

EVOLUTION OF EGG SIZE IN NEOTROPICAL CICHLID FISHES

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Abstract

Not all fish eggs are the same. The Cichlidae present a unique opportunity to examine the selection pressures shaping egg size because the family is large, diverse, and found in many ecological niches. The result is dramatic variation in egg size across species. I will describe a series of experiments exploring these selection pressures in Neotropical cichlids, including development time versus temperature, development time versus egg size, egg survivorship versus temperature, and spawning site choice versus temperature. In brief, higher temperatures shorten development time, while larger egg size extends it. And, despite the finding that eggs survive well at high temperatures, parental cichlids choose lower temperatures at which to spawn.

Introduction

Egg size in fish is the result of a spectrum of selection pressures operating on parents laying and caring for eggs, the eggs, and the resulting fry. The parent, for example, faces a tradeoff between egg size and egg number. The size of the egg influences the time it takes to hatch, an important consideration for an egg in risk of predation or falling water levels. Because a parent may be committed to parental care at least until the eggs hatch, the longer eggs take to develop, the greater the cost of parental care in terms of time and energy. Finally, the size of an egg may determine the size, health and capabilities of the fry and the duration of the post-hatch care. Understanding egg size is thus vital to unravelling the selection pressures influencing parental investment in fish.

The Cichlidae is one of the largest fish families, comprising some 105 genera (Nelson, 1994) and at least 1300 species, all of which provide some form of parental care, ranging from simple guarding to mouthbrooding. Within the Cichlidae, egg size is variable. The effective diameter (Coleman, 1991; in essence the three-dimensional average of the major and minor axes of nonspherical eggs) varies from 0.9mm to over 5.0mm. This represents a difference in egg volume of almost two orders of magnitude.

In this paper, I present a series of experiments and results focussing on Neotropical cichlids to elucidate the factors underlying the variation in egg size.

Experiment I: The extent of variation

How much variation is there in egg size? To examine the extent of variation in egg size amongst Neotropical cichlids, I have obtained either through breeding the fish myself, finding eggs in the wild, or by egg samples sent to me by other cichlid breeders, a large collection of cichlid eggs.

Methods

Eggs were preserved in either 70% isopropyl alcohol, or 4% formalin and then measured under a microscope using an ocular micrometer. Effective diameter was calculated as the cube-root of length x width x width.

Results

Egg size varied from 0.9mm to 2.6mm, with most species falling in the range of 1.4 to 1.8 (Fig. 1).

Experiment II: The effect of temperature and egg size on hatching time

In theory, larger eggs should take longer to hatch because there is more material to convert from one state (the yolk) to another (the fry). In order to understand the effect of egg size on hatching time, it was first necessary to establish the relationship between temperature and hatching time because the effect of temperature is likely larger and must be controlled for in analyzing egg size.

Methods

Eggs from a single spawning were placed in "hatching cups" (the bottom portion of a plastic vial glued to a piece of glass) in aquaria maintained at different temperatures. The cups ensure that I can keep track of the eggs and yet allow good circulation of water. I put ten eggs into each cup, and then placed eight cups in each of six aquaria. Temperatures for the different aquaria ranged from 20 to 36°C.

Eggs were monitored around the clock for hatching. The "time-to-hatch" for a cup was taken as the time when 50% of the eggs in a cup had hatched. The scores for the eight cups were then averaged to give the hatching time for the particular temperature.

The experiment was repeated seventeen times using various species of Neotropical cichlids (convict *Cichlasoma nigrofasciatum*, midas *C. citrinellum*, rose-breast *C. longimanus*, rainbow *Herotilapia multispinosa*, bifasciatum *C. bifasciatum*, and tuba *C. tuba*. Species were chosen for their particular egg size.

Because hatching may not represent the same developmental stage in each of these different species, I chose to also evaluate the time to "swim-up", namely the point at which the fry can swim up off the bottom of the aquarium. This is a surprisingly distinct point in time. I recorded the data as that time at which 50% of the fry in an aquarium had reached swim-up.

Results

Temperature has a dramatic effect on hatching time and on swim-up time. For midas cichlids, at 34°C, the eggs hatch in a little over two days whereas at 22°C they take almost 5 days (Fig. 2).

