

## Morphological and Growth Rate Differences between Bluegill Males of Alternative Reproductive Life Histories

TIMOTHY J. EHLINGER

Department of Biological Sciences, University of Wisconsin  
3209 North Maryland Avenue, Milwaukee, Wisconsin 53211, USA

MART R. GROSS

Department of Zoology, University of Toronto  
25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

DAVID P. PHILIPP

Center for Aquatic Ecology, Illinois Natural History Survey  
607 East Peabody Drive, Champaign, Illinois 61820, USA

**Abstract.**—We characterized the morphology of mature cuckolder and mature parental male bluegills *Lepomis macrochirus* from Lake Opinicon, Ontario. By rearing bluegill larvae to maturity in experimental ponds in Illinois we also examined whether morphological differences between males of the two reproductive life histories were conserved across widely varying environmental conditions. Cuckolder and parental males collected in Lake Opinicon differed in their size-adjusted body shape. They also differed in their pattern of mass allocation to testis versus somatic tissue. Cuckolder males allocated significantly more of their total body mass to testes compared to parental males. Body shape and testis:somatic ratio differences between male types reared in experimental ponds in Illinois were nearly identical to those observed in bluegills from Lake Opinicon. This divergence between male types remained consistent even when bluegills were reared over a 10-fold variation in growth rate. Average growth rate within ponds was strongly associated with the probability that a male would mature as a parental male within the first year. However, the proportion of males maturing as cuckolders was relatively constant among ponds and was not influenced by growth rate differences. These findings have important implications for management of bluegills and other *Lepomis* species where growth differences or reproductive divergence occur within single populations.

Alternative male reproductive behaviors are known in many fish species (reviewed in Taborsky 1994; Gross 1996). Males of bluegill *Lepomis macrochirus* exhibit two distinct reproductive life histories, parental and cuckolder (Gross 1979, 1991a; Dominey 1980; Gross and Charnov 1980). Tactics used by males employing the parental strategy include late maturation, territory acquisition via aggressive interaction with other parental males, nest construction, and parental care of developing offspring. By contrast, cuckolder males usually mature early and do not procure territories or construct nests. Rather, they steal fertilizations from parental males by using either "sneaking" or "satellite" tactics (Gross 1982; Philipp and Gross 1992). Cuckolders initially adopt the sneaking tactic, hiding around a nest edge and then stealing fertilizations by darting quickly into the nest during spawning. As they become older, they increasingly switch to the satellite tactic, hovering near nests and mimicking female behavior to gain nest entry.

Understanding a fish's life history, especially

complex alternatives, is essential to proper management. Life history differences among individuals within populations of bluegills make the challenge of successful management even greater. In this paper we address the morphology and growth rates of bluegill males in the cuckolder and parental life histories. Our objective is to determine whether the reproductive life histories have associated differences in morphology and growth rate. If so, these differences should be taken into account when collecting data on stunted populations and when designing management strategies.

### Methods

**Study population.**—Male bluegills, 40 mature parentals and 40 mature cuckolders, were collected with hand-held dip nets while they were spawning in two colonies from Lake Opinicon, Ontario, during 28–30 June 1988. Only cuckolder males hiding near nests (i.e., using the sneaker tactic) were collected. Samples were frozen and taken to the laboratory for morphometric analysis (see below). To-

