

Predation and the Evolution of Colonial Nesting in Bluegill Sunfish (*Lepomis macrochirus*)

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Summary. 1. Male bluegill sunfish (*Lepomis macrochirus*) construct nests in densely packed colonies characterized by high breeding synchrony. Females deposit eggs in the nests and males alone provide parental care for eggs and larvae. During the 7-day care period, males do not leave the nests to forage nor do they nourish the young. Parental males do actively defend their broods against predators.

2. This study investigated the effects of coloniality on predation. Bluegill brood are attacked by predators moving along the lake substrate and from the water column. Substrate-level predators include a major predator in the system, the snail *Viviparous georgianus*, and also bullhead, *Ictalurus* spp. Predation from the water column is primarily by conspecifics (94%) but also by *Lepomis gibbosus* and the hybrid, *L. macrochirus* × *L. gibbosus*. There is little or no predation on parental males.

3. Significant differences in brood predation are found among nests in central, peripheral colony and solitary sites. Brood loss at peripheral nests is at least three times that at central nests, and solitary nests experience greater predation than colony nests. These differences are due to effects of nest dispersion rather than to habitat characteristics.

4. Bluegill brood predation is reduced through colonial nesting as (1) peripheral nests screen central broods from snails and bullhead, (2) predators can be swamped by the high nesting density, and (3) overlapping defended zones provide cumulative defense against water-column predators and bullhead. Synchrony in breeding augments these anti-predation attributes of colonial nesting, and can also reduce conspecific predation and result in a 'head-start' against predators.

5. Certain costs to brood survivorship arise from colonial nesting: predation by neighboring males and ripe females, concentration of odor cues which may influence bullhead predation, and possibly fungal transmission between nests.

6. Pumpkinseed sunfish (*L. gibbosus*), which breed concurrently with bluegill, are relatively unsocial nesters. Pumpkinseed do not suffer the same predation pressures. As a result of morphological and behavioral adaptations for feeding, pumpkinseed are able to remove snails from their nests and probably repel bullhead attacks. As snails contribute over 50% of the estimated predation on bluegill, this difference between species is significant.

7. Brood predation is proposed as an important selective force for the evolution of colonial nesting in sunfishes. Selection should be mediated through female choice of a nest dispersion which maximizes brood survivorship. Morphological and behavioral preadaptations probably determine the type and degree of brood predation experienced by a species, and hence species-specific selection for patterns of nest dispersion.

Introduction

Breeding aggregations are a relatively widespread phenomenon in vertebrates that exhibit parental care. These aggregations may arise from physical limitations in the environment, or from social attraction among conspecifics. When proximity is a result of social attraction rather than habitat shortages, stationary breeding aggregations with parental care are aptly termed 'colonies'. The evolution of colonial breeding has attracted considerable interest, particularly in birds, and four major hypotheses have

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emerged to explain its adaptiveness: mutual stimulation or social facilitation (Darling 1938); regulation of population size (Wynne-Edwards 1962); more efficient exploitation of food resources (e.g. Horn 1968; Emlen and Demong 1975); and reduced predation (e.g. Kruuk 1964; Hoogland and Sherman 1976).

The evolution and adaptive significance of coloniality has not been studied in fishes. In noncolonial species, brood survivorship is often dependent upon some form of parental defense against predators (Breder and Rosen 1966; Keenleyside 1978a). In some species parents conceal their broods, but usually they protect broods by actively counterattacking predators and driving them away. Aquatic systems contain a wide spectrum of potential predators, and predation can be extensive (e.g., McKaye and Barlow 1976; Perrone 1978; Gross and Nowell 1980). Through coloniality, fishes could obtain several anti-predation advantages. These are: (1) collective defense ('mobbing') (Hoogland and Sherman 1976); (2) 'selfish herd' effects (Hamilton 1971); (3) predator 'swamping' (Wiley and Wiley 1980). Although no studies have demonstrated these benefits for fishes, the importance of predation with regard to colonial breeding has been suggested by Loiselle (1977) and Gerald (1970). This paper investigates the significance of coloniality on predation in the bluegill sunfish (*Lepomis macrochirus*; Centrarchidae).

Bluegill sunfish are highly colonial breeders: (1) their nest dispersion is clumped despite unoccupied and continuous habitat of similar water depth, water temperature, and substrate character; (2) breeding groups expand through the addition of new members independent of changing water depth and substrate condition; (3) solitary nests are rare in the breeding population (less than 7%); (4) breeding synchrony within groups exceeds breeding synchrony between groups; (5) behavioral interactions among males involves initial aggression but is followed by mutual acceptance and social facilitation (Colgan et al. 1979; Gross 1980). In striking contrast to bluegill, pumpkinseed sunfish (*L. gibbosus*), which breed in similar habitats, often nest solitarily or in loose nesting aggregations. Coloniality occurs throughout the range of bluegill, as does the relatively unsocial breeding of pumpkinseed (e.g., Clark and Keenleyside 1967; Gerald 1970; Carlander 1977). This variation in breeding dispersion among closely related species poses an interesting evolutionary problem.

The approach taken here is to examine the behavior of predators in the system and contrast predation loss at central colony, peripheral colony, and solitary bluegill nesting sites. The hypothesis that coloniality is adaptive as an anti-predation behavior predicts that central colony males suffer reduced predation. The

results from our study support this hypothesis. Some comparative data were gathered on response to predators by the noncolonial pumpkinseed. In combination with studies of mate choice (Gross 1980) and structural morphology, this paper contributes to an explanation of how breeding dispersion evolved in sunfishes.

