



Do parental convict cichlids of different sizes value the same brood number equally?

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ABSTRACT

We report a negative correlation between the weight of a female convict cichlid, *Cichlasoma nigrofasciatum*, and the magnitude of her defence against a model brood predator for a brood reduced to 100 eggs. We account for this relationship by the fact that a larger female is more likely to spawn a larger number of eggs than is a smaller female, making a fixed number of eggs relatively less valuable to the larger female. We performed two supplementary experiments that eliminated other logical explanations of the data. One experiment involved scaling the model brood predator. Results indicated that the size of model relative to the parent (over the range of ratios investigated) has no significant effect on magnitude of defence. The other experiment demonstrated no systematic trend in defence when brood number was unmanipulated. Thus, on average, larger females defended their naturally larger broods to the same extent as smaller females defended their smaller broods. Together, these three results suggest that female convict cichlids of different sizes do not value the same brood number equally.

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The issue of how much to invest in a current brood is a problem that every parent faces. Trivers (1972, page 139) defined parental investment as 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'. By definition, parental investment in a current brood forfeits investment in later broods. Consequently, the value of an existing brood relative to a parent's expectation if it were to reproduce again is an important variable in investment allocation decisions (Coleman et al. 1985; Sargent & Gross 1985).

Fish have indeterminate growth, making body size a key life history character. As a female fish grows, the number of eggs that she produces increases. On average, a larger female will produce more eggs than will a smaller female. Therefore, a larger female has an expectation of a greater number of eggs than does a smaller female. In concrete terms, we would expect a larger fish to value a given brood number of, for example, 100 eggs, less than a smaller fish. The larger fish has the option of respawning and laying far more than 100 eggs, but a smaller fish

would not be able to respawn as many eggs (Coleman 1993).

Brood defence, like many forms of parental investment, costs in terms of both energy and risk. We used magnitude of defence shown by a parent against a model brood predator as a reflection of brood value. The appropriateness of this quantity relies on the assumption that defence increases with perceived brood value. Not only does this measure incorporate both energy and risk components of parental investment, but it is also relatively straightforward to measure.

The purpose of our study was to determine whether the same number of offspring (brood size) is valued equally by female convict cichlids, *Cichlasoma nigrofasciatum*, of different body weight. We conducted a series of three experiments that measured the magnitude of brood defence under different circumstances. Experiment 1 established whether a large parent will defend a brood of fixed number, for example, 100 eggs, less than a smaller parent will. Experiment 2 tested whether a parent would respond differently to models of different size, thereby investigating the effects of scaling the model relative to the size of the parent. Experiment 3 tested whether the size of the parent per se influences the magnitude of defence that a parent will expend on its natural number of offspring.

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GENERAL METHODS

The Convict Cichlid

We used the convict cichlid because it is well suited to captive spawning and manipulation (e.g. Lavery & Keenleyside 1990; Lavery & Colgan 1991). Furthermore, it provides extensive parental care in the form of guarding and fanning. The convict cichlid is a substrate spawning fish found from Guatemala to northern Panama in Central America (Bussing 1987; see also McKaye 1977; Keenleyside et al. 1990; Wisenden 1994, 1995; Wisenden & Keenleyside 1995). Fertilization is external, and both parents remain with the brood until several weeks after the offspring have reached the free-swimming stage. At 28°C, the eggs hatch after about 3 days and reach the free-swimming stage after about 6 days. Defence of the young by the parents is crucial to the young's survival (McKaye 1977).

Experimental Set-up

We bred each pair of fish in a 76-litre aquarium (60 × 30 × 30 cm), three sides of which were covered with paper to provide visual isolation from other pairs. The aquarium contained 2 cm of gravel, a plastic plant and a bottomless flowerpot (8.8 cm diameter) to serve as a suitable spawning substrate. Each tank also had a heater to maintain a temperature of 28°C, which is conducive to breeding. The room was maintained on a 12:12 h light:dark cycle with 15 min of simulated dusk and dawn. The fish were fed daily with frozen brine shrimp and TetraCichlid flakes.

