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Reddon, AR (2021) FE Spotlight: The right fish for the job: Local ecology affects morphology in a cooperative breeder. Functional Ecology, 35 (10). pp. 2136-2137. ISSN 0269-8463

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The right fish for the job: Local ecology affects morphology in a cooperative breeder

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The right fish for the job: Local ecology affects morphology in a cooperative breeder

Differences in social organisation or structure are often observed among populations exposed to differing predation regimes and physical environments (Lott 1991). For example, guppies, *Poecilia reticulata*, exposed to greater predation risk tend to form larger, more peaceful groups than those under less threat of predators (Magurran & Seghers, 1991). Social species may also show differentiation among populations at other levels of biological organisation, for example in physiology or morphology, and these responses may shape and constrain one another (Montiglio et al. 2016; Young & Bennett, 2010). For example, animals that are physically less susceptible to predation may be less motivated to engage in social interactions. It is necessary to examine responses to ecological heterogeneity at multiple levels of organisation to predict how changing environments are likely to affect social structure, organisation, and behaviour (Fisher et al. 2021).

An emerging model system for the study of sociality is the daffodil cichlid fish, *Neolamprologus pulcher*. Daffodil cichlids are endemic to Lake Tanganyika, East Africa and are one of only around two dozen known cooperatively breeding fish species (Dey et al. 2017). Daffodil cichlids live in groups, typically of about 4-14 fish (Heg et al. 2005), which work together to defend a small benthic territory that they use to evade predation and raise the offspring of the dominant breeding pair (Balshine et al. 2001; Taborsky 1984). Recently, it has been shown that geographically close, but reproductively isolated populations of daffodil cichlids show differences in social structure depending on the local ecological conditions (Groenewoud et al. 2016).

In this issue of *Functional Ecology*, Freudiger et al. (2021) examine variation in body shape across eight populations of daffodil cichlids. Morphological change is a common response to ecological heterogeneity in fishes (Eklöv et al. 2007; Imre et al. 2002; Ruehl et al. 2011). The authors looked at populations which are exposed to differing levels of predation, habitat complexity, and available shelter size. Freudiger et al. report that populations living in areas with higher predation risk, larger shelters, and greater habitat complexity tend to be deeper bodied than those from less complex, lower predation environments. Deeper bodies help fish to avoid being eaten by gape limited predators, increase burst swim speed, and improve manoeuvrability in complex habitats. On the other hand, available shelter size may constrain how deep their bodies can be. Freudiger et al. found that this difference in morphology is not explained by genetic drift nor geographic distance because neither genetic similarity nor spatial proximity between populations correlated with the degree of difference in morphology. Rather, there appears to be convergent emergence of a deeper bodied phenotype among populations that are exposed to greater predation risk in more complex habitats. These deeper bodied fish may be limited in which shelters they can use, which could place a limit on group size due to the availability of suitable shelters. Deeper bodied fish may also be less vulnerable to predators and therefore more willing to engage in dangerous antipredator behaviours. Changing body shape could also alter head size and shape which may affect some of the key helping behaviours shown by subordinates such as digging and brood care. Helping behaviour can affect the size and number of subordinates that are tolerated by the dominant pair, altering the composition of these social groups (Fischer et al. 2014, 2017).

Freudiger et al. report that these population differences are retained across two generations of common garden breeding in the laboratory, which suggests that phenotypic plasticity is not a sufficient explanation and that genetic divergence, and/or epigenetic effects likely play a significant role. However, plasticity may be relevant when looking at more flexible behavioural characteristics. It would be interesting to look for differences in social interactions, communication, and cooperative behaviour among daffodil cichlid populations, and examine the role of phenotypic plasticity in any variation observed. The results of the laboratory study that Freudiger et al. present suggest a possible role for parental effects, as each generation closely resembles its parents but less so its grandparents. The role of parental effects in determining population differences in daffodil cichlids is ripe for closer examination.

The authors were not able to disentangle the effects of shelter size, habitat complexity, and predator abundance on morphology due to the strong correlation among these habitat characteristics within the studied populations. Future studies should aim to separate these factors, either through finding new study populations which do not show this covariance between these ecological characteristics, or through laboratory or field experimentation that manipulates these parameters independently. Another open question is how these populations may differ in neural and physiological characteristics in addition to morphology and social structure. For example, exposure to predators has been shown to affect brain size and organisation between populations of fishes (Gonda et al. 2011; Reddon et al. 2018; Walsh et al. 2016), and these differences may underpin social and behavioural variation. Populations of fish that vary in exposure to predation and in social behaviour also show neuroendocrine differences, for example in the nonapeptide hormone vasotocin (Reddon et al. submitted). Conducting similar comparisons among daffodil cichlid populations could offer a window into the physiological mediators of social variation in response to predation threat.

The population differences identified by Freudiger et al. (2021) show how morphology may respond to ecological heterogeneity among neighbouring populations in the daffodil cichlid. These changes in morphology may have effects on social organisation and structure by influencing susceptibility to predation, competition for shelters, and the tendency for subordinates to participate in brood care and territory maintenance. I look forward to future work further unravelling the causes and consequences of behavioural, physiological, and neural differentiation among populations exposed to differing ecological conditions in these fascinating fish.

Conflict of interest

The author has no conflict of interest to declare.

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