





Insufficient data render comparative analyses of the evolution of cooperative breeding mere speculation: A reply to Dey et al.

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1 | INTRODUCTION

Dey et al. (2019) claim to have “demonstrated that transitions to cooperative breeding in Lamprologine cichlids were not related to a species’ *social mating system*” in their previous study of these fishes (Dey et al., 2017). They assert that our challenge of this conclusion (Tanaka et al., 2018) was unjustified. By focussing on the most important points of their critique, we here explain why this allegation is unfounded.

Our critique of the conclusions drawn from the comparative analysis of Dey et al. (2017) concerned two major shortcomings of that study: a low coverage of trustworthy behavioural data and an insufficient phylogenetic tree. Our conclusion from a careful validation of the information on which their analysis of lamprologine cichlids had been based was simply that “better information on their behaviour and phylogenetic relationships is needed to allow meaningful analyses” (Tanaka et al., 2018). To illustrate the significance of this plea for caution, we first call attention to the mating system classification applied by Dey et al. (2017). To a large extent, this classification drew upon the casual categorization of mating patterns provided 30 years ago in two books for aquarists (Konings, 1988; Brichard, 1989, and a newer edition from 1999), which were never meant to serve as hard data basis on which a quantitative comparative analysis should be based. Another source of Dey et al.’s (2017) mating system classification is a morphometric study of body shape differences published by Clabaut, Bunje, Salzburger, and Meyer (2007), in which no data on mating patterns are reported at all, but which instead refers

to Kuwamura (1997); the latter is a book chapter drawing upon the above-mentioned aquarist books and on unpublished personal communications. Kuwamura (1997) acknowledged the provisional nature of his mating system estimation by adding question marks to many of the alleged mating patterns. Importantly, none of these assessments derive from genetic analyses, but instead merely reflect qualitative observations of social behaviour. Since mating systems were classified by Dey et al. (2017) in order to serve as a proxy for within-group relatedness, the relevant variable is the genetic mating pattern. This problem is apparently recognized also by Dey et al. (2019), who state that “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”. Dey et al. (2017) used genetic mating system data when available but lacking genetic data for the vast majority of species, they perforce made do with—often anecdotal—information on social mating systems.

Referring to our reanalysis of Dey et al.’s (2017) approach, Dey et al. (2019) state “The results put forth by Tanaka et al. (2018) 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. (2018) confound social systems and mating systems. ... in Tanaka et al.’s (2018) classification scheme, all 21 cooperatively breeding species are classified as monogamous [sic; in fact, this should read non-monogamous] (including the 13 cooperatively breeding species in their Table 1, and the 8 additional cooperatively breeding species for which we agree on the mating system classification)”. This is an interesting comment. The multi-male/multi-female

category described in Heg and Bachar (2006), which has been referred to by Tanaka et al. (2018), denotes groups consisting of multiple sexually mature males and females. To what extent these adult subordinates gain reproductive share is known from 6 cooperatively breeding cichlids for which genetic data are available (*Neolamprologus pulcher*, *N. savoryi*, *N. obscurus*, *N. multifasciatus*, *Julidochromis ornatus*, *J. transcriptus*; see Kohler, 1998; Awata, Munehara, & Kohda, 2005; Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Kohda et al., 2009; Tanaka et al., 2015; Hellmann et al., 2016; Heg et al. in revision; see Taborsky, 2009, 2016 for review). Without exception, all these studies revealed that groups in the respective species contain larvae, young or helpers of different degrees of relatedness to the breeders, revealing that they are genetically non-monogamous. In contrast, evidence for a genetically monogamous, cooperatively breeding cichlid is hitherto missing. Thus, according to current knowledge the assumption that few, if any, cooperatively breeding cichlids are truly monogamous does not seem farfetched.