Material and Methods

Synopsis of Reproductive Behavior

Bluegill reproductive behavior in Lake Opinicon is typical for the species (Avila 1973; Carlander 1977; Gross 1980). Males construct nests in colonies of 10–150 members; nests are built rim to rim and they sometimes assume a hexagonal shape (Barlow 1974). Some males which mate by cuckoldry (Gross 1979; Gross and Charnov 1980), do not construct nests nor show parental care. Gravid females arrive as schools at established colonies of waiting males and spawn for several hours. After spawning, all females return to deeper water. Parental males fan their eggs and respond aggressively to territory intruders. Eggs hatch in approximately 3 days and larvae (immature fry) mature for 4 days before leaving the nests as free-swimming fry. Since spawning is synchronous within a colony, broods of almost all bluegill males are at the same developmental state. After fry leave nests, the males return to deeper water and resume feeding until the next spawning bout. This is usually 3–10 days later. Similar reproductive behavior occurs in pumpkinseed (Miller 1963), but nests are dispersed and breeding synchrony is considerably less.

Study Area

Lake Opinicon (Leeds County, Ontario, Canada) is a 900 ha mesotrophic lake similar to many in the Ontario basin (Keast 1978b). It has a natural bluegill population and a resident fish community of 18 species (Keast and Webb 1966). The primary study site was a homogeneous sandbar 20 m wide and 90 m long, stretching across the mouth of a bay (Birch Bay; see map in Gross and Nowell 1980). Substrate conditions (90% sand, 10% light gravel) and plant cover (5%) are generally uniform along this bar and water temperature does not vary. Water depth on the bar averages 1 m and depth increases to 3 m on the bay side and 10 m on the lake side. Thus the breeding habitat is well delimited. From four to seven bluegill colonies are simultaneously established on the bar. Collectively they use less than 20% of the total bar area. Between 25 and 80 pumpkinseed nest concurrently in unoccupied regions between colonies. Spawning habitat requirements for pumpkinseed are similar to bluegill. Qualitative observations of predation were made in other areas of the lake, described in Gross and Nowell (1980).

Data Collection and Analysis

The data were collected during the June–July breeding months of 1976–1979. Behavioral observations were made from 3-m towers on the shoreline near nesting areas, or with mask and snorkel while kneeling near a colony or swimming along the sandbar. Observer presence caused no apparent disturbance to the fish community (Colgan et al. 1979). Preliminary observation and sampling were made to identify the predators in the system. The potential predators on bluegill brood were identified from approximately 200 h of observation during 1976 and 1977. These were later sampled to verify eggs or larvae in their stomachs. Predator samples were collected randomly using screen funnel traps near colonies, and selectively by using a hand net manipulated by a skin diver.

The predators upon bluegill eggs and larvae were found to be: male and female bluegill; male and female pumpkinseed (*L. gibbosus*); hybrid sunfish (*L. macrochirus* × *L. gibbosus*); immature

(20–35 mm total length) smallmouth bass (*Micropterus dolomieu*); bullhead catfish (*Ictalurus* spp.); and snails (*Viviparus georgianus*). Rockbass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*) and minnows (see Keast and Webb 1966) were seen near colonies but did not prey upon the brood. Adult male bluegill were not preyed upon during the nesting period. Thus, the study is concerned only with predation on bluegill brood.

A representative colony (A) with 52 nesting males was used for detailed observations of natural predation. 'Central' males were defined as having at least one nest separating them from the colony edge. 'Peripheral' males had at least one nest edge exposed and formed a ring around the colony. Colony A had 11 central and 41 peripheral males. Sixteen 'solitary' bluegill males were found in unoccupied areas between colonies. Solitary males were separated by a minimum of 1.5 m from other nests; a distance sufficient for behavioral and probably visual isolation. Several methods were used to study predation.

1. Predator density was assessed by swimming strip counts along the sandbar (Keast and Harker 1977). The bar was divided into twelve 75-m² sections and free-swimming fish were recorded from each quadrat. Counts were made three times each week, and began 2 weeks before nesting activity.

2. To assess possible predation during the spawning bout, ten observation periods each of 10 min duration were made during the spawning of colony A on June 27, 1978. Predation during the 7 days of egg and larval brooding was assessed by establishing daily observation periods. To monitor both crepuscular and diurnal hours of predator activity, observation periods were held 06.00–07.30, 13.30–15.00 and 20.00–21.30. This provided 26.5 h of observational data covering approximately 23% of the daylight hours during which brood were developing in nests (16.5 h daily visible light). Predator size was estimated as large (>150 mm total length), medium (120–150 mm) or small (<120 mm). Male parental 'defense' was defined as aggression towards an intruder in the parent's territory. This usually took the form of a 'chase'. Each complete chase (exit from and re-entry into the nest) was scored as one defense. A direct count of egg or larval loss to predation was not feasible as approximately 15,000 eggs are spawned in each nest. Instead, predation was quantified by documenting the occurrence and success of a predation attempt. An 'attempt' was defined as penetration by an intruder into the territory of a parental bluegill, involving direct movement toward the nest. 'Successful attempts' involved biting at eggs or larvae resting on the nest bottom. Our definitions allowed for parental defense in the absence of an actual predation attempt on the nest, as occurs if a predator is chased while swimming through a territory.

3. To determine the influence of nesting density on predator number, a count of free-swimming potential predators over four different sites was made. The sites, each measuring 12 m², included: a colony with 13 males (colony B); an area with a solitary nesting male (two such areas were examined); a section of vacant bar; and a deserted colony site, which served as a control (i.e., the males and fry had already dispersed). Each site was visited 20 times in random order and the number of predators counted. The relationship between predation pressure and density within a colony was examined by dividing colony A into three sections of differing density.

4. When nests contained broods, the positions of predators in the water column were recorded at four sites: colony A; colony B; a stretch of unoccupied sandbar (control); and at the site of a solitary male. Meter sticks were placed in an upright position and potential predators within an approximate 12 m² area were scored as swimming low (<1/3 m from the substrate), medium (1/3–2/3 m), or high (>2/3 m) in the water column. Water depth over the bar closely approximated 1 m. The scoring was repeated five to eight times at each site in random order.

5. To investigate whether coloniality imparts protection for

unguarded nests, such as while parental males chase predators, we experimentally removed seven males from each type of nest site (central, peripheral, and solitary). Males were readily captured using a hand net placed over the nest bottom. When the net was lifted slowly, disturbance to other males was minimal. Removals were performed at a third colony (C) of 68 males to avoid affecting the main study areas.