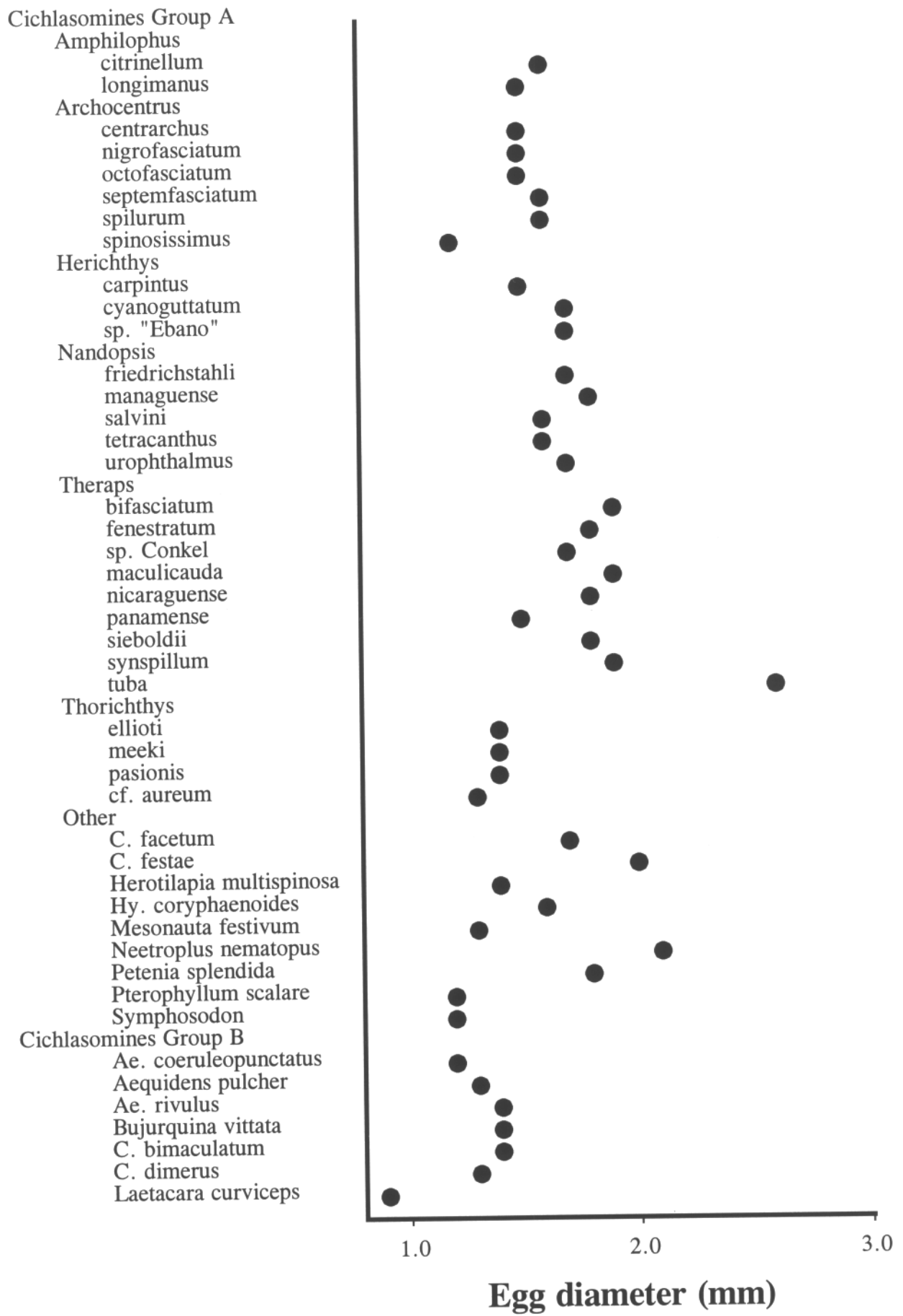


Figure 1. Egg size of forty-five species of Neotropical cichlids.

