

Cuckoldry in sunfishes (*Lepomis*: Centrarchidae)

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Male sunfishes build nests and provide care for eggs spawned therein. It is shown here that small non-nesting male pumpkinseed (*Lepomis gibbosus*) and bluegill (*L. macrochirus*) will intrude during conspecific spawnings, to fertilize eggs. Such behaviour cuckolds the males which care for the brood.

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Les crapets mâles construisent des nids et voient au soin des œufs qui y sont déposés. Les mâles de petite taille du crapet-soleil (*Lepomis gibbosus*) et du crapet à orièlles bleues (*L. macrochirus*), qui ne font pas de nid, interviennent lors de la fécondation des œufs, concupiant ainsi les mâles responsables de l'élevage des portées.

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Introduction

The behavioural ecology of sunfish populations in Lake Opinicon, Ontario, is the subject of a long-term study by the author. Breeding in North American sunfishes is characterized by female spawning in nests constructed by males; males remain at the nest to provide parental care of the brood (Breder 1936). I report here on reproductive behaviour by non-nesting male bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*). My observations indicate that small males of these two species intrude into nests during conspecific spawning for the purpose of fertilizing eggs.

Methods

The study sites are described in the report by Gross and Nowell (1979). Pumpkinseed and bluegill reproductive behaviours were observed both from observation platforms placed on the shore near breeding males, and with mask and snorkel from within the water. Collections of free-swimming fish and selective samples from nests under observation were made with funnel traps and dip net. The weights reported here were measured with a Torsion balance accurate to 10^{-3} g. Data are examined for statistical significance with an analysis of variance test (ANOVA; Sokal and Rohlf 1969).

Results and Discussion

In Lake Opinicon, male bluegill construct nests in colonies of 15-100 individuals, and gravid females arrive as a school to spawn. Pumpkinseed are non-colonial but aggregated in favoured habitat. Female pumpkinseed individually approach territories of nesting males, and not all males in an area will spawn. During observation of spawning behaviour, I noted frequent intrusion by small conspecifics into nests containing spawning pairs.

During the June 1977 spawning, a random sample of 24 bluegill, much smaller in body size than ripe females and nest-building males (termed 'parentals'), was netted from near the edge of a spawning bluegill colony. The sample produced 23 males and 1 female (sex determined by internal inspection of gonadal tissue; female with undeveloped ovaries). All males released sperm under slight abdominal pressure, and excised testes were well developed. This was surprising since these males measured 42% smaller in total length than the smallest nesting bluegill ($N = 52$ parental bluegill) and were apparently many years younger. To verify biological activity, sperm was added to stripped bluegill eggs in petri dishes successful fertilization occurred. Examination of stomach contents showed 3 empty stomachs, 19 with various organic foodstuffs (female stomach included here), and 2 with two fresh bluegill eggs.

Since few stomachs contained eggs, and because of the ease of sperm release, it was postulated that these non-nesting males were at the colony to cuckold parental males. The following predictions were made: (1) if intrusions are for egg predation, then the number of eggs in intruders' stomachs should increase during spawning time; (2) if intrusions are for fertilizing eggs, then the amount of sperm in the gonads should decrease during spawning time; (3) if intrusions are for both eating and fertilizing, then egg number in stomachs should increase and sperm in gonads decrease; (4) if intrusions are for neither (1) nor (2), then both will remain constant.

To test the underlying hypotheses of egg eating vs. fertilization, 80 intruders were captured individually while in nests with a spawning pair of

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TABLE 1. Stomach contents and gonad weights of bluegills captured during intrusion into nests containing spawning bluegill pairs (June 28, 1977; Lake Opinicon)

	Colony 1		Colony 2		Total	
	Early	Late	Early	Late	Early	Late
<i>N</i>	13	15	19	18	32	33
\bar{x} body weight	12.83	13.51	11.90	13.11	12.38	13.30
\bar{x} testis weight	0.41	0.39	0.39	0.33	0.40	0.36
Stomach contents:						
empty	1	14	2	10	3	24
full	9	0	15	6	24	6
eggs	3	1	2	2	5	3
total no. of eggs	31	4	16	18	47	22
Testis wt. Body wt.	0.032	0.029	0.033	0.025	0.033	0.027
ANOVA	$P < 0.10$		$P < 0.025$		$P < 0.05$	
Eggs Fish	2.4	0.3	0.8	1.0	1.5	0.7
ANOVA	$P > 0.50$		$P > 0.50$		$P > 0.50$	

bluegills. Samples were first made 'early' during colony spawning, and then again after 2 h as a 'late' sample (Table 1). Additionally, 15 intruders from an 'early' sample were kept live in aquaria with running lake water, and killed during the 'late' sampling. The aquarium specimens contained eggs when killed, demonstrating that digestion should not preclude accumulation of eggs during the 2 h allowed between samplings. All 80 fish sampled were found to be male.

The data of Table 1 conform with prediction (2), therefore supporting the hypothesis that the significance of small fish intrusion during spawnings is egg fertilization. Overall, 12.5% of intruding males contained eggs, but this represented only 1.1 eggs per fish (bluegill nests contain about 4000 eggs). While the number of eggs in stomachs did not increase during the spawning bout, sperm in gonads did decrease (ANOVA, $P < 0.05$) by approximately 10%. It is also striking that all captured intruders were male. The occasional egg eaten by intruders probably reflects an attempt to compromise energetic costs accumulated from rapid dashes into nests and from time lost feeding.

Behavioural observations further reinforce the intrusions-for-fertilization hypothesis. Intruders came beside the female in the manner of parentals, during her egg releases (recognized by a characteristic dipping movement; Miller 1963). It is presumed by sunfish biologists (e.g., Breder 1936; Miller 1963; Keenleyside 1972; this author) that sperm is released at this time. Parental males responded with much aggression to nest intruders; however, small males frequently escaped detection by taking a position at the females' side opposite to

that of the parental male. Intruders thus positioned could remain in a nest during several female 'dips.'

Similar reproductive behaviour occurs in the pumpkinseed. Collections during pumpkinseed spawn intrusions also produced small conspecific males with developed gonads, and pumpkinseed intruders acted in a manner resembling what has been described for the bluegill. These intrusions presumably are a widespread phenomena, since small males with developed gonads can also be found in bluegill populations in New York State (personal communication by Wallace Dominey, May 1978). The fertilization intrusion behaviour by non-nesting bluegill and pumpkinseed in Lake Opinicon is in general agreement with that found by Keenleyside (1972) for longear (*L. megalotis*) in the Middle Thames River. This author concurs with Keenleyside that similar intrusion behaviour is likely to be found in other *Lepomis* spp.

I wish to draw attention to a consequence of the reproductive behaviour described here. The reproductive success of a non-nesting male which intrudes during spawning is dependent upon (1) conspecific males attracting females to their nests, (2) success in sperm competition with these males, and (3) provision of brood care by the nesting males (uncared for brood will not survive; Gross, unpublished data). Since parental males experiencing spawn intrusions will be caring for other males' offspring (in addition to their own), they have in fact been 'cuckolded,' and their parental behaviour has been 'parasitized.' From the existence in several *Lepomis* species of small males with functionally developed gonads and complex intrusion behaviours, it is apparent that cuckoldry is a

significant feature of the reproductive biology of sunfishes. This significance is not widely known by sunfish workers (e.g. review by Carlander 1977).

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