In this context, Dey et al. (2019) accuse Tanaka et al. (2018) of an assertion that in fact has not been made: "Tanaka et al claim on a re-analysis of the data that transitions to cooperative breeding are promoted by non-monogamous (promiscuous) breeding systems". This allegation illustrates the central misunderstanding in this debate. The aim of Tanaka et al.'s (2018) reanalyses was explicitly *not* to draw alternative conclusions on the effect of mating systems on the evolution of cooperative breeding in lamprologine cichlids. Instead, the intention was merely to illustrate the severe problem inherent in drawing conclusions from the application of comparative methods to a dubious data base. For this very reason, Tanaka et al. (2018) remarked in the Abstract: "In order to illustrate the impact of the mating system misclassifications, we scored mating patterns as reported in the original literature and re-analysed the dataset based on Dey et al.'s tree topology. The result suggests that the mating system does in fact significantly explain the evolutionary transition to cooperative breeding in lamprologine cichlids, but we submit that a reliable conclusion cannot be reached before improving the behavioural information and the underlying phylogenetic reconstruction". We concede that this formulation may have been too subtle. So once and for all: we do not believe that the question Dey et al. (2017) asked, namely whether mating patterns explain evolutionary transitions to complex societies in lamprologine cichlids, can be answered with the information at hand on mating patterns and phylogenetic relationships of these fishes. The fact that a contrasting significant outcome resulted from our reanalysis of the data they used, applying their own statistical approach with the mating system classification provided in the original literature they cited, reveals how sensitive the result of such analysis is to assumptions on mating patterns that are just not sufficiently understood.

Regarding mating patterns, what really matters to comprehend the role of direct and indirect benefits in the evolution of cooperative breeding is the degree of relatedness between helpers and the breeders' offspring. Even if breeders are generally monogamous, changes in breeder identity due to frequent deaths or turnovers in territory ownership lead to reduced relatedness between existing

helpers and new offspring (Taborsky & Limberger, 1981), as has been shown in *N. pulcher* (Dierkes et al., 2005). Additionally, immigration, which occurs regularly in the cooperatively breeding cichlids investigated thus far (see Taborsky, 2016 for review), significantly reduces relatedness between helpers and beneficiaries. Consequently, in the cooperatively breeding cichlids for which genetic data are available, the mean within-group relatedness values are clearly below 0.5 (Awata et al., 2005; Dierkes et al., 2005; Kohler, 1998; Taborsky, 2009; Tanaka et al., 2015), varying with age and size of the subordinates (Dierkes et al., 2005).

Dey et al. (2019) state that the alternative phylogenetic trees presented in Tanaka et al. (2018) also suggest 4–5 transitions to cooperative breeding. We should like to stress that the recurrent evolution of cooperative breeding in Lake Tanganyika cichlids has not at all been doubted by Tanaka et al. (2018). However, to comprehend the drivers of these evolutionary transitions it is essential to correctly understand the phylogenetic relationships among the different species. Our point was that this is not possible with the phylogenetic tree of Dey et al. (2017). As Tanaka et al. (2018) illustrated in detail, the topology of that tree was strongly biased towards mitochondrial relationships. Due to stochasticity of the lineage sorting process, gene trees typically differ from each other and from the species tree (Avice & Wollenberg, 1997). Even if lineage sorting is realized faster in the mitochondrial than in the nuclear genome, incomplete lineage sorting might still be a problem, in particular in rapidly radiating lineages, which usually experience repeated cladogenesis events within the time it takes for lineage sorting to be completed (Whitfield & Lockhart, 2007). Thus, the phenomenon of incomplete lineage sorting, and in particular ancient incomplete lineage sorting (Takahashi, Terai, Nishida, & Okada, 2001) of mtDNA is not unique to cichlids but is found in many rapidly diversifying taxa. What complicates the situation in lamprologines even more is that on top of ancient incomplete lineage sorting, hybridization and introgression (sometimes even with range-wide replacement of mtDNA) are particularly frequent in this cichlid lineage, which heavily affects phylogenetic inference based on mitochondrial data (e.g. Salzburger, Baric, & Sturmbauer, 2002; Koblmüller et al., 2007, 2017). Consequently, the topology of the tree used by Dey et al. (2017) is greatly at odds with current knowledge based on modern phylogenomic evidence (Irisarri et al., 2018; McGee et al., 2016). As with mating system data, comprehensive genomic data have not yet been published for many lamprologine species. Accurately capturing the dynamics of character evolution across a phylogeny is particularly challenging in dynamic clades like Lake Tanganyika cichlids; these challenges are made nearly insurmountable if dense marker sets are ignored in favour of a few mitochondrial and nuclear genes.

