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**Brood Size, Male Fanning Effort and the Energetics  
of a Nonshareable Parental Investment in Bluegill Sunfish,  
*Lepomis macrochirus* (Teleostei: Centrarchidae)**

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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.

**Abstract**

We present a model and an experimental test for a nonshareable parental-investment behavior (fanning of eggs) using parental male bluegill sunfish. The model predicts that as brood size increases, nonshareable investment into the brood should increase if a parent is to maximize its remaining lifetime reproductive success. The experimental test manipulated the number of eggs in nests and quantified the frequency and tempo of fanning in the field using underwater video equipment. As predicted, male bluegill fanned larger broods more frequently than smaller broods. The fanning tempo (beats per min) did not change with changes in brood size. Parental males lost substantial amounts of body weight during the period of parental care, and lipid extractions revealed a loss in nonpolar lipids. The difference in fanning frequency between large and small broods did not result in differential weight loss for the parents, but parents that fanned more tended to lose more nonpolar lipids from the body tissue than males that fanned less.

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**Introduction**

Animals provide two fundamentally different kinds of parental investment (WITTENBERGER 1981; LAZARUS & INGLIS 1986): shareable and nonshareable. With shareable investments, such as guarding offspring in a nest, all offspring benefit simultaneously from a unit of parental investment. In contrast, with nonshareable investments such as feeding offspring, the benefit is distributed such that no two offspring benefit from the same unit of investment. A previous study examined a shareable parental investment, brood defense by bluegill sunfish, *Lepomis ma-*

*crochirus*, and showed that total parental investment decreased with a decreased brood size (COLEMAN et al. 1985). The present study examines a nonshareable parental investment, fanning of eggs by a parental fish, in response to varying brood size.

Fanning eggs to facilitate gas exchange is one of the most common forms of parental investment in fishes (BLUMER 1979; KEENLEYSIDE 1979). A fish fans by repeatedly moving one or more of its fins over the eggs and pushes water to the egg surfaces (BARLOW 1964; MERTZ & BARLOW 1966; TORRICELLI et al. 1985). The value of fanning has been demonstrated both in the laboratory and in the field. Artificial agitation of orange chromide (*Etroplus maculatus*) eggs in a manner analogous to fanning greatly enhanced the oxygen consumption of eggs (ZORAN & WARD 1983). Furthermore, eggs that were not fanned developed more slowly than fanned eggs, and with a greater frequency of deformities (ZORAN & WARD 1983). In the field, pumpkinseed sunfish (*Lepomis gibbosus*) eggs that were protected from predation but were not fanned suffered 55 % greater mortality than eggs that were fanned (GROSS 1980). Thus fanning is an important behavior for the successful survival of the parent's progeny.

Fanning that provides oxygen to eggs is a nonshareable parental investment. Each egg consumes molecules of oxygen, which become unavailable to other eggs; therefore, oxygen consumption increases with the number of eggs in a nest (VAN IERSEL 1953; JONES 1966; REEBS et al. 1984). A parental fish may fan continuously for long periods of time indicating the need to constantly replenish the supply of oxygen molecules near the eggs. VAN IERSEL (1953) and TORRICELLI et al. (1985) have demonstrated that reducing the concentration of dissolved oxygen near a fanning fish leads to an increase in fanning effort, suggesting that parental fish are sensitive to the oxygen demands of their progeny. The following model predicts how fanning effort should change with changes in brood size.

Life-history models for parental investment (e.g. SARGENT & GROSS 1985; COLEMAN et al. 1985) assume that a parent is selected to maximize its remaining lifetime reproductive success subject to a tradeoff between present and future reproduction. The principal difference between models for shareable and nonshareable investment is in the cost of the parental behavior. Brood size does not influence the cost of a shareable investment, whereas it does influence the cost of a nonshareable investment. This cost is manifested as a decrease in future reproduction as a function of brood size.

Let

$N$  = brood size. This can be either an absolute number of offspring, such that  $0 \leq N$ ; or it can be a measure relative to some maximum brood size, such that  $0 \leq N \leq 1$ . The latter is used for convenience but the results would be the same

$i$  = nonshareable investment in each offspring in the present brood,  $0 \leq i \leq 1$

$i_T$  = total investment into the present brood ( $N \times i$ )

$P$  = reproductive success via the current brood. Reproductive success is assumed to increase with a diminishing rate of return through invest-

ment of resources into present or future reproduction (Fig. 1); we represent this by  $P = N(1 - e^{-i})$   
 $F =$  reproductive success via future broods. This is represented by  $F = 1 - e^{-(1 - N \times i)}$ . Note that  $F$  decreases as the present brood size increases (Fig. 1).

