# PARENTAL INVESTMENT THEORY: TESTS IN BLUEGILL SUNFISH (*LEPOMIS MACROCHIRUS*: CENTRARCHIDAE)

by

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# ABSTRACT

A fundamental goal of parental investment research is to elucidate the rules by which an organism allocates its parental effort. Recent theory has emphasized that an organism providing care will consider not only the value of its brood at stake, but also that of its own expected future reproduction. Because investing into present reproduction reduces the organism's expected future reproduction, the organism faces a tradeoff between present and future allocation of resources (Williams' Principle). This theory, the relative value rule for parental investment, has not been critically tested.

This study documents that bluegill sunfish (*Lepomis macrochirus*) incorporate both the size of their brood (which affects the value of the brood at stake) and their past parental investment (which affects the parent's expected future reproduction) into a decision making process about continued parental investment. The experiment reported here, involving manipulations of a natural population of bluegill sunfish, eliminates the correlation between brood size and past investment which has marred previous experimental research into parental investment theory.

A critical assumption of this experiment was that parental fanning effort of eggs increases with brood size. By manipulating brood sizes and by quantifying parental fanning of eggs, I show that parental male bluegill spend more time fanning larger broods than smaller broods. These results confirm the assumption that fanning effort increases with brood size.

I also document the pattern of parental investment made through the brood cycle of bluegill, and compare it to recent theory concerning the interplay of past investment with the changing probability of brood survivorship. A parent's willingness to defend follows an inverted V-shape through the cycle, peaking between 1 and 2 days after the eggs hatch. The initial increase in defense is explicable as the effect of accumulating past investment (i.e. the decreasing value of the parent's expected future) and the declining phase may be the result of the increasing ability of the fry to avoid nest predators.

My research has therefore provided the first critical test of recent parental investment theory. The results support the theory that the value of the brood relative to that of the parent's expected future reproduction determine a parent's investment into its young.

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# PART A

# GENERAL INTRODUCTION

# PARENTAL INVESTMENT RESEARCH

Parental investment (or parental care) research is concerned with the question of why parents, at a cost to their own future and subsequent reproduction, allocate resources to one or more of their offspring. Along with the study of mating systems, including sexual selection, and life history strategies, including alternative reproductive strategies, it is one of the areas of reproductive biology that is of particular interest to evolutionary and behavioural ecologists. These areas are not strictly discrete, but rather form the foci of a network of research: there are numerous questions within each topic, and each has substantial ties with the others. Particularly important has been the recent application of life history theory to the study of reproductive behaviour. This approach emphasizes the role of tradeoffs (Williams' Principle: Williams 1966), a powerful insight for understanding animal behaviour. This thesis examines parental investment from a life history theory or "tradeoff" approach.

Parental investment can be defined as any investment by a parent which increases its offspring's chances of survival. Parental investments which are behavioural in nature have typically been referred to as parental care; the two terms are often used synonymously.

Carlisle (1982) listed two fundamental goals of parental investment research: (1) to elucidate the rules by which a parent allocates care to its offspring; and (2) to explain the origin and distribution of parental care within and among taxa. To her list I add the following: (3) to predict the form of investment provided by a parent (i.e., what behaviours and morphologies will evolve); and (4) to determine how parental care influences other components of an organism's life history, e.g. its mating system.

The topic of this thesis is the <u>allocation of parental investment</u>. I begin by briefly reviewing the literature on parental investment research to place the work presented in this thesis in proper perspective.

### *Origin and Distribution of Parental Care*

The origin and distribution of care has received extensive treatment in the literature, though mostly at the natural history level. Parental care exists in many animal species and some patterns have emerged in the distribution of parental care states (i.e., male, female, biparental or no care) among major taxonomic groups (see Sargent and Gross, in press). From the descriptive studies (see Breder and Rosen 1966 and Blumer 1979, 1982 for reviews of fish literature) several attempts have been made at evolutionary explanations for the distribution of care states. For example, Gross and Sargent (1985) and van Rhijn

(1984) have recently devised models for the evolution of parental care states in fishes and birds, respectively. Because these models have appeared only recently, they have not yet been tested. Furthermore, the complexity of these models combined with the intrinsic difficulty in measuring the life history parameters involved, will make empirical testing difficult (see Blumer [1985] for a test of one aspect of one model).

### *Form of Parental Care*

Similarly, the form of care present in numerous species has been described, but little predictive theory has been developed. There are over a dozen forms of care in fishes ranging from the guarding of eggs to bubble-nesting (Blumer 1982); however, why a species shows one behaviour and not another is largely unexplained. No doubt morphology influences which forms of care are more likely to evolve in a species -- the elongated bodies of stichaeids (pricklebacks) and anarhichadids (wolf eels) pre-adapt them to wrap around their egg masses, whereas the gibbose body shape of centrarchids (sunfish) prevents this -- but many fish species of similar morphology exhibit different forms of care. Thus, morphology cannot be the sole explanation for the form of care given. Isolated attempts have been made at explaining specific forms of care (e.g. the evolution of mouth brooding [Oppenheimer 1970]) but there has been little effort at developing a general theory for the form of care given.

### *Implications of Parental Care*

The influence of parental investment on other aspects of reproduction has received some attention. For example, several studies have reported mate choice based on mate quality, one aspect of which is the mate's willingness and/or ability to provide parental investment (Downhower and Brown 1980; Bateson 1983; Sargent et al. in press; others). Other researchers have largely ignored parental investment in cases where it should have been examined. For example, Ridley and Rechten (1981) offer several hypotheses for why a female might prefer to mate with a male that is already guarding eggs, but they do not consider the role of parental investment. Understanding how a parent decides to allocate its care will be important in understanding how animals choose their mates and in understanding other aspects of reproductive biology.

### *Allocation of Parental Investment*

This thesis addresses the allocation of parental investment, or how a parent decides how much parental care to provide to its offspring at any particular point in time. Remarkably, although numerous papers have been published on parental investment allocation, particularly in the last 15 years, the research has lacked a concise statement of the theory being tested. Recently, Andersson et al. (1980), Pressley (1981), Carlisle (1982) and Sargent and Gross (1985, in press) applied a life history approach to parental investment, recognizing that because parental investment has a cost, a parent faces a tradeoff between investing in present versus future reproduction (Williams' Principle). The solution to this tradeoff is for the parent to invest according to the value of its brood relative to its own expected future reproduction (Sargent and Gross 1985). This theory, described in detail in Part C, predicts that parameters that affect the value of the brood relative to the parent's future should be incorporated into the decision making process about how much investment to make at any given time.

This question may be complicated by several factors. For example, when a parent and its offspring differ in the amount of parental care they would like the parent to provide ("parent-offspring" conflict: Trivers 1974), the actual amount of care given will depend on the offspring's ability to influence the parent's decisions (Parker 1985). Similarly, if both parents provide care, then the amount of care each provides will be a function of the amount the other provides (Houston and Davies 1985). The complexities of parent-offspring conflict and biparental care suggest that a situation of uniparental care, and one in which we can assume the offspring are not able to influence the parent's decisions about the allocation of care, would be best for testing current developments in parental investment / life history theory.

The critical step in testing current theory is determining whether an animal acts upon the value of its brood relative to its expected future by adjusting its level of investment according to changes in this tradeoff. If this holds true, we may explore the effects of various ecological and life history parameters on parental investment allocation. This should allow us to explain specific patterns in nature (such as changes in parental investment through time) and to predict as yet unobserved phenomena (such as the effect of cuckoldry on parental investment). Finally, we will be able to approach some of the more complex allocation issues such as parent-offspring conflict and biparental care.

## OBJECTIVES OF THIS THESIS

In this thesis I perform experimental work with parental investment in bluegill sunfish (*Lepomis macrochirus*: Centrarchidae). In the remainder of Part A, I describe my study area and provide a synopsis of the reproductive biology of my experimental organism, the bluegill sunfish.

Next, I examine the relationship between brood size and fanning effort (Part B). This tests an important assumption of the experimental design used in Part C.

