

**PARENTAL SIZE AND PERCEIVED BROOD VALUE:
ARE ALL EGGS CREATED EQUAL?**

Alison P. Galvani
New College
Oxford University
Oxford, OX1 3BN
United Kingdom
alison.galvani@new.ox.ac.uk

Ronald M. Coleman
Department of Integrative Biology
University of California
Berkeley, CA 94720-3140
colemanr@garnet.berkeley.edu

Abstract

We report a negative correlation relating maternal weight and magnitude of defense within convict cichlids (*Cichlasoma nigrofasciatum*). These results illustrate that cichlids maximize return on reproductive investment by evaluating the relative returns that can be reaped from present and expected future broods.

Introduction

In a broad sense, we explored parental investment decisions which comprise an important dimension of life history strategies. Life history theory allows us to predict, test and understand different adaptive aspects of an organism's life cycle (Stearns, 1977). A life history perspective defines the phenotype by demographic characters, such as age, size, number of offspring and growth and reproductive investment. These fitness components influence each other through interrelated trade-offs, arising from functional constraints.

These components vary not only between species, but also between individuals within a species and even within the life cycle of an individual. Demographic characters will change throughout a life history, as will, therefore, the life history strategy at any given point. Indeterminate growth in fish means that size will be a continuously varying factor for an individual, giving rise to a plastic strategy within the life history of a single individual.

We focused on the relationship between present and future investment. Viewing present investment in the context of future reproductive prospects is appropriate, as resource allocation in the present influences not only current reproductive success, but also future reproduction. This is to say expenditure on a current brood has repercussions on the condition of the parent and therefore may compromise ability to invest in future broods (Coleman et al., 1985; Coleman and Gross, 1991).

Maximization of reproductive investment, and for that matter any form of investment, is directly derived from the rate of return on the investment. If an animal maximizes this quantity at each point within its life history, taking into account present conditions and future prospects, on average it will ultimately achieve the highest possible return on its investment (Sargent and Gross, 1985; Sargent and Gross, 1992).

We approached this issue by asking if parents who have different expected future reproductive success would value the same brood size equally. In fish, brood size increases with female size. Therefore, we questioned whether smaller parents value a fixed number of offspring more highly than do larger parents. This is a reasonable prediction, given that if a smaller parent respawed, it would expect a smaller brood than if a larger parent respawed.

Reproductive effort encompasses costs in terms of both energy and risk. We assumed that these efforts rise with perceived brood value. The particular parameter we took as a reflection of perceived value was the magnitude of defense a parent was prepared to expend against a brood predator. Not only does this measure incorporate both energy and risk components, but it is also relatively straightforward to measure through manipulative experiments.

We selected the convict cichlid (*Cichlasoma nigrofasciatum*) as our study animal, because this fish exhibits extensive parental care in the form of guarding and fanning (Lavery and Keenleyside, 1990; Keenleyside, 1991; Keenleyside et al., 1990). Moreover, pair bonding is not for life in convicts, so there is no complication arising from the value of maintaining a bond between parents.

Methods

We set up sixteen aquaria using females ranging from 4 g to 14 g. Females of various sizes were deliberately chosen to maximize the span of sizes examined. No attempt was made to control for male size because males were removed for the parental defense tests.

Each pair of fish was bred in fifteen gallon aquaria, three sides of which were covered with paper to provide visual isolation. Each aquarium contained two cm of gravel, a plastic plant and a bottomless flower pot measuring 8.8 cm in diameter to serve as a suitable spawning substrate. Each tank also had a heater to maintain the temperature at 28°C which is conducive to breeding. Room lighting was 12L:12D with fifteen minutes of simulated dusk and dawn. The fish were fed daily with frozen brine shrimp and TetraCichlid flakes.

The fish were checked at least once a day for spawning. The day after spawning, recorded as day 2, the pot was removed to count the number of eggs laid on it. A scraper was then used to remove any eggs in excess of one hundred. The weights of both parents were measured on an electronic balance and the standard and total lengths were measured with calipers. The female was returned to the brood, but the male was removed to another aquarium. Testing the investment of only one of the parents avoids complications arising from biparental interactions of convict cichlids (Coleman, 1992).

