

Brood size and the economy of brood defence: examining Lack's hypothesis in a biparental cichlid fish

Brian D. Wisenden¹ & Miles H.A. Keenleyside

Department of Zoology, University of Western Ontario, London, Ontario, N6A 5B7, Canada

¹ *Current address: Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, S7N 0W0, Canada*

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Synopsis

We tested the explanatory value of two hypotheses reviewed by Lack (1954) in the maintenance of brood size in free-ranging convict cichlids *Cichlasoma nigrofasciatum*: (1) physiological constraints on egg production, and (2) behavioural constraints imposed by brood defence. Number of free-swimming young in 13 experimental (E) broods was augmented to the upper limit of the size distribution of natural broods (150 young); 18 control (C) broods were handled in the same way but brood size was not changed (mean \pm SE = 69.5 \pm 11.0). E and C brood sizes were measured at 5 day intervals. At day 20 (just before independence from parental care), 50.3 \pm 9.4 (n = 9) young remained in E broods and 30.8 \pm 7.8 (n = 8) young remained in C broods ($p > 0.05$). Offspring number did not differ significantly ($p > 0.05$) between C and E broods after day 10. Mean growth rate of offspring was significantly lower in E broods than in C broods, perhaps in response to increased density of young in the former. Both the convergence of offspring number in E and C broods and suppression of growth in E broods support a behavioural constraint; that during the first 10 days in which the young are free swimming, two parents are unable to defend large broods as successfully as small broods. A trade-off exists in parental investment between current and future reproduction. Extra-parental investment in current reproduction (eggs) does not result in an increased number of young at independence, therefore a behavioural constraint during brood defence should stabilize the evolution of clutch size.

Introduction

The evolution of clutch size has received much attention in the ornithological literature (for review see Godfray et al. 1991), stimulated by the seminal work of David Lack (1947, 1954, 1968). Lack (1954) noted that many bird species have characteristic clutch sizes and he reviewed four hypotheses about factors regulating the evolution of clutch size in birds. Fish species also have characteristic fecundities (Wootton 1991) and Lack's hypotheses can be extended to the evolution of clutch size in fishes.

The first hypothesis examined is that there is a physiological limit, controlled by food supply or body size, to the number of eggs a female can produce. This may also apply to fish (Wootton 1984, Townshend & Wootton 1984).

The second hypothesis states that birds lay as many eggs as they can cover during incubation. Although fish do not incubate their eggs, for species with parental care, oxygenation by egg fanning behaviour is common (Blumer 1979). However, there is no evidence to suggest that egg number is con-

strained by a parent's ability to provide oxygen in most habitats (Wootton 1984).

The third hypothesis considered was that clutch size is adjusted to balance mortality so that the species may ensure its survival. Lack dismissed this hypothesis as an argument for group selection.

Lack's fourth, and favoured, hypothesis is that clutch size in birds is determined by the number of young for which the parents can adequately provide food. This has been supported by many studies of birds and has been subsequently broadened to take into account various life history trade-offs affecting an individual's lifetime reproductive success (Godfray et al. 1991).

Parental care in fish differs from that of altricial birds in that fish with prolonged care of mobile offspring generally do not feed their young directly (McKaye 1981, but see Wisenden et al. 1994). In fish, brood defence is the main form of parental care of free-swimming young (Perrone & Zaret 1979, Sargent & Gross 1993). Therefore, to apply Lack's fourth hypothesis to fish with extended biparental care, the hypothesis becomes 'clutch size is adjusted to the number of young that parents can economically defend from brood predators'. There is indirect evidence to support this hypothesis from a study of convict cichlids, *Cichlasoma nigrofasciatum*, in their natural habitat (Wisenden 1994a, b). Mean number of young per brood at independence from parental protection was virtually the same at four sites that differed in mean size of breeding females, mean growth rates of offspring, and mean brood survival.

Among fishes, the family Cichlidae is well known for its variety of parental care styles (Keenleyside 1991). Convict cichlids, the species used in this study, are small freshwater fish native to Central America. They are substrate spawning hole-nesters that have biparental care of eggs and free embryos for about a week, and free-swimming juveniles for an additional three to four weeks (Wisenden & Keenleyside 1992). Both parents actively defend the brood against potential predators.