Experimental Procedure

We checked the fish at least once a day for spawning and designated the day of spawning as day 1. The day after spawning, day 2, we removed the flowerpot to count the number of eggs. In experiments 1 and 2, we used a scraper to remove eggs in excess of 100. Therefore, all females were left with a brood number of 100 eggs, irrespective of the number spawned. Brood manipulation by egg addition was not attempted, because it was both impractical and inappropriate for our purposes. Even if two convicts spawned at the same time, convict eggs cannot be reattached to a spawning substrate. There may also be problems if a parent can distinguish its offspring from unrelated offspring. Furthermore, we would not expect a female to have evolved the ability to respond to an increase in the number of eggs within a single brood cycle, because such a situation would not arise in the wild.

On day 2, we weighed both parents on an electronic balance and measured the standard and total lengths with calipers. Only the female was returned to her brood. Testing the investment of only one of the parents avoids complications arising from the biparental care of convict cichlids (Coleman 1993).

We performed predator encounter experiments starting on day 6, by which point the offspring were typically

free-swimming. We constructed predator models from a photographic plate of a nonconspecific brood predator, *Tilapia mariae*. We used this particular photograph (Axelrod et al. 1985, plate 361) because it looks like a generalized brood predator. We did not use a photograph of a convict cichlid to avoid the female confusing the model with a potential mate. All three experiments involved a model with a total length of 55.6 mm and standard length (SL) of 45.5 mm, corresponding to a female weighing roughly 3.6 g, using weight (g) = $0.0000202 \times SL^{3.17}$ (mm) from Coleman (1993). We refer to this model as the small model. Experiment 2 involved an additional model constructed from the same photograph, but enlarged by 48% to give a total length of 82.0 mm and standard length of 67.1 mm (corresponding to a female weighing 12.5 g). We refer to this model as the large model. The photographs were coated in clear epoxy resin and attached to a Plexiglas handle.

Each defence test involved moving the model in a figure-8 pattern in front of the schooling fry. We recorded the number of times that the female bit the model within 30 s, after which the model was withdrawn. After another 30 s, the model was reinserted and the encounter repeated. We performed this entire procedure on 6 consecutive days, twice a day. We allowed at least 30 min between repeats to reduce the possibility that the first predator encounter could influence the next encounter.

After the last encounter on the final day of testing, we siphoned out the fry and counted them to confirm that the quantity of young did not decline significantly through the test period. We also weighed the female again and recorded her standard and total lengths. For analysis and graphing, we used the weight of the female on the day after spawning. All means are reported as ± 1 SE.

EXPERIMENT 1: MANIPULATED BROODS

In this, the main experiment, we tested the defence of parents of different size each protecting a fixed number of eggs against a model brood predator of constant size.

Methods

We selected females of various sizes for this experiment to maximize the range of sizes used. No attempt was made to control for male size, because males were removed for the parental defence tests.

The day after spawning, any eggs in excess of 100 were scraped from the bottomless flowerpot. Therefore, brood number was constant for all fish, irrespective of how many eggs they had spawned. All females were tested using only the small model. For analysis, we averaged the total 24 test scores obtained for an individual female to produce a single defence test score for that female.

Results

We obtained 14 spawnings. We found a significant positive regression ($r_{13}^2 = 0.83$, $P < 0.01$; Fig. 1) between

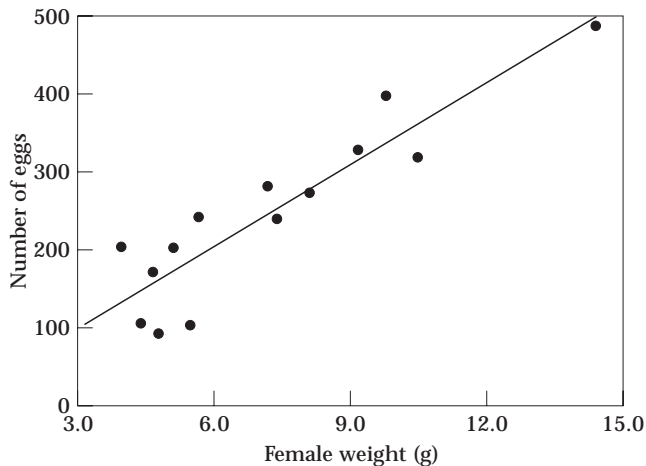


Figure 1. Number of eggs spawned versus female weight (number = $35.1 \times \text{weight} - 5.3$) in experiment 1.