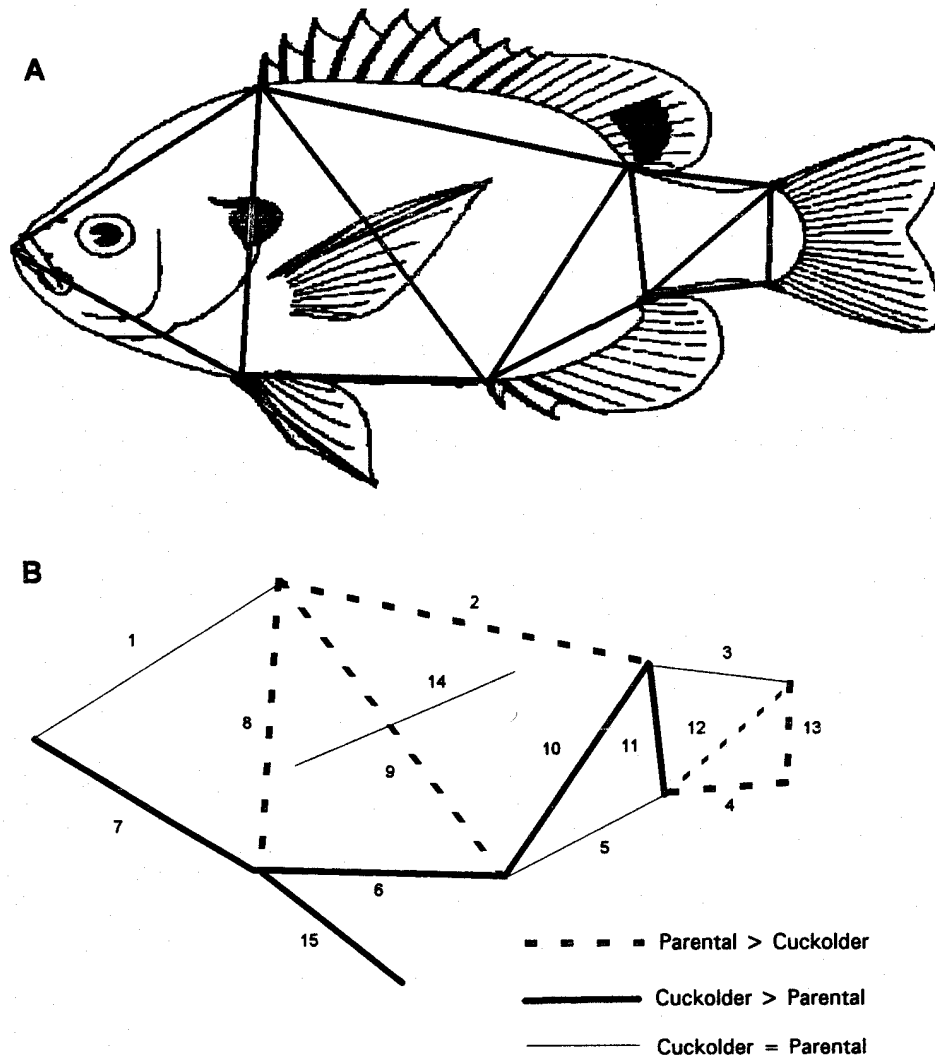


FIGURE 1.—(A) Bluegill landmark points and lengths measured from video images and used in morphometric analyses. (B) Diagrammatic representation of the discriminant function coefficients showing size-adjusted patterns of morphological divergence between male bluegill reproductive forms in Lake Opinicon. Solid and dashed lines indicate dimensions where cuckolders or parental males are larger, respectively. Coefficient values are presented in Table 1.

tal wet mass and testis mass were recorded for each fish. Somatic mass was calculated by subtracting testis mass from total wet mass.

*Experimental pond populations.*—Bluegill larvae were collected from the nests of parental males in Lake Opinicon during 25–26 June 1987 at 1–2 d posthatch (5–6 d old). Ten nests were selected randomly from each of three colonies (30 nests total) and approximately 2,000 larvae were removed from each nest. The larvae were combined in a holding tank and mixed with mild stirring. Aliquots containing approximately 500 larvae

were then placed into 1-L glass jars that were transported to the experimental pond facility of the Illinois Natural History Survey, Champaign. Larvae from nine jars were placed in each of five ponds (4,500 larvae per pond) and one pond was stocked with larvae from three jars (1,500 larvae per pond). When stocked, the progeny were 8–9 d old and had become free-swimming fry, capable of feeding on exogenous food. Ponds were similar in physical dimensions (0.08 ha with a 3-m maximum depth and earthen containment) but varied in the abundance of invertebrate zooplankton and

benthic fauna at the time of stocking. Differences in prey availability and bluegill densities produced variation in growth rates among the six ponds.

These bluegills remained in the ponds for 11 months, after which the ponds were drained and the fish were collected. Reproductively mature males were distinguished from immature fish (male and female) at the collection site by the presence of sperm exuding from the urogenital pore when fish were compressed lightly on the abdomen. Confirmation of reproductive condition and the determination of the sex of immature fish were done by dissection and microscopic examination of the gonads in the laboratory. Total wet mass and gonad mass were recorded for at least 100 fish selected randomly from each pond. The gonad mass for immature males and immature females was less than 0.005 g. No mature females were detected in any of the experimental ponds. A subset of 50 fish from each pond was frozen and used for morphometric analysis.