6. Snail density along the sandbar and at colony A during different stages of the reproductive cycle was measured by daily counts in randomly selected 1-m² plots. Snails were also removed from nests to examine stomachs for the presence of brood. The rate of snail movement was estimated by releasing individuals into aquaria with running lake water and measuring distance travelled within a set time period. A total of 15 trials with five snails were run. Consumption rate was estimated by feeding live brood to snails. Five replicate samples of three snails were placed in contact with known quantities of eggs and larvae (usually 100), and after a given time (usually 24 h) the remaining brood were counted. Digestion rate was studied by liberal feeding of bluegill larvae. Snails were allowed to feed for 3 h and then moved into empty aquaria. The stomach contents of five snails were examined every 10 min until stomachs were found empty. The experiment was then repeated using ten snails sampled every 5 min. Since larvae were frozen and their tissues may have been broken down, the estimates of digestion rate are only approximate.

7. Nocturnal predation was investigated by diving with underwater lights. The only active nocturnal predators were bullhead, and they tended to shy away from the lights. This unfortunately limited our observations.

8. Approximately 20–25 h of observations were accumulated on pumpkinseed nesting on the sandbar. Comparative studies were made between these and bluegill for predation by snails. As part of a larger study into the mating systems of sunfishes (Gross 1980), 70–110 pumpkinseed nesting in a shallow cove, White Pine Bay (Gross and Nowell 1980), were under daily observation 1976–1978. Incidents of natural predation were recorded during more than 700 observation hours. Although this site is structurally different from the sandbar, a colony of bluegill was annually established among the pumpkinseed nests and all the predators identified for bluegill at the sandbar were also seen in the cove. Some of these data are used for comparative study with bluegill.

9. Statistical evaluations of the data were based upon χ^2 (Siegel 1956) and analysis of variance (ANOVA) (Sokal and Rohlf 1969) tests.

Results

Colony site selection by bluegill did not reduce predation. The five sections in which colonies were established did not differ from the seven sections without colonies in total number of potential predators (ANOVA, two-tailed, $P > 0.05$). Predation pressure was exerted in two ways. Snails and bullhead moved along the lake substrate to attack nests (substrate-level predators) while the remaining species attacked from positions in the water column (water-column predators).

Water-Column Predation

Predator Behavior and Male Bluegill Response. The predominant predators in the water column were conspecifics, accounting for over 90% of all attacks during the brooding period (Table 1). Although pumpkin-

Table 1. Predation pressure from fish in the water column during the post-spawning parental care period. Data are summarized from 26.5 h of observation and include: relative predator abundance, predation threat, and defensive chases made by parental males. Predator abundance is the number of each fish species swimming into bluegill territories during the observation period

Predator	Abundance		Predation attempts			Defensive chases	
	No. observed	% of total	No.	No. per predator	% of total	No.	No. per predator
Total bluegill	367	73.4	114	0.31	94.3	1303	3.55
Large bluegill (> 150 mm)	100	20.0	74	0.74	61.2	727	7.27
Medium bluegill (120–150 mm)	102	20.4	38	0.37	31.4	527	5.17
Small bluegill (<120 mm)	165	33.0	2	0.01	1.7	71	0.43
Pumpkinseed	75	15.0	3	0.04	2.5	313	4.17
Hybrid	24	4.8	4	0.17	3.3	314	13.08
Smallmouth bass	34	6.9	0	—	—	0	—

seed were relatively abundant, they made fewer predatory attempts. Predation by smallmouth bass was infrequent and they were not important predators in the system.

Free-swimming *Lepomis*, searching for food, moved along the sandbar singly or in loose groups of up to 15. Many fed on bluegill eggs and larvae (Table 2). Attacks on broods were usually made by single fish, from either low or high in the water column. Those attacking from low in the water column would swim rapidly toward the nest and bite at the bottom of the nest near the edge. In contrast, those attacking from high in the water column would 'hang' motionless and then dive down into a nest. Successful predation attacks by large bluegill captured on average 17.9 eggs and larvae (SD=12.8, $n=12$ large bluegill and 74 successful attacks). To avoid male parental defense, predators often paused near the edge of territories awaiting an opportunity to at-

Table 2. Stomach contents of 60 free-swimming *Lepomis* captured in traps near colonies or netted from over colonies during the 7-day parental care period. The category 'miscellaneous invertebrates' includes aquatic insects, crustaceans, and gastropods. Stomachs with bluegill brood usually contained some sand

	Stomach contents				\bar{x} no. of brood and range in stomachs with brood
	Bluegill eggs or larvae only	Invertebrates and bluegill eggs or larvae	Misc. invertebrates only	Empty	
No. of <i>Lepomis</i>	12	4	41	3	396 (15–1,300)
Percentage	20.0	6.7	68.3	5	

tack while the parent's attention was diverted. These lingering fish were frequently chased with parental aggression being directly proportional to predator threat. Large bluegill and especially hybrids elicited the most defensive chases and were also most likely to attempt predation (Table 1). Parental defense intercepted approximately 53% of all attacks during the parental care period. When a predator successfully penetrated a nest the parental male attempted fierce and repeated bites on its side. Predators rarely counterattacked and usually retreated rapidly, with the defending parent chasing about 1 m. Because *Lepomis* are visual predators, attacks by a single male can attract others, giving rise to group attacks. Male parental defense was usually ineffective in such situations. On one occasion a group of 20 large bluegill and hybrids successively consumed all the brood from three peripheral nests.

A tagging study (Gross 1980) permitted the recognition of some individuals returning to colony A for repeated predation. The reappearance of these same individuals and the rare co-occurrence of brood and invertebrates in their stomachs (Table 2), suggests a degree of predator learning and specialization.