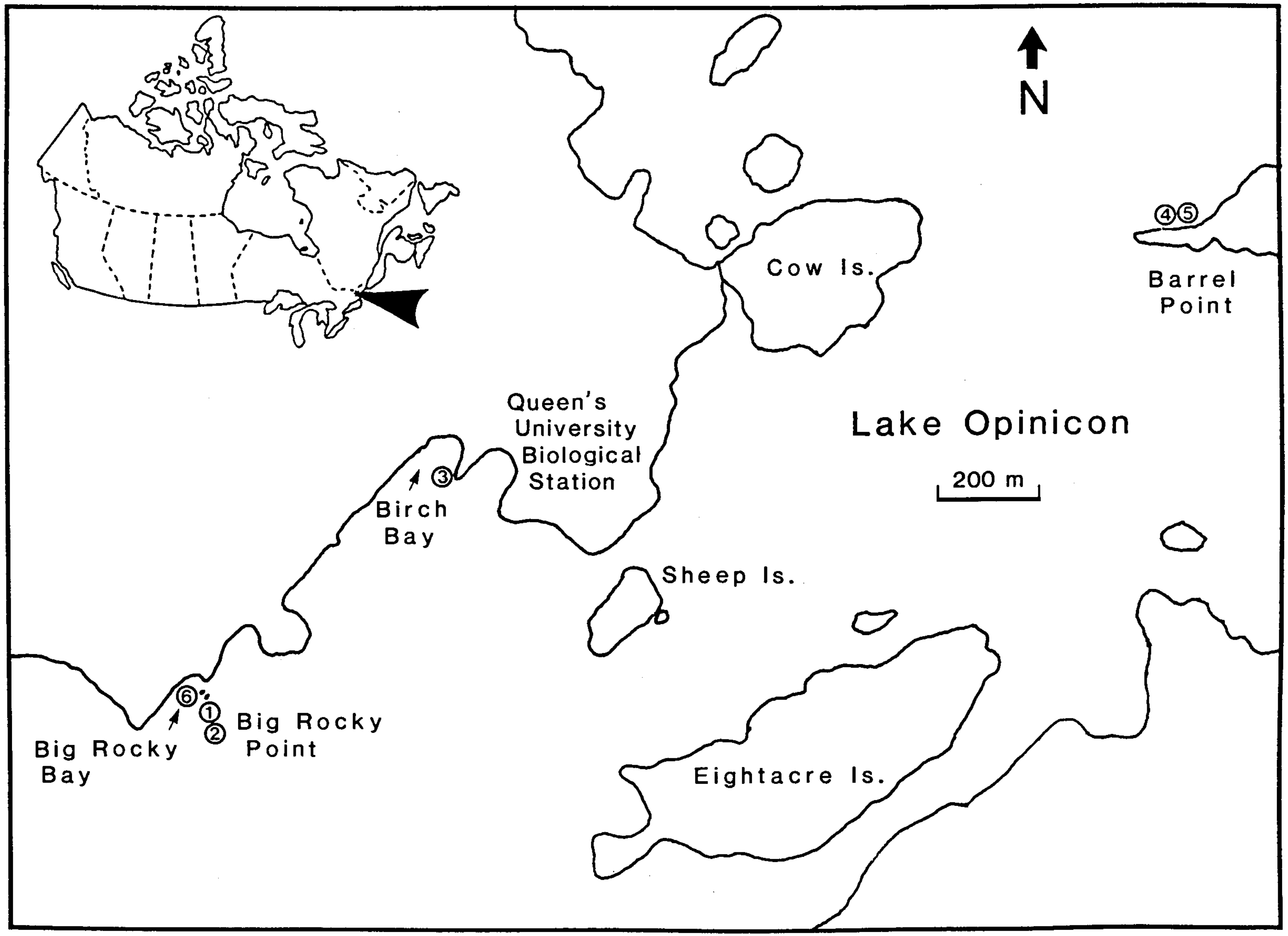
Third, I perform a critical test of the theory of parental investment (Part C).

Fourth (Part D), I describe changes in parental investment through the brood cycle and relate this to the theory of Part C.

## STUDY SITE

The study was carried out in 1984 and 1985 at Lake Opinicon, Ontario (Canada) using the facilities of the Queen's University Biological Station. Lake Opinicon is approximately 900 ha in area, mesotrophic (the physical characteristics of the lake are summarized in Crowder et al. 1977) and contains 18 species of fish, including six species of centrarchids (Keast 1978). The native bluegill population is large and breeding colonies are found in several locations in the lake. This population is well-known and has been the subject of on-going investigations in reproduction (Colgan et al. 1979; Gross 1979; Gross and Charnov 1980; Gross and MacMillan 1981; Gross 1982), behavioural ontogeny (Brown and Colgan 1984, 1985), early life history (Brown and Colgan 1982; Amundrud et al. 1974), and feeding ecology (Keast 1978, 1980, others). Several bluegill colonies were used in my research; their locations are illustrated in Figure 1.

Figure 1: Map of the central section of Lake Opinicon showing the location of the colonies used in the research (Table 1 describes these colonies).


N
Lake Opinicon
200 m
④⑤
Barrel Point
Cow Is.
Queen's University Biological Station
③
Birch Bay
Sheep Is.
Eightacre Is.
⑥
①
②
Big Rocky Point
Big Rocky Bay

# REPRODUCTIVE BIOLOGY OF BLUEGILL SUNFISH

Bluegill sunfish are a colonial breeding centrarchid with exclusive male nest building and male parental care (Miller 1964; Avila 1976; Dominey 1981; Gross and MacMillan 1981). In Lake Opinicon the bluegill breeding season extends from early June to mid-July, although this is variable depending upon water temperature and general climatic conditions. During the non-breeding season, adult bluegill are usually in the deeper portion of the lake, and the first indication of spawning is when increasing numbers of adult males are seen in the shallows. Breeding males are readily identifiable by their large size (typically 175 mm total length) and by the presence of a bright-orange colouration on the breast that persists through the spawning season. Males aggregate at traditional spawning locations where they sweep nests in the substrate using their caudal fins. Nests are frequently packed rim to rim over homogeneous substrate. Nest location appears to be determined predominately by social attraction, indicative of a truly colonial species (Gross and MacMillan 1981). Colony size is highly variable both among sites and for the same site at different spawnings and may number between 5 and 150 males (Table 1).

Male nest building (described in detail by Miller 1964) may last from 1 to 3 days. After this, gravid female bluegill

Table 1: Description of the six bluegill colonies used in the research. Colonies 1 - 3 are from 1984, and 4 - 6 from 1985. Data are means ± 1 SE, and sample sizes are in parentheses.

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Location[1] | Big Rocky Point[2] | Big Rocky Point | Birch Bay Bar[2] | West Barrel Point | East Barrel Point | Big Rocky Bay |
| Water Depth (m) | 1.0 | 1.0 | 1.2 | 0.8 | 0.8 | 0.8 |
| Substrate | gravel | gravel | sand | sand & woody debris | sand & woody debris | sand & organic debris |
| Nesting males | 35 | 66 | 44 | 12 | 30 | 45 |
| Nesting began | June 19[3] | June 29 | July 10[3] | June 21 | June 22 | July 1 |
| Spawning began | June 20 | June 30 | July 11 | June 23 | June 24 | July 2 |
| Eggs hatched | June 24 | July 3 | July 13 | no hatch[4] | June 28 | July 4 |
| Colony deserted | June 28 | July 7 | July 17 | June 28 | July 1 | July 9 |
| Male weight[5] (g) | 99.2±2.1 (27) | 94.9±1.9 (66) | 93.6±1.9 (41) | 97.6±5.2 (12) | 97.6±5.0 (17) | 86.9±4.0 (24) |
| Male length[6] (mm) | 174.0±1.3 (27) | 175.0±1.0 (66) | 176.8±1.2 (41) | 175.3±2.7 (12) | 175.1±1.8 (30) | 171.4±2.0 (23) |
| Male age[7] (years) | --------- | 7.9±0.1 (63) | 7.8±0.1 (39) | --------- | --------- | --------- |

[1] see Fig. 1 for locations in Lake Opinicon

[2] Gross and Nowell (1980) describe these sites

[3] there may have been some nesting activity the previous day

[4] silted over and destroyed by wave action

[5] males were weighed on the last day of the brood cycle, except for colony 4 males which were weighed on June 24

[6] total length

[7] based on scale reading

arrive as a school at the colony and enter the nests to spawn. Spawning activity in the colony lasts for several hours to a day, although occasionally spawning resumes a second day. Each male may spawn with several females and may acquire several thousand eggs in its nest (Gross 1980; pers. obs.). Females depart after spawning, leaving only males to care for the fertilized eggs.