*Morphometric analysis.*—An image of each fish specimen was recorded on videotape and the coordinates of landmark points (Figure 1A) were digitized from the image by using OPTIMAS<sup>®</sup> image analysis software (Bioscan Inc., Edmonds, Washington) as described by Ehlinger (1991). Centroid size was calculated as the sum of the squared distances between all pairs of landmark coordinates, including the anterior of the lower jaw and fin attachment points (excluding the pectoral fin). Centroid size is highly correlated with other multivariate size measures (Bookstein et al. 1985) and accurately describes the patterns of allometric growth in bluegills (Ehlinger 1991). Size adjustment of individual length measures was accomplished by regressing each log-transformed length or log-transformed centroid size (Ehlinger 1991). Individual lengths were standardized to a mean of 0 and variance of 1 prior to regression. Because of significant differences in regression slopes between Lake Opinicon and the Illinois ponds, size corrections were done separately for each location prior to analysis for differences in shape between male sexual life histories. The residuals of these regressions were used in the subsequent multivariate analyses.

Canonical discriminant analysis was conducted to compare the body shapes of cuckolder and parental males from Lake Opinicon (SYSTAT MGLH module; Wilkenson 1990). With the discriminant function calculated from the Lake Opinicon population, we classified the reproductive

TABLE 1.—Size-corrected body shape discriminant function coefficients and their probabilities, when comparing cuckolder versus parental bluegill males collected from Lake Opinicon. Truss numbers correspond to Figure 1B. Wilks lambda = 0.51,  $P < 0.003$ .

Truss number	Coefficient	P
1	-0.75	0.595
2	-1.71	0.003
3	-1.80	0.070
4	-0.95	0.034
5	0.34	0.930
6	0.91	0.015
7	1.11	0.036
8	-0.44	0.023
9	-0.15	0.000
10	0.43	0.007
11	0.93	0.020
12	-1.19	0.034
13	-0.28	0.009
14	0.40	0.875
15	0.63	0.001

males from the experimental ponds as either parental or cuckolder males.

Using log-transformed data, differences in testis mass between male life histories from Lake Opinicon were tested by using analysis of covariance (ANCOVA) with somatic mass as the covariate. Reproductive males from the Illinois ponds were classified as either cuckolder or parental males by comparing their ratio of testis to total mass to that for cuckolder and parental males from Lake Opinicon. The classification based on testis mass was compared to the classification based on morphometric measurements using a chi-square test.

## Results

### *Reproductive Male Types in Lake Opinicon*

Canonical discriminant analysis of the size-adjusted residuals for males from Lake Opinicon showed that males behaving as cuckolders were shaped differently than parental males (Table 1; Figure 1B). Parental males were larger along the dorsal margin, whereas cuckolders possessed larger ventral margins, longer pelvic fins, and shorter caudal peduncles. In addition, cuckolders were deeper bodied in the posterior of their abdomen, whereas parental males were deeper bodied anteriorly.

Analysis of covariance of testis mass with somatic mass showed that cuckolder and parental males from Lake Opinicon differed in their allocation of mass to reproductive tissue ( $P = 0.0001$ ). On average ( $\pm$  SE), cuckolder males allocated 5.56% ( $\pm 0.11$ ) of their body mass to testes com-