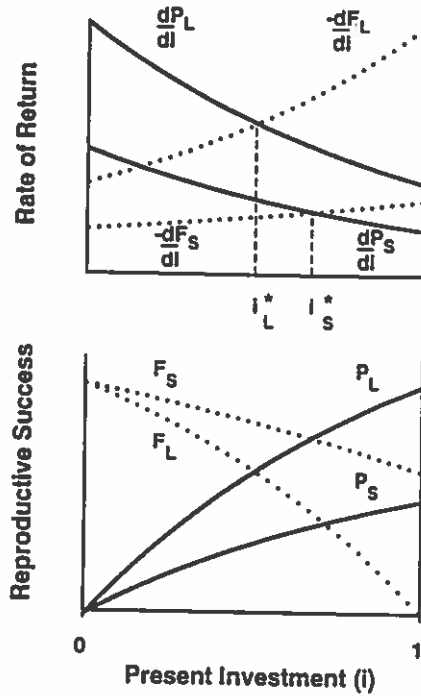


Fig. 1: Graphical representation of the model for nonshareable parental investments. Reproductive success from present (P) and future (F) broods is illustrated using curves of diminishing returns (lower panel). Different brood sizes are denoted by subscripts for Large (L) and Small (S) broods. The optimal investment per offspring ( $i^*$ ) for each brood size occurs where the rates of return (upper panel) into P and F are equal in magnitude, but opposite in sign

The optimal investment ( $i^*$ ) occurs when the rate of return on investment into present reproduction equals the rate of return on investment into future broods (SARGENT & GROSS 1985),

$$\begin{aligned} \text{i.e.,} \quad & dP/di = -dF/di \\ \text{therefore} \quad & N \times e^{-i} = -(-N \times e^{-(1 - N \times i)}) \\ \text{and} \quad & i^* = 1 / (1 + N) \\ & i_T = N / (1 + N) \end{aligned}$$

Thus, as the brood size ( $N$ ) increases, the optimal nonshareable investment into each offspring ( $i^*$ ) decreases; however, the optimal amount of total investment into the brood ( $i_T$ ) increases (Fig. 2).

An important component of this model is the future cost function, which assumes that the cost of fanning increases with brood size. While the physical exertion of fanning would seemingly cost considerable energy reserves of the parent, few data exist to examine this assumption. For example, a field study of the pumpkinseed sunfish found that males lost 9 % of their wet body weight during the period of parental care and approximately 74 % of this weight was lost

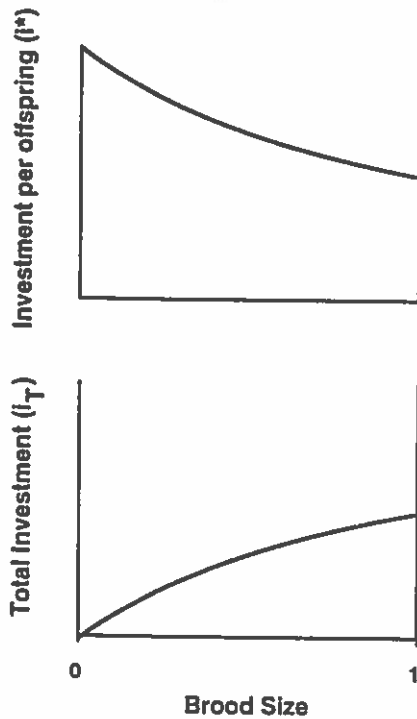


Fig. 2: As brood size increases, the optimal investment per offspring ( $i^*$ ) is predicted to decrease while the total investment into the brood ( $i_T$ ) should increase

while the eggs were being fanned (GROSS 1980). We were therefore interested in determining if the energetic expense of different amounts of parental investment could be measured using changes in the wet weight of the fish, or by using lipid extractions.

The specific goals of this study were to determine whether parental male bluegill (*Lepomis macrochirus*) decrease the amount of fanning they provide a brood of reduced size, and to determine if fanning a brood of normal size caused a greater loss of body weight or lipids in the parent fish than fanning a reduced brood.