The eggs are guarded against predators and fanned until they hatch, usually after 2 or 3 days. The fry are guarded but not fanned until they leave, an additional 3 to 4 days, after which the adult males also leave the colony to forage. During the 6-7 days of parental care, males do not leave their nest site, even to feed.

During the brood cycle the eggs and fry are under constant predation threat by conspecifics as well as other species, including pumpkinseed sunfish (L. gibbosus), hybrid sunfish (L. gibbosus x L. macrochirus), and bullhead catfish (Ictalurus spp.). These predators can consume significant numbers of eggs or larvae and can in extreme cases remove all offspring from a nest (Gross and MacMillan 1981). Thus, guarding by the parental male is necessary for the survival of the brood (Gross and MacMillan 1981; Bain and Helfrich 1983). The effort required to guard will be largely independent of brood size because males guard the nest "site"; many or few progeny probably demand similar guarding effort for equal probabilities of survival (Williams 1975, p.135).

Fanning is used to move fresh oxygenated water over the fertilized eggs. Male bluegill fan by using pectoral fin movements directed at the eggs. Shortly after the eggs are spawned, a male uses his tail to sweep eggs out to the periphery of the nest. During fanning, a male typically places his tail in the center of the nest and faces the nest edge. He then alternates fanning several strokes with rotating on his tail, thereby moving around a portion or all of the nest circumference. Fanning has been shown to increase with brood size in three-spined sticklebacks (van Iersel 1953) and in pumpkinseed sunfish (Gross 1980); in Part B I demonstrate this for bluegill. Presumably, fanning increases because of the greater oxygen demands in the nest environment due to the increased number of respiring eggs.

A male bluegill may spawn several times in a breeding season; a colony usually goes through two to five brood cycles and specific males are known to have returned to spawn in the same colony (even in the exact same nest) several times (pers. obs.). In some cases males renested as soon as two days after completing a brood cycle. Parental males of ages 7 through 11 are found in colonies, although most are 7 or 8 years old (Table 1).

Parental care has a large cost in terms of survivorship and/or ability of males to participate in future brood cycles. For example, comparing the weights of 11 nesting parental males from Colony 2 at 1900 h on 2 July (just prior to egg hatch; $\bar{x}=102.1$ gm, SE=3.32) with their weights at 1700 h on 6 July (just prior to colony desertion; $\bar{x}=96.5$ gm, SE=3.17) shows an average decrease of 5.4% during 94 hours (paired t-test, $t_{10}=3.66$, $P<0.004$). This time represents approximately 60% of their brood cycle. In the related pumpkinseed sunfish, males lose 9% of their body weight during the egg and fry stages of parental care and approximately 74% of this weight is lost while the eggs are being fanned (Gross 1980). In a related study on the threespine stickleback (Gasterosteus aculeatus), Sargent (1985) found that a male's expenditure on territory defense reduced the number of future brood cycles achieved. Male bluegill also suffer from abrasion to their fins and loss of scales when providing parental care. These damaged tissues are highly susceptible to fungal infections which can decrease adult survivorship.

The synchrony of spawning and parental care activities within a bluegill colony facilitates experimentation in parental investment theory. Although there are differences in male characteristics and behaviour among colonies and even among the individuals of a colony (Gross 1980; Gross and MacMillan 1981), these differences can largely be overcome by randomly assigning individuals to treatments and by using large sample sizes. Another potentially confounding factor in bluegill colonies is the occurrence of a small-bodied alternative male phenotype, called "cuckolder" males, which obtain fertilizations by intruding into spawnings and do not provide parental care (Gross 1982). An uneven distribution of cuckoldry across a colony might influence parental care, although it remains to be documented that parental bluegill alter their parental investment in response to cuckoldry. This problem can be avoided, however, by using colonies free of nearby vegetation since cuckolders do not breed in such colonies.

To test parental investment theory it is frequently necessary to compare the amount of care given by one individual with that of another, or with that of the same individual at a different time. Because the care given by a parent may consist of a large number of associated behaviours, it is usually impractical to evaluate all care given. Furthermore, even if one is able to evaluate a number of behaviours (e.g. Robertson and Biermann 1979; Colgan and Gross 1977), to then compare individuals one must create a weighting system to combine the behaviours into a single score. The results obtained may strongly depend on the weighting system devised. Quantitative scores based on a single important parental care behaviour do not have this drawback.

In the context of guarding, male bluegill perform many behaviours including biting, opercular spreading, and lateral displays amongst others. I chose to consider only biting as a measure of willingness to provide parental care because biting clearly represents the most aggressive behaviour a bluegill can direct at an intruder (Henderson and Chiszar 1977). Wootton (1971), in comparing defensive behaviours in three-spined sticklebacks, found biting to be one of the most consistent measures of aggression.

Parental behaviour can be scored either by observing natural situations involving brood defense (e.g. Anderson 1984), or by introducing a stimulus to initiate the behaviour. The obvious problem with natural situations is that the stimulus is uncontrollable and unreliable. Three different types of introduced stimuli have been used by various researchers, namely: a live animal (e.g. Sevenster 1961; Wootton 1972; Gross 1980); a human intruder (e.g. Barash 1975; Weatherhead 1979, 1982; Carlisle 1985); or a model predator (e.g. Morris 1958; Peeke et al. 1969; Colgan and Gross 1977; Robertson and Biermann 1979; Gross 1980; Pressley 1981).

Using a live animal can be problematic, since it may not present a constant stimulus (threat) to the subject. Human intruders are an ambiguous threat; does the subject perceive the human as a threat to itself, to its brood, or to both? Furthermore, since humans are a novel object to many animals, it is unlikely that responses to humans have been as intensively selected upon as responses to natural predators.

I chose model presentation techniques because they allowed control of the stimulus and avoided the problems described above. The most unrealistic aspect of using a model is that it does not respond to the actions of the subject. The recent ideas of game theory (Maynard Smith 1982) propose that in conflict situations, a combatant should evaluate its opponent's actions (or reactions) as part of determining its own present or subsequent action. A model is passive to attacks; therefore, I used brief periods of presentation and assumed that "opening bids" by a bluegill were indicative of its overall willingness to defend its brood.

# PART B

# BROOD SIZE AND FANNING EFFORT

# INTRODUCTION

Recent models of parental investment theory (Andersson et al. 1980; Pressley 1981; Carlisle 1982; Sargent and Gross 1985) attempt to explain how a parent should allocate its parental effort at any given point in time. To test their theory, Sargent and Gross proposed an elegant experimental design that eliminates the problematic correlation between past investment and brood size (see Part C). A key assumption of the design is that parents with larger clutches perform some behaviour that causes them to invest at a higher rate than parents with smaller clutches. For birds, there is evidence that the cost of incubation increases with clutch size (Biebach 1981; Whittall and Coleman, in prep.). For some fishes, fanning behaviour is a likely candidate.

Fanning is one of the most common forms of parental care in fishes (Blumer 1979). A fish fans by repeatedly moving one or more of its fins (pectoral, pelvic, anal or caudal) over the eggs to push water to the egg surfaces, thereby facilitating gas exchange (Mertz and Barlow 1966; Torricelli et al. 1985). The value of fanning has been demonstrated both in the laboratory and in the field. Artificial agitation of eggs in a manner analogous to fanning greatly enhances the oxygen consumption of eggs (Zoran and Ward 1983). Orange chromide (Etroplus maculatus) eggs that are not fanned develop significantly more slowly than fanned eggs, and with a greater frequency of deformities (Zoran and Ward 1983). Pumpkinseed eggs that are protected from predation but are not fanned suffer 55% greater mortality due to fungal infection than eggs that are fanned (Gross 1980). Numerous experiments on salmonid eggs have also demonstrated the detrimental effects of insufficient oxygen supply to the eggs (Hayes et al. 1951; Garside 1959; Silver et al. 1963; others). Salmonid eggs are not fanned, but are buried in the gravel in streambeds where the current running through the gravel has a similar effect to the fanning provided by a parental fish in other species.

There is good reason to predict that fanning effort should increase with brood size. Daykin (1965) applied mass transfer theory to the problem of fish egg respiration, and although quantitative solutions to the system require the quantification of an immense number of parameters, qualitative predictions were possible. For example, the rate of oxygen transfer from the water to a group of eggs is suggested to vary with several factors including the number of eggs present; the rate of oxygen use within each egg; the water temperature (which affects both the metabolism of the egg and the rate of diffusion of oxygen); the structure of the egg group (planar or clumped); and the water velocity. Empirical evidence supports this: oxygen consumption of eggs increases with egg number, stage of development, temperature, and oxygen concentration (Hayes et al. 1951; van Iersel 1953; Jones 1966; Reebs et al.