During the spawning period female bluegill were active predators (Table 3). Upon entering nests gravid

Table 3. Predation attempts ($n=245$) by conspecifics on bluegill eggs during colony spawning

	Sex of predator		Female in nest during predation attempt		Male defensive chases		Predation success		
	Male	Female			Female in nest	Female not in nest	Total	Female in nest	Female not in nest
			Yes	No					
No. of predation attempts	17	228	154	91	430	250	185	—	—
Percentage	6.9	93.1	62.9	37.1	63.2	36.8	75.5	76.2	74.5

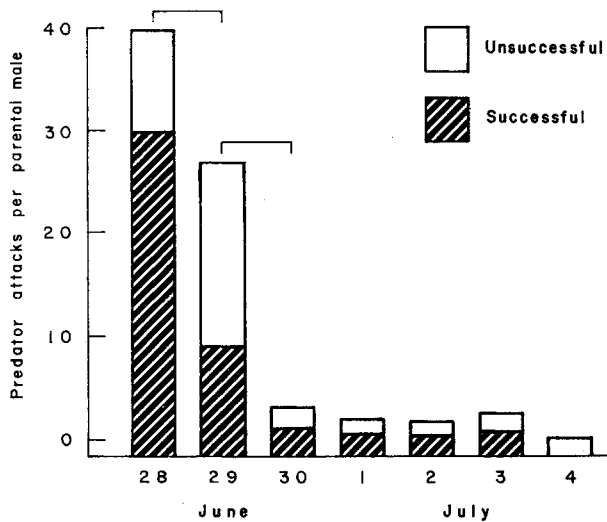


Fig. 1. Daily predation pressure by free-swimming *Lepomis* during the 7 days of post-spawning bluegill brood care. The data were extrapolated to a 16.5-h day from 4.5 h of daily observation and show the average number of predation attempts and predation success on males in colony A. A bar (—) indicates significant differences between days in predation attempts and success (ANOVA, two-tailed, $P < 0.05$)

females typically bit at the bottom. Males would then chase them from the nest unless they commenced spawning and stopped taking eggs. Of 20 gravid females collected, 65% had eggs in their stomachs (\bar{x} egg no. for predacious females = 26, $SD = 13.1$; overall $\bar{x} = 16.9$, $SD = 16.5$).

Predation was greatest during spawning while a female was in the nest (Table 3, ANOVA, two-tailed, $P < 0.01$). The attacks of males and females in the water column had approximately equal success, and each sex made an equal proportion of their predation attempts at this time. Resident males responded with an increase in defensive attacks (ANOVA, two-tailed, $P < 0.01$), but their success in preventing an attack was less than during the remaining parental care period (ANOVA, two-tailed, $P < 0.01$). This can be attributed to: (1) confusion arising from large numbers of spawning females mingling in the colony, (2) difficulty of guarding against predation while attempting to complete spawning sequences, and (3) approaching females 'suddenly' eating eggs rather than being sexually motivated. Colonies that attracted smaller schools of females did not suffer as much spawning predation.

During the 7 days in which young were brooded by males, frequency and success of attacks decreased (Fig. 1). Virtually no predation occurred on the day when fry dispersed. There was no change, however,

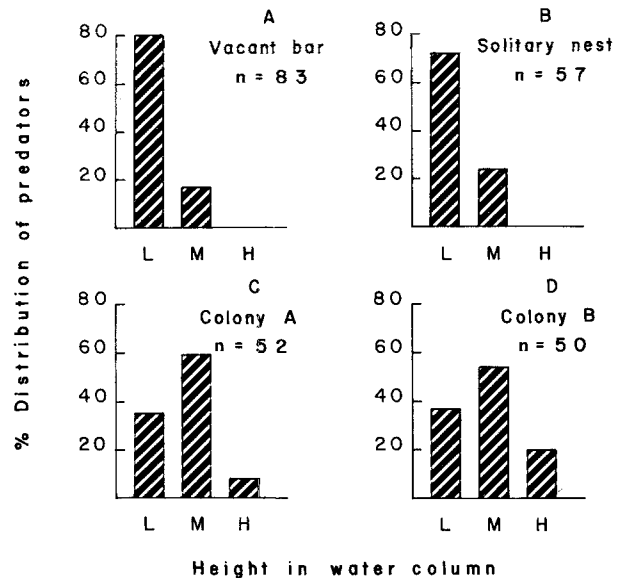


Fig. 2. Distribution within the water column of potential predators on bluegill brood at four sites along the sandbar. Fish were either low (L: $< 1/3$ m from substratum), medium (M: $1/3 - 2/3$ m), or high (H: $> 2/3$ m) in the water column. Fish low in the water column were of greatest threat to nesting bluegill. n = number of potential predators in the calculations

in predation pressure within any one day (testing for difference in the number of parental defenses and predation attempts in morning, afternoon, and evening periods of observation, ANOVA, two-tailed, $P > 0.05$ for both tests). Several small bluegill (< 120 mm) entered the colony each evening but were generally ignored by parental males. The reason for this influx was not clear, as small bluegill were not active brood predators (Table 1).

The Effect of Nest Density. Typically, potentially predacious fish swam low in the water column along the sandbar. When approaching a colony, however, they rose higher in the water column, thereby swimming further away from bluegill nest (Fig. 2c compared with 2a, χ^2 , $P < 0.01$ for all levels; Fig. 2c compared with 2d, χ^2 , $P < 0.05$ for all levels). By contrast, swimming height was unaffected by solitary nesting bluegill (Fig. 2a compared with 2b, χ^2 , $P > 0.05$ for all levels). Higher swimming heights over the colony can be attributed to predators avoiding the multiple attacks from aggregated bluegill males. This increased distance between broods and predators decreased predation threat; attacks were proportionately more common from fish lower in the water column (χ^2 , $P < 0.05$).

