Egg Size Determines Offspring Size in Neotropical Cichlid Fishes (Teleostei: Cichlidae)

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Within the family Cichlidae, the size of eggs varies tremendously across species (Breder and Rosen, 1966; Fryer and Iles, 1972; Coleman, 1991). Sizes range from the small eggs (0.9 mm in diameter) of rams (*Microgeophagus ramirezi*) to the massive eggs (4.5 mm in diameter) of some of the African mouthbrooding cichlids such as *Cyphotilapia frontosa* (unpubl. data). The hatchlings of the large-egged mouthbrooders are clearly much larger than the hatchlings of the rams and other small-egged species (pers. obs.). However, the relationship between egg size and hatchling size for smaller differences in egg size has not been explored. For example, within the Neotropical cichlids, the range of egg sizes is much smaller: small-egged species such as *Cichlasoma dimerus* have an average egg diameter of 1.3 mm, whereas the largest-egged species, "*Cichlasoma (Theraps)*" *tuba* has an average egg diameter of 2.4 mm (RMC, unpubl. data). Does this relatively small difference in egg size actually translate into a consistent difference in the size of the hatchlings? Furthermore, does the variation in egg size within a single laying account for differences in hatchling size? Understanding the consequences of differential allocation to egg size between eggs in a single clutch and within and among species will help us understand the factors shaping the evolution of egg size.

A larger egg may not necessarily translate into a larger hatchling for several reasons. For example, a given measure of egg size may not be a true representation of the energetic and material resources of an egg. This could be the case if larger eggs are simply filled with more water than smaller eggs, and size differences may solely be accounted for by water content. In such a case, the difference in egg size may be insignificant to the resulting hatchling. This is particularly plausible because fish eggs are hydrated and expand to some extent when they leave the female (Kamler, 1992). An ideal measure of egg size may involve a complete biochemical analysis of the contents of an egg, reporting protein, lipid, and carbohydrate content (e.g., Kamler, 1992); however, this is not practical for many studies. Indeed, for situations when the eggs are particularly small and yet must be kept alive, even weighing individual eggs or measuring their volume can be difficult.

We investigated the relationship between egg size and hatchling size in 26 species of Neotropical cichlids. We also examined eggs and hatchlings produced by 17 females within one species [convict cichlids, "*Cichlasoma (Archocentrus)*" *nigrofasciatum*], and eggs and hatchlings from within single clutches of two species (convict cichlids and rainbow cichlids, *Herotilapia multispinosa*) to look at the effects of intraspecific and intraclutch variation in egg size.

MATERIALS AND METHODS

Cichlid eggs are not spherical but generally are better described as prolate spheroids (elongated spheres). To compare nonspherical eggs, Coleman (1991) proposed using the "effective diameter," which is the diameter the egg would have if its contents were reshaped into a perfect sphere. In the case of a prolate spheroid, the effective diameter (d_e), as used throughout this paper, is the cube root of the major axis multiplied by the square of the minor axis (i.e., cube root of length × width × width).

The systematics of Neotropical cichlids are in a state of flux, creating confusion in the generic status of many of the species used in this study (Kullander, 1983; Stiassny, 1991). We follow Stiassny (1991) in referring to certain of these fishes by the genus "*Cichlasoma*," including the section names provided by Regan (1906, 1906–1908) as though they designate subgenera; however, the exact phylogenetic meaning of these sections is uncertain. The 26 species examined were *Aequidens pulcher*, *Cichlasoma bimaculatum*, *C. dimerus*, *C. festae*, *C. pusillum*, "*Cichlasoma (Amphilophus)*" *alfari*, "*C. (Am.)*" *citrinellum*, "*C. (Am.)*" *longimanus*, "*C. (Am.)*" *rostratum*, "*C. (Nandopsis)*" *managuense*, "*C. (Archocentrus)*" *centrarchus*, "*C. (Ar.)*" *nigrofasciatum*, "*C. (Ar.)*" *septemfasciatum*, "*C. (Ar.)*" *spilurum*, "*C. (Theraps)*" *bifasciatum*, "*C. (Th.)*" *intermedium*, "*C. (Th.)*" *nicaraguense*, "*C. (Th.)*" *sieboldii*, "*C. (Th.)*" *tuba*, *Cleithracara maronii*, *Crenicichla lepidota*, *Herotilapia multispinosa*, *Microgeophagus altispinosa*, *Nannacara anomala*, *Neetroplus nematopus*, and *Pterophyllum scalare*.