2 | CONCLUSION

An extraordinary claim requires extraordinary proof.
(Truzzi, 1978)

Modern comparative approaches based on phylogenetic data offer a great opportunity to investigate the evolution of complex behavioural traits. However, the reliability of conclusions drawn from such analyses depends entirely on the quality of the underlying data. Dey et al. (2019) seem to agree to some extent with the preliminary nature of the data on which their analysis was based, by stating ‘... 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’. Until such insight is gained, we adhere to our original claim that “better information on their behaviour and phylogenetic relationships is needed to allow meaningful analyses”—and reliable conclusions, we should like to add.

3 | DEDICATION

We wrote this reply in memory of the first author of our original publication, the late Hirokazu Tanaka. We all benefitted tremendously from his passion for cichlids and his deep insight in their behaviour and evolution.

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REFERENCES

- Avice, J. C., & Wollenberg, K. (1997). Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 7748–7755.
- Awata, S., Munehara, H., & Kohda, M. (2005). Social system and reproduction of helpers in a cooperatively breeding cichlid fish (*Julidochromis ornatus*) in Lake Tanganyika: Field observations and parentage analyses. *Behavioral Ecology and Sociobiology*, 58, 506–516. <https://doi.org/10.1007/s00265-005-0934-6>
- Brichard, P. (1989). *Pierre Brichard's book of cichlids and all the other fishes of Lake Tanganyika*. Neptune, NJ: Tfh Pubns Inc.
- Clabaut, C., Bunje, P. M., Salzburger, W., & Meyer, A. (2007). Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. *Evolution*, 61, 560–578. <https://doi.org/10.1111/j.1558-5646.2007.00045.x>
- Dey, C. J., O'Connor, C. M., Wilkinson, H., Shultz, S., Balshine, S., & Fitzpatrick, J. L. (2017). Direct benefits and evolutionary transitions to complex societies. *Nature Ecology & Evolution*, 1, 0137. <https://doi.org/10.1038/s41559-017-0137>
- Dey, C. J., O'Connor, C. M., Wilkinson, H., Shultz, S., Balshine, S., & Fitzpatrick, J. L. (2019). Confounding social and mating systems predictably leads to biased results when examining the evolution of cooperative breeding in cichlids: A response to Tanaka, et al. *Ethology*, 125, 409–414.
- Dierkes, P., Heg, D., Taborsky, M., Skubic, E., & Achmann, R. (2005). Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecology Letters*, 8, 968–975. <https://doi.org/10.1111/j.1461-0248.2005.00801.x>
- Heg, D., & Bachar, Z. (2006). Cooperative breeding in the Lake Tanganyika cichlid *Julidochromis ornatus*. *Environmental Biology of Fishes*, 76, 265–281. <https://doi.org/10.1007/s10641-006-9032-5>
- Hellmann, J. K., Sovic, M. G., Gibbs, H. L., Reddon, A. R., O'Connor, C. M., Ligocki, I. Y., ... Hamilton, I. M. (2016). Within-group relatedness is correlated with colony-level social structure and reproductive sharing in a social fish. *Molecular Ecology*, 25, 4001–4013. <https://doi.org/10.1111/mec.13728>
- Irisarri, I., Singh, P., Koblmüller, S., Torres-Dowdall, J., Henning, F., Franchini, P., ... Meyer, A. (2018). Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes. *Nature Communications*, 9, 3159. <https://doi.org/10.1038/s41467-018-05479-9>
- Koblmüller, S., Duftner, N., Sefc, K. M., Aibara, M., Stipacek, M., Blanc, M., ... Sturmbauer, C. (2007). Reticulate phylogeny of gastropod-shell-breeding cichlids from Lake Tanganyika—the result of repeated introgressive hybridization. *BMC Evolutionary Biology*, 7, 7.
