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Alternative male life histories in bluegill sunfish

(sexual selection/breeding systems/parental care/cuckoldry/frequency-dependent selection)

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ABSTRACT Male bluegill sunfish are shown to have two alternative mating strategies: cuckoldry or parental care. Cuckolder males first mature at age 2. They follow a developmental sequence of sneaking and then mimicking female behavior to deceptively gain access to spawnings. Males who become parentals (construct nests, attract females, provide brood care) delay maturation until age 7. The parental investment of these males is parasitized by the cuckolders. This system is an example of a truly parasitically dependent mating strategy in vertebrates. A natural selection model is developed to predict the equilibrium frequencies of the two male types. A preliminary test of the model provides qualitative agreement.

Nesting colonies of bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) are among the most spectacular reproductive assemblages known to temperate freshwaters of North America (1-5). As long ago as 1906, Gill (6) established that male sunfish construct substrate nests and provide parental care for eggs and larvae. Recently, Gross (7) and Dominey (8) reported that not all males at a spawning bluegill colony take part in parental care duties. Instead, small nonnesting males penetrate spawning territories and release sperm, gaining potential fertilizations through the cuckolding of males who provide care (7). Current theory and knowledge of vertebrate mating systems suggests that such behavior may derive from competition for breeding sites and subsequent reproductive displacement. This is known for several fishes (9-11), elephant seals (12), and redwinged blackbirds (13). However, cuckolding sunfish males do not attempt to nest (14) and therefore do not compete for breeding sites. In this report we show that those males who mate by cuckoldry have a completely different life history from males who construct nests and provide care. Thus, there are two types of males present in the population. We then develop an evolutionary model to predict the equilibrium proportion of these males and provide a preliminary calculation for one population.

Field observations and experiments were conducted from 1976 through 1979 on a natural population of bluegill inhabiting Lake Opinicon, Ontario, Canada (14). Colonies contain 8-150 males with nests approximately rim to rim in 0.4-2.5 m of water. Data on spawning behaviors were collected by observers on towers placed near shallow colonies, and by skin and scuba diving in deeper waters. Spawning begins when a school of gravid females arrives at an established colony of males; females enter the nests singly and release eggs. At that time, males not previously associated with the nests intrude and release sperm (7).

We identified three male behavioral types in a random sample [focal-animal sampling (15)] of 72 fish studied at three colonies during spawning (14). "Parental" males constructed and remained in nests, were highly territorial to nest intruders,

and were light in body color with dark yellow-orange breasts. "Sneaker" males remained close to the substrate and showed rapid nest entry and exit. They were nonaggressive and light in body color. "Satellite" males showed slow nest entry, were sometimes aggressive to fish of equal size, and had a dark body with dark vertical bars. The coloration and movement of satellite males mimicked female behavior (16). We tested the hypothesis that these behavioral categories are mutually exclusive by examining the behavior of a random sample of 41 additional fish during their spawning. All test fish were successfully placed in a category. The labels parental, sneaker, and satellite were chosen simply because they are behaviorally descriptive. An additional randomly sampled 148 males were identified in the colonies by these behavioral criteria and then were captured, and their lengths, weights, and ages were determined. They gave three distinct age groups (Fig. 1A). Each group differed statistically with respect to age, length, and weight (pairwise two-tailed *t* tests; $P < 0.001$). Satellite males were intermediate to the small sneaker and larger parental males. There was a notable absence of 6-year-old males at the colonies.

Three distinct hypotheses may account for these data. (i) Cuckoldry and parental care are sequential behaviors performed during the lifetime of a single male; (ii) males have two distinct strategies, with some males maturing early to become cuckolders and others delaying reproduction to become parentals; (iii) males have three distinct life histories, corresponding to the three behavioral and age types. Of course, combinations of these explanations are possible.

To determine the proportion of reproductively active males within each age class, fish were randomly captured with traps and seines throughout the lake (14). Fig. 1B shows that only a minority of the males corresponding to the sneaker and satellite ages are reproductively active. Activity peaks at age 2 (21%) and then declines through age 6 (3%). For parentals, age 7 shows a sharp increase (32%) and about all year 8 and older males are reproductively active. Because only a minority of the young males are reproductively active, it is clear that cuckolding and parental care are *not* simply sequential behaviors.