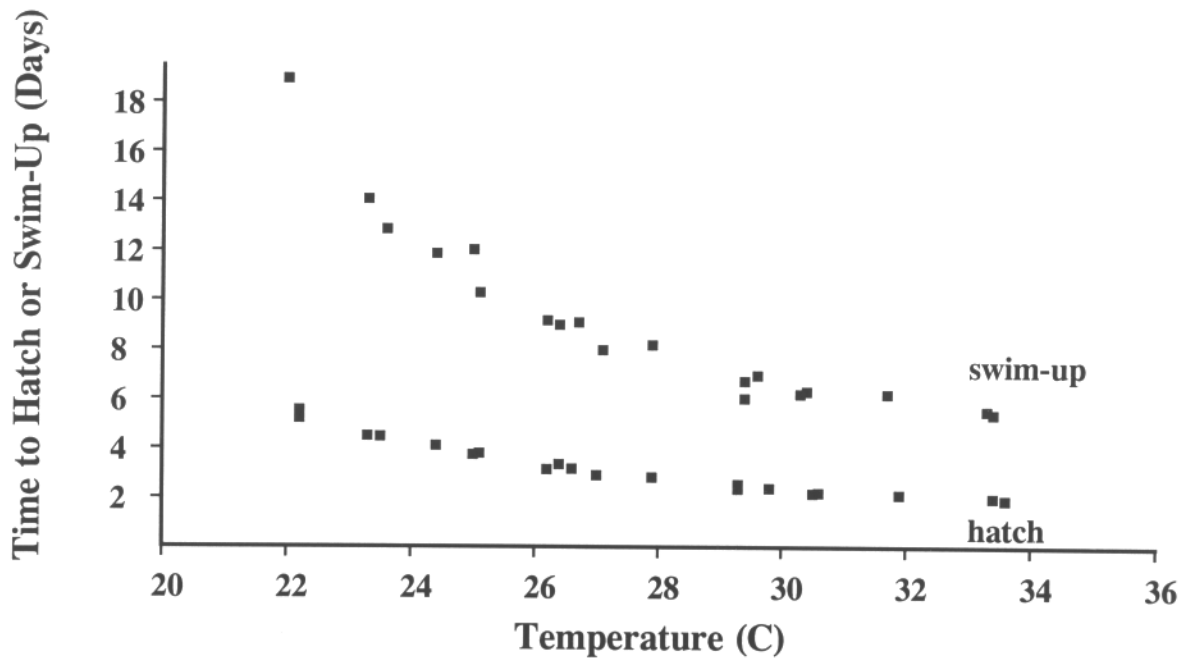


Figure 2. Development time versus temperature for midas

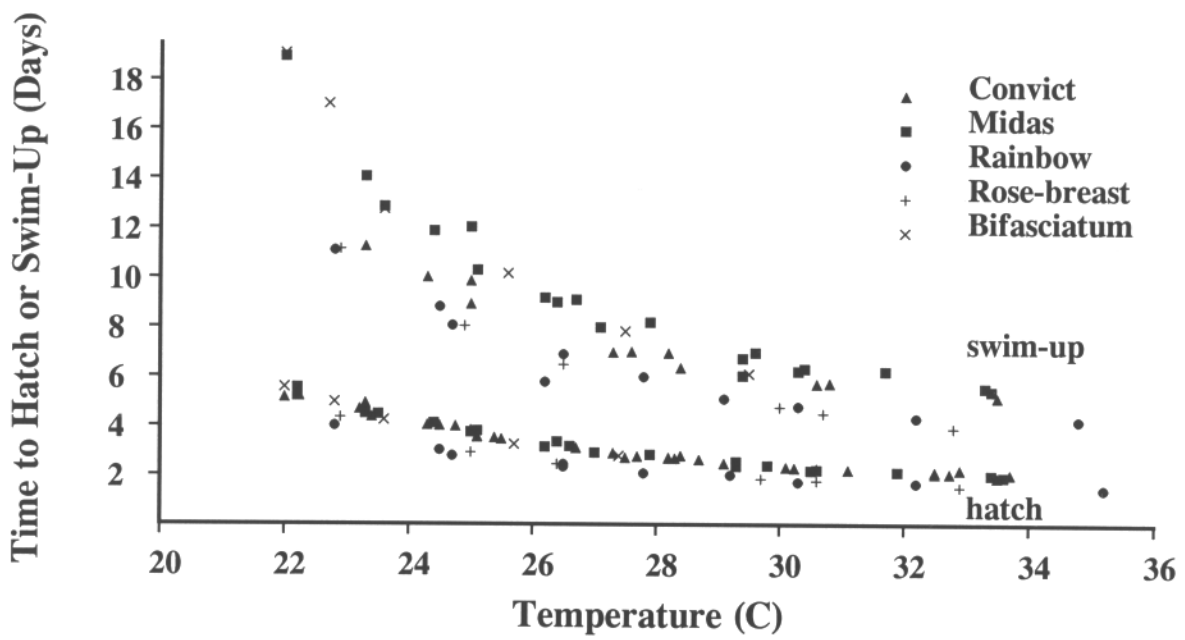


Figure 3. Development time for five cichlids

The effect of egg size is also present, though less clear (Fig. 3). Species with larger eggs, such as bifasciatum, midas and convict cichlids appear to take longer to develop than species with smaller eggs such as the rainbow cichlid. There is an exception, rose-breast cichlids, which have a larger egg, yet develop as quickly as those species with smaller eggs. This requires further investigation.