The objective of this paper is to determine the potential roles of physiological constraints on egg production (Lack's first hypothesis) and behavioural constraints imposed by brood defence (based on

Lack's fourth hypothesis), as selective forces maintaining the present range in brood sizes in free-ranging convict cichlids. Brood size at our study site in Costa Rica during earlier work (1990 and 1991) ranged from 8 to 159 young (mean \pm SE = 73.7 ± 4.1 , $n = 78$ broods) when the brood first emerged from the cavity in which the eggs were laid. In the present study we increased the number of offspring at the beginning of the free-swimming interval in experimental (E) broods to 150 young, at the upper extreme of that distribution (at the 99 percentile) and left control (C) brood size intact with 70 young (at the 47 percentile). If behavioural constraints on the parents, imposed by the demands of brood defence, limit brood size in convict cichlids, then mean number of young in E broods should converge on mean number of young in C broods during the period of parental care. In addition, large brood size may result in higher density of young and lead to slower growth of offspring in E broods than in C broods. If physiological constraints dictate brood size in convict cichlids, then the number of offspring remaining in experimentally augmented broods should be significantly higher than in control broods at the end of the period of parental care.

Materials and methods

Data were collected from 5 March to 25 April 1993, at the río Cabuyo, a clear, freshwater stream located in Lomas Barbudal Biological Reserve, Guanacaste province, northwest Costa Rica ($10^{\circ}30'N$, $85^{\circ}23'W$). The río Cabuyo is fed by a constant flow of ground water in the dry season (December to May) during which convict cichlids breed. During the study, mean stream width (\pm SE) was 10.56 ± 0.39 m, mean depth was 44.8 ± 2.4 cm, mean flow was $231.71 \cdot s^{-1}$ and mean current speed was $4.9 \text{ cm} \cdot s^{-1}$. Relatively deep, wide sections of the río Cabuyo were chosen for the study because brood predation pressure is known to be intense in this habitat (Wisenden 1994a, b).

Breeding pairs of convict cichlids along about 100 m of the stream were used in this experiment. When the young were between 5 and 6 mm standard length (SL) (three to five days after becoming

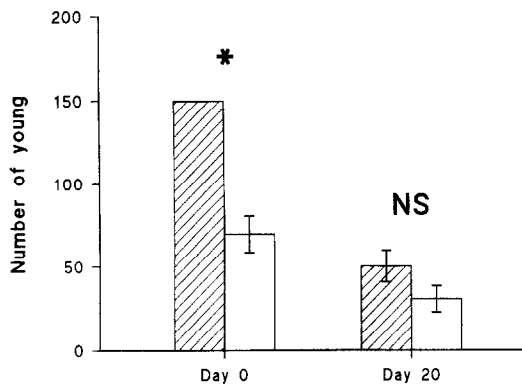


Fig. 1. Mean (\pm SE) offspring number for experimentally augmented broods (hatched bars, $n = 9$), and control broods (open bars, $n = 8$) on Day 0 (soon after emergence of the young from the spawning cave) and on Day 20 (near independence of the young from parental care). Asterisk indicates a significant difference between experimental and control groups (t-test, $p < 0.05$). NS, not significant ($p = 0.137$).

free-swimming), the family unit was captured using a seine net for the parents and hand nets for the young, as described in Wisenden & Keenleyside (1992). We anaesthetized each parent with MS222 (tricaine methanesulfonate) and recorded its SL and weight. We excised a dorsal spine and made a detailed sketch of the body markings to help identify individuals on subsequent sampling dates. We arbitrarily chose 10 offspring, anaesthetized them with MS222, measured the SL of each to the nearest 0.5 mm, and counted the number of offspring in the brood. When the parents and their offspring had recovered from the MS222, we returned them to the stream at the point of capture using a clear plastic tube (Wisenden & Keenleyside 1992). Normal brood defence resumed immediately.