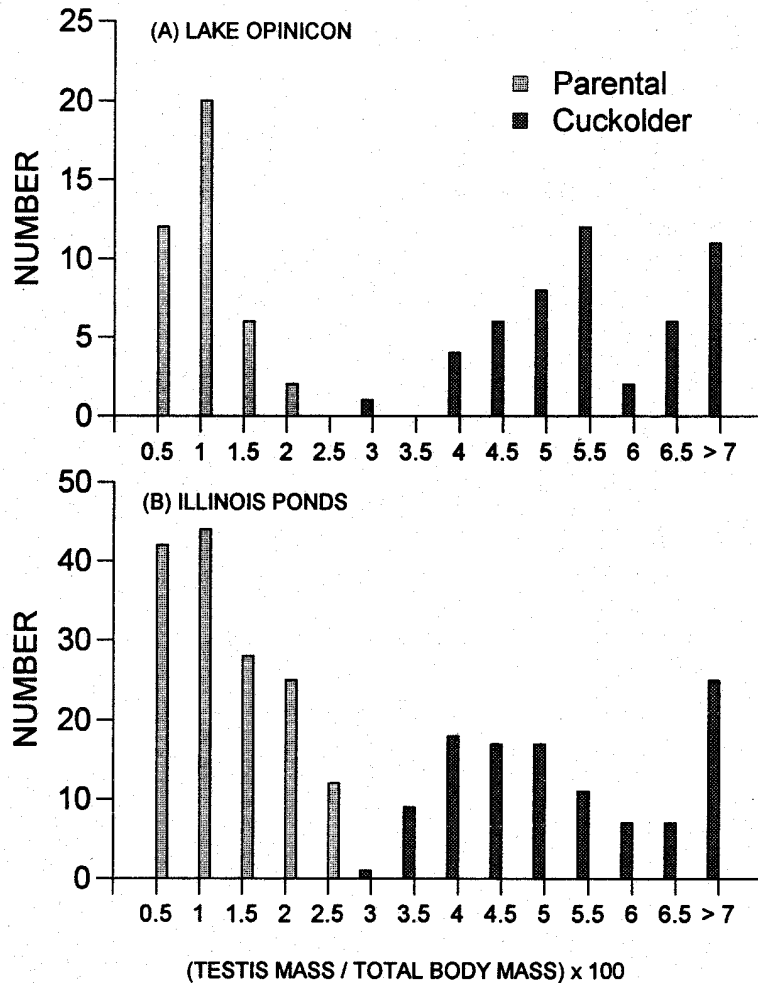


FIGURE 2.—Frequency distribution of the ratio of testis mass to total mass comparing cuckolders (heavy shading) with parental (light shading) male bluegills. (A) Lake Opinicon, Ontario, (B) Experimental ponds in Illinois.

pared to 1.18% ( $\pm 0.07$ ) for parental males (Figure 2A).

#### *Reproductive Types in the Experimental Ponds*

The relationship between testis mass and body mass indicated three distinct types of male bluegills in the experimental ponds; small males with large and mature testes, intermediate-sized males with small testes that were not producing sperm, and large males with ripe testes (Figure 3). The distribution of the ratio of testis to total mass exhibited a clear bimodality among males that had matured within 11 months in Experimental ponds (Figure 2B). Based upon the similarity of this distribution with that of the Lake Opinicon population, we categorized reproductively mature males

as cuckolders if testis mass accounted for 3% or more of their total body mass. Males were classified as parental males if testis mass was less than 3% of their total body mass.

A comparison of male reproductive types from the experimental ponds with their Lake Opinicon counterparts revealed no difference in the ratio of testis mass to total mass ( $P > 0.10$  by Kruskal-Wallis test). On average, cuckolders males in the ponds allocated 5.27% ( $\pm 0.12$ ) of their total mass to testes, as roughly did the cuckolders in the lake. Parental males that had already matured in the ponds at 11 months of age allocated roughly the same percentage of their total mass to testes (1.24%  $\pm 0.07$ ) as did the parental males maturing in Lake Opinicon at 7–8 years of age. The differ-

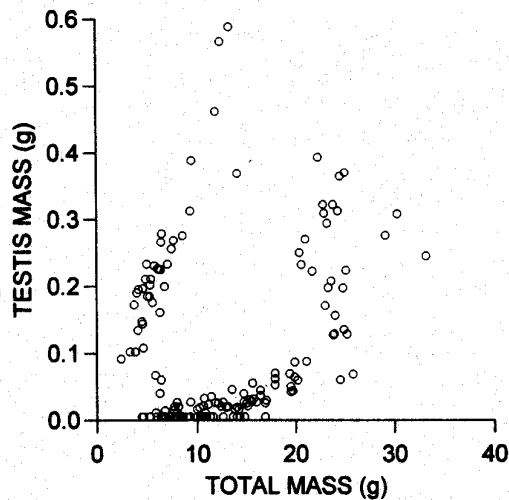


FIGURE 3.—Relationship between testis mass and total body mass for a random sample of bluegill males collected from one of the experimental ponds in Illinois.

ence between cuckolder and parental males in the percentage of mass allocated to testes was qualitatively consistent across the six experimental ponds (Figure 4A), even though the mean total mass of bluegills in these ponds differed as much as 10 fold (Figure 4B).