Experiment III - Temperature Choice

If temperature is so important to the development time in these cichlids, and consequently the duration of parental care, do parental cichlids actually choose the temperature at which they spawn? In the wild, they may have some opportunity to choose, either by not spawning during a certain season, or by choosing warmer or cooler parts of a river or lake.

Methods

To allow choice, I designed an aquarium with four chambers. Each was separated from the next chamber by a 3/4" plexiglass divider with a 2" x 4" notch cut in the bottom front corner. The thick plexiglass insulated each chamber from the next, while the notch allowed the fish to pass from one chamber to the next with a minimum of water flow. A bottomless flowerpot, lying on its side, was placed in each chamber as a potential spawning site.

Three aquarium heaters were inserted in the leftmost chamber, and the rightmost chamber was hooked up to a stock-tank continuously cooled by a chiller. This setup created a temperature gradient across the four chambers of as much as 10°C.

A pair of fish was placed in the apparatus and allowed to choose their spawning site, which they usually did within a few weeks. Three species were examined: convicts, rainbows and blue acaras (Aequidens pulcher).

Results

The results clearly indicate two points (Fig. 4). First, the different species appear to prefer slightly different temperatures to spawn at. Secondly, and perhaps most importantly, none of them prefer to spawn at the highest possible temperature as a general rule. Given the benefits demonstrated in the previous experiment, this seems puzzling.

Experiment IV - Temperature and Mortality

Parents may choose not to spawn at the warmest sites either because the eggs will not do well, or because the parents will not do well.

Methods

Using data gathered from the hatching experiment, I compared the mortality of eggs at different temperatures.

Results

While mortality is complete above 36°C and below 20°C, in between there is no clear relationship (Fig. 5). Thus, it is not egg mortality that drives the parental choice discovered in Experiment III.

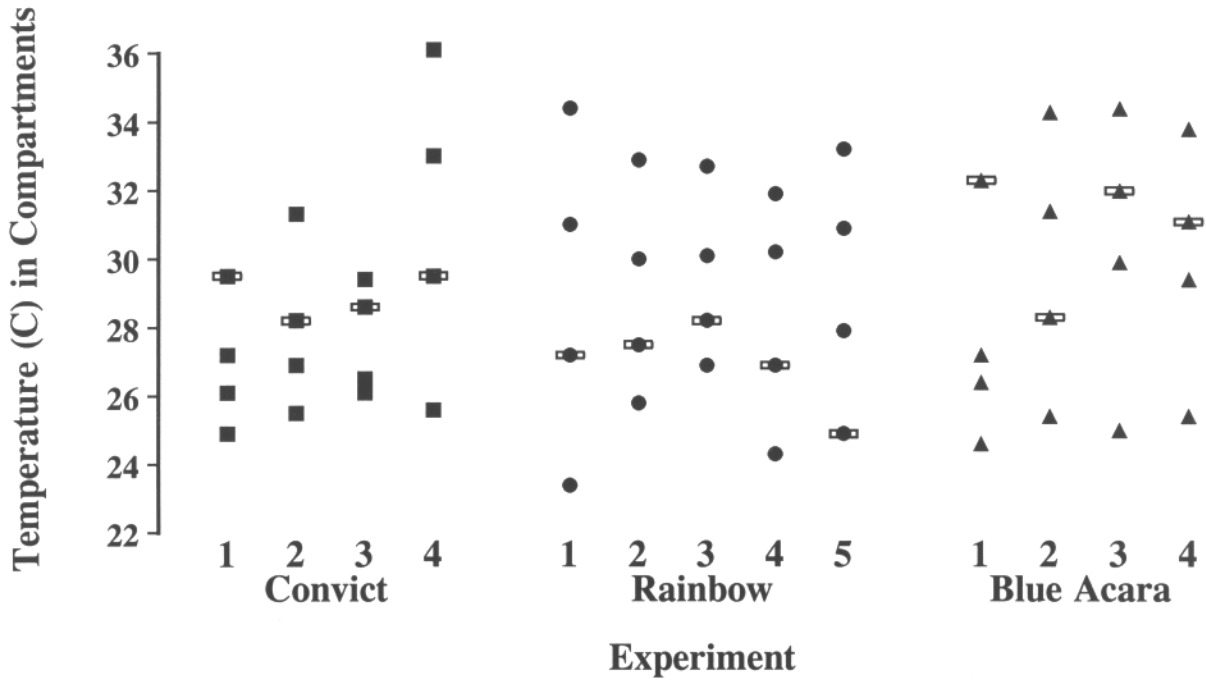


Figure 4. Spawning choice of three cichlids. The outline indicates which of the four compartments was chosen.