The fishes were maintained in the laboratory using a typical freshwater aquarium setup. Each setup consisted of a glass aquarium (38–280 liters), gravel, sponge filter, heater, and either

pieces of slate, flowerpots, or broken flowerpots. All species examined were biparental substratum spawners (Loiselle, 1994), though differing in the precise choice of spawning site (e.g., flowerpot, piece of slate, exposed glass tank bottom). Water temperatures were maintained between 24 and 28 C, and the light cycle was 12D/12L. Fishes were fed twice daily on Purina trout chow and Tetramin cichlid flakes with weekly supplements of live brine shrimp.

Aquaria were observed daily for the presence of eggs or hatchlings. When a clutch of eggs was found, a sample of 30–50 eggs was scraped from the substratum with a blunt metallic spatula. The rest of the eggs were left to hatch. Eggs were then either measured immediately or stored in 70% isopropyl alcohol. Storage in isopropyl alcohol does not significantly alter egg diameter (unpubl. data).

To calculate effective diameter, we measured the length and width of 20 eggs from each sample using a Wild dissecting scope fitted with an ocular micrometer, calibrated to 0.01 mm. The 20 values were averaged to produce a mean egg size for the species. On the day of hatching, hatchlings were collected with a turkey baster. Because live hatchlings are difficult to measure accurately, they were immediately preserved in 4% formalin and measured several days later. Three parameters were measured with each hatchling lying on its side: the total length of the hatchling (TL), and the length and width of the yolk sac. Typically, 20 hatchlings were measured to obtain a mean hatchling value for the species, though in a few cases, particularly when hatchlings were rare, fewer than 20 were used [C. festae 13; "C. (Am.)" alfari 13; "C. (Am.)" rostratum 18; "C. (Ar.)" septemfasciatum 16; "C. (Th.)" bifasciatum 19; "C. (Th.)" intermedium 13; "C. (Th.)" tuba 3; "C. (Th.)" sieboldii 12; Cl. maronii 16; M. altispinosa 11; N. anomala 10; P. scalare 11]. We used only a single spawning from a single female for each species to avoid pseudo-replication in the interspecific analysis.

To determine the importance of collecting the hatchlings on the first day of hatch, we also took daily samples of hatchlings to see how much their size changed from day to day. We sampled a single spawn for each of two species, "C. (Am.)" citrinellum and "C. (Th.)" bifasciatum, from the day of hatch until the stage of free-swimming.

To test whether egg size explains offspring size, we regressed mean hatchling length on mean egg size, and we correlated mean yolk diameter with mean egg size. If larger eggs are simply filled with more water, we would not expect significant positive relationships in either analysis.

To examine intraspecific variation, we sampled eggs and hatchlings from single spawnings of 17 convict cichlid females. To assess the effect of variation within a clutch in size of egg on size of offspring, we obtained individual hatchlings from eggs of known size using single clutches of convict cichlids and rainbow cichlids. In both cases, eggs were scraped off the laying site as described above and their size measured in a petri dish. For the within-clutch analyses, we selected extreme sizes as well as eggs of more intermediate size to maximize the range of egg sizes used. Each egg was measured under the microscope and then placed in a numbered hatching cup in the hatching aquarium. As each egg hatched several days later, the hatchling was removed and placed in a numbered vial of 4% formalin. Eggs that did not hatch were dropped from subsequent analysis. The hatchlings were measured as above and similar regressions performed.