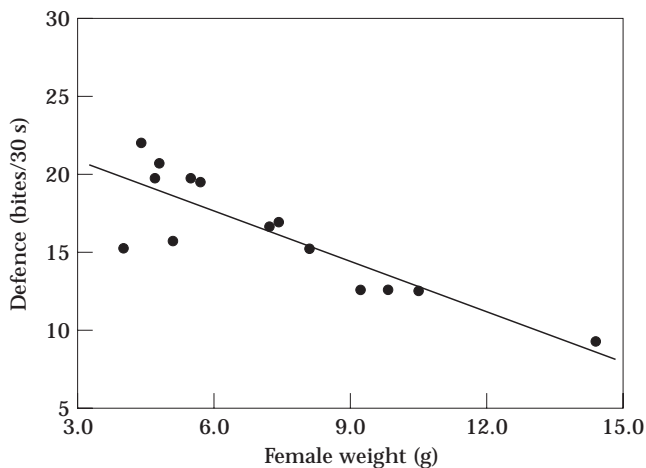


Figure 2. Magnitude of defence versus female weight for females defending 100 eggs (defence = $-1.08 \times \text{weight} + 24.1$) in experiment 1.

the number of eggs spawned and the weight of the female. This result supports the assumption that fecundity increases with the size of the female.

Most importantly, we obtained a significant negative regression between the magnitude of defence and the size of the female ($r_{13}^2 = 0.73$, $P < 0.01$; Fig. 2). In other words, larger females defended the same number of eggs less than did smaller females.

Despite being fed liberally, females on average lost $3.8 \pm 0.7\%$ of their body weight from the time of spawning until the end of the defence tests. The average number of fry recovered from each tank was 94.6 ± 2.1 .

Discussion

Large females defended a brood of 100 fry less than did smaller females. These results can be explained if the female is acting to maximize the return on her reproductive investment, because a larger female can expect to have a larger brood than a smaller female. This expect-

tation makes a brood of a given number relatively less valuable to a larger female. Therefore, a large female may be better off not wasting energy on, what is to her, a meagre brood. Our results on female convict cichlids are consistent with results for male convict cichlids under similar experimental conditions (Coleman 1993).

The results of experiment 1 also could be explained if the females defended their offspring to achieve a specific level of intimidation against the brood predator. For example, if each bite from a larger female is more intimidating, larger females achieve the same effect with less defence than smaller females. Alternatively, large females may perceive small predators as less of a threat. In both of these scenarios, the important variable is the size of the brood predator relative to the parent. In experiment 2, we tested whether the relative size difference between the parent and the model predator could explain the results of experiment 1.

EXPERIMENT 2: PREDATORS OF DIFFERENT SIZES

In experiment 1, we varied parent size and kept model size constant. Therefore, the results of this experiment could be confounded by the relative difference in size between parent and model for large and small parents; that is, the smallest parents were roughly the size of the model, but larger parents were larger than the model.

If the relative size difference between parent and model underlies the results of experiment 1, those results could be explained if a parent bites a larger model more than a smaller model. To determine whether this was happening, we conducted a second experiment in which each fish was presented with two models of different size, but otherwise identical.

Methods

We used 16 females (size range 2.8–10.5 g). In each trial, we presented a model of one size followed by the other-sized model after 30 s. In the second trial on the same fish later that day, both models were again presented, but in the reverse order. This was repeated for 6 days, hence each fish encountered both models 12 times. In addition, to control for order effects, if the first model presented to a fish was large, then the first model presented to the next fish to spawn was small. Therefore, half of the fish to spawn encountered the small model first, and the other half encountered the large model first. We compared the defence of each female against the small model versus her defence against the large model using a paired *t* test.