## Material and Methods

### Bluegill Sunfish

The bluegill sunfish is a colonial-breeding centrarchid with male nest building and exclusive male parental care (GROSS & MACMILLAN 1981; COLEMAN et al. 1985). Males gather at traditional spawning locations where they sweep nests in the substrate using their caudal fins. Gravid females arrive as a school at the colony, enter the nests and spawn. Spawning activity in the colony lasts for several h and then the females depart. Only the males care for the eggs. These parental males do not leave the nest to feed during the brood cycle. The eggs are guarded against predators and fanned for 2 to 5 days until they hatch. After hatching, the fry are guarded (but not fanned) an additional 3 to 6 days after which they and then the adult males leave the colony and forage. Adults may have 1 to 3 brood cycles per season, and breed for 1 to 3 years.

### Colony Site

The fanning study involved a pair of neighboring bluegill colonies located 0.8 m deep on a sandy bottomed bay on the north side of Barrel Point, Lake Opinicon, Ontario (44°34'N, 76°19'W). Two colonies were used because neither alone contained enough males to provide an adequate sample for the experiment. The colonies were within 4 m of one another and occupied ecologically similar habitat. Nests were located rim-to-rim, as is typical of bluegill. The shallow, hard-packed, sandy bottom of the bay allowed the use of video in data collection (described below).

Nest building was first seen in Colony 1 on 21 June, 1985, and continued into the next day. Males began nest building in Colony 2 on 22 June, 1985, and this colony developed in parallel with the first but lagged one day behind. Spawning occurred on 23 June in Colony 1, and 24 June in Colony 2. In both colonies a small proportion of the spawning resumed the second morning but the bulk of spawning occurred on the first day. Cuckolder males, a small-bodied alternative male phenotype that provide no parental care (GROSS 1982), were present at only a low frequency. The day after spawning, 42 parental males were fanning and guarding their nests, 12 in Colony 1 and 30 in Colony 2.

### Manipulations

At approximately 13.45 h on 24 June and 11.30 h on 25 June for Colonies 1 and 2, respectively, the 42 nests were individually marked with a small numbered tile. Each male was caught by hand-net, weighed to the nearest g using a portable electronic balance, measured for total length to the nearest mm, and returned to its nest. Later that day, at approximately 16.00 h in both cases, each nest was assigned randomly to one of two treatments: "Control" or "Manipulated". The brood size in each nest of the Manipulated treatment was reduced by about 50 %, as judged by eye, using a plastic scoop and SCUBA. To control for the disturbance of removing the brood in the Manipulated nests, the nests in the Control treatment were also manipulated with the scoop but no eggs were removed. The effects of cuckolders, if any, on the spawning and parental behavior of the nesting males were assumed to be randomly distributed across the Control and Manipulated treatments.

On 28 June, after data on fanning behavior had been collected, an unusual change in wind direction caused silt and woody debris to fill the nests of Colony 1. These males subsequently abandoned their nests. Colony 2 was shielded by rocks and was not severely affected by the silt. 17 males in Colony 2, 9 from the Control treatment and 8 from the Manipulated treatment, remained on their nests through the rest of the brood cycle. On 1 July, the fry had reached the gold-eye stage and were starting to move in the bottom of the nest (indicating that they would soon leave the nest). The 17 males in Colony 2 were therefore collected with a hand-net, reweighed, sacrificed and frozen for tissue analysis.

To confirm that the Manipulated broods were in fact smaller than the Control broods, all the fry from each of five nests of each treatment were collected by siphoning with a turkey baster and placed in separate jars for subsequent counting in the laboratory. This was easily done because the fry were visible and loose in the nest bottom.

### Measuring Fanning

To compare the fanning activities of males with Control versus Manipulated broods, a video camera (RCA model CC011) encased in an underwater plexiglass housing was mounted on a tripod approximately 1 m from the edge of a nest, outside the fish's territory. Males of Colony 1 were videotaped on the afternoon of 25 June and the morning of 26 June and males of Colony 2 were videotaped on the afternoon of 26 June. To control for a possible time-of-day effect, we alternated taping males from the Control and Manipulated treatments. Therefore, any uncontrolled effect should have been distributed evenly between the two groups. Due to time and sunlight constraints, only half the males in each treatment were videotaped. Approximately 12 min of activity for each of 21 males (11 Control and 10 Manipulated nests) were recorded and later analysed for duration and tempo of fanning.