1984). Thus, given that the function of fanning is to provide fresh water to the eggs, factors that affect the rate of gas exchange should also affect fanning. For example, van Iersel (1953) and Torricelli et al. (1985) have demonstrated that reducing the concentration of dissolved oxygen in the vicinity of a fanning fish will lead to an increase in fanning effort by that fish. Many other studies have examined fanning; in fact, fanning is probably the most studied of all fish parental behaviours (van Iersel 1953; Morris 1954; Sevenster 1961; Barlow 1964; Mertz and Barlow 1966; van den Assem 1967; Reebs et al. 1984; Torricelli et al. 1985; numerous others). However, most of these studies were done within an ethological framework, describing the behaviour rather than testing specific hypotheses of adaptation. Detailed behavioural records were made, but often of only a very few fish (sometimes as few as one, Morris 1954), and manipulations were generally not done (but see van Iersel 1953). Thus, although this research was valuable for illustrating that behaviour can be quantified, few general statements can be made about the considerable fanning data that were collected.

The present investigation was undertaken to determine whether parental male bluegill alter the amount of fanning they provide, given different brood sizes, and furthermore to determine if such differences cause detectable change in the final condition of the parent fish.

# METHODS

## Colony Site

The study involved a pair of neighbouring bluegill colonies located 0.8 m deep on a sandy bottomed bay on the north side of Barrel Point (see Figure 1). The two colonies will be referred to as the West and East colonies. Two colonies were used because neither alone contained enough males to provide an adequate sample for the experiment. The colonies were within 4 m of one another and occupied ecologically similar habitat. Nests, located rim-to-rim as is typical of bluegill, were readily visible. The shallow, hard-packed, sandy bottom of the bay allowed the use of video in data collection (described below).

Nest building was first seen in the West colony on 21 June 1985 and continued into the next day. Males began nest building in the East colony on 22 June 1985 and this colony developed in parallel with the first but lagged one day behind. For example, spawning occurred on 23 June in the West colony, and on 24 June in the East colony. In both colonies light spawning continued into the second morning but the bulk of the spawnings occurred on the first day. The day after spawning there were 12 bluegill nesting in the West colony (plus 1 *L. macrochirus* x *L. gibbosus* hybrid), and 30 in the East colony (plus 3 hybrids).

## Manipulations

After spawning, each nest (n=42) was marked with a small (5 cm x 7 cm) numbered tile and assigned randomly to one of two samples: Full or Reduced. The day after spawning (approximately 1345 h on 24 June and 1130 h on 25 June for the West and East colonies respectively) all males were caught by hand-net, weighed (to the nearest g) using a Philips portable electronic balance (Philips Electronics Ltd, Scarborough, Ont.), measured (total length, to the nearest mm), and any major abrasions or abnormalities noted. Males were then returned to their nests. Later that day (approximately 1600 h in both cases) I reduced the brood size by approximately 50% (as judged by eye), using a plastic scoop and SCUBA, in the Reduced sample nests. To control for the disturbance of removing the brood, I also intruded with the scoop upon the nests in the Full sample but did not remove any eggs.

Several days into the brood cycle, after the fanning data had been collected, a change in wind direction caused silt and woody debris to fill the nests of the West colony. All these males subsequently abandoned their nests. The East colony was shielded by a pile of rocks and was not severely affected by the silt. Most of the males in the East colony remained on their nests through the rest of the brood cycle.

At the end of the brood cycle (1 July), all remaining males (9 from the Full sample, 8 from the Reduced sample) were collected, re-weighed, and sacrificed for further analysis. (Note that the last day of the cycle is generally characterized by gold-colouration in the eyes of the fry, and by the fry swimming and bouncing along the bottom of the nest. These signs usually indicate that the parental males and the fry will leave the colony that night.)

To ensure that the Full broods were in fact larger than the Reduced broods, all the fry from 5 nests of each sample were collected (using a turkey baster) and placed into separate Mason jars. These fry were then counted in the laboratory.

### Data Collection and Analysis

To compare the fanning activities of males with full versus half broods, I used video equipment to obtain approximately 12 minutes of activity for each of 21 males and then analyzed the video tape for fanning rate and frequency. To obtain recordings, the video camera (RCA model CC011), encased in a custom-built underwater plexiglass housing (by A. Hook, Victoria, B.C.), was mounted on a tripod approximately 1 m from the edge of the nest using mask and snorkel. Actual recordings were taken after the experimenter had retreated beyond the apparent visible range of the fish.

For West colony males, video-taping was done on the afternoon of 25 June and the morning of 26 June. Males of the East colony were video-taped on the afternoon of 26 June. To control for a possible time of day or date effect, I alternated the taping of males from the Full and Reduced samples. As such, any uncontrolled effect should be distributed evenly between the two groups. Due to time and sunlight constraints, not all males in each sample were video-taped.

Fanning activity can be quantified by two parameters: by its duration (how much time does a parental fish spend fanning), and by its tempo or intensity (how fast or strong are the movements of the fanning fish). Some researchers have used "bouts" of fanning -- defined as periods of continuous fanning separated by an arbitrary period without fanning -- as measures of fanning activity (e.g. Mertz and Barlow 1966). The bout concept is useful in describing the temporal pattern of fanning, but complicates analyses of parental effort which are concerned mainly with the total effort expended by the fish. To quantify duration of fanning, a 10 min segment of each male's video tape was examined for the following behaviours: (1) Pectoral Fanning, (2) Tail Sweeping, or (3) other behaviours (including rim circling [see Colgan et al. 1979], chasing intruders or hovering more than 5 cm above the nest bottom). The behaviour of the male on the tape was noted every 5 s. The frequency of each activity was then scored as the number of records of that behaviour out of the 120 total records in the 10 min period (12 records per min). This frequency score provides an estimate of the relative duration of each of the three types of behaviours in the 10 min period.

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

Except where noted, the probability level for significant differences among samples was set at 0.05.

## RESULTS

The object of the manipulation was to make the broods of the Reduced sample roughly half the size of broods of the Full sample. In fact, the average number of fry in the Reduced sample ($\bar{x}$=3459 ± 804[SE], n=5) was 59.7% of the average number of fry in the Full sample ($\bar{x}$=5797 ± 711[SE], n=5). The difference between samples was statistically significant (one-tailed t-test, $t_8$=2.18, P=0.03).

For the analysis of weight loss, only males that remained until the end of the brood cycle could be used (Table 2). For these males, there was no significant difference in either initial weight or length. Males from both samples lost significant amounts of weight through the parental care period (7.3% and 7.5% [paired one-tailed t-tests, $t_8$=5.38, p<0.001; and $t_7$=8.61, p<0.0001] for the Full and Reduced samples respectively); however, there was no significant difference between the samples in either final weight or in the amount of weight lost.

Time spent fanning was significantly different between the two samples (Table 3). Full males spent an average of 66% of their time fanning, compared to the 56% of Reduced males. There was no significant difference in fanning tempo between Full and Reduced males -- the average fanning tempo was 89.3 ±

Table 2: Weight loss of males with Full versus Reduced broods. Data are means ± 1 SE. The t-tests are two-tailed for total length and initial weight, and one-tailed for final weight and weight lost, in keeping with the predictions made.

| | Full | Reduced | $t_{15}$ | P | Combined |
|---|---|---|---|---|---|
| n | 9 | 8 | | | 17 |
| Total length (mm) | 174.1±3.1 | 173.9±3.7 | 0.05 | 0.96 | 174.0±2.3 |
| Initial weight (g) | 108.3±7.4 | 102.0±8.2 | 0.58 | 0.57 | 105.4±5.4 |
| Final weight (g) | 100.4± 6.9 | 94.4±7.7 | 0.59 | 0.28 | 97.6±5.0 |
| Weight lost (g) | 7.9±1.5 | 7.6±0.9 | 0.15 | 0.44 | 7.8±0.9 |

Table 3: Activities of males with Full versus Reduced broods. Data are means ± 1 SE. All tests are one-tailed t-tests.

| | Full | Reduced | $t_{19}$ | P | Combined |
|---|---|---|---|---|---|
| n | 11 | 10 | | | 21 |
| Fanning tempo (beats/min) | 89.3 ± 2.0 | 89.4 ± 3.9 | 0.03 | 0.49 | 89.3 ± 2.1 |
| Frequency of Fanning (periods) | 79.7 ± 4.8 | 67.6 ± 2.3 | 2.22 | 0.02 | 74.0 ± 3.0 |
| Frequency of Tail Sweeping (periods) | 2.5 ± 0.6 | 2.9 ± 0.8 | 0.44 | 0.33 | 2.7 ± 0.5 |
| Frequency of other behaviours[1] (periods) | 37.8 ± 4.8 | 49.5 ± 2.2 | 2.13 | 0.02 | 43.4 ± 3.0 |

[1] includes hovering more than 5 cm above the nest, rim circling and chasing intruders, though the latter two behaviours are rare in comparison with hovering

9.5[SD] (n=21) beats per minute. Likewise, frequency of Tail Sweeping did not differ between the samples. The increase in Other Behaviours is accounted for by an increase in hovering greater than 5 cm above the nest: rim circling and chasing intruders remained rare.