The average cuckolder size in the ponds ( $5.4 \text{ g} \pm 0.4$ ) was very similar to the size of sneaker males in Lake Opinicon ( $5.2 \text{ g} \pm 0.3$ ), whereas the average parental male size in the ponds ( $12.4 \text{ g} \pm 0.51$ ) was much smaller than that of parental males in Lake Opinicon ( $106.3 \text{ g} \pm 2.7$ ).

The discriminant function calculated to distinguish parental and cuckolder males from Lake Opinicon (Figure 5A) also distinguished between the male reproductive types reared in the ponds. When scored on the Lake Opinicon discriminant function, 95% of the pond-reared males that were identified as cuckolder or parental males on the basis of testis:somatic mass ratio (Figure 2B) were classified similarly on the basis of morphometric measures (Figure 5B;  $P < 0.01$ ). Discriminant function scores for fish reared in the ponds were not correlated with growth rate differences among ponds ( $R = -0.35$ ,  $P > 0.5$ ). When the immature males from the ponds (mean total mass,  $8.3 \text{ g} \pm 4$ ) were classified using the morphometric discriminant function, 87.5% were categorized as parental males, which may suggest that most of them were following the parental male life history trajectory but had not yet matured.

The pattern of males classified as different male

reproductive types varied greatly among ponds (Figure 6). The proportion of males maturing as parental males exhibited a strong relationship with average growth rates among ponds (Figure 6, solid line), ranging from 1% to 76% between the ponds with the slowest and fastest growth rate. Associated with the increase in proportion of parental males was a concurrent decrease in the proportion of immature males remaining in the ponds (Figure 6, dashed line). In contrast, the proportion of males maturing as cuckolders was not associated with growth rate and changed little among ponds, averaging around 20% of males sampled (Figure 6, dotted line).

### Discussion

This study examined and documented the patterns of morphological divergence between bluegill males adopting alternative reproductive life histories. First, cuckolder and parental males collected from a natural lake differed in their size-adjusted body shape. Second, bluegill males differed in their pattern of mass allocation to testes versus somatic tissue; cuckolder males allocated more of their total body mass to testes compared to parental males (also see Gross 1982). Third, body shape and testis:somatic mass ratio differences between male types reared in experimental ponds in Illinois are nearly identical to those observed in the natural lake environment in Ontario. The divergence between male types remained consistent even when bluegills were reared over a 10-fold variation in growth rate. Lastly, average growth rates within ponds was strongly correlated with the probability that a male would mature as a parental male within the first year, however, the proportion of males maturing as cuckolders was constant among ponds and was not influenced by growth rate differences.

The fact that parental males matured in the pond environment after only 11 months and at sizes as small as 3 g was unexpected, especially because parental males in Lake Opinicon seldom mature before their seventh summer at less than 75 g body mass (Gross 1982). This finding indicates that parental male bluegills have an environmentally dependent flexibility in their age and size of maturation, and points to the need to recognize the plasticity of these males in the size or age of first reproduction (*sensu* West-Eberhard 1989) as distinct from true male alternative reproductive life histories (Gross 1996).

The divergence in body shape between cuckolders and parental males does not necessarily

