and collect such data.

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How to cite this article: Dey CJ, O'Connor CM, Wilkinson H, Shultz S, Balshine S, Fitzpatrick JL. Confounding social and mating systems predictably lead to biased results when examining the evolution of cooperative breeding in cichlids: A response to Tanaka et al. *Ethology*. 2019;125:409–414. <https://doi.org/10.1111/eth.12883>

APPENDIX A1

DISAGREEMENT OVER MATING SYSTEM CLASSIFICATIONS

In this section, we focus on the specifics of the mating system reclassifications offered by Tanaka et al. (2018; Table 1). Tanaka et al. (2018) claim that 23 species in our study were incorrectly classified.

For three species Tanaka et al.'s (2018) classifications are identical to the monogamous classification used in our analyses (*Lepidolamprologus kendalli*, *L. nkambae*, and *N. cylindricus*). Tanaka et al. (2018) also performed alternative analyses where these three species were classified as non-monogamous (which did not change their findings), but their main mating classification for these three species are identical with ours.

As such, Tanaka et al. (2018) actually offer different mating system classifications for 20 species:

For four of these species, Tanaka et al. (2018) either ignore the information provided in the reference we cite or reclassify species based on rare anecdotal observations, rather than on the species' typical mating behaviour. These include:

Julidochromis marlieri

Yamagishi and Kohda (1996) (which we cite in Dey et al., 2017) state "we found that monogamous pairs were most common ... Our data also suggested that large females may mate with 2 males." We interpreted this information as evidence that the typical mating behaviour for this species was monogamous pairing. In contrast, Tanaka et al., (2018) cite Heg and Bachar (2006) to support their assignment of non-monogamous. In turn, Heg and Bachar (2006) cite Sunobe, 2000) as evidence for polyandry in this species. However, Sunobe, 2000) reports only one polyandrous group in his study out of a total sample size of six groups observed. Therefore, we argue that Tanaka et al., (2018) classification emphasizes the rare behaviour over the species typical behaviour.

Lamprologus teugelsi

Clabaut, Bunje, Salzburger, and Meyer (2007) clearly classify this species is polygynous. Tanaka et al. (2018) claim that no reliable information is found.

Lepidolamprologus attenuatus

Both Tanaka et al. (2018) and our group used Nagoshi and Gashagaza (1988) to classify the mating behaviour for this species, which states that *L. attenuatus* is "often found in pairs, but sometimes one male mated with two females at the same time". We interpreted this as evidence for species-typical monogamous behaviour. In contrast, Tanaka et al. (2018) claim this is evidence for "frequent polygamy".

TABLE A1 Comparison of analyses of a relationship between mating system and cooperative breeding for the Lamprologines cichlids based on (a) classic and (b) female-centric mating system classifications

Approach	log10 Bayes Factor*
Classic mating system classifications	
Model A Correlation between <i>classic</i> mating system and cooperative breeding reported in Dey et al. (2017).	0.698
Model B Tanaka et al.'s (2018) approach – <i>classic</i> mating system classification where no cooperative breeding species are classified as monogamous.	2.117
Model C Correlation between <i>classic</i> mating system and cooperative breeding where the mating system of the seven least well studied cooperative breeders are treated as non-monogamous, and we accept three reclassifications from Tanaka et al. (2018) that we agree with.	0.666
Model D Correlation between <i>classic</i> mating system and cooperative breeding where the mating system of the seven least well studied cooperative breeders are treated as NAs in the dataset.	0.428
Female-centric mating system classifications	
Model E Correlation between <i>female-centric</i> mating system and cooperative breeding reported in Dey et al., (2017).	0.02
Model F Correlation between <i>female-centric</i> mating system and cooperative breeding where the mating system of the seven least well studied cooperative breeders are treated as NAs in the dataset.	0.004

Note: What is clear from Table A1, is that Tanaka et al.'s (2018) finding of a positive correlation between non-monogamy and evolutionary transitions to cooperative breeding is an outlier. The correlation between a non-monogamous mating system and cooperative breeding that Tanaka et al. (2018) report can only be found under an extreme scenario where all cooperative breeders are classified as non-monogamous. In all other analyses, there is no clear evidence for a link between mating system and cooperative breeding. Importantly, the lack of a correlation between mating system and cooperative breeding is also evident in all analyses using the female-centric mating system classification, which is arguably the most appropriate when testing the monogamy hypothesis. Critically, the lack of a correlation between mating system and cooperative breeding is entirely consistent with the findings presented in our original paper.

*Log10 Bayes Factors < 1 indicate little evidence, 1–2 strong evidence and >2 decisive evidence.

Neolamprologus moori

Tanaka et al. (2018) cite Karino (1998) to support their classification of monogamy, despite the fact that two of the co-authors of the Tanaka et al. (2018) commentary published a paper in 2008 (Sefc, Mattersdorfer, Sturmbauer, & Koblmüller, 2008) providing genetic evidence of "an exceptionally high level of multiple paternity ...where each of ten broods was sired by two to >10 males". We cited Sefc et al., (2008) to classify this species as non-monogamous in our original paper.

We can also address the discrepancy for six additional species, as the references that were accidentally cut from our Supplementary Table 1 (Dey et al., 2017) clearly support the mating system classification that we used. These references either provide more recent or more direct evidence of the mating system of these species than the references offered by Tanaka et al. (2018). These species include:

Altolamprologus calvus

Clabaut et al. (2007) classify this species as monogamous.