We performed one of two treatments on each brood. Control (C) broods were sampled as described above, then returned to the stream with all their young. Experimental (E) broods had their brood size increased to 150 young. Additional young used to augment E broods came from nearby broods in the study area, sections of the río Cabuyo outside the study area, or from the Quebrada Urraca, a tributary of the río Cabuyo. The extra young did not differ in SL from the young of the receiving brood by more than 0.5 mm. Added young that are larger than the natural young are rejected by the parents (Wisenden & Keenleyside 1992, Fraser et

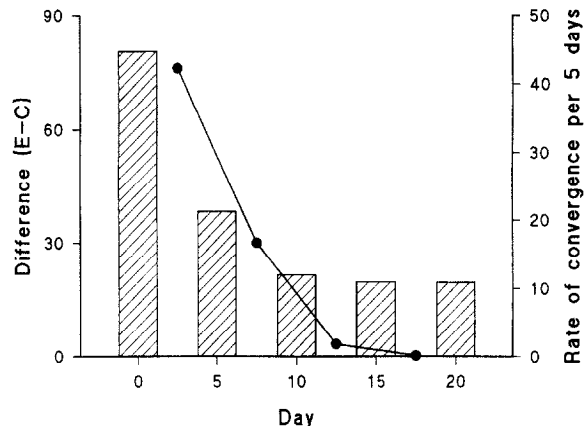


Fig. 2. The rate of convergence (line) as the change per five day interval in the difference in mean offspring number between E and C broods (bars) for brood samples taken every five days.

al. 1993). Young that are smaller than the natural offspring are accepted by the parents but suffer disproportionately higher levels of predation (Wisenden & Keenleyside 1994). Foreign young of similar size (i.e. < 0.5 mm SL) are neither rejected nor suffer disproportionate predation pressure and there is no evidence that adult convict cichlids distinguish between their own young and foreign, conspecific young of the same size. In E broods, extra young were either included with the original young when adults and their young were returned to the water, or they were added within 1 h using the clear plastic tube. We observed E broods for a few minutes to confirm that the extra young were accepted by the parents.

We designated the day of the initial sample as day 0. Each brood was then monitored at intervals of 5 days until day 20 (just before the end of the period of parental care) or until brood failure. At each sample, offspring were collected using hand nets, leaving 5 to 10 offspring with the parents. We arbitrarily chose 10 offspring, anaesthetized them, recorded their SL and counted the number in the entire sample. Young remaining in the water were counted using a face mask. After the young had recovered from the MS222 (ca. 10 min), they were returned to their parents as described above. We balanced the distribution of C and E broods within río Cabuyo to ensure that any potential differences in brood predation pressure between different areas

Table 1. Number of control and experimental broods surviving to each 5 day sample.

Sample day	Control		Experimental	
	n	%	n	%
0	18	100	13	100
5	15	83	13	100
10	14	78	12	92
15	13	72	11	85
20	8	44	9	69

of the study stream did not influence the comparison of survival of young between E and C broods.

Results

Mean number (\pm SE) of young in E broods before manipulation (58.4 ± 10.5 offspring, $n = 9$) did not differ significantly from that in C broods (69.5 ± 11.0 offspring, $n = 8$; $t = 0.73$, $df = 15$, $p = 0.479$). For broods that remained with their parents to day 20, mean number of young in E broods ($n = 9$) declined from 150 at day 0 to 50.3 ± 9.4 at day 20, while C broods ($n = 8$) declined from 69.5 ± 11.0 at day 0 to

30.8 ± 7.8 at day 20 (Fig. 1). Mean number of young in E and C broods differed significantly at day 0 ($t = 7.32$, $df = 7$, $p < 0.001$) and day 5 ($t = 2.61$, $df = 14$, $p = 0.020$) but not at day 10 ($t = 1.54$, $df = 14$, $p = 0.145$), day 15 ($t = 1.52$, $df = 15$, $p = 0.150$) or day 20 ($t = 1.57$, $df = 15$, $p = 0.137$). Therefore, convict cichlid parents did not defend E (large) broods as effectively as C (small) broods.

The rate of convergence of mean offspring number in E broods toward mean offspring number in C broods was not uniform over the 20 day period. The magnitude of the difference in mean offspring number between E and C broods declined rapidly from day 0 to day 10, but then stabilised from days 10 to 20 (Fig. 2). Thus, the rate of convergence, as measured by the change in this difference in mean offspring number over each 5 d interval, declined to almost zero after the day 10 sample. The C broods failed to reach day 20 in 10 out of 18 cases; E broods failed 4 out of 13 times ($\chi^2 = 1.873$, $df = 1$, $p = 0.171$; Table 1).