Sunfish have indeterminate growth that is sensitive to energetics (19, 20). Because reproduction and growth are a known trade-off in many organisms (21), we investigated male growth history as recorded on their scales (22). Within an age group, males with mature testes had a significantly smaller linear growth increment than equal-aged males with immature testes, in the season they were captured (e.g., 2-year-old males have a difference of 25%; $n = 61$, one-tailed *t* test, $P < 0.005$). Relative growth increments can therefore be used to examine past reproductive activity and we can read the past growth history of an individual fish from its scales. Fig. 2A shows that body length is strongly correlated with scale length, and provides the means for this back calculation.

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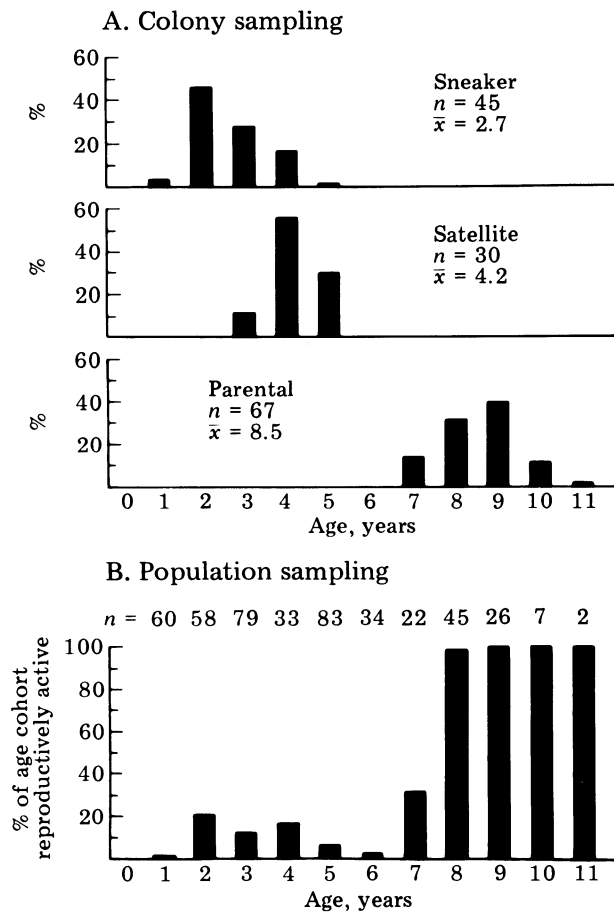


FIG. 1. (A) The age-frequency distribution of male bluegill, showing behavior defined as sneaker, satellite, or parental in spawning colonies. Ages of fish were determined from scales pressed onto acetate slides. The technique of scale aging has been verified for bluegill (17, 18). Age "0" is the year of birth and the first season of growth. Data were averaged over four colonies in Lake Opinicon, 1978. (B) Results of population sampling in 1977 and 1978 to determine the proportion of reproductively active males within age cohorts. A random population sample was obtained by using unbaited screen funnel traps (1 × 0.5 m) placed at various depths, and by seining (2 × 50 m beach seine net), at six widely dispersed sites in Lake Opinicon. Collections were made throughout the peak breeding season between mid-June and mid-July, on days without colony spawning to ensure representative sampling. There were no significant differences (χ^2 , $P > 0.05$) between collection sites in the proportions of reproductively active males. Reproductive activity was assessed by the presence of a mature testis. Reproductively active males have a large testis with sperm composing 1.1% (parental males) to 4.5% (sneaker males) of their total body weight. Reproductively immature males have thread-like testes that are poorly developed and are no more than 0.4% of the body weight. This difference is clearly evident upon dissection. The maturation state is maintained throughout the entire breeding season and, to a lesser degree, during the quiescent winter period.

The hypothesis of two alternative reproductive pathways predicts that the back-calculated growth of reproductively mature sneaker and satellite males will consistently show poor yearly increments relative to the growth history of equal-aged males with immature testes. These smaller growth increments correspond to past years of reproductive activity. If there are three pathways, then males in the satellite category should show larger growth increments in their early (presumably pre-reproductive) years. Both of these hypotheses predict that the back-calculated growth of parental males will be similar to that of young males not reproductively active, while greater than that of cuckolding males. All males might be expected to show

equivalent growth in years 0 and 1, when little or no cuckoldry occurs.