Results

The effect of size of the model on the magnitude of defence was not significant ($t_{15} = 0.44$, $P = 0.67$; mean difference = 0.2 bites). As in experiment 1, females lost weight ($3.3 \pm 0.8\%$). The average number of fry recovered at the end of the tests was 95.1 ± 0.9 .

Discussion

The ratio of the size of the model to the size of the parent did not influence the magnitude of defence for the size range that we investigated. This range was acceptably wide for ascertaining an effect if one did exist, because the ratio of the standard lengths of the smallest to largest fish tested (39.1:76.5 mm), was similar to the ratio of the standard lengths of the small model to the large model (45.5:67.1 mm).

Over the size range of the two model predators, the parent was defending its brood, not itself. Therefore, it appears that the two models posed relatively equal threats to the brood. Because the models were roughly the same size as the female parent, they were probably not close to the size threshold at which the model would be regarded as a threat to the parent itself.

Thus experiment 2 clarifies the results of experiment 1. The decrease in defence by large females in experiment 1 was probably not caused by the increased difference in size between parent and model for larger parents versus smaller parents.

EXPERIMENT 3: DEFENCE OF UNMANIPULATED BROODS

If the relationship between expected and realized brood numbers is indeed the important variable explaining the trend in defence found in experiment 1, we predicted that there should be no systematic difference in defence when this variable is kept constant. There may be differences in defence between females, because other factors such as parasite load may have an influence, but these should not affect a trend related to the size of the female.

Methods

To keep relative brood number constant between fish of different size, we left the brood number unmanipulated, that is, each female defended the number of offspring that it had spawned.

Again, the females were tested for two sets of two trials every day for 6 days using only the small model. We averaged the 24 test scores obtained for each female to produce a single defence test score for each of the 16 females.

Results

There was no significant relationship between size of the female and her defence in protection of her unmanipulated brood ($r_{15}^2 < 0.01$, $P = 0.98$; Fig. 3). The average number of fry recovered from each aquarium was $4.5 \pm 0.7\%$ less than the number of eggs spawned, consistent with experiments 1 and 2. Females lost similar amounts of weight from spawning through to the end of testing as in previous experiments ($3.0 \pm 0.7\%$ of their initial body weight).

To ensure that the lack of a relationship between female size and brood defence in this experiment was not

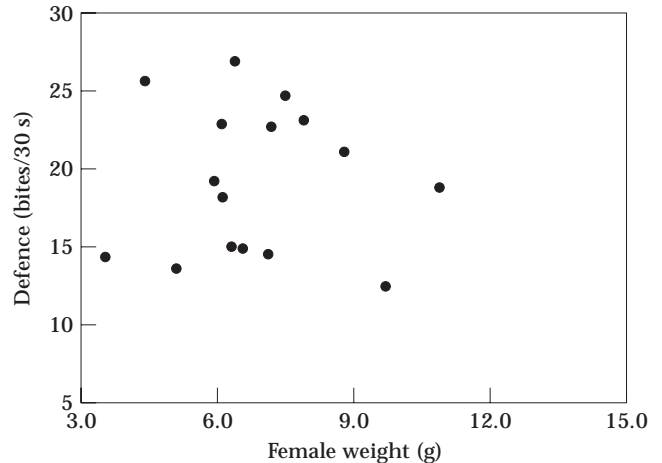


Figure 3. Magnitude of defence versus female weight for females defending unmanipulated broods in experiment 3.

the product of an aberrantly large or small spawning, we compared the number of eggs spawned in this experiment with a regression of egg number on body size from experiment 1. None of the spawnings in experiment 3 fell outside the 99% confidence interval of that regression. We conclude that each female in experiment 3 produced a brood typical for her size. Not surprisingly, therefore, as with the lack of a relationship with body size, there was no significant relationship between brood number and a female's defence in protection of her unmanipulated brood ($r_{15}^2 < 0.01$, $P = 0.96$).