In general, predacious *Lepomis* did not converge on colonies. Fewer potential predators were found

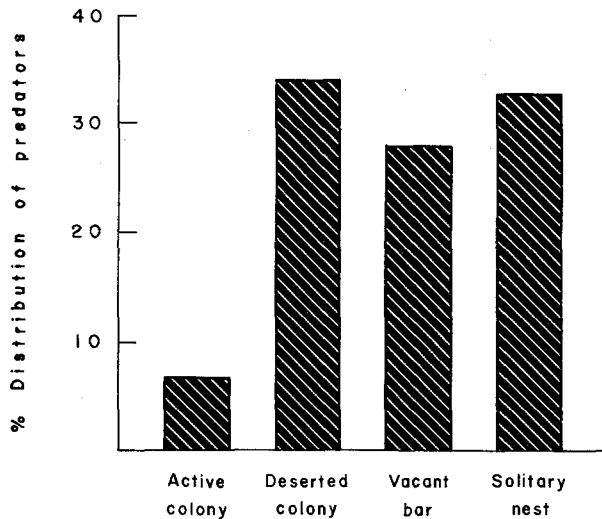


Fig. 3. Relative proportions of potentially predacious *Lepomis* in four sites of equal area along the sandbar habitat, during bluegill breeding. The data are summarized from 20 randomized observations at each site and a total of 257 fish

near colony B than along equal areas of vacant bar, at a deserted colony site, or around a solitary male (Fig. 3, χ^2 , $P < 0.05$). Differences among the latter three areas were not significant (χ^2 , $P > 0.05$). The data suggest that the number of potential predators around a solitary nest site is fivefold greater than at a colony.

The effect that nesting density *within* a colony has on predation pressure was examined by visually dividing colony A into three sections (X, Y, Z) of approximately equal areas but differing in nest density or structure (Table 4). Nearest neighbor analysis (measured from nest centers) showed a greater nest density in X relative to Y (ANOVA, two-tailed, $P < 0.01$) and to Z (ANOVA, two-tailed, $P < 0.01$). Density in Y did not differ significantly relative to Z (ANOVA, two-tailed, $P > 0.05$). Section Y differed from Z primarily in structure: nests in Y were more linearly arranged while those in Z were grouped in a circular pattern. Predator number was found to

be inversely related to nest density. Differences were significant between all sections (χ^2 , $P < 0.01$) except between Y and Z (χ^2 , $P > 0.05$). Actual predation attempts experienced by individual parental males were greatest at lowest nest densities. The number of attempts in sections X and Z differed significantly (χ^2 , $P < 0.01$) while those in Y were intermediate but not statistically different from Z (χ^2 , $P > 0.05$). The frequency of defensive behaviors shown by males differed significantly between all three sections (ANOVA, two-tailed, $P < 0.05$ for each pair in Table 4). This result suggests that males in section B may have faced greater predation exposure because of their linear nesting structure. Thus, the high density context of colonial nesting clearly reduces exposure of bluegill brood to water-column predators. This effect is also influenced, however, by the geometric arrangement of nests.

The Effect of Nest Position. There were no differences during colony spawning between peripheral and central nest sites with spawning females in either total number of predation attempts (ANOVA, two-tailed, $P > 0.05$) or in proportion of successful predation attempts (χ^2 , $P > 0.05$). During the brooding period, however, males at central colony positions suffered significantly less predation than those nesting at peripheral sites (Table 5). Comparative attack rate data were not obtained for solitary nesting males because of a shortage of field time. But, a study of the defensive behavior of solitary males indicated they took part in more defensive behavior than did central males (Table 6, ANOVA, two-tailed, $P < 0.001$). Solitary males also tended to show more defense than peripheral males but the difference was not significant (ANOVA, two-tailed, $P > 0.05$).

Predation on central nest sites was reduced because of overlapping defended areas. This could be seen in several ways: (1) A greater proportion of 'group responses', where two or more parental males simultaneously chased a potential predator, occurred at central colony positions (Table 6, central vs. peripheral, χ^2 , $P < 0.001$). These changes frequently caused predators to leave the nest area. Solitary males

Table 4. Predation pressure from free-swimming fish on three sections of a bluegill colony (A) differing in nest density or nest arrangement (see text for details)

Colony section	No. nesting males	Nest density (no./m ²)	Potential predators		Predation attempts		Aggressive chases by nesting males	
			Total ^a	Per nest	Total ^b	Per nest	Total ^b	Per male
X	12	2.9	146	12.2	38	3.2	621	51.8
Y	16	4.7	115	7.2	37	2.3	586	36.6
Z	24	5.0	126	5.3	44	1.8	524	21.8

^a From 23 spot checks during 5 days

^b 435 min observation per colony section

Table 5. Comparison of predation pressure from water-column *Lepomis* at central ($n=11$) and peripheral ($n=41$) sites in a bluegill colony (A). Data are summarized from daily observation (Fig. 1) during the 7-day post-spawning parental care period. The statistical analysis was done on the raw data with a two-tailed χ^2 , $df=6$

Colony position	Predation pressure per male			
	No. predator attacks	No. defensive chases	Defensive chases per predatory attack	% attack success
Central	23.8	193.4	8.1	25.1
Peripheral	97.4	1009.7	10.4	52.9
χ^2	$P < 0.01$	$P < 0.05$	—	$P < 0.001$

Table 6. Defensive behavior by bluegill nesting at three locations: central, peripheral and isolated from a colony. Eleven nests containing eggs were observed at each location for 110 min. Group responses, the proportion of defensive chases involving two or more parental males simultaneously chasing a predator, are shown

	Nest position		
	Central	Peripheral	Solitary
Chases to predators	16	96	114
Chases per nest	1.5	8.7	10.4
Group response	50%	8.2%	—

Table 7. Predation pressure on unguarded bluegill nests at three locations: central, peripheral, and isolated from a colony. Males were selectively captured from seven nests at each location. The length of time before predation occurred, the number of attacking predators, and the number of aggressive chases to these predators by neighboring parental males were recorded during 5 min of observation on each nest. Mean values and single standard deviations are shown

Nest position	Time to first predation (min)	No. predators attacking nest	Aggressive chases from neighboring males
Solitary	1.7 ± 1.7	5.1 ± 2.2	—
Peripheral	1.9 ± 1.2	5.9 ± 1.4	16.3 ± 9.8
Central	5.7 ± 2.5	1.9 ± 0.9	20.6 ± 6.8

could not, of course, benefit from any group response. (2) Unguarded nests gained a delay in predation at central colony positions relative to peripheral and solitary sites (Table 7, ANOVA, two-tailed, $P < 0.01$ for each pair). Although solitary nests were on average the earliest to be discovered by predators, the difference was not statistically significant from peripheral locations (ANOVA, two-tailed, $P > 0.05$). (3) Predators in central nests were chased by neighboring males about 3.5 times more than predators in peripheral nests (Table 7). This was due to centrally located

nests having more neighboring males than peripheral nests, since peripheral and central neighbors were equally active chasers (ANOVA, two-tailed, $P > 0.05$).