Fanning activity can be quantified by two parameters: its duration (how much time a parental fish spends fanning), and its tempo or intensity (the speed or strength of the movement of the fins). Some researchers have used "bouts" of fanning, periods of continuous fanning separated by a period without fanning, to measure fanning activity (e.g. BARLOW 1964; MERTZ & BARLOW 1966). Although

the bout concept is useful for describing the temporal pattern of fanning, it is less suitable for analyses of parental effort, which are concerned with the total effort expended by the fish. Instead, a random 10-min segment from each of the 21 males' videotapes was analysed for the occurrence of the following behavior: (1) Pectoral Fanning, in which the body is oriented either horizontally or with the head slightly lower than the tail and the pectoral fins are moved back and forth over the eggs, (2) Tail Sweeping, in which the caudal fin is moved over the nest substrate with the body oriented vertically, or (3) Other Behavior (including rim circling [see COLGAN et al. 1979], chasing intruders or hovering more than 5 cm above the nest bottom). Male behavior was recorded at every 5 s, giving 120 records per 10-min period. The frequency of each activity was then scored as the number of records of that behavior out of the 120. This frequency score provides an estimate of the relative duration of each of the three categories of behavior in the 10-min period.

For fanning tempo, the number of fanning beats per min was counted from a random 3 min of fanning activity by each of the 21 males. A "beat" was defined as a complete forward stroke of a pectoral fin while the male was within 5 cm of the bottom of the nest. Because fanning may involve either synchronous or asynchronous movements of the two pectoral fins, the movement of only one fin was used in the analysis.

### Measuring Energetics

We employed two techniques to assess the energetic cost of parental investment. First, we used the change in total wet weight from measurements on 25 June and 1 July. This assumed that total wet weight reflects the amount of energy available to a parent. We predicted that a parental male expending more parental effort would lose more weight than one expending less effort. The accuracy of this method is reduced if the fish absorbs water during the parental care phase, as has been found for fathead minnows, *Pimephales promelas* (UNGER 1983), and three-spined sticklebacks, *Gasterosteus aculeatus* (FITZGERALD et al. 1989).

Second, we used fat extraction (SAWICKA-KAPUSTA 1975) to examine the quantity of nonpolar lipids remaining in various body parts at the end of the brood cycle. Such lipids, a compact and biochemically efficient storage for energy, are the major source of energy for reproduction in fish (REZNICK & BRAUN 1987) and other taxa (RICKLEFS 1974; DERICKSON 1976; FITZPATRICK 1976; WALSBERG 1983; BLEM 1990). The caloric value of fats is twice that of proteins and carbohydrates (HADLEY 1985). Therefore, lipid extractions likely provide an accurate measure of the energy content of the parent fish (SAWICKA-KAPUSTA 1975; POND 1978). Unfortunately, lipids can only be extracted once from an individual and this precludes comparisons before and after a manipulation.

To extract fat, the 17 frozen bluegill from Colony 2 were thawed and dissected into three components: liver, g-rads and body. Each component was dried for seven days at 50 °C to a constant weight (nearest 0.001 g) and ground into a homogeneous mixture with a mortar and pestle. The total dry weight of the fish was calculated as the sum of the dry weights of the three components. A subsample from each component was then fluxed in an ether Soxhlet apparatus for approximately 5 h to remove nonpolar lipids. The amount of nonpolar lipids per g of subsample was determined by subtracting weight after extraction from weight before extraction and dividing by weight before extraction. The amount of nonpolar lipids in each component was obtained by multiplying the amount of nonpolar lipids per g of subsample by the dry weight of the entire component.

We sampled a third bluegill colony in 1986 to investigate further the change in lipid content through the brood cycle. This colony formed on the east side of Barrel Point, consisted of approximately 55 males, and spawned on 10 June 1986. Hatching occurred on 12 June. 10 males were collected on each of the 10th, 12th, 14th, and 16th of June. On 18 June, 5 males were collected. All fish were frozen immediately after collection. Lipid extraction and analysis were conducted as described above. We used regressions of more than one Y per X (SOKAL & ROHLF 1981, p. 477) to test for a decrease in lipid reserves, because the data consisted of multiple values for each day in the brood cycle. Pooling of mean squares was not employed.