Discussion

With unmanipulated broods, there was no relationship between either body size or brood number and the level of defence by a female parent. These results confirm the absence of an effect of maternal weight per se on the magnitude of her defence. Therefore, the difference between expected brood number and realized brood number explains the defence trend in experiment 1. Insufficient sample size cannot be proposed as a convincing argument to explain the insignificant result in experiment 3, because the sample size (16) was larger than that in experiment 1, where a significant result was found using manipulated broods.

GENERAL DISCUSSION

Considered together, these three experiments indicate that female convict cichlids of different sizes do not value the same brood number equally. Experiment 1 showed that larger females defended a fixed number of eggs less than did smaller females. Experiment 2 eliminated the possibility that the size ratio of the female parent to the model explained the results of experiment 1. Experiment 3 demonstrated that size of the parent per se had no effect on defence by a parent guarding its natural brood number.

The response to brood number that the fish appear to make in relation to their own size should be advantageous in the wild, where brood predation is common (R. Coleman, personal observation). Therefore, it is not surprising that convicts have evolved a response to brood reduction. Guarding is an important component of the life history strategy of various species (Blumer 1982), in helping to maximize reproductive success. Maximization of reproductive or any other 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 maximize its reproductive success (Sargent & Gross 1985).

Guarding is a shareable form of parental investment. A shareable investment benefits all offspring regardless of their number (Coleman & Fischer 1991). If guarding was non-shareable, and each doubling of brood number required a doubling in investment to maintain the same level of benefit for each offspring, all broods would be of equal value. In these three experiments, however, the rate of return on the effort expended by the female depended on the number of offspring. If a female had twice as many eggs, the return on her effort would be twice as large. For a large female presented with 100 eggs, respawning over 200 eggs and hence doubling the return on her defence is a likely possibility. Therefore, the larger female may be better off conserving her effort for future broods which are likely to be larger. A smaller female, on the other hand, can expect to have fewer eggs per spawning than a larger female. Therefore, a smaller female will devote more effort to her 100 eggs than a larger female.

The fact that larger females spawned more eggs than did smaller females within the brood cycle studied, and hence had greater past investment (Coleman & Gross 1991), does not invalidate our findings. It is true that the absolute amount of investment that each female had already devoted to her brood before brood manipulation was different for females of different sizes, but the relative amounts of investment were constant. In other words, each female produced a brood number according to her weight.

It could be argued that the females may have assessed the proportion removed and not the direct value of the remaining brood. In most cases, however, these two quantities will predict the same level of investment. On average, a female that has a greater proportion of eggs removed also has greater future expectation. Therefore, even if the females responded to a rule of thumb based on the number of eggs removed as a proportion of the original brood number, this response would also be based on the expected future reproduction. In other words, a female defending in relation to the eggs remaining as a proportion of the original amount spawned is also defending relative to the number of eggs she can expect to produce if she respawed. This effect is generated from the correlation between the weight of the female and the number of eggs spawned.

On the other hand, there may be a discrepancy between the proportion of eggs removed and the expected reproductive success based on maternal weight

if the female spawned an unusual brood number in the brood cycle tested. In such a case, rules of thumb based on these two quantities would yield different results. This potential complication was not a problem for this study, however, because none of the brood numbers widely deviated from the regression obtained between female weight and brood number.

Our results agree with those of Coleman (1993) who found that larger male convict cichlids defended a fixed brood number less than did smaller males. Coleman did not test the effect of model size or parental size per se. Two other studies have examined the effect of parental size on the magnitude of parental investment. Keenleyside et al. (1985), also working with convict cichlids, found that large males defended more intensely than smaller males. These results may appear to contradict our results; however, a closer look at Keenleyside et al.'s methods shows this not to be true. In nature, large males have larger broods than do smaller males, because larger males are generally more successful at obtaining larger females as mates (McKaye 1986). Therefore, in the wild, males of different sizes should have the same relative brood number. However, Keenleyside et al. paired the males with females and did not manipulate brood number, such that a male was not necessarily defending its expected brood number. Furthermore, although only male defence was considered, the females were not removed from the experimental apparatus. This design could have caused complications from biparental interactions, which Coleman (1993) found to be significant.