Hatching cups (2.0 cm diameter, 1.5 cm high) were made from the bottom portion of a plastic specimen vial secured with silicon to a small square of glass to make the cup sink. The cups were placed in a half-filled 38-L aquarium, with a heater and airstone. This hatching-cup design proved successful in other experiments because it allows water to circulate over the eggs but keeps the eggs from blowing out of the cups.

RESULTS

Mean hatchling length was positively correlated with mean egg diameter in the 26 species examined (Fig. 1; $r = 0.83$; df $= 24$; $P < 0.01$). Diameters of most of the eggs were 1.3–1.9 mm. The extreme point at 2.4 mm was "C. (Th.)" tuba, the only known cichlasomine with such a large egg (RMC, unpubl. data). The means for hatchling yolk diameter (y_e) also correlated positively with mean egg diameter in these species ($y_e = 1.00 \times d_e - 0.11$ mm; $r = 0.97$; df $= 24$; $P < 0.01$).

Hatchlings change size rapidly after hatching (Fig. 2). Hatchling length increased 15% on the first day for midas cichlids and 13% for "C. (Th.)" bifasciatum. Also, as expected, yolk diameter declined as hatchling length increased. It is therefore important that hatchlings be obtained on the day of hatching (as was done in this study) for hatchling size comparisons; otherwise changes in hatchling size may cloud the relationship between egg size and hatchling size.
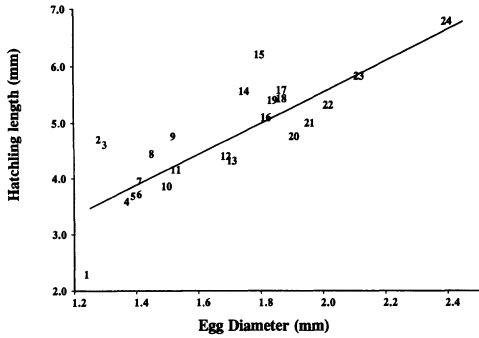
Fig. 1.   Mean hatchling length (TL) as a function of mean effective egg diameter (d_e) for 26 species of Neotropical cichlids (TL = 2.76 × d_e + 0.02 mm). Each number represents one or more species, as follows: 1 = *N. anomala*; 2 = *P. scalare*; 3 = *C. dimerus*; 4 = *M. altispinosa* and *Cl. maronii*; 5 = "*C. (Am.)*" *longimanus* and *H. multispinosa*; 6 = *C. bimaculatum*; 7 = *A. pulcher*; 8 = *C. pusillum*; 9 = "*C. (Ar.)*" *nigrofasciatum*; 10 = *Cr. lepidota*; 11 = "*C. (Ar.)*" *centrarchus*; 12 = "*C. (Ar.)*" *spilurum*; 13 = "*C. (Ar.)*" *septemfasciatum*; 14 = "*C. (Th.)*" *intermedium*; 15 = "*C. (N.)*" *managuense*; 16 = "*C. (Am.)*" *citrinellum*; 17 = "*C. (Th.)*" *sieboldii*; 18 = "*C. (Th.)*" *bifasciatum*; 19 = "*C. (Am.)*" *alfari*; 20 = "*C. (Am.)*" *rostratum*; 21 = *C. festae*; 22 = "*C. (Th.)*" *nicaraguense*; 23 = *N. nematopus*; and 24 = "*C. (Th.)*" *tuba*.
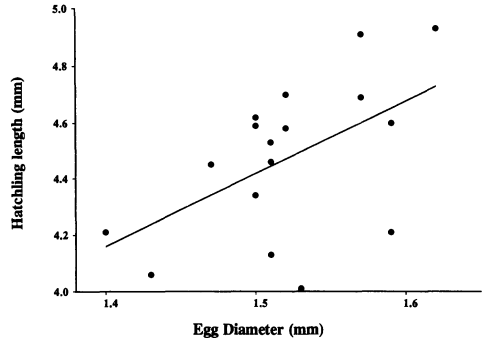
Intraspecific comparison of single spawnings from 17 convict cichlid females also revealed a positive correlation between mean hatchling length and mean egg diameter (Fig. 3; r = 0.54; df = 15; P < 0.05). The mean for hatchling yolk diameter was also significantly correlated with egg diameter (r = 0.64; df = 15; P < 0.05).