Mean SL of adult fish in the E and C groups did not differ (females: $t = 1.23$, $df = 29$, $p = 0.227$; males: $t = 0.52$, $df = 29$, $p = 0.605$). Mean SL of females was 43.5 ± 1.4 mm ($n = 13$) and 41.6 ± 0.9 mm ($n = 18$), and of males was 56.6 ± 1.2 mm ($n = 13$) and 55.8 ± 1.0 mm ($n = 18$) for E and C groups, respec-

Table 2. Summary of the effect of parent size on Ln number of young in control ($n = 8$) and experimental ($n = 9$) broods at each 5-day sample, based on multiple regressions of the model: $\text{Ln number} = \beta_0 + \beta_1 \ln \text{female SL} + \beta_2 \ln \text{male SL}$.

Sample	Control broods					
	r^2	p (model)	β_1	p (β_1)	β_2	p (β_2)
Day 0	0.95	< 0.001	4.714	< 0.001	0.783	0.398
Day 5	0.90	0.003	5.129	0.002	0.494	0.709
Day 10	0.92	0.007	5.926	0.004	0.470	0.758
Day 15	0.83	0.011	6.022	0.008	0.503	0.807
Day 20	0.15	0.657	2.851	0.531	1.598	0.796
Sample	Experimental broods					
	r^2	p (model)	β_1	p (β_1)	β_2	p (β_2)
Day 0 ¹	0.15	0.619	2.197	0.494	- 0.241	0.961
Day 5	0.45	0.221	- 3.050	0.148	6.269	0.102
Day 10	0.64	0.046	- 3.311	0.076	7.867	0.017
Day 15	0.74	0.018	- 4.169	0.037	9.923	0.007
Day 20	0.75	0.015	- 4.719	0.033	11.412	0.005

¹ Based on mean offspring number before brood augmentation.

tively. Parent SL had no effect on whether or not a brood reached day 20 for C broods (females: $t = 0.31$, $df = 16$, $p = 0.762$; males: $t = 0.55$, $df = 16$, $p = 0.591$) or for E broods (females: $t = 0.09$, $df = 11$, $p = 0.926$; males: $t = 1.71$, $df = 11$, $p = 0.115$). For C broods there was no difference in initial offspring number between broods that reached day 20 and those that did not ($t = 1.04$, $df = 16$, $p = 0.313$).

In C broods, size of the female parent was positively correlated with offspring number for all sample times except day 20, indicating a strong relationship between female size and fecundity (Table 2). No fecundity effect was found for females in E broods at day 0 (before brood size manipulation). In contrast to C broods, female SL in E broods was negatively correlated with offspring number for samples taken on days 15 and 20.

Male SL was not correlated with offspring number in C broods for any sample. In E broods, male SL was not significantly correlated with offspring number at day 0 (before manipulation) or day 5, but it was for samples taken on days 10, 15 and 20, providing support for the hypothesis that large males are more effective at brood defence than small males (Table 2). In E broods, the strength of the correlation between both female and male SL and offspring number increased over time.

Growth rates ($\text{mm} \cdot \text{day}^{-1}$) of young in C broods were significantly faster than in E broods, and significantly faster in broods that reached day 20 than in broods that did not (ANOVA Treatment: $F = 6.75$, $df = 1, 27$, $p = 0.016$; Day: 20 $F = 5.22$, $df = 1, 27$, $p = 0.032$, Table 3). There was no significant interaction between treatment and whether or not a brood reached day 20 ($F = 0.86$, $df = 1, 27$, $p = 0.363$). Mul-

tipple regression of \ln female SL and \ln male SL on \ln growth rate of young showed no significant effects in C broods ($r^2 = 0.450$, $df = 7$, $p = 0.225$) or E broods ($r^2 = 0.474$, $df = 8$, $p = 0.145$).