### Results

The average number of fry in the subsample of Manipulated nests was 60 % of the average number of fry in the subsample of Control nests (Manipulated:  $\bar{x} = 3459 \pm 804$  SE,  $n = 5$ , range 1063 to 5972; Control:  $\bar{x} = 5797 \pm 711$  SE,  $n = 5$ ,

range 3411 to 7313). Although there was overlap between the two subsamples, the difference between subsample means was statistically significant (one-tailed *t*-test,  $t_8 = 2.18$ ,  $p = 0.03$ ).

Fanning frequency was significantly lower in the Manipulated (small-brood) treatment (Table 1). Males in the Control (large-brood) treatment spent an average of 66 % of their time fanning (79.7 of 120 records), compared to 56 % for the Manipulated males (67.6 of 120 records). There was no significant difference in fanning tempo between Control and Manipulated males. Likewise, frequency of Tail Sweeping did not differ between the treatments. The increase in Other Behavior in the Manipulated treatment is accounted for by an increase in hovering greater than 5 cm above the nest; rim circling and chasing intruders remained rare. The small number of males for which we collected both fanning and brood-size data precluded statistical analysis, but based on the means for fanning and brood size for each treatment, males in the Manipulated treatment provided more fanning per egg (0.020) than males in the Control treatment (0.014).

*Table 1:* Behavior of parental male bluegill with Control (large) versus Manipulated (small) broods. Frequency data are the mean number of records of each behavior ( $\pm 1$  SE) out of 120 records in the 10-min period (see Methods); *t*-tests of fanning tempo and fanning frequency are one-tailed because of the predictions of the model; other *t*-tests are two-tailed

	Control	Manipulated	$t_{19}$	<i>p</i>	Combined
<i>n</i>	11	10			21
Fanning tempo (beats/min)	89.3 $\pm$ 2.0	89.4 $\pm$ 3.9	0.03	0.49	89.3 $\pm$ 2.1
Frequency					
Fanning	79.7 $\pm$ 4.8	67.6 $\pm$ 2.3	2.22	0.02*	74.0 $\pm$ 3.0
Tail Sweeping	2.5 $\pm$ 0.6	2.9 $\pm$ 0.8	0.44	0.66	2.7 $\pm$ 0.5
Other Behavior <sup>1)</sup>	37.8 $\pm$ 4.8	49.5 $\pm$ 2.2	2.13	0.04*	43.4 $\pm$ 3.0

<sup>1)</sup> includes hovering more than 5 cm above the nest, rim circling and chasing intruders.

Only males that remained until the end of the brood cycle were used for the analysis of energetic costs (Table 2). There was no significant difference in either initial weight or length for the males of the two treatments. Males from both Control and Manipulated nests lost significant amounts of wet weight through the parental-care period (paired one-tailed *t*-tests: Control: 11.3 %,  $t_8 = 9.14$ ,  $p < 0.001$ ; Manipulated: 10.8 %,  $t_7 = 8.43$ ,  $p < 0.001$ ). There was no significant difference between the treatments in either amount of weight lost, final wet weight or dry weight; however, males with Manipulated broods tended to have more nonpolar lipids per g of body tissue than males with Control broods ( $p = 0.066$ ). The amount of lipids per g of gonadal tissue showed less difference ( $p = 0.087$ ) while there was no significant difference between the treatments in the amount of lipids per g of liver tissue ( $p = 0.28$ ).

In Colony 3, where males were sampled every two days, there was a significant linear decrease through the brood cycle in both the amount of

Table 2: Weight loss of parental male bluegill with Control versus Manipulated broods. Data are  $\bar{X} \pm 1$  SE; t-tests are two-tailed for total length and initial weight, and one-tailed for final weight and weight lost, in keeping with the predictions of the model