# DISCUSSION

The results show that bluegill with large broods provide greater fanning effort than those with small broods. They do so by spending more time fanning larger broods than small broods. The tempo of fanning, however, does not change with changes in brood size.

These results are consistent with findings for other species. Gross (1980) compared the fanning frequency of parental male pumpkinseed sunfish (<u>Lepomis gibbosus</u>) with various numbers of eggs in their nests and found that males with more eggs fanned significantly more frequently than males with fewer eggs. He did not examine fanning tempo. Unfortunately, because he used natural variation in egg number we do not know whether the difference in fanning was due to the differences in egg number or due to some characteristic of the male correlated with egg number. For example, large, healthy males are more likely to attract females and therefore they will probably acquire more eggs in their nests than less robust males (Gross 1980). Robust males will also have larger body reserves and thus be able to fan more. Therefore, the correlation between fanning effort and brood size may be spurious.

Van Iersel (1953) examined the fanning frequency of male three-spined sticklebacks (*Gasterosteus aculeatus*). By manipulating the number of clutches that each male cared for, he showed that time spent fanning increased with the number of clutches in the nest. Van Iersel did not report quantitative data on fanning tempo, but he did state that tempo appeared to remain the same for an individual, although there were differences among individuals.

Why do parental male bluegill change their fanning frequency and not their fanning tempo? Although the question is not central to my research, the answer is probably rooted in the mechanics of how fins move water. According to Daykin (1965), the return in oxygen exchange capacity due to increases in current velocity increases with diminishing returns; thus, it may not pay a fish to fan faster as much as it pays it to fan for greater duration. For species in which the parent attempts to court additional females during the parental phase (e.g. parental sticklebacks will court other females, Sargent 1985; whereas bluegills court only during the brief spawning period) the increased time devoted to fanning larger broods may be at the expense of additional matings, thus it may be worthwhile to fan faster rather than longer. There are insufficient data in the literature to test this prediction.

The prediction that males which fan more should lose weight faster than other males was not supported. Both groups of males did lose significant amounts of weight over the brood cycle, but the losses were not different between the groups. Parental males do not leave the nest during the brood cycle to feed so it is not surprising that they lose large amounts of weight. I do not know how much of this weight loss is due to fanning activity, although males do spend substantial amounts of time fanning (males with Full broods spent approximately 66% of their time fanning in the video recordings). The large variation in initial body weights and the problems of using wet body weight as an indicator of condition (Unger 1983), combined with the fact that the design did not involve paired samples may explain why no differences were found. Demonstration of the cost of this additional fanning may have to wait for more accurate and precise measures of physiological cost (e.g. Sargent 1985).

# SUMMARY

I have provided an experimental test of the hypothesis that fanning effort of male bluegill sunfish increases with the number of eggs in their nest. By manipulating the number of eggs and by quantifying the frequency and tempo of fanning in the field using underwater video equipment, I have shown that parental male bluegill fan larger broods more frequently than smaller broods. However, the fanning tempo (beats per minute) does not change with changes in brood size. This result is consistent with that found in other studies of fish species.

# PART C

## PARENTAL INVESTMENT DECISION RULES: A TEST IN BLUEGILL SUNFISH

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# INTRODUCTION

The theory of life history evolution (Williams 1966; Stearns 1980; Charlesworth 1984) proposes that natural selection will favour behaviours which maximize lifetime reproductive success. However, it is not always clear which of many possible alternative behaviours will do so. Consider an animal with offspring. This animal has two potential means by which it may gain reproductive advantage: (1) through continued investment into present progeny (thus increasing offspring survivorship and fertility), or (2) by investment into expected future progeny (through increased adult survivorship and fertility). Because investment allocated to present reproduction is usually forfeited from future reproduction, the parent should optimize the tradeoff between present and future allocation (Williams 1966). But, by what "decision rule" does a parent determine its optimal level of present investment?

I begin with a brief review of the theory related to how parents decide upon their investment into present progeny. Next, I provide an experimental test of parental investment in a fish which has solitary male parental care of its young, the bluegill sunfish (*Lepomis macrochirus*). I show that male bluegill appear to allocate their parental investment through a decision rule based upon the value of both their present brood and, through its relationship to past investment, their own expected future reproduction.

## Parental Investment Decision Theory

During the last three decades, parental investment theory has been influenced by concepts from ethology, ecology, and life history theory. Ethology suggested that offspring have a "stimulus" value which induces parental behaviour in an adult (e.g. van Iersel 1953; Kramer and Liley 1971). A greater number of offspring should therefore lead to an increase in parental care (Kramer 1973). Ecological theory, by contrast, suggested that the "cost" of parental care would greatly influence a parent's willingness to invest (Orians 1969). Trivers (1972), incorporating life history theory (Williams 1966), suggested that parental investment is best measured by its cost to subsequent reproduction. He defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (Trivers 1972, p. 139).

Few people have appreciated how the cost of investment may influence parental investment behaviour. For example, Trivers developed an argument for parental investment that assumed that selection acted to minimize wastage of past investment. Minimizing wastage of past investment, however, will not maximize lifetime reproductive success if it involves throwing good investment after bad (Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977). Doing so has become known as committing the Concorde fallacy (Dawkins 1976). Several authors have suggested that animals do in fact commit the Concorde fallacy. Weatherhead (1979, 1982) and Dawkins and Brockmann (1980), for example, have applied the term "Concorde fallacy" to any situation in which present investment is based on past investment. However, as I will show, a relationship between past investment and present decision making need not constitute committing the Concorde fallacy. In fact, using past investment to decide the current level of investment can be a useful investment strategy.

Recently, Andersson et al. (1980), Pressley (1981), Carlisle (1982) and Sargent and Gross (1985, in press) proposed that animals should invest according to the value of their brood relative to their own expected future reproduction. The optimal level of parental investment occurs when the rate of return on investment into the present is equal in magnitude to the rate of return on investment into future reproduction. Therefore, parameters that affect the value of the brood relative to that of the parent's expected future reproduction should be incorporated into the decision making process about how much to invest at any given time, i.e. the optimal parental investment decision rule.

The value of the brood, or the probability that the parent will gain fitness through it, is a function of their number (brood size), their probability of surviving to reproduce, and their relatedness to the parent. The value of the parent's expected future reproduction can be influenced by many things, including past investment, the sex ratio, and the amount of time remaining in the breeding season. However, because selection works within constraints, animals may or may not incorporate each of these parameters into their parental investment decision rule.