On day 6, by which point the offspring had typically reached the free-swimming stage, predator encounter experiments were performed. We constructed a predator model from a photographic print of a non-conspecific brood predator (*Tilapia mariae*) of total length 55.6mm and standard length 45.5mm, corresponding to a female weighing roughly 5g. The photograph was coated in clear epoxy resin and attached to a plexiglass handle.

For each defense test, the model was slowly inserted into the corner of the tank furthest from the fry and held in this position for five seconds. The model was moved near the site of schooling fry, and the stopwatch was started when the model reached this position. Then the

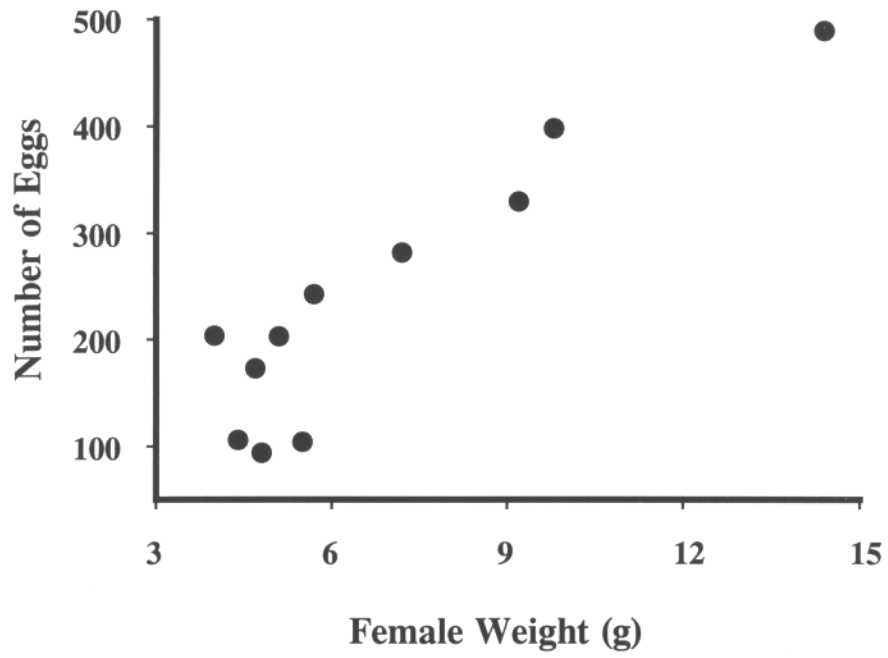


Figure 1. Fecundity versus body size in convict cichlids

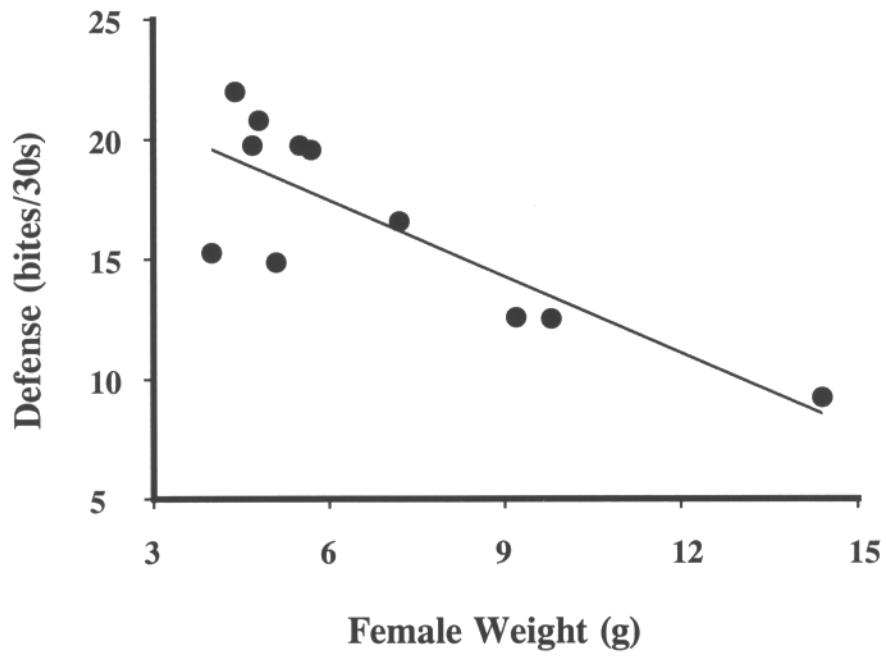


Figure 2. Defense versus body size in convict cichlids

model was moved in a figure-eight pattern, and the number of bites the mother gave to the model within a thirty second period was counted, whereupon the model was withdrawn. After a further thirty seconds, the model was reinserted and the encounter repeated. Over six consecutive days, this entire procedure was performed twice daily, allowing at least thirty minutes between repeats. After the last repeat of the final day, the fry were siphoned out and counted to ensure that the number had not fallen substantially below one hundred. We also weighed the female again and recorded her standard and total lengths. For analysis, we averaged the twenty four test scores obtained for individual females to produce a single defense test score for each female.

Results

We had a total of eleven spawnings from females dispersed over a wide spread of sizes. We found a highly significant positive correlation between number of eggs spawned and the weight of the mother (Fig. 1; $r=0.84$, $df=9$, $p<0.001$). This supports the assumption that fecundity increases with female size.

Magnitude of defense decreased with the size of the female (Fig. 2; $r=0.68$, $df=9$, $p=0.002$).

Discussion

These results are explicable if the mother is indeed acting to maximize the return on her reproductive investment. Optimal allocation is determined by the relative investment returns that can be reaped from present and expected future broods. A larger female can expect to have a larger brood than a smaller female, making a brood of a given size relatively less valuable to the larger female. Consequently, a larger female may be better off conserving expenditure on an existing brood to provide it for subsequent broods by decreasing shareable expenses (*sensu* Wittenberger, 1981) such as defense against predators.