In the second study of effects of parental size on parental investment, Reid & Roitberg (1995) found that larger male pine engravers (Coleoptera: Scolytidae) invested less in their broods than did smaller males. However, they investigated the duration of investment as opposed to intensity of investment as we did. In addition, larger males had a greater chance of finding further mates than did smaller males. This dimension was not an issue in our study, because larger females were not able to obtain more spawnings within a given period than were smaller females. On average, small and large females both experience a similar refractory period after spawning, during which they cannot respawn.

Our study has broad implications. For example, in biparental cichlids, both parents take care of the offspring and the parents are often of different size (McKaye 1986). Thus, the same brood may be of different value to each parent. Understanding how parental investment is affected by the size of one parent may help us to unravel the dynamics of biparental investment (Coleman 1993).

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References

- Axelrod, H. R., Burgess, W. E., Pronek, N. & Walls, J. G. 1985. *Dr. Axelrod's Atlas of Freshwater Aquarium Fishes*. 1st edn. Neptune City, New Jersey: T.F.H. Publications.
- Blumer, L. S. 1982. A bibliography and categorization of bony fishes exhibiting parental care. *Zoological Journal of the Linnean Society*, **76**, 1–22.
- Bussing, W. A. 1987. *Peces de las Aguas Continentales de Costa Rica*. San Jose: Editorial de la Universidad de Costa Rica.
- Coleman, R. M. 1993. The evolution of parental investment in fishes. Ph.D. thesis, University of Toronto, Canada.
- Coleman, R. M. & Fischer, R. U. 1991. Brood size, male fanning effort and the energetics of a nonshareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae). *Ethology*, **87**, 177–188.
- Coleman, R. M. & Gross, M. R. 1991. Parental investment theory: the role of past investment. *Trends in Ecology and Evolution*, **6**, 404–406.
- Coleman, R. M., Gross, M. R. & Sargent, R. C. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behavioral Ecology and Sociobiology*, **18**, 59–66.
- Keenleyside, M. H. A., Rangeley, R. W. & Koppers, B. U. 1985. Female mate choice and male parental defense behaviour in the cichlid fish *Cichlasoma nigrofasciatum*. *Canadian Journal of Zoology*, **63**, 2489–2493.
- Keenleyside, M. H. A., Bailey, R. C. & Young, V. H. 1990. Variation in the mating system and associated parental behaviour of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae). *Behaviour*, **112**, 202–221.
- Lavery, R. J. & Colgan, P. W. 1991. Brood age and parental defence in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). *Animal Behaviour*, **41**, 945–952.
- Lavery, R. J. & Keenleyside, M. H. A. 1990. Parental investment of a biparental cichlid fish, *Cichlasoma nigrofasciatum*, in relation to brood size and past investment. *Animal Behaviour*, **40**, 1128–1137.
- McKaye, K. R. 1977. Competition for breeding sites between the cichlid fishes of Lake Jiloa, Nicaragua. *Ecology*, **58**, 291–302.
- McKaye, K. R. 1986. Mate choice and size assortative pairing by the cichlid fishes of Lake Jiloa, Nicaragua. *Journal of Fish Biology*, **29** Suppl. A, 135–150.
- Reid, M. L. & Roitberg, B. D. 1995. Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). *Canadian Journal of Zoology*, **73**, 1396–1401.
- Sargent, R. C. & Gross, M. R. 1985. Parental investment decision rules and the Concorde fallacy. *Behavioral Ecology and Sociobiology*, **17**, 43–45.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Wisenden, B. 1994. Factors affecting reproductive success in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Canadian Journal of Zoology*, **72**, 2177–2185.
- Wisenden, B. 1995. Reproductive behaviour of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. *Environmental Biology of Fishes*, **43**, 121–134.
- Wisenden, B. & Keenleyside, M. H. A. 1995. Brood size and the economy of brood defence: examining Lack's hypothesis in a biparental cichlid fish. *Environmental Biology of Fishes*, **43**, 145–151.