	Control	Manipulated	$t_{15}$	$p$	Combined
n	9	8			17
Total length (mm)	174.1 $\pm$ 3.1	173.9 $\pm$ 3.7	0.05	0.96	174.0 $\pm$ 2.3
Initial weight (g)	108.3 $\pm$ 7.4	102.0 $\pm$ 8.2	0.58	0.57	105.4 $\pm$ 5.4
Final wet weight (g)	96.1 $\pm$ 6.6	90.9 $\pm$ 7.1	0.53	0.31	93.7 $\pm$ 4.7
Wet weight lost (g)	12.3 $\pm$ 1.3	11.1 $\pm$ 1.3	0.64	0.26	11.7 $\pm$ 0.9
Final dry weight (g)	21.8 $\pm$ 1.6	21.4 $\pm$ 2.1	0.16	0.44	21.6 $\pm$ 1.3
Final lipids (per g of component tissue)					
Body	0.021 $\pm$ 0.003	0.041 $\pm$ 0.013	1.59	0.07	0.030 $\pm$ 0.007
Liver	0.229 $\pm$ 0.032	0.256 $\pm$ 0.030	0.60	0.28	0.242 $\pm$ 0.021
Gonads	0.049 $\pm$ 0.018	0.083 $\pm$ 0.014	1.43	0.09	0.065 $\pm$ 0.012
Final lipids (total g in component tissue)					
Body	0.46 $\pm$ 0.08	1.01 $\pm$ 0.44	1.32	0.10	0.72 $\pm$ 0.21
Liver	0.027 $\pm$ 0.006	0.028 $\pm$ 0.006	0.08	0.47	0.027 $\pm$ 0.004
Gonads	0.008 $\pm$ 0.004	0.015 $\pm$ 0.005	1.11	0.14	0.011 $\pm$ 0.003

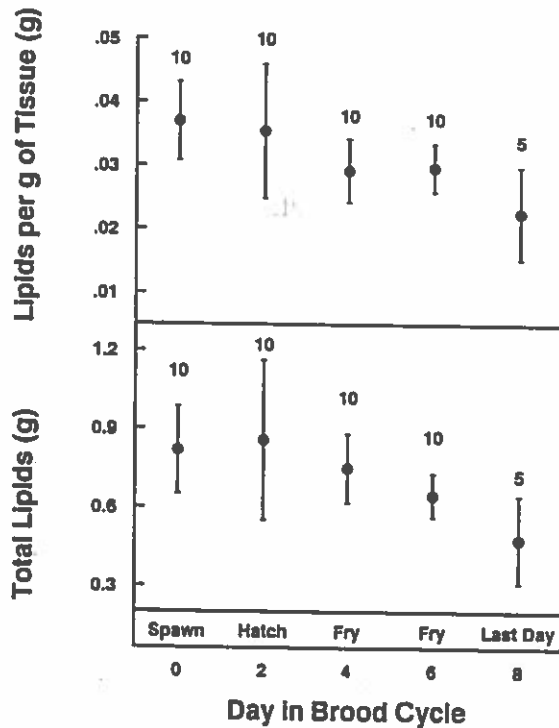


Fig. 3: The relationship between day in the brood cycle and lipid content in the body component for parental male bluegill in Colony 3. Each symbol presents  $\bar{X} \pm$  SE for the given sample size



nonpolar lipids per g of body tissue (Fig. 3;  $F_{1,3} = 23.1$ ,  $p < 0.017$ ,  $Y = -0.0016 X + 0.0375$  g where  $X$  is day in the brood cycle) and total lipids in the body ( $F_{1,3} = 13.8$ ,  $p < 0.034$ ,  $Y = -0.041 X + 0.880$  g). There was no relationship between lipids in the liver or gonads and day in the brood cycle for either lipids per g of tissue (liver:  $\bar{x} = 0.178 \pm 0.013$  g; gonad:  $\bar{x} = 0.090 \pm 0.013$  g) or total lipids (liver:  $\bar{x} = 0.023 \pm 0.002$  g; gonad:  $\bar{x} = 0.013 \pm 0.002$  g). There was no difference in either male length ( $\bar{x} = 177.2 \pm 1.2$  mm,  $n = 45$ ), wet weight ( $\bar{x} = 95.9 \pm 2.0$  g,  $n = 45$ ), or dry weight ( $\bar{x} = 22.8 \pm 0.5$  g,  $n = 45$ ) for the five samples.

### Discussion

The results show that male bluegill with larger broods fanned more frequently than did males with smaller broods, as predicted by the model for nonshareable investments. They may also have fanned less per egg than did males with smaller broods, a secondary prediction of the model. The tempo of fanning did not change. The large amount of time devoted to fanning indicates the importance of the parent supplying a continuous supply of oxygen to the eggs.