It is also important to consider that a small fish is likely to become a large fish if it survives. Furthermore, within a single brood cycle, the loss of eggs through predation will be a common occurrence. Consequently, within a lifetime, or even within a brood cycle, parents are continually readjusting their strategies. Consider that in biparental species, such as convicts, there will also be an interplay between the relationship of parent relative to parent in addition to the relationship of parent relative to brood. From an ethological perspective, we can surmise that convicts are able to incorporate dimensions of present conditions in the formation of a life history "decision". A further extension would be to repeat these experiments on a female as it progresses through its life. This should demonstrate that parents are able to change their perception of relative brood value with growth.

Acknowledgements

We thank G.W. Barlow for use of his facilities, financial support and discussions. This research was supported in part by grant BNS 9109852 from the National Science Foundation to G.W. Barlow.

References

- Coleman RM and Gross MR (1991) Parental investment theory: the role of past investment. *Trends in Evolution and Ecology* 6:404-406
- Coleman RM, Gross MR and Sargent RC (1985) Parental investment decision rules: a test in bluegill sunfish. *Behavioural Ecology and Sociobiology* 18:59-66

- Keenleyside MHA (1991) Parental care, p. 191-208; in Cichlid Fishes: Behaviour, ecology and evolution. Keenleyside MHA (ed) Chapman and Hall, New York, New York
- Keenleyside MHA, Bailey RC and Young VH (1990) Variation in the mating system and associated parental behaviour of captive and free-living Cichlasoma nigrofasciatum (Pisces, Cichlidae). Behaviour 112:202-221
- Lavery RJ and Keenleyside MHA (1990) Parental investment of a biparental cichlid fish, Cichlasoma nigrofasciatum, in relation to brood size and past investment. Animal Behaviour 40:1128-1137
- Sargent RC and Gross MR (1985) Parental investment decision rules and the Concorde fallacy. Behavioural Ecology and Sociobiology 17:43-45
- Sargent RC and Gross MR (1992) Williams' principle: an explanation of parental care in teleost fishes, p. 275-293; in The behaviour of teleost fishes (2nd edn). Pitcher TJ (ed) Croom Helm, London
- Stearns SC (1977) The evolution of life history traits. A critique of the theory and a review of the data. Annual Review of Ecology and Systematics 8:145-171
- Wittenberger JF (1981) Animal Social Behavior. Duxbury Press, Boston.