Within an individual clutch, we found positive correlations between hatchling and egg diame-

Fig. 3.   Mean hatchling length (TL) as a function of mean effective egg diameter (d_e) for spawnings from 17 female convict cichlids (TL = 2.62 × d_e + 0.49 mm).

ter and between yolk diameter and egg diameter. For a rainbow cichlid clutch, hatchling length increased with egg diameter (Fig. 4; r = 0.62; df = 14; P < 0.05), and yolk diameter increased with egg diameter (r = 0.93; df = 14; P < 0.01). Removing the possible outlier at egg size of 1.27 (Fig. 4) did not significantly change either result. The coefficients of variation (Sokal and Rohlf, 1981) for egg diameter, yolk diameter, and hatchling length were 8.6%, 9.4%, and 5.8%, respectively. For a convict cichlid clutch, the results were similar for hatchling length (r = 0.63; df = 12; P < 0.05) and yolk diameter (r = 0.90; df = 12; P < 0.01). The coefficients of variation for egg diameter, yolk diameter and hatchling length were 5.5%, 6.1%, and 2.9%, respectively.

DISCUSSION

Our results indicate that a considerable source of hatchling-size variation derives from
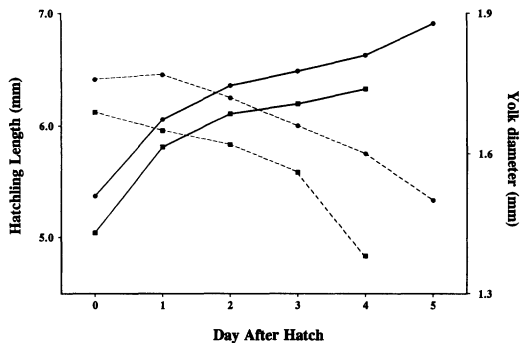

Fig. 2.   The change in hatchling length (solid lines) and yolk diameter (dashed lines) on the days after hatching. Circles represent "*C. (Th.)*" *bifasciatum*, squares represent "*C. (Am.)*" *citrinellum*. Each symbol represents the average for 20 individuals sampled on that day, except for "*C. (Th.)*" *bifasciatum* on day 1 (n = 19), day 4 (n = 17), and day 5 (n = 10).
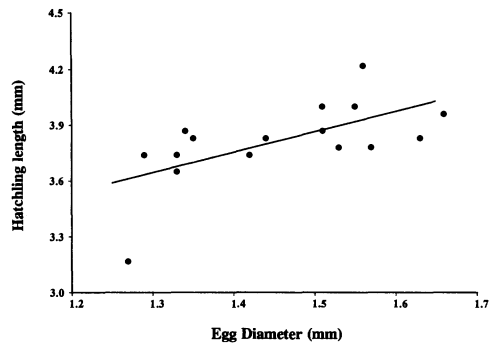

Fig. 4.   Hatchling length (TL) of individual hatchlings as a function of effective egg diameter (d_e) within a single clutch of rainbow cichlids (TL = 1.09 × d_e + 2.23 mm). A plot of yolk diameter (y_e) on effective egg diameter (d_e) looks similar (y_e = 0.97 × d_e − 0.05 mm).

differences in egg sizes. This relationship holds across species of Neotropical cichlids, within one of the species, and even within single clutches of two species. This result suggests that small differences in egg size can have significant consequences for the life history of the hatchlings. It also suggests that offspring size at hatch is under the control of the female, to the extent that she can control egg size allocation, more than it is determined by historical constraints of phylogeny, i.e., which particular species of cichlid the egg comes from.