Substrate-Level Predation

Predator Behavior and Male Bluegill Response. Bullhead and snails were important predators in the system. In contrast to *Lepomis*, bullhead were active nocturnal predators, sensitive to odor cues (Keast 1970). Although their predation threat was not quantified, behavioral observations were obtained for 11 diurnal attacks involving 27 bullhead and for 28 nocturnal attacks involving 109 bullhead. The two species involved, *Ictalurus nebulosus* and *I. natalis*, were several times larger than parental males in body size, and they usually attacked in groups of two to five. Although parental bluegill responded aggressively by biting, they were unable to drive bullhead from their nest. As a result, all the brood in a nest was sometimes consumed. One bullhead captured within 5 min of penetrating a nest had approximately 400 eggs in its stomach even though it had been under constant attack by the parent.

To assess the number of bullhead in the breeding habitat, traps were set overnight. No bullhead were captured prior to bluegill spawning, and only one was captured after reproduction was finished. In contrast, eight were trapped during the parental care period. This suggests an influx of bullhead, although sample sizes are small.

Snails were voracious predators, highly responsive to the presence of bluegill brood. Male nest building decreased local snail density but snails entered the colonies in large numbers after eggs were spawned (Fig. 4). Snail density increased tenfold in 2 days, with an average of 23.7 snails per nest in colony A at peak density ($n=20$ nests, $SD=9.5$; snail size: $n=64$, shell length = 1.9 ± 0.35 cm, width = 1.6 ± 0.26). At this time nests had immature larvae and 20–50% of the bottom of a nest would be covered with snails.

During peak density snails contained on average 4.1 immature bluegill larvae in their stomachs ($n=25$ snails). Three days later this number dropped to 0.16 mature larvae ($n=25$ snails). Maturing larvae became increasingly difficult for snails to capture because they were able to move about the nest bottom. Due to the synchronous development of broods in colony nests, there were no alternative broods to prey upon. Snails therefore began to leave and their density in the colony returned to a prespawning level.

Experiments on snail movement demonstrated that snails did not approach nests randomly. Forty tagged snails were placed 15 cm from a colony edge. One day later a survey of their positions revealed

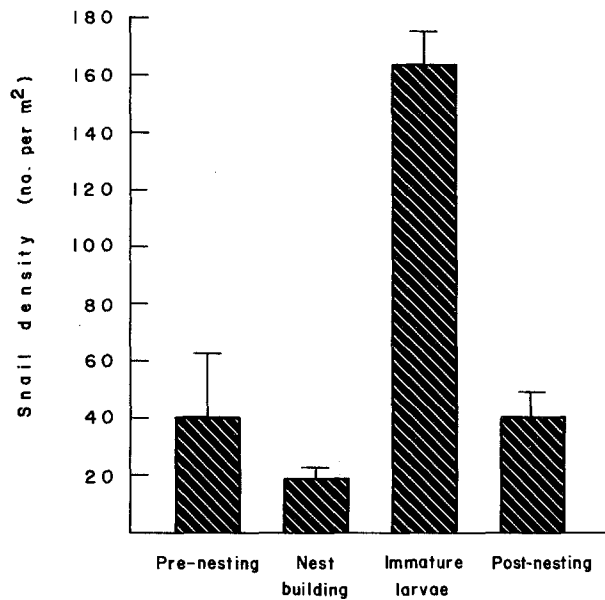


Fig. 4. The response of snails (*Viviparous georgianus*) to bluegill breeding. Presented are mean values and standard deviations calculated from 15 randomly chosen 1-m² plots at the site of colony A: (1) prior to any nest building (30.5.78); (2) during nest building (6.6.78); (3) while immature larvae were in nests (2.7.78); (4) after breeding activity (10.8.78). Differences in snail density between adjacent periods are statistically significant (ANOVA, two-tailed, $P < 0.01$ for each pairwise test). Pre-nesting and post-nesting snail density do not differ significantly (ANOVA, two-tailed, $P > 0.05$)

that a substantial proportion (55%) had moved into colony nests while 18% had moved away and 28% had remained where placed (χ^2 , $P < 0.05$). Snails probably detected the presence of broods by odor. Snail movement as measured in aquaria was estimated at 1.8 cm/min (approx. 1 m/h). This suggests snails are capable of quickly reaching a colony from several meters distance.

Active defensive behavior by bluegill males against snails was observed only once. This occurred when a single peripheral male went approximately 0.3 m from its nest and repeatedly bit at a snail. In response the snail withdrew into its shell. A few minutes later the snail emerged and began moving toward the colony, and, despite several additional attacks from the parent, eventually gained access to the nest.

Effect of Nest Position and Density. Central males were screened from bullhead and snails by the ring of peripheral males. Snail number in peripheral nests was twice that in central nests during the brooding period (Table 8). Observations of bullhead predation revealed that 32 of 38 (84%) were on peripheral nests.

Since nest density generally increases toward the center of a colony (Gross 1980), a further screening

Table 8. The number of snails (*Viviparous georgianus*) in nests of bluegill and pumpkinseed breeding concurrently in the same habitat. The data were collected during three reproductive bouts and an approximately even sampling was made while eggs and larvae were present. n = nests sampled; \bar{x} = mean no. of snails; SD = standard deviation; ANOVA = test of statistical significance between adjacent columns

	Position of bluegill nest			Pumpkinseed nests (solitary)
	Central	Peripheral	Solitary	
n	46	86	16	25
$\bar{x} \pm SD$	6.9 ± 10.9	13.7 ± 5.3	29.7 ± 15.0	0.36 ± 0.8
ANOVA	$P < 0.01$		$P < 0.001$	$P < 0.001$

of interior nests occurs. The higher density also provides cumulative defense against bullhead. When penetrating the colony, bullhead elicited increasing numbers of simultaneous defensive attacks and were driven out.