Fig. 2B shows that: (i) All males have similar growth rates at ages 0 and 1. (ii) Sneaker and satellite males show reduced growth in all previous years corresponding to ages at which cuckoldry behavior is observed (Fig. 1A). (iii) Males who become parentals at age 7 were the larger members of their cohort. They showed enhanced growth at all previous ages also. However, they showed reduced growth at age 7. They show no growth evidence of reproduction prior to age 7. Further testing (14) showed that aged 8 and 9 males had growth histories that paralleled the growth of nonreproductive males, aged 4 and 5, but consistently exceeded that of cuckolders. This comparison is less strong than the others because the males, aged 8 and 9, are compared (at their age 4 and 5) with males who were aged 4 and 5 in a different year. However, the year-to-year variation in growth is small (e.g., age 8 and 9 males show identical growth histories) compared to the growth decrement due to reproduction.

Fig. 1B shows that the cuckolding proportion of a cohort declines (21% age 2, 3% age 6) with age. This decline could be due to cuckolders dropping out of that pathway and entering the nonreproductive portion of their cohort. However, if this were the reason, we would expect to find evidence in the growth rates of fish classified as nonreproductive. Given the size of growth decrement due to breeding, this should show up as a bimodal growth curve. For example, fish who reproduced at age 3 and dropped out at age 4 should show greatly reduced growth when contrasted at age 3 with nonreproductive 3s. We can find no evidence for such bimodality. Given evidence in other organisms that reproductive activity is costly in terms of increased mortality rates (21, 23), the relative decline in cuckolders with age (Fig. 1B) is most likely due to increased mortality compared to their nonreproductive cohort members. There is direct evidence for this increased risk. Fins of most satellite males collected late into spawning bouts are torn, but not those in early collections (14). Sneaker males often bear wounds, as a result of attacks by parental males (14). Such wounds are highly susceptible to fungal and other infections (24).

The data support the hypothesis that there are two alternative life history pathways, that sneakers become satellites as they age. The data do not rule out the possibility that a cuckolder might sometimes survive to an age and size where it could become a parental. However, calculations with the increased mortality on cuckolders (Fig. 1B) suggest that for every parental living to age 7, about 0.12 cuckolder does. This is a generous overestimate of the relative chance of a cuckolder becoming a parental, because their decreased growth would delay even further the age at which they could compete for a territory and function as a parental (14). A schematic diagram of these two life histories is shown in Fig. 3. Cuckolder males mature at age 2 and parental males about 5 years later; the former attempt to parasitize the parental investment of the latter. Unguarded bluegill eggs do not survive (2, 5) and cuckolder males do not provide care, even when parental males are experimentally removed from the nests (14), thus, the cuckoldry strategy is parasitically dependent upon parental males.

In a recent independent study of bluegill reproduction, Dominey (8) described "female mimics" and suggested that mimics represent an alternative reproductive behavior. The mimicry he observed is similar to that which we have ascribed to satellite males. It is interesting that in Dominey's population (New York State) the mimics and parentals show considerable overlap in age (8). The mimics, however, are smaller in body size. This is expected from the present conclusion that mimicry