Across species, differences in egg size accounted for 69% of the variation in hatchling total length and 94% of the variation in the size of the yolk of hatchlings. Few interspecific studies are available to compare with our findings. Blaxter (1969) presented data on egg size and length of hatchlings for 14 species of oviparous fishes drawn from a wide range of fish taxa. The smallest egg was that of a surgeonfish (diameter of 0.7 mm), whereas the largest was a dogfish (egg length of 65 mm). The data were heavily clustered toward small eggs, but even so, small eggs clearly produced small hatchlings, and large eggs produced large hatchlings.

A number of researchers have exploited differences between the egg size of different populations, for example, Atlantic herring *Clupea harengus* (Blaxter and Hempel, 1963), and dace *Leuciscus leuciscus* (Mann and Mills, 1985), or between different females, for example, orangethroat darter *Etheostoma spectabile* (Marsh, 1986), striped bass *Morone saxatilis* (Eldridge et al., 1982), Atlantic cod *Gadus morhua* (Knutsen and Tilseth, 1985), chum and coho salmon *Oncorhynchus keta* and *O. kisutch* (Beacham et al., 1985), rainbow trout *O. mykiss* (Springate and Bromage, 1985), and Atlantic salmon *Salmo salar* (Thorpe et al., 1984), to examine hatchling size. All of these studies of intraspecific variation found that larger eggs produced larger hatchlings, as we found with convict cichlids.

Within a single clutch of rainbow cichlids, egg size accounted for 38% of the variation in hatchling total length and 87% of the variation in yolk size of hatchlings. Similarly, for a clutch of convict cichlids, we found 40% and 81%, respectively. Our intraclutch results differ from a previous report by Lagomarsino et al. (1988) who detected only a weak correlation between egg size and hatchling length in the midas cichlid, "*C. (Am.)*" *citrinellum.* They argued that their correlation was so weak as to be biologically insignificant.

We suspect three possible reasons why Lagomarsino et al. (1988) found only a weak correlation. First, it appears, though it is not explicitly stated, that they measured live fry, not preserved ones. Second, they measured the hatchlings at the free-swimming stage, when the yolk sac was completely absorbed, several days later in development than in our study. Third, they used random samples of eggs from each of the broods they examined, whereas we specifically selected a range of eggs of different sizes. Calculating the coefficient of variation in egg size for each of their broods with the data provided in their table 1, the CVs are in almost all cases comparable to the CVs we obtained (range = 6.9–19.3, mean = 11.0). As they pointed out, the CVs they found for fry length were much smaller (range = 1.3–6.1, mean = 2.7). We do not know whether their lesser variation in size of free-swimming hatchlings was the result of measuring live hatchlings or whether the variation they found in size of eggs truly disappeared after the eggs hatched.

The positive association between the yolk size of hatchlings and egg size indicates a metabolic cost to producing larger eggs. Larger eggs are not larger because they are filled with more water but because they contain more of the materials necessary to produce a larger hatchling. Consequently, from a parental-investment perspective, making a large egg costs a female more per egg than making a small egg. Larger eggs entail a reduction in the number of eggs that can be produced (Smith and Fretwell, 1974; RMC, unpubl. data). Therefore, larger size must confer a compensatory advantage, such as the ability to escape predators, to exploit an inhospitable environment, or to consume a broader array of foods. No studies to date have examined this question at such a fine level of variation in the Cichlidae.

Our study shows that relatively tiny differences in initial egg size may lead to differences in size of hatchlings. Within a few weeks after hatching, dramatic differences in the size of siblings are obvious (unpubl. data). Further, the phenomenon of "growth depensation," namely that through time the largest fish in a cohort get larger and the smaller fish lag further behind, widespread in fishes (Brown, 1957; Brett, 1979), is commonplace in cichlids (pers. obs.). The intriguing question remains: is it the initial differences in egg size that ultimately determine the size of a fry in the hierarchy, or do these initial differences disappear and other forces generate subsequent variation?

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