Discussion

Parental convict cichlids guarding broods that were experimentally enlarged at the beginning of the free-swimming interval did not have significantly more offspring than those guarding control broods 20 days later, near the end of the normal duration of parental care (Fig. 1). The evolution and maintenance of brood size in convict cichlids appears to be limited by a behavioural constraint of parental brood defence in the first 10 days that the young are free-swimming. During the first 10 days, mean offspring number in the two treatment groups rapidly converged (Fig. 2). By day 10, brood size in E broods was reduced to a size roughly equivalent ($p > 0.05$) to that of C broods and offspring in both groups became equally defendable thereafter.

The E and C broods did not differ in their chance of total brood failure (Table 1). Although parents guarding E broods lost more young than parents of C broods during the first 10 days, this did not affect their success in rearing the remainder of the brood from day 10 to offspring independence at day 20.

Unlike the young of some other species of New World cichlids (Perrone 1978), convict cichlid young tend to stay close to the substrate. If the young ascend into the water column they are vulnerable to attack by *Astyanax fasciatus*, an abundant, quick-swimming characin in the study streams (Wisenden personal observation). The school of young is essentially two-dimensional. At constant density, large broods cover a larger area of the substrate than small broods and may be more difficult for parents to defend against predators. If the efficiency of brood defence is determined by the area occupied by the school of offspring, then losses to predation should increase sharply after the threshold radius of the maximum defendable area has been reached.

This area of maximum defence efficiency should increase with parent size (Grant & Kramer 1990). In

Table 3. Mean growth rates ($\text{mm} \cdot \text{day}^{-1}$) of young in control and experimental broods that reached day 20 and for those that did not reach day 20. SE and sample size are in parentheses.

	Control	Experimental	Total
Reached day 20	0.2824 (0.013,8)	0.2425 (0.009,9)	0.2613 (0.009,17)
Failed before day 20	0.2461 (0.009,7)	0.2272 (0.009,4)	0.2392 (0.007,11)
Total	0.2655 (0.009,15)	0.2378 (0.007,13)	0.2526 (0.006,28)

a larger study on unmanipulated broods, conducted in shallow water habitat where predation pressure was relatively light, large females and males were significantly more successful at guarding their young from predators than small parents were (Wisenden 1994b). In the present study, there was no evidence of a positive effect of female size on brood defence, particularly in E broods (Table 2). We have no explanation for why female SL was negatively correlated with brood size in E broods. Similarly, we have no explanation for the absence of a fecundity effect for females in the E group at day 0 (before manipulation). Male SL was positively correlated with offspring number at day 20 in E broods but not in C broods. Thus, for E broods, large males were more effective at brood defence than smaller males. The significant effect of male SL on defence of E broods may be that large parental males have a greater area of intimidation of potential predators than small parental males.

The behavioural constraint hypothesis is further supported by the reduced rate of growth of young in E broods compared to C broods (Table 3). Young on the periphery of a brood are most vulnerable to predator attacks (Hamilton 1971, McKaye & Oliver 1980, Goff 1984, McKaye et al. 1992). To reduce the probability of being taken by a predator, individual young should move toward the centre of the brood. This in turn would result in an increase in offspring density, higher levels of intra-brood aggression and greater competition for food, with a negative effect on mean growth of the young. Offspring growth is probably food limited in the río Cabuyo because growth is significantly slower there than at other, nearby locations (e.g. Quebrada Amores) where leaf litter is more abundant (Wisenden 1994a). A behavioural constraint on brood size imposed by the area occupied by a convict cichlid brood is consistent with Lack's fourth hypothesis.

If biparental care arose from uniparental male care to counter intense brood predation pressure (Barlow 1974, Keenleyside 1991), then egg size in convict cichlids, a conservative trait not affected by female size or food supply (Townshend & Wootton 1984), probably represents an evolutionary optimum to increase survival of the young through fast growth and development (Wootton 1991). If female

convict cichlids cannot reduce egg size to increase fecundity, then increased fecundity can only come from increased allocation of finite resources to reproduction (Smith & Fretwell 1974). However, females may refrain from laying large clutches because of a trade-off between current and future reproductive success (Williams 1966, Charnov & Krebs 1973, Wisenden 1993). If an increase in parental investment in eggs does not result in an increase in reproductive success from the current reproductive effort (because of the limited ability of parents to defend very large broods), but has a negative effect on future reproductive success (because of the demands on finite resources), then a behavioural constraint imposed by brood defence will stabilize selection pressure on the evolution of clutch size in convict cichlids.

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