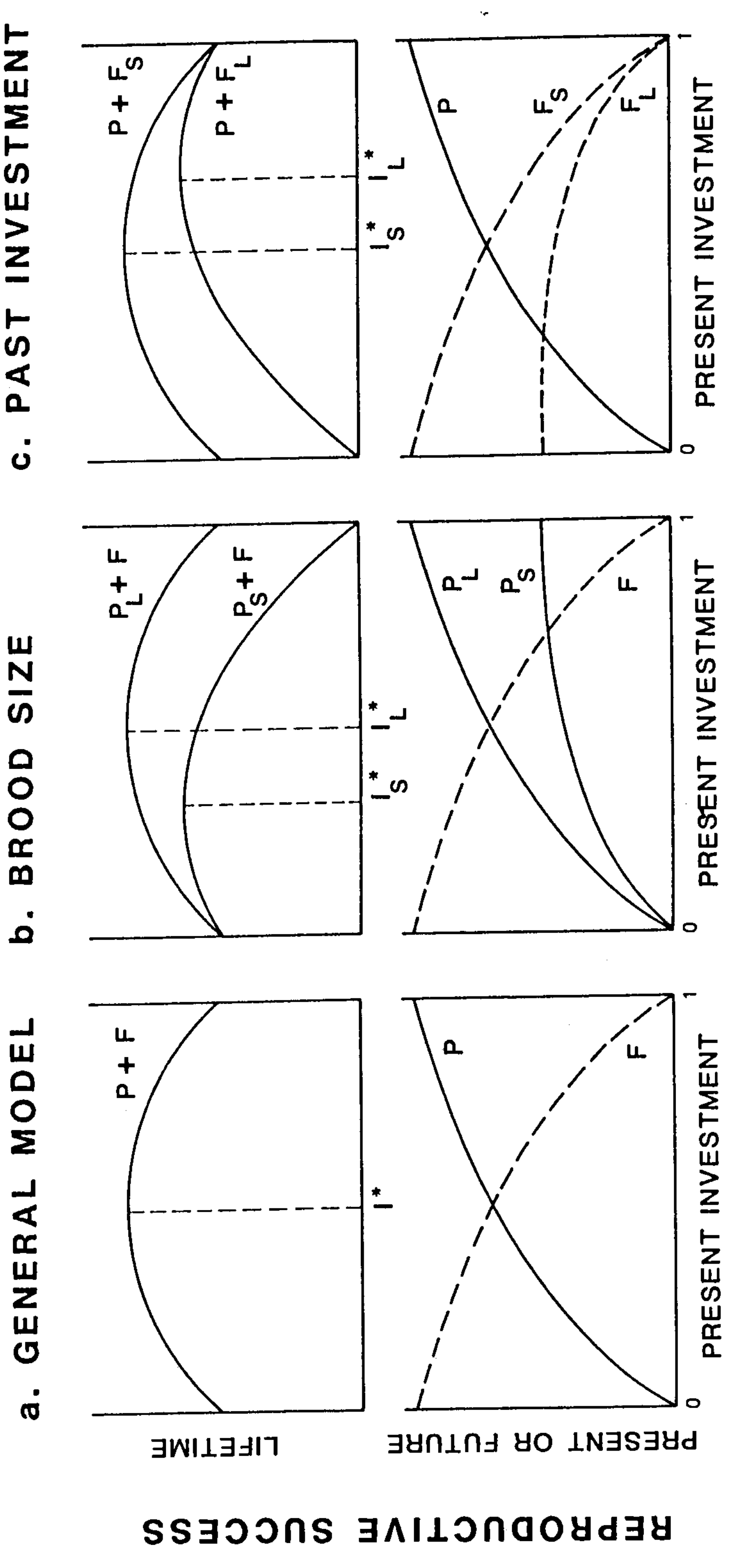
In this chapter, I provide an empirical test of the effects of two parameters, namely brood size and past investment. From Sargent and Gross (1985) I derive the prediction that the optimal level of present investment maximizes the sum of present and future reproductive success (Fig. 2a). Therefore, a decrease in brood size (such as by predation) decreases present reproductive success and should result in a decrease in the total amount of care a parent provides (Fig. 2b). Because reproduction has a cost, past investment is related to the expected future reproduction of the parent (Williams 1966). A parent which has invested heavily in the past has less expected future reproduction (e.g. Fagerstrom 1982; Sargent 1985), and therefore an increase in past investment will increase the optimal level of present investment (Fig. 2c). More precisely, animals could use either past investment _per se_, or present condition, the direct result of past investment, as a predictor

Figure 2: The optimal level of present investment

a. The effect of present investment on reproductive success. Present reproductive success (P) is assumed to increase with diminishing returns with present investment, while future reproductive success (F) is assumed to be a decreasing function of present investment. Lifetime reproductive success (P+F) is the sum of present and future reproductive success. The optimal level of present investment, that which maximizes lifetime reproductive success, is indicated by $I^*$. Sargent and Gross (1985) have shown that present and future reproductive success need not be equal at $I^*$, but the rate of return from each will be equal in magnitude.

b. The effect of different brood sizes, large (L) and small (S), on $I^*$ assuming equal past investment. A decrease in brood size reduces present reproductive success from $P_L$ to $P_S$, and $I^*$ for a small brood ($I_S^*$) is thus less than that for a large brood ($I_L^*$).

c. The effect of different levels of past investment, large (L) and small (S), on $I^*$ assuming equal brood sizes. An increase in past investment decreases future reproductive success from $F_S$ to $F_L$, and $I^*$ for large past investment ($I_L^*$) is thus greater than that for small past investment ($I_S^*$).


a. GENERAL MODEL
b. BROOD SIZE
c. PAST INVESTMENT
REPRODUCTIVE SUCCESS
LIFETIME
PRESENT OR FUTURE
P + F
I*
P
F
P_L + F
P_S + F
I*_S
I*_L
P_L
P_S
F
P + F_S
P + F_L
I*_S
I*_L
P
F_S
F_L
0
1
PRESENT INVESTMENT

of expected future reproduction. Separating these two is beyond the scope of this chapter, and for simplicity and consistency with the literature I use the term past investment to indicate the effect of past investment on present condition and hence expected future reproduction.

## Parental Investment Decision Rules

From the principle that animals should invest according to the value of their brood *relative* to their own expected future reproduction, we can construct four plausible decision rules incorporating combinations of brood size and past investment.

1. *Invest according to brood size*: The "brood size" hypothesis states that a parent should invest according to the number of progeny in its care.

2. *Invest according to past investment*: The "past investment" hypothesis suggests that a parent invests according to the amount of investment already put into its brood. I emphasize that to do this does not necessarily constitute committing the Concorde fallacy, although it is consistent with committing the Concorde fallacy.

3. *Invest according to both brood size and past investment*: I assume here that if an animal were sensitive to both brood size and past investment, the net effect on present

investment is qualitatively predictable in some cases. For example, if both parameters change so that each separately predicts an increase in present investment, then the net effect of the two together will be a greater increase in present investment than for either one alone. However, they may also change so as to have contradictory effects on present investment, in which case I make no attempt to predict the net effect on present investment since this would require quantification of each effect.

4. Invest according to neither brood size nor past investment: The "null" hypothesis for parental investment decision rules is that a parent is either not sensitive to brood size or past investment, or it does not act on this information. Semelparous animals (or iteroparous animals during their last reproductive bout) might be expected to behave in this way since they have no reproductive future beyond the brood at stake.

## Testing Investment Decision Rules

Testing alternative decision rules is difficult because in natural situations brood size and past investment are likely to be positively correlated, thus making it difficult to separate the effects of each on present investment. An experimental design for discriminating among parental investment decision rules has been suggested by Sargent and Gross (1985). The design calls for three treatments, each treatment consisting of a sample of families (i.e., individual parents with a clutch of eggs) that can be manipulated independently of other families. In one sample, the number of brood in the nests is reduced soon after oviposition (the Early sample). The brood size of the second sample is reduced later in the brood cycle, when parental investment has accumulated (the Late sample). Finally, the brood size of the third sample is not reduced (the Control sample).

If the interval between the first and second brood reduction is characterized by parental behaviours that increase in intensity or frequency with brood size (cf. incubation in birds [Biebach 1981], fanning in fishes [van Iersel 1953; Part B of this thesis]), parents with larger broods will make a greater investment into the brood than those with small broods. When the three samples are compared after the late reduction, the Control sample therefore has large brood size and large past investment, the Late sample has small brood size and large past investment, and the Early sample has small brood size and small past investment.

