

# Digest: Life history evolution in Darwin's dream ponds\*

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Can variation in sex-specific parental investment lead to sexual dimorphism in immune response? Keller et al. (2018) measured immune cell parameters, expression of candidate genes, and composition of buccal microbiota in mouthbrooding cichlid species from Lake Tanganyika that show either maternal or biparental care. They found that maternal mouthbrooding species have increased sexual dimorphism in immune parameters, while biparental mouthbrooders exhibit an upregulated adaptive immune response, suggesting resource allocation shifts between parental investment and the immune system.

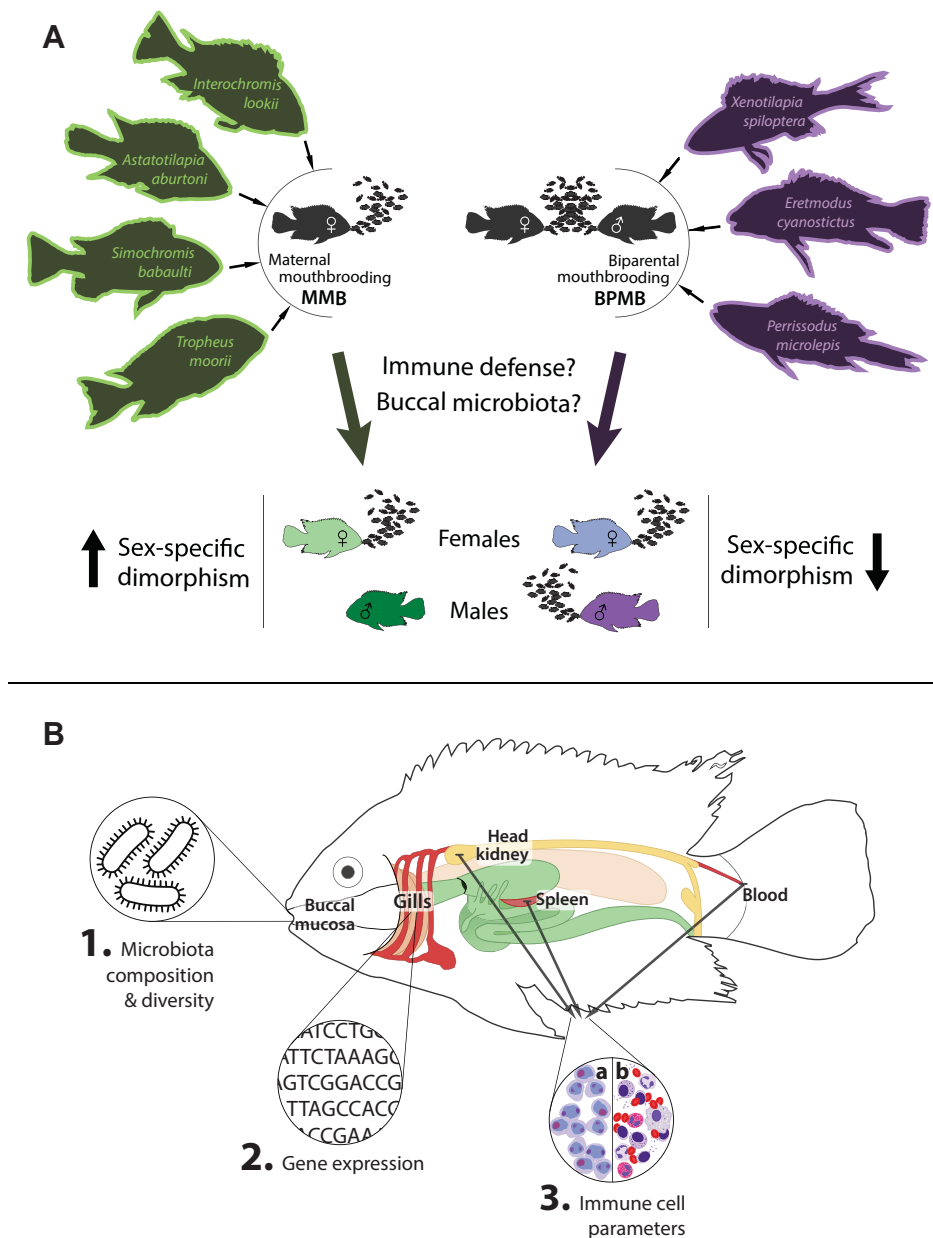
There is a tremendous diversity in life history strategies within and among species across the tree of life, and understanding the evolutionary mechanisms that drive these differences is a key objective in biology. Life history traits such as survival rate, growth rate, and reproductive success are major components of overall fitness, and intraspecific trait variation can thus lead to differences in Darwinian fitness between individuals (Stearns 1992). In the absence of life history trade-offs, all individuals would be able to reach a general fitness optimum and variation in fitness would not exist. The limited availability of metabolic resources thus forces organisms to find an optimal resource allocation strategy and weigh investments across a diversity of traits to maximize overall fitness (Y model; Noordwijk and de Jong 1986; Rowe and Houle 1996).