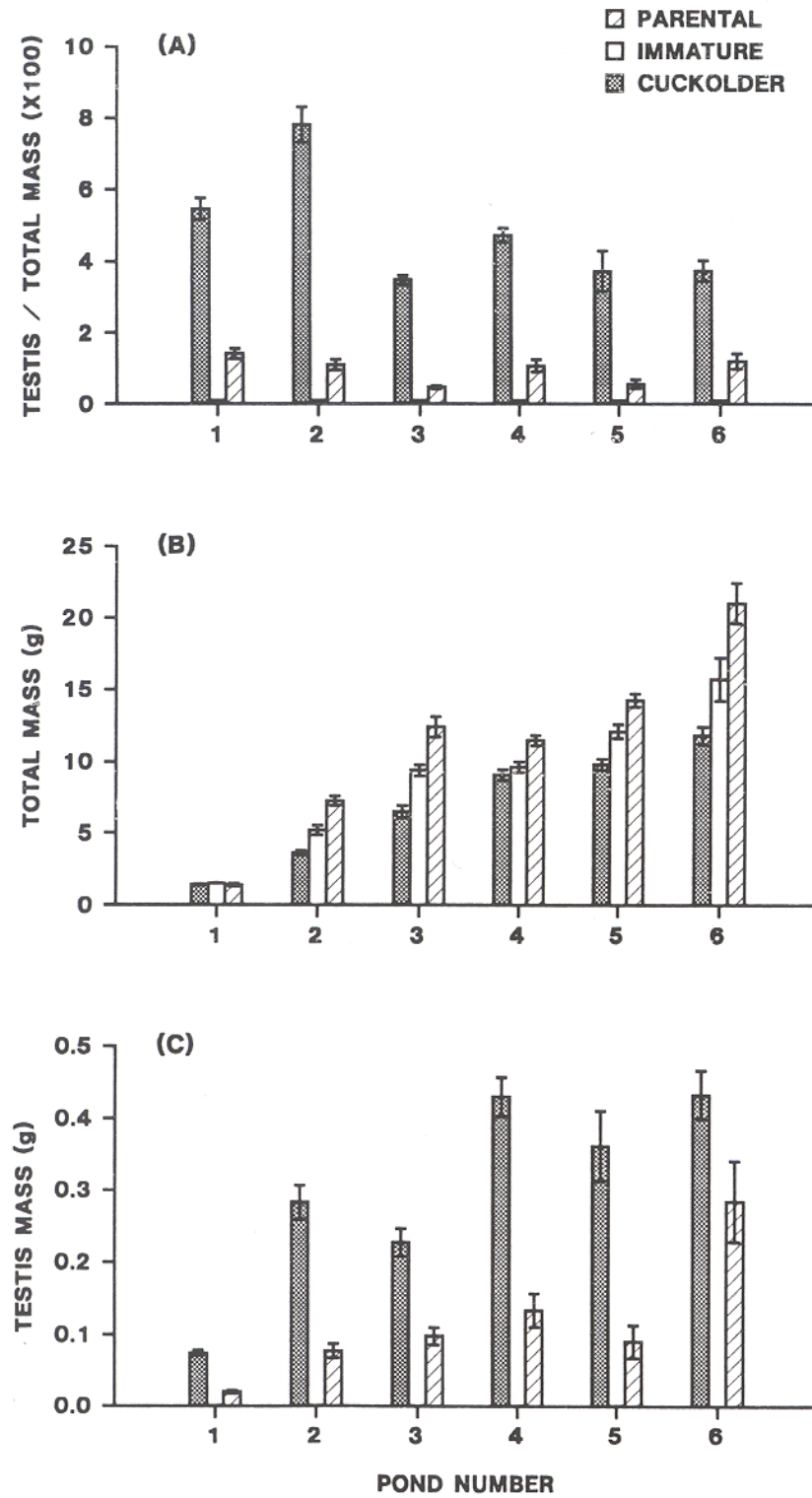


FIGURE 4.—Patterns of tissue allocation between testis mass and total mass for bluegill males of each reproductive form reared in experimental ponds. (A) Ratio of testis mass to total body mass. (B) Total mass. (C) Testis mass. Data are means  $\pm$  SE for each group of males.