The high density and synchrony of colonial nesting swamped the predators. Solitary nests contained over twice as many snails as the average colony nest (Table 8). For a short time snail density continued to increase in all nests even as the number of brood in their stomachs decreased (due to larval maturation). Bullhead showed a similar tendency to increase in numbers *after* breeding had begun. There is thus a time lag to predation.

Predation on Pumpkinseed

Two aspects of predation on noncolonial pumpkinseed are of direct comparative interest. First, pumpkinseed nests had markedly fewer snails than bluegill (Table 8). This difference was independent of bluegill nest location (ANOVA, two-tailed, $P < 0.001$ for central, peripheral, and solitary locations). As an experiment, four marked snails were placed into seven pumpkinseed and seven bluegill nests. We found that pumpkinseed were able to remove snails. Single snails were grasped in the mouth and deposited 0.5–1.5 m outside of the nest. After 45 min, six pumpkinseed nests contained no snails and one nest had one snail. In contrast all seven bluegill nests still contained the four snails.

Second, it was noted that pumpkinseed were relatively unthreatened by bullhead. During an observation time approximately 3.5 times longer than for bluegill, a total of 37 bullhead were observed near pumpkinseed nests in White Pine Bay. Only one of these bullhead attempted predation on a pumpkinseed nest, and it was eventually repelled by vigorous biting from the parental male.

Discussion

The Predators

Conspecifics, snails, and catfish, the most important bluegill brood predators in Lake Opinicon, are also likely to be major predators throughout the bluegill range. This is suggested by the extensive range overlap of *Viviparous georgianus*, other omnivorous gastropods, *Ictalurus* and other Ictaluridae or catfish-like species, with bluegill (Clench 1962; Eckblad and Shealy 1972; McDonald 1969; Scott and Crossman 1973; Lee et al. 1980). Other recorded predators of bluegill brood are carp and common suckers (Webster 1954), perch (Carlander 1977), other *Lepomis* (this study; Carlander 1977), and various cyprinids (Gerald 1970). As a consequence of their large body size, nesting male bluegill are probably excluded from the diet of piscivorous fishes (e.g., *Esox lucius* and *Micropterus salmoides*; A. Keast, personal communication). One of us (M.R.G.) has observed attempted predation on parental males by water snakes (*Natrix sipedon*) and Great Blue herons (*Ardea herodias*). Such observations are rare, suggesting that no important predators prey upon nesting adults.

Bluegill colony sites are found in a variety of substrates in Lake Opinicon as elsewhere (Carlander 1977). Although not apparent on the sandbar, bluegill may derive some escape from brood predators through colony site selection. For instance, snail distribution is not uniform within lakes (Turnbull 1975) and bullhead prefer weedy habitats (Keast 1970). As large bluegill are rarely observed swimming in very shallow water, colonies formed there probably are detected less frequently by conspecifics. Such sites also decrease the space for water-column attack. Nesting sites must also be selected by physical and biotic requirements for brood development. Site selection should thus optimize the trade-offs between predacious and developmental sources of mortality.

The Anti-Predation Advantage of Colonial Nesting

A quantitative estimate of predation by *Lepomis* and snails during the parental care period can be made for central and peripheral males in a colony. As the number of brood captured per successful attack is approximately 18, *Lepomis* consume about 108 brood at central sites in contrast to 936 at peripheral sites (Table 5). Snails remained in nests for at least 4 days, and daily brood consumption was estimated as 19.7, thus snail predation at central sites was approximately 543 brood and at peripheral 1079 (Table 8). Total brood loss to predation was therefore around 651 and 2015 at central and peripheral sites, respectively.

Assuming equal egg distribution, central males would lose 4.3% of their clutch and peripheral males 13.4% (average bluegill clutch = 14958; Gross, unpublished data). As bullhead predation strongly affected peripheral males, a ratio of 1:3 for predation at central versus peripheral colony sites is a conservative estimate.

Although water-column predation cannot be quantified for solitary nest sites, the data strongly suggest that solitary males suffer more *Lepomis* predation than the average colony male. Peripheral and solitary males may not be very different in *Lepomis* predation. However, snails alone consume about 2340 brood at solitary nests. This represents a 14.5% increase in the predation that occurs at peripheral sites by snails and *Lepomis* combined.

The anti-predation advantage gained from colonial nesting can be attributed to a decreased 'encounter' rate and 'cumulative defense'. Colonial males encountered fewer snails and possibly *Lepomis* by 'swamping' the numerical and functional capabilities of these predators (Holling 1959; Robertson 1973). Due to the defensive 'screen' (Loiselle 1977) provided by peripheral nests, central males encountered still fewer predators. Peripheral males possibly suffer relatively higher encounter with bullhead than solitary males. The concentrated odor cue from a colony may be a strong attractant, and after their first contact bullhead seem to adopt special search strategies (Treisman 1975).

Unlike the concentrated mobbing in many birds (Lack 1968; Hoogland and Sherman 1976), there was no indication of 'co-operation' among male bluegill during group responses. Cumulative defense in bluegill seems to be a passive result of overlapping defended zones (Fig. 5). Nevertheless, it produced a strong effect on *Lepomis* predation and contributed to repulsion of bullhead. It is unlikely that solitary bluegill males can defend their brood from bullhead attack.

Synchrony during nesting greatly augmented the swamping, screening and cumulative defense, anti-predation attributes of coloniality. Synchrony between colonies reduced the number of predacious conspecifics, and synchrony provides males with a 'head-start' against snail and bullhead predators. This is described by Wiley and Wiley (1980) as a reduction in the response of predators due to a delayed attraction into breeding areas relative to nest availability.