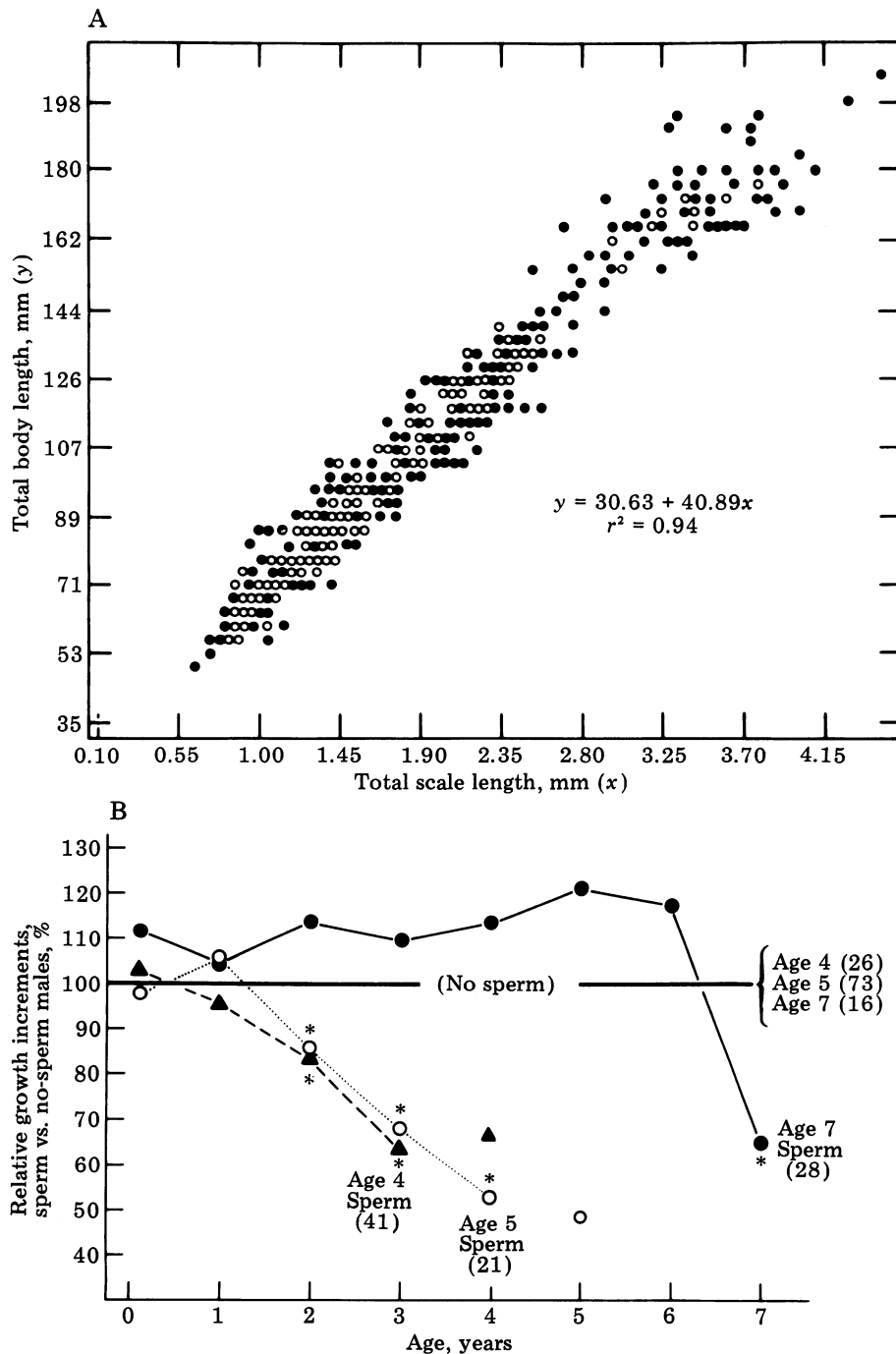


FIG. 2. (A) Relationship between body growth and scale length for male bluegill in Lake Opinicon. A total of 446 fish were examined. ●, Individual fish; ○, samples of two to eight fish. The technique of growth back-calculation from fish scales is reviewed in ref. 22. It has been successfully tested with bluegill (17). We used an ocular micrometer and microprojector read to 0.02 mm, to measure the width between annuli and the radius from the nucleus midpoint to the anterior scale margin. The body-scale relationship was determined by a least-squares regression of body length (y) on scale radius (x) ($P < 0.001$). From this, Lea's methods of proportions (22) were used to back-calculate annual increments in body size from the measured widths between scale annuli.

(B) Relationship between body growth and sperm production for three age classes of male bluegill in Lake Opinicon. Ages were determined from scale annuli. Growth increments for each age class were back-calculated from the relationship in A. Males without sperm on capture were considered to have "full" growth (100%). Growth of males with sperm was contrasted to these males without sperm. Whereas growth seasons are identical for fish within age cohorts, this is not necessarily the case between year classes. Fish aged 5 and 7, for example, may have faced quite different environments at age 2. For this reason comparisons are made at any age only within an equal-aged cohort. For example, the fourth year growth increment of 5-year-old males containing sperm was only 53% of that by cohort males without sperm. Significant growth differences (two-tailed t tests; $P < 0.05$) within cohorts are indicated by *. Sample sizes are in parentheses. Points not joined by lines are the partial growth increments in the year the fish were captured. ○, Age 5; ▲, age 4; ●, age 7.

behavior is but one part of the ontogeny of the cuckoldry strategy. Evidence that cuckoldry is widespread is suggested from reports of early maturing males (young males captured with ripe testes) throughout the bluegill range (5, 14, 25); similar

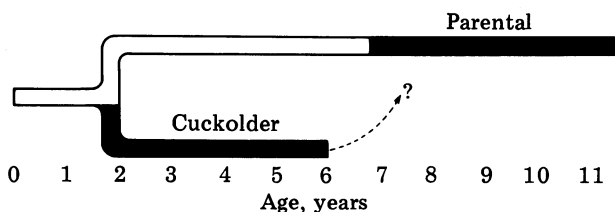


FIG. 3. Schematic summary of the reproductive life history pathways for male bluegill sunfish, as indicated by data from Lake Opinicon, Ontario. Shaded areas correspond to the reproductive ages of parental and cuckold males. See text for details.

forms of cuckoldry probably occur in most if not all members of the genus (7, 26).