These results are consistent with studies of other species. For example, GROSS (1980) found that male pumpkinseed sunfish with more eggs fanned significantly more frequently than males with fewer eggs. However, because GROSS used natural variation in egg number, it is uncertain whether the difference in fanning was due to the differences in egg number or due to some characteristic of the male, such as the amount of body fat that may have been correlated with egg number. VAN IERSEL (1953) examined the fanning frequency of male three-spine sticklebacks (*Gasterosteus aculeatus*) in aquaria and, by manipulating broods, showed that time spent fanning increased with egg number. VAN IERSEL did not report quantitative data on fanning tempo, but stated that tempo appeared to remain constant for individuals, although there were differences among individuals.

Our data suggest that parental bluegill have a fixed fanning tempo and adjust only the frequency of fanning according to brood size. Why do male bluegill change their fanning frequency and not their fanning tempo? One consideration is the mechanics of fin movement. According to DAYKIN (1965), the return to oxygen-exchange capacity increases with diminishing returns with increases in current velocity (i.e., doubling the water velocity less than doubles the increase in oxygen exchange with the egg). Thus, a bluegill may not benefit as much by fanning faster as by fanning more frequently (for which the benefits may increase linearly). For species in which the parent attempts to court additional females during the parental phase (e.g., parental male sticklebacks court additional females, SARGENT 1985; whereas bluegill court only during the brief spawning period) the increased time devoted to fanning larger broods may be at the expense of additional matings, if courting and fanning cannot be performed simultaneously. Thus fanning faster rather than more frequently may be expected in such species. Data in the literature are insufficient to test this prediction.

The results of this study are useful for understanding and testing other models of parental investment. To examine shareable-parental-investment decision rules, SARGENT & GROSS (1985) proposed an experimental design that eliminates the problematic correlation between past investment and brood size. A key assumption of the design is that parents with larger broods perform some behavior that causes them to invest at a higher rate than parents with smaller broods. Evidence from birds suggests that the cost of incubation increases with clutch size (BIEBACH 1981; COLEMAN & WHITTALL 1988). For fishes, COLEMAN et al. (1985) assumed that fanning increases with brood size in their test using the experimental design of SARGENT & GROSS. This study confirms that assumption.

The prediction that males that fan more should lose weight faster than other males was not supported in our study. Both groups of males lost significant amounts of weight over the brood cycle, but the losses were not different between groups. We do not know how much of this weight loss is due to fanning activity, although males spend substantial amounts of time fanning (males with Control broods spent approximately 66 % of their time fanning in the video recordings). The large variation in initial body weights and the problems of using wet body weight as an indicator of condition (UNGER 1983; FITZGERALD et al. 1989) may explain why no differences in weight loss were found between the two treatments.

Lipid extractions on samples through the brood cycle illustrate that parental male bluegill are losing nonpolar lipids through the period of parental investment. Lipid extractions on males with different fanning activities suggest ( $p = 0.066$ ) that males that fanned more lost more nonpolar lipids from body tissues than did males that fanned less. Unfortunately, the lipid-extraction technique can only be done once on a fish, thus the variation between individuals in initial lipid content may make detection of statistically significant differential losses difficult.

The shareable/nonshareable investment dichotomy presented by WITTENBERGER (1981) is useful for examining some parental-investment situations such as fanning as analysed here. However, shareable and nonshareable likely represent the endpoints of a continuum; some investments may be partially shareable. For example, male bluegill sunfish can guard any number of fry equally well because they remain in the nest. In the related smallmouth bass (*Micropterus dolomieu*), after the fry leave the nest they remain in the vicinity of the nest for several weeks, and the male patrols a progressively larger and larger area which may exceed several meters across. At this point, defense of the young becomes less shareable because the male can no longer defend all fry equally at the same time. More elaborate models will need to be considered to understand these kinds of parental investment.

#### Acknowledgements

We thank Barb DESROCHERS and Lisa VENIER for field assistance; Isabelle CÔTÉ, Larry DILL, Ian FLEMING, Mart GROSS, John REYNOLDS and Mark WINSTON for helpful suggestions; and the management of Queen's University Biological Station, Lake Opinicon for access to facilities. COLEMAN was supported by an NSERC of Canada Postgraduate Scholarship, a B.C. Packers Limited

Scholarship, and a University of Toronto Special Fellowship. The research was supported in part by an NSERC of Canada Operating Grant to M. R. GROSS and by a grant to COLEMAN from the Raney Fund of the American Society of Ichthyologists and Herpetologists. The lipid analysis was funded by contract DE-AC09-76SR00-819 to the Savannah River Ecology Laboratory.

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*Received: August 2, 1990*

*Accepted: November 13, 1990 (G. Barlow)*