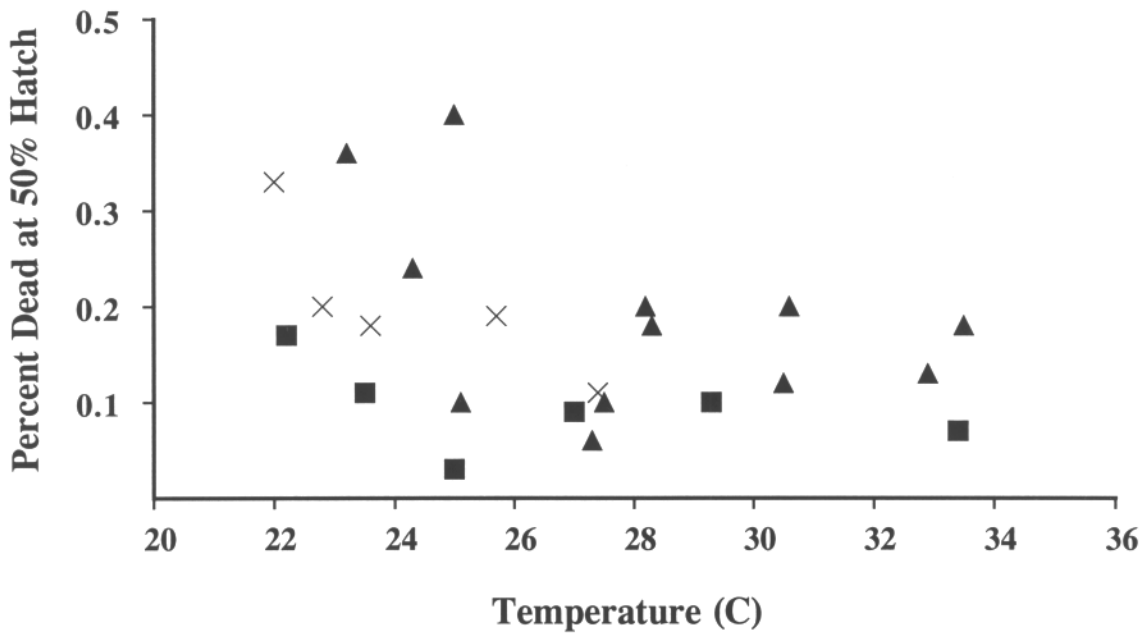


Figure 5. Mortality of eggs versus temperature.

Discussion

This series of experiments illustrates the extent of variation in egg size across a selection of Neotropical cichlids. The first experiment demonstrates substantial variation in egg size, with a few particularly noteworthy species with extreme egg size. For example, *C. tuba* has an unusually large egg, much larger than any other species. There are also species with tiny eggs. These species deserve particular attention in the future.

The tradeoff between egg size and egg number is well established elsewhere (Smith and Fretwell, 1974) so it is clear that parents pay a cost for having large eggs. There must be corresponding benefits. For example, Coleman and Galvani (this volume) have shown that larger eggs produce larger offspring. But, the question remains as to the exact advantages offered by larger offspring.

There are also additional costs of larger eggs. Experiment II illustrates that larger eggs take longer to hatch and longer still for the fry to reach the point of swimming. Since the parents must provide parental care at least to the point of free-swimming to ensure reasonable offspring survival, larger eggs mean an increase in the duration (and hence the cost) of parental care.

Experiment II also illustrated the profound effect of temperature on development time: higher temperatures dramatically shorten development time. Yet, Experiment III showed that parents in at least three species do not choose to spawn at the highest available temperature. Experiment IV showed that this is not because of increased offspring mortality at higher temperatures. Combined, these experiments suggest that it is something about the parents that prevents them from spawning at higher temperatures.

The most likely explanation for the puzzling choice of spawning temperatures is the cost of fanning. During the early stages of parental care, parental cichlids not only guard their offspring, but they must also fan the eggs to move oxygen-rich water over the eggs. Because warmer water contains less oxygen than cooler water, it seems likely that at warmer temperatures parental cichlids would have to fan faster than at cooler temperatures. Therefore I suggest that the species examined choose lower spawning temperatures because the cost of fanning would increase too much at higher temperatures. This is a testable prediction that I hope to examine in the near future.

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