Although we do not know what maintains the cuckold strategy at a particular frequency, its maintenance in the population most likely depends upon a frequency-dependent mating advantage (27-29). We provide here a theoretical calculation for the expected proportion cuckolders at age 2, under the frequency-dependent assumption. Because the growth prior to any reproduction is the same on average for cuckolders and future parentals, we assume that the cuckold strategy is not simply an option "chosen" by males who would in some way do worse as parentals later in life.

The equilibrium (or ESS) proportion of males in each pathway should be such that the lifetime fitness of an individual is the same for either life history (27, 29, 30). In theory these expected proportions can be calculated. Let lx = probability an

individual is alive at age x (all males are assumed alive at age 2); bx = number of offspring an individual will produce (fertilize) while it is age x . Because bx and lx will differ for each pathway, let p and s designate parental and sneaker-satellite respectively. The population is assumed to be stationary (30, 31). If the fitness is to be the same over each pathway, it follows that

$$\int_{x=2}^{\infty} l_s(x) \cdot b_s(x) dx = \int_{x=2}^{\infty} l_p(x) \cdot b_p(x) dx. \quad [1]$$

We now show that a testable life history model can be derived from relationship 1. Let n males reach age 2 each year. If q proportion of these go down the sneaker-satellite pathway, then the number of age x s males is $q \cdot n \cdot l_s(x)$. Because each of these fertilizes $b_s(x)$ eggs, the total number of eggs fertilized by all s males is

$$q \cdot n \int_{x=2}^{\infty} l_s(x) \cdot b_s(x) dx. \quad [2]$$

The same function for the parental males is

$$(1 - q)n \int_{x=2}^{\infty} l_p(x) \cdot b_p(x) dx. \quad [3]$$

The ratio of Eq. 2 to Eq. 3 is the ratio of the eggs fertilized by sneaker-satellite males to the eggs fertilized by the parental males, in each breeding season. Let h = proportion of eggs in a breeding season fertilized by s males. Recall the conditions for an equilibrium q (Eq. 1). Forming the ratio of Eq. 2 to Eq. 3, we have

$$\frac{q \cdot n \int_{x=2}^{\infty} l_s(x) \cdot b_s(x) dx}{(1 - q)n \int_{x=2}^{\infty} l_p(x) \cdot b_p(x) dx} = \frac{h}{1 - h} \quad [4]$$

or

$$q = h. \quad [5]$$

That is, the equilibrium proportion of males at age 2 entering the sneaker-satellite pathway should be equal to the proportion of eggs fertilized in each breeding season by all the sneaker-satellite males. We have thus transformed the life history calculations into a set of behavioral observations (i.e., estimating h). A discrete-generation version of this prediction was derived and tested on fig wasps by Hamilton (32).

The proportion of males at age 2 becoming cuckolders (q) is 21% (Fig. 1B) (95% binomial confidence interval 11–31%). The number of spawning acts intruded upon by cuckolders varies from 3% to 31%, depending upon colony water depth (14). To date, we have sampled seven colonies, which represent the depth distribution in Lake Opinicon. For each of these, 57–272 egg depositions were observed. The mean rate of successful intrusion was $14\% \pm 10\%$. This is an approximate although possibly liberal measure of the proportion of eggs fertilized by cuckolders (h). We conservatively score only intrusions that place cuckolders at the nest center during the egg releases. About 30% of these involve only the cuckolder releasing sperm. Of the remaining 70%, sperm competition probably favors the cuckolders because they position themselves closest to the eggs while releasing sperm. These data are too imprecise to constitute a quantitative test of the model, but they

are suggestive in that while cuckolders compose over 80% of the reproductively active males in the population (14), they obtain only $\approx 14\%$ of the eggs laid. In order to provide a quantitative test, we need data from several lakes. The prominence of bluegill in North American waterways (5) and the fact that all male fertilization is in a nest where it can be measured hold promise for a comprehensive test of a life history theory.

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