If each parent's willingness to invest is quantified after the second brood reduction, using a behaviour that does not increase by necessity with brood size, the alternative decision rules make distinct predictions about how parental investment will compare among the three samples. These are:

| Decision Rule | Predicted Investment |
|---|---|
| 1. Brood size | Control > Late = Early |
| 2. Past investment | Control = Late > Early |
| 3. Brood size and Past investment | Control > Late > Early |
| 4. Null | Control = Late = Early |

# METHODS

## Colony Site

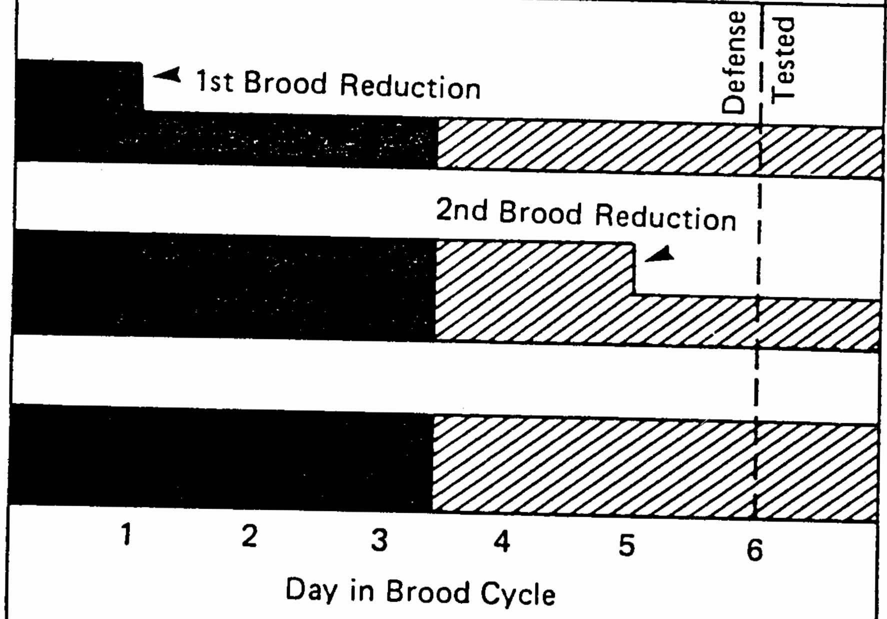
This study involved a breeding colony located 1 m deep on a flat rock shelf, Big Rocky Point (Gross and Nowell 1980). The shelf is covered with fine gravel and has little vegetation. The lack of vegetation and the threat of predators excluded "cuckolders", a small-bodied alternative male phenotype (Gross 1982), from spawning at this site. Thus, all broods in the nests were fathered by the parental males.

## Manipulations

Approximately 66 bluegill males began to construct nests on 29 June 1984. Spawning began late the next day and continued for a few hours into the morning of 1 July. After the spawning, I assigned nests randomly to one of four samples: Early (n=7), Late-1 (n=15), Late-2 (n=10) and Control (n=18). The Late-2 sample, an addition to the Sargent-Gross design, is discussed below. Each nest was marked with a small (5 cm x 7 cm) numbered tile; nests with unusually few or many eggs were not used.

For the Early sample, brood size was reduced in the afternoon of 1 July (Fig. 3). Approximately 50% of the brood

Figure 3: The experimental design. Males fan and guard their brood before hatching (solid bars), but only guard after hatching (hatched bars). The day in the brood cycle corresponds coincidentally to the date in July when the experiment was conducted. The chart of the size of the brood, parent's past investment, and relative value of the brood to the parent's expected future are for day 6, when the parent's brood defense was tested (see text).

| SAMPLE | MANIPULATION | BROOD SIZE | PAST INVESTMENT | RELATIVE VALUE |
|---|---|---|---|---|
| Early |  | Small | Small | Low |
| Late<br>(Late 1<br>& Late 2) | | Small | Large | Medium |
| Control | | Large | Large | High |

as judged by eye was removed from each nest using a plastic scoop and SCUBA. For the Late samples, a 50% reduction was made in the morning of 5 July, after all the eggs had hatched (and males had ceased fanning). To control for the disturbance of removing brood, at the time of both the first and second reductions all nests not being reduced in brood size were intruded upon with the plastic scoop. The exception is the Late-2 sample which, while otherwise treated the same as the Late-1 sample, was not manipulated with the plastic scoop during the first reduction. By comparing the Late-1 and Late-2 samples, I could determine whether the act of intrusion with the plastic scoop had an effect separate from that of reducing the brood. All possible perturbations on the male nesting cycle were therefore controlled.

### Data Collection and Analysis

Parental defense was measured by scoring each male's aggression to the same potential brood predator -- a model of a bluegill. Free-swimming bluegill are important predators on conspecific eggs and larvae but are not a threat to the nest site because males do not take over each others' nests during the brood cycle (Gross and MacMillan 1981). Parental aggression towards a predaceous bluegill involves a risk of injury and an energetic cost. Thus aggressiveness of a male towards a model presented at the nest perimeter can be used to measure willingness to invest in the brood (see also Colgan and Gross 1977).

The model was constructed from a photographic print of a bluegill in Hubbs and Lagler (1958, Plate 38). The print was glued to a clear plexiglass backing, covered with epoxy resin, and attached to a plexiglass handle. The size of the model (153 mm total length) was chosen to be approximately 10% smaller than the average nesting male, and smaller than any individual parental male: large enough to be a real threat to the brood and small enough to not over-intimidate the guarding male.

For each trial, the observer (wearing a mask and snorkel) moved the model predator in a figure-8 pattern for 30 s at the edge of a nest and recorded the number of bites it received from the nest owner. The presence of the observer did not appear to affect the behaviour of nesting males. The bites were tabulated using push button counters, then recorded on underwater tablets at the end of each trial. All males were tested within 2 two-hour periods on July 6. Tests were made around 1100 h and again at 1500 h (EST).

Immediately after the second defense test, males were caught, weighed using a 300 g Pesola spring balance (2 g divisions) and measured (total length, to the nearest mm), and 2-3 scales were taken from the "key scale area" for aging

(Gross 1982). The length and weight data were used to calculate Fulton's condition factor (weight x $10^5$ / length$^3$), presumed to be an estimate of body condition or robustness (Carlander 1977).

The defense scores, averaged for the two tests, were transformed to their common log (defense score + 1) equivalents to meet the assumptions of normality and homogeneity of variance for statistical analysis. Therefore, defense scores reported here are in the transformed scale and symmetrical standard errors are given. Except where noted, the probability level for significant differences among samples was set at 0.05.

# RESULTS

There were no statistically significant differences among the 4 samples in either parental male age, length, weight or Fulton's condition factor (Table 4, analysis of variance [ANOVA], age: $F_{3,41}=1.68$, $P=0.19$; length: $F_{3,44}=0.36$, $P=0.78$; weight: $F_{3,44}=0.64$, $P=0.59$; Fulton's condition factor: $F_{3,44}=0.72$, $P=0.54$). Furthermore, the defense scores for the Late-1 and Late-2 samples did not differ significantly (two-tailed contrast with pooled variances, $t_{46}=0.54$, $P=0.59$). I concluded that the disturbance caused by removing brood had no significant effect on male defense, and combined Late-1 and Late-2 into one sample (Late) for subsequent analysis.

An ANOVA revealed significant differences in male brood defense among the three samples: Early, Late and Control (Figure 4, $F_{2,47}=6.62$, $P<0.003$). Furthermore, one-tailed planned non-orthogonal contrasts with pooled variances adjusted to an error probability of 0.025 (Sokal and Rohlf 1981, p.242) are significant for the Control vs. Late ($t_{47}=2.01$, $P<0.025$) and Late vs. Early samples ($t_{47}=2.28$, $P<0.014$). Note that adjustment of the critical acceptable error rate to 0.025 is considered a conservative approach to analyzing multiple comparisons (Sokal and Rohlf 1981). The parental defense of males in the three samples is therefore ranked statistically as Control > Late > Early, consistent with hypothesis 3: invest