- Koblmüller, S., Nevado, B., Makasa, L., Van Steenberge, M., Vanhove, M. P., Verheyen, E., ... Sefc, K. M. (2017). Phylogeny and phylogeography of *Altolamprologus*: Ancient introgression and recent divergence in a rock-dwelling Lake Tanganyika cichlid genus. *Hydrobiologia*, 791, 35–50. <https://doi.org/10.1007/s10750-016-2896-2>
- Kohda, M., Heg, D., Makino, Y., Takeyama, T., Shibata, J.-Y., Watanabe, K., ... Awata, S. (2009). Living on the wedge: Female control of paternity in a cooperatively polyandrous cichlid. *Proceedings of the Royal Society B: Biological Sciences*, 276, 4207–4214. <https://doi.org/10.1098/rspb.2009.1175>
- Kohler, U. (1998). *Zur Struktur und Evolution des Sozialsystems von Neolamprologus multifasciatus (Cichlidae, Pisces), dem kleinsten Schneckenbuntbarsch des Tanganjikasees*. Herzogenrath, Germany: Shaker Verlag.
- Konings, A. (1988). *Tanganyika cichlids*. Zevenhuizen, Netherlands: Verduijn Cichlids.
- Kuwamura, T. (1997). The evolution of parental care and mating systems among Tanganyikan cichlids. In H. Kawanabe, M. Hori, & M. Nagoshi (Eds.), *Fish communities in Lake Tanganyika* (pp. 59–86). Kyoto, Japan: Kyoto University Press.
- McGee, M. D., Faircloth, B. C., Borstein, S. R., Zheng, J., Hulsey, C. D., Wainwright, P. C., & Alfaro, M. E. (2016). Replicated divergence in cichlid radiations mirrors a major vertebrate innovation. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20151413. <https://doi.org/10.1098/rspb.2015.1413>
- Salzburger, W., Baric, S., & Sturmbauer, C. (2002). Speciation via introgressive hybridization in East African cichlids? *Molecular Ecology*, 11, 619–625. <https://doi.org/10.1046/j.0962-1083.2001.01438.x>
- Taborsky, M. (2009). Reproductive skew in cooperative fish groups: Virtue and limitations of alternative modeling approaches. In R. Hager, & C. B. Jones (Eds.), *Reproductive skew in vertebrates: Proximate and ultimate causes* (pp. 265–304). Cambridge, UK: Cambridge University Press.
- Taborsky, M. (2016). Cichlid fishes: A model for the integrative study of social behavior. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 272–293). Cambridge, UK: Cambridge University Press.
- Taborsky, M., & Limberger, D. (1981). Helpers in fish. *Behavioral Ecology and Sociobiology*, 8, 143–145. <https://doi.org/10.1007/BF00300826>
- Takahashi, K., Terai, Y., Nishida, M., & Okada, N. (2001). Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in Lake Tanganyika as revealed by analysis of the insertion of retroposons. *Molecular Biology and Evolution*, 18, 2057–2066. <https://doi.org/10.1093/oxfordjournals.molbev.a003747>
- Tanaka, H., Frommen, J. G., Koblmüller, S., Sefc, K. M., McGee, M., Kohda, M., ... Taborsky, M. (2018). Evolutionary transitions to cooperative societies in fishes revisited. *Ethology*, 124, 777–789. <https://doi.org/10.1111/eth.12813>

- Tanaka, H., Heg, D., Takeshima, H., Takeyama, T., Awata, S., Nishida, M., & Kohda, M. (2015). Group composition, relatedness, and dispersal in the cooperatively breeding cichlid *Neolamprologus obscurus*. *Behavioral Ecology and Sociobiology*, *69*, 169–181. <https://doi.org/10.1007/s00265-014-1830-8>
- Truzzi, M. (1978). On the extraordinary: An attempt at clarification. *Zetetic Scholar*, *1*, 11–19.
- Whitfield, J. B., & Lockhart, P. J. (2007). Deciphering ancient rapid radiations. *Trends in Ecology & Evolution*, *22*, 258–265. <https://doi.org/10.1016/j.tree.2007.01.012>

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