Variation in resource allocation strategies can be particularly pronounced between the sexes. Males and females often follow distinct reproductive strategies and thus prioritize different traits when allocating resources. In a conventional mating system, with males under strong sexual selection, females increase their fitness by investing in somatic maintenance and increased lifespan,

while males often forego long-term survival by focusing on short-term reproduction (Adler and Bonduriansky 2014). Even though such differences in resource allocation between reproduction and survival have been thoroughly studied, the sex-specific trade-offs between reproduction and other prominent life history traits are less well understood. For instance, it is well known that the ability to mount an effective immune response is energetically costly, but few studies have asked whether sex-specific differences in reproductive investment such as parental care can explain sexual dimorphism in immune response.

In this issue, Keller et al. (2018) addressed this question by focusing on resource allocation in cichlid fishes from Lake Tanganyika. The evolutionary radiation of cichlid fishes in East African rift lakes has translated into an extraordinary diversity of forms (hence, the symbolic denomination of "Darwin's pond") and includes a surprising variety of parental investment strategies. For example, multiple cichlid species have independently developed the ability to store eggs and fry in their oral cavity and thus shield offspring from predation risk. This mouthbrooding behavior can be provided by a single parent (maternal mouthbrooding; MMB) or both parents (biparental mouthbrooding; BPMB). However, mouthbrooding is energetically costly, since it is difficult for parents to feed, and can ultimately affect growth and survival (Morley and Balshine 2003).

\*This article corresponds to Keller, I. S., T. Bayer, W. Salzburger, and O. Roth. 2018. Effects of parental care on resource allocation into immune defense and buccal microbiota in mouthbrooding cichlid fishes. *Evolution*. <https://doi.org/10.1111/evo.13452>.



**Figure 1.** (A) The seven cichlid species from Lake Tanganyika sorted by the mode of parental care (maternal or biparental mouthbrooding—MMB or BPMB). Keller et al. (2018) investigated the effect of parental care on immune defense and buccal microbiota of males and females from each species. According to resource allocation theory, sex-specific dimorphism is expected to be high in MMB species, and marginal in BPMB species. (B) Keller et al (2018) used a holistic approach by characterizing the composition of buccal mucosa microbiota (1) and quantifying two different aspects of immune response. They collected samples (2) from the gills for gene expression analysis and (3) from the head kidney, spleen, and blood for cellular immune parameter analysis (3a: cell activity—the ratio of active/inactive cells; 3b: cell population composition—the ratio of innate/adaptive immune cells).

Keller et al. (2018) used this empirical system to investigate whether sex-specific investment in parental care leads to sexual dimorphism in immune response by comparing species with contrasting parental care systems (i.e., MMB vs. BPMB). To do so, they used a holistic approach and quantified (I) the microbiota composition in the buccal cavity, (II) cellular immune parameters in various tissues, and (III) gene expression of 28 candidate

genes (Fig. 1). They observed sex-specific differences in cellular components within MMB species and recorded an overall lower expression of immune-related genes in MMB females, suggesting that contrasting parental care strategies can indeed lead to variation in the degree of sexual dimorphism in immunity. In addition, individuals within BPMB species exhibited upregulation of adaptive immune response.

Their findings suggest that the evolution of parental care systems can induce changes in resource allocation between parental care and immune response, but that further research is still needed since idiosyncratic results across genes and tissue types highlight that it often remains difficult to predict the direction of immune response. Thus, the striking biological diversity within the Great East African lakes continues to provide novel insights into the processes promoting evolutionary change and will likely do so for years to come.

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