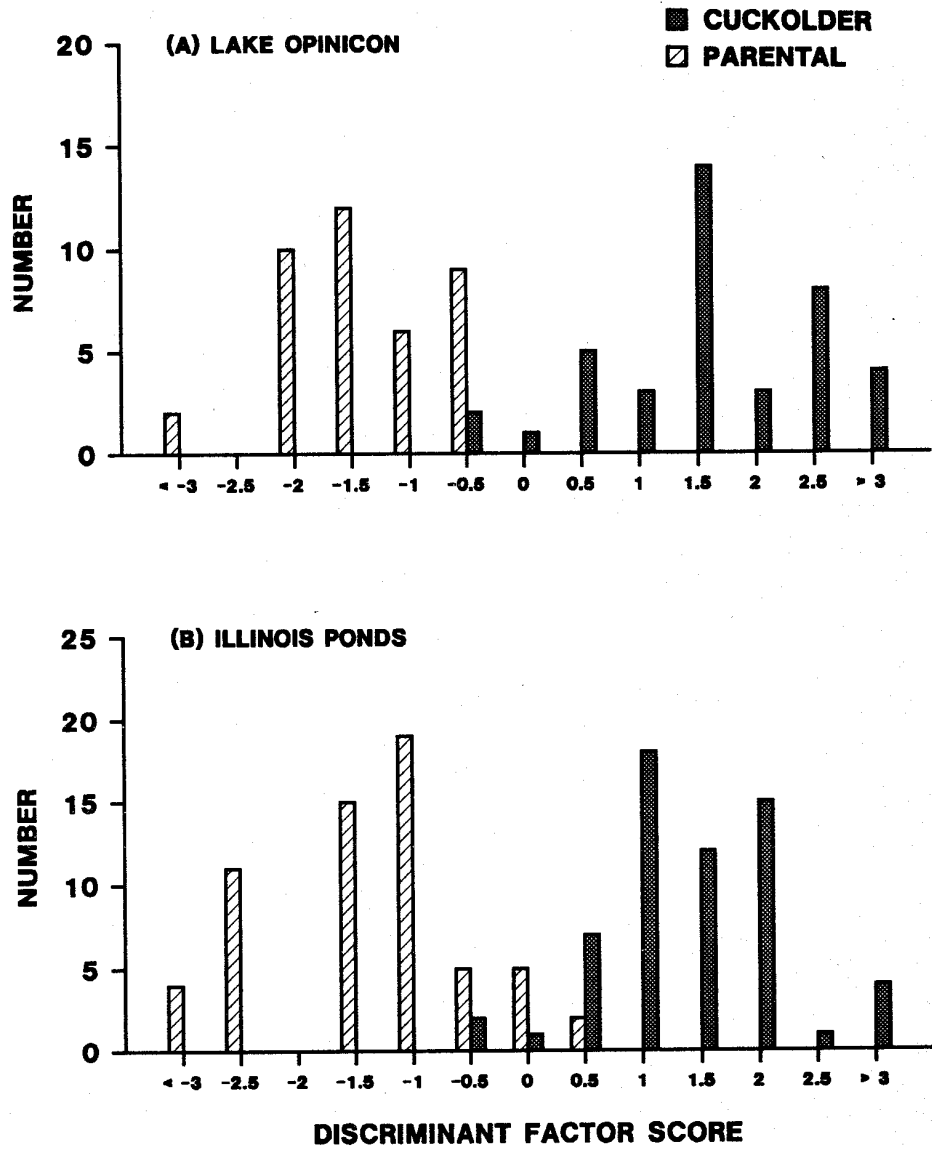


FIGURE 5.—Frequency distributions of discriminant function scores comparing bluegill reproductive forms of male bluegills from (A) Lake Opinicon and (B) experimental ponds in Illinois. Individual fish are classified by using the discriminant function calculated from the Lake Opinicon population.

demonstrate that these differences are due to underlying genetic divergence, because differences among males in micro-habitat selection within the lake or pond environment (Layzer and Clady 1987; Meyer 1987), social environment (Gross 1991b, 1996), or both could have influenced morphological development. However, the consistency of the pattern across rearing conditions

strongly supports the argument that the morphological differences are functionally tied to differences in life history, whether or not they are genetically programmed. The fact that the proportion of males exhibiting the cuckolder phenotype does not appear to be influenced by growth rate and differed little among ponds suggests a genetic component to cuckoldry, al-