Female bluegill can maximize their benefits from male coloniality by preferentially spawning in (1) the densest regions of a colony, (2) areas where other females are already spawning (during a predation act the probability that a given females' eggs are consumed is inversely related to the number of eggs pre-

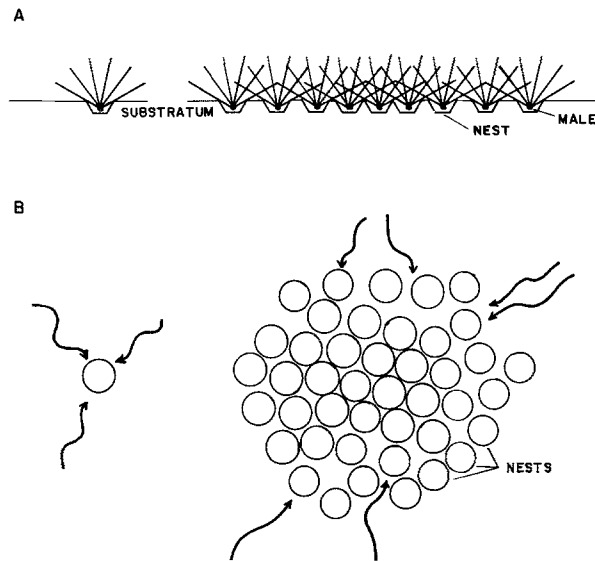


Fig. 5A, B. Schematic representation of colonial defense in bluegill. **A** Cross-section through a colony and a solitary nest. The cluster of lines from each nest represent the strike zone of a parental male. Close nesting results in overlapping defended zones and group defense. **B** Top view. Arrows indicate predator approach. Solitary males are confronted by predators along a 360° territory. This arc of defense is considerably reduced for peripheral males, and central males are screened from predators. Encounter rate in colonies is also reduced by swamping

sent from other females), and (3) in synchrony. These behaviors have been documented for bluegill (Gross 1980).

Evolution of Colonial Nesting

Solitary breeding is probably the ancestral condition in sunfishes (Gross 1980). For coloniality to evolve, the net benefit from group nesting must outweigh that of solitary nesting (Alexander 1974). Benefits and costs are measured under natural selection by their influence on an individual's genetic contribution to succeeding generations. A hypothesis for the evolution of coloniality through benefits associated with foraging can be rejected for sunfishes since neither young nor adults actively feed during the parental care period. This is in contrast to the situation in many birds (e.g., Crook 1966; Krebs 1974). The hypotheses that coloniality arose under selection for population regulation (Wynne-Edwards 1962) or social facilitation (Darling 1938) are also unlikely explanations. Stimulatory effects, restricted to males, probably evolve secondarily (Orians 1961; Hoogland and Sherman 1976), and sunfish do not possess attributes for group or trait-group selection (Maynard Smith 1976; Wilson 1980).

The present results have shown that a selective advantage of colonial nesting is reduced predation

pressure on brood. However, no social behavior is likely to be without attendant costs (Wilson 1975; Hoogland 1979). We noted that clumped nesting (1) permitted predation by neighboring males and ripe females and (2) concentrated odor cues and probably influenced the likelihood of bullhead predation. It also makes possible the transmission of fungal disease (Hoffman 1967; Carlander 1977). These 'cost' factors are being studied but preliminary results indicate that their negative influence on bluegill is very small *relative* to the predation advantages bluegill gain.

How did coloniality evolve? Males are favored by natural selection to maximize their *product* of clutch survivorship and size (number of matings). As the supply of males is not limited (Gross 1980), females are free to choose a dispersion that maximizes brood survivorship. The benefit of increased clutch size through female choice is likely to outweigh male mating costs from close nesting (e.g., cuckoldry, courtship interference, smaller feeding territories). Therefore males will be selected to accept the dispersion pattern largely favored by females.

A possible scenario for the evolution of sunfish coloniality is as follows. In a nonsocial nesting dispersion determined by aggressive territoriality between males, females may prefer mating with dispersed males because, for example, this reduces brood loss through fungal transmission. Under conditions of intense predation, however, it could be favorable for females to choose males with overlapping territories. The antipredation advantages accrued through such choice have been demonstrated above. When this occurs, the aggressive nature of male territoriality would be modified through sexual (and natural) selection, permitting clumped nesting. (This assumes, of course, that female choice outweighs male costs of close nesting.) Differential reproduction, resulting from position within clumps, would discriminate against isolated males and result in male competition for central sites. Continuing selection could then give to a social organization in which conspecifics are a primary stimulus in nest site selection, and females are synchronous spawners. These behaviors characterize the reproduction of bluegill. The evolutionary influences, if any, of non-nesting cuckold males (Gross and Charnov 1980) on colony structure is being considered elsewhere (Gross, in prep.).

An interesting comparison to the evolved coloniality in bluegill is the nonsocial breeding of sympatric pumpkinseed. The proposed evolutionary model for social breeding requires that predation pressures be significantly reduced to outweigh any costs of close nesting. Although Lake Opinicon pumpkinseed were exposed to the same predators as bluegill, they did not suffer the same predation pressure. Snails ac-

counted for over 50% of bluegill predation, yet pumpkinseed were largely unaffected. Pumpkinseed were also relatively exempt from bullhead predation. A parsimonious explanation can be provided for these differences. Pumpkinseed possess morphological and behavioral adaptations for feeding on heavy-bodied molluscs, while bluegill are morphologically adapted to soft-bodied prey such as chironomid larvae and cladocera (Carlander 1977; Keast 1978a). These adaptations allow pumpkinseed to pick up and 'crush' their prey, while bluegill 'delicately' protrude the mouth for semisuctorial feeding in the water column (Keast 1977). As a result of their heavier musculoskeletal system, pumpkinseed probably have superior structural 'preadaptations' for brood defense against bullhead (see Lauder and Lanyon 1980). Pumpkinseed are also behaviorally and morphologically preadapted to manipulate and remove snails attempting nest entry. Functional differences between sunfish species probably play a significant role in determining the type and extent of brood predation experienced, and ultimately selection for patterns of nest dispersion.

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