Chalinochromis brichardi

Brichard (1989), Sturmbauer, Verheyren, and Meyer (1994), and Kuwamura (1994) clearly classify this species as monogamous.

Chalinochromis popelini

Brichard (1989) describes this species as living in long term pair bonds, which we interpreted as monogamous.

Julidochromis dickfeldi

Brichard (1989) classifies this species as monogamous.

Julidochromis regani

Clabaut et al., (2007) classify this species as monogamous.

Neolamprologus hecqui

Konings (1988) classifies this species as polygynous.

Seven of the remaining 10 species in question are cooperative breeders (*N. falcicula*, *N. gracilis*, *N. helianthus*, *N. marungensis*, *N. niger*, *N. olivaceous*, and *N. splendens*). For each of these seven species, Tanaka et al. (2018) use Heg and Bachar (2006) to support their claim that these species are non-monogamous. Heg and Bachar (2006) classify these species as non-monogamous based on the fact that they live in multi-male, multi-female groups. However, as argued above, living in multi-adult groups is not in itself indicative of the mating system of the species ("multi-male, multi-female groups" only means that males and females are living together in a social group – it is not synonymous with "multi-pair" groups).

Finally, in the three remaining species, we agree with Tanaka et al.'s (2018) reclassification, although we note that two of these species were included in the Sensitivity Analysis of Dey et al. (2017) to account for uncertainty in their mating system.

Neolamprologus boulengeri

We agree with Tanaka et al. (2018) assertion that based on the available evidence this species is monogamous. However, we did run alternative analyses with this species classified as monogamous in our original paper (see Dey et al., 2017; Sensitivity analysis and Supplementary Figure).

Neolamprologus walteri

We also agree that a mating system classification of NA is appropriate. In our original paper, we ran analyses with this species classified as both monogamous and non-monogamous (see Dey et al., 2017 Sensitivity analysis and Supplementary Figure 4), and therefore accounted for uncertainty in the mating system of this species. However, we acknowledge that mating behaviour of this species is largely unknown.

Neolamprologus prochilus

We concede that our mating system classification for this species may have been premature. Tanaka et al. (2018) suggest that this species should be treated as NA with respect to mating system, and we agree.

APPENDIX A2

THE IMPACT OF DISAGREEMENTS IN TRAIT CLASSIFICATION ON THE EVOLUTIONARY RELATIONSHIP BETWEEN COOPERATIVE BREEDING AND MATING SYSTEM

We assume that debates about cichlid mating systems are likely to be of greater interest to cichlid enthusiasts rather than to a broad variety of scientists. Therefore, in this section we instead focus on Tanaka et al.'s (2018) claim that cooperative breeding evolved from non-monogamous species in the Lamprologine cichlids.

In our paper, we report that there is little evidence for an evolutionary correlation between mating system and cooperative breeding (log₁₀ Bayes Factor = 0.698, values <1 indicate little support for dependent evolution, see also Dey et al., 2017). In contrast, Tanaka et al. (2018) claim that cooperative breeding emerged from non-monogamous species. However, as we outline above, there are considerable issues with Tanaka et al.'s (2018) analysis. Specifically, in the absence of genetic data, Tanaka et al.'s (2018) default was to classify

all cooperative breeders as non-monogamous. In fact, in Tanaka et al.'s (2018) re-analysis, no cooperatively breeding species were classified as monogamous. Using this classification scheme, Tanaka et al. (2018) find that non-monogamous mating systems unsurprisingly promote evolutionary transitions to cooperative breeding (log₁₀ Bayes Factor = 2.117, note that we had to calculate this value as it was not provided in Tanaka et al.'s (2018) paper).

We can also assess variations in the mating system classifications outlined above:

If, for arguments sake, we accept Tanaka et al.'s (2018) classification that seven disputed cooperative breeders are in fact non-monogamous (based on the fact that they live in multi-adult groups), and we also accept that we misclassified three species as pointed out by Tanaka et al. (2018), we still find no clear evidence for a correlation between mating systems and cooperative breeding (log₁₀ Bayes Factor = 0.666, Table 1, Model C). This result is consistent with the findings presented in Dey et al. (2017) and not with the re-analysis of Tanaka et al. (2018).

We also re-ran the analysis after removing the mating systems classifications for the seven species of cooperatively breeding cichlids under dispute. Instead of reclassifying these species as non-monogamous (as Tanaka et al., 2018 did), we treated these species as NAs in the analyses. As in our original paper, there is again no clear evidence for a correlation between mating system and cooperative breeding is generated (log₁₀ Bayes Factor = 0.428, Table 1, Model D).

Critically, as discussed above, the key target of selection is within-group relatedness. To focus on within-group relatedness we really need to classify mating systems using a female-centric classification. For example, in species where males control harems, females should be classified as monogamous because females within a harem still only mate with one male. Note that this is precisely what Tanaka et al. (2018) suggests should be done, however they fail to incorporate their own advice into their re-analysis. When we used a female-centric mating system classification in our paper, again we found no clear evidence for a correlation between mating system and cooperative breeding (log₁₀ Bayes Factor = 0.02, Table 1, Model E, see also Dey et al., 2017).

When we repeated this female-centric analysis, but this time excluded the seven cooperatively breeding species under dispute, once again we found no clear evidence of a correlation between mating system and cooperative breeding (log₁₀ Bayes Factor = 0.004, Table 1, Model F).