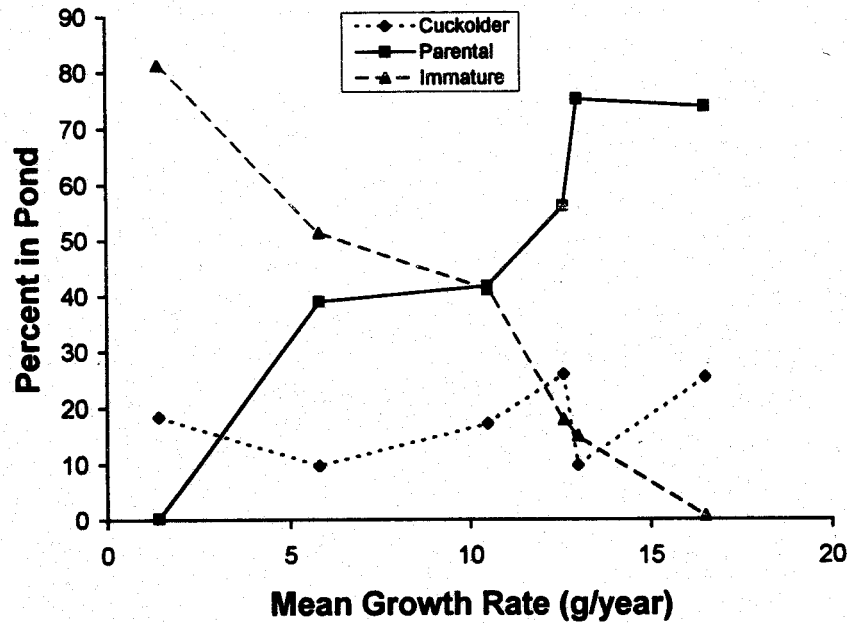


FIGURE 6.—Proportion of bluegill males from each pond exhibiting either parental, immature, or cuckolder male phenotypes. Classifications were made by testis mass to total body mass ratios for 100 randomly selected males per pond and confirmed for subsets of fish based upon morphological discriminant analysis. Growth rates for each pond were calculated as the average wet mass for the 100 males.

though this result is difficult to interpret because these bluegills came from a single population and presumably common genetic background. Conducting similar studies with bluegills from other populations with different genetic backgrounds will be necessary to demonstrate whether genetic variation may help explain differences in the frequency of cuckolders among lakes (see Ehlinger 1997; and Drake et al. 1997, both this issue).

Understanding the ecological and evolutionary differences between life histories is critical to predict and manage their relative abundances in populations. The conserved differences detected in this study provide fertile ground for generating hypotheses regarding possible adaptive functions of the cuckolder body plan relative to the parental male. For example, Figure 1B suggests a suite of characters well-suited for “sneaking” tactics. The smaller forehead region may contribute to reducing conspicuousness while hiding near the nests of parental males. A

over caudal peduncle is well known in other species to be correlated with burst speed performance (Webb 1984), and this trait may aid cuckolders in darting quickly in and out of nests during spawning. The longer pelvic fins and the an-

terior positioning of the pectoral fins of cuckolders may contribute to maneuverability within the vegetation surrounding nests (Blake 1980; Webb 1984). The larger dorsal margin and anteriorly deeper body in parental males may be beneficial for aggressive threats and displays by making fish of the same size look larger when viewed anteriorly (Neil 1983). The morphological differences between cuckolders and parental males may also have ecological or trophic correlates. For example, higher burst velocity in cuckolders (Ehlinger and Gross, unpublished) may help them escape from the predators which frequently forage in and around bluegill colonies (Gross 1982). Differences in body shape may also affect growth rates directly, because variation in body depth and pectoral fin length are correlated with feeding efficiency in vegetated habitats (Ehlinger and Wilson 1988; Ehlinger 1990).

#### Management Implications

Understanding the factors influencing alternative male life histories may help in formulating new approaches for managing bluegill populations. A central component of this is recognizing that cuckoldry is distinct from early mat-



uration of parental males. It is important to note that growth rate differences among ponds significantly changed the rate and proportion of males maturing as parentals, but did not affect the proportion maturing as cuckolders. Although the experimental ponds are simple environments compared to natural lakes (e.g., no predators or interspecific competitors), this pattern suggests that stunting in bluegill populations cannot be attributed simply to increased cuckolder abundance in reduced-growth environments. In fact, our data show that high growth rate during the first year promotes early maturation of parental males. Because the removal of large nesting males in bluegill colonies may also promote the maturation of younger males (Jennings et al. 1997, this issue) and contribute to lower growth rates among lakes (Ehlinger 1997), it is important to know whether small mature bluegill males in lakes are cuckolders or early maturing parentals. Differences in the ratio of testis mass to total mass between cuckolder and parental males provides a simple tool for quantifying the relative frequency of cuckolders within populations (Drake et al. 1997). These data may assist managers in deciding among different management strategies designed either to increase the abundance of larger parentals or to decrease the abundance of cuckolders.

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