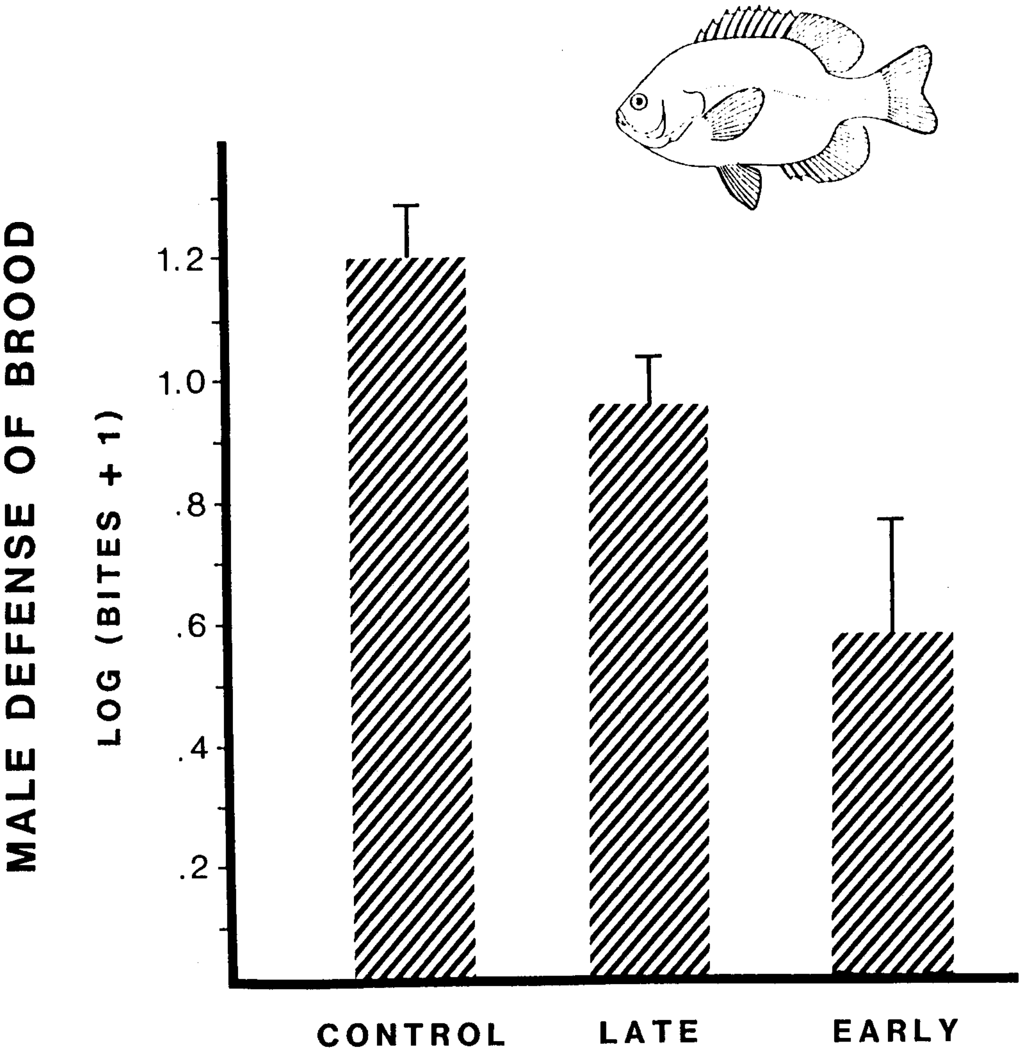
Table 4: Comparison of male characteristics. A description of Early, Late-1, Late-2, and Control sample males. The combined data for the two Late samples are also presented as the Late column. Data are means ± 1 SE, sample sizes are in parentheses.

| Variable | Sample | | | | |
|---|---|---|---|---|---|
| | Early | Late-1 | Late | Late-2 | Control |
| Age | 8.0±0.3 (6) | 8.3±0.2 (14) | 8.0±0.2 (23) | 7.6±0.2 (9) | 7.9±0.2 (16) |
| Length | 175.2±2.0 (6) | 175.4±2.4 (15) | 174.6±1.8 (24) | 173.3±2.8 (9) | 177.1±2.3 (18) |
| Weight | 90.2±3.6 (6) | 94.7±3.9 (15) | 93.1±2.8 (24) | 90.6±3.9 (9) | 97.4±3.8 (18) |
| Fulton's Condition Factor | 1.67±.04 (6) | 1.74±.03 (15) | 1.74±.02 (24) | 1.73±.04 (9) | 1.74±.02 (18) |

according to both brood size and past investment.

A secondary prediction from the experimental design is that the Control and Late males should show a greater decrease in body condition over the brood cycle than the Early sample because the former were investing at a greater rate. However, I did not measure male weights at the start of the experiment because I might have seriously disrupted colony activity. An analysis of covariance (ANCOVA; Sokal and Rohlf 1981) of final weight on length$^3$ reveals no significant differences between the Early sample and the Late and Control samples combined ($F_{1,45}=2.01$, $P=0.18$).

Figure 4: Defense scores for Early, Late and Control males. Error bars indicate 1 SE.


MALE DEFENSE OF BROOD
LOG (BITES + 1)
1.2
1.0
.8
.6
.4
.2
CONTROL
LATE
EARLY

# DISCUSSION

The results of the experiment unambiguously support hypothesis 3, and reject the alternatives. Thus, parental investment in bluegill sunfish is consistent with a decision rule that incorporates both the past investment made by the parent and its current brood size. This supports the theory that the value of the brood relative to that of the parent's expected future reproduction determines a parent's investment into its young (Sargent and Gross 1985).

Several previous studies are consistent with these findings, but they did not control for alternate explanations. For example, Kramer (1973) working on blue gouramis (Trichogaster trichopterus), van Iersel (1953) and Pressley (1981) working on three-spined sticklebacks (Gasterosteus aculeatus), and Carlisle (1985) working on a cichlid (Aequidens coeruleopunctatus) found an increase in parental care behaviour with an increase in brood size, which is consistent with these results but does not test the effect of past investment. Robertson and Biermann (1979) attempted to hold past investment constant and reported an increase in brood defense with an increase in clutch size for redwinged blackbirds (Agelaius phoeniceus): However, their experimental design assumes that the cost of incubation does not increase with clutch size (contrary to Biebach [1981]). Furthermore, studies using natural variation to test the effect of brood size on present investment (e.g. Pressley 1981) do not control for differences among parents in ability to provide care. For example, parents which are more robust may provide larger parental investment than less robust parents, even though the proportional allocation of investment to present reproduction may be the same; and they may obtain larger clutches because of their ability to obtain superior territory sites. This emphasizes the importance of manipulative experimentation for resolving questions of parental investment allocation. In addition, several studies (e.g. Barash 1975; Weatherhead 1979; Dawkins and Brockmann 1980) have found a correlation between past investment and present investment: However, these studies have not critically tested among alternative explanations for the correlation.

The prediction that Control and Late males should have inferior body condition than Early males at the end of the brood cycle was not supported. This may be because wet body weight is not a reliable indicator of body condition. For example, Unger (1983) has found that parental fathead minnows (<u>Pimephales promelas</u>) selectively maintain their body weight through the brood cycle by retaining water. Selective retention among bluegill males may also obscure energy deficiencies. Unfortunately, other factors such as abrasion to fins and scale loss that are associated costs of parental behaviour, which will affect future reproductive success, were not evaluated. In addition, measurement error incurred while using the Pesola spring balance in the field may have obscured weight differences.

In this experiment I did not determine whether past investment may affect the value of the brood as well as the parent's expected future reproduction. It is this aspect of past investment that has received the greatest attention in the literature. Past investment reduces the amount of future investment necessary to bring offspring to independence. If, for example, an offspring requires 100 units of food before it can become independent, then a parent that has invested 75 cumulative units may well do better by investing 25 more than by abandoning its offspring to start a second with 0 cumulative units. Thus some forms of past investment increase the value of the brood. This is not true, however, for guarding as seen in bluegill. A bluegill brood that has been continually guarded is probably no closer to independence than one that has been sporadically guarded; therefore, the brood has the same value whether the parent invests a little or a lot. It is not clear whether fanning increases the value of the brood, or whether the differences in fanning between the small and large broods in the experiment translate into differential probabilities of survival per offspring. If the eggs in the reduced broods received a greater amount of fanning per egg, (and they do, Part B), and if this translates into an increase in brood value, then we might expect the Early sample males to have defended slightly more than originally predicted.

My findings suggest that constraints to animal behaviour under which selection molds parental investment may be less restrictive than other studies have suggested (e.g. Weatherhead 1979, 1982; Dawkins and Brockmann 1980). Using the parental investment decision rule, we may now properly address a wide range of parental investment issues including: (i) changes in brood defense through the brood cycle (Sargent and Gross, in press); (ii) mate desertion (Trivers 1972; Grafen and Sibly 1978); (iii) filial cannibalism (Rohwer 1978); and (iv) changes in brood defense with variable environments (Carlisle 1982). Research into these and other areas of parental investment may reveal additional parameters to which animals are sensitive, and these should ultimately be included in a more refined understanding of parental investment.

This work also gives us new insight into mating system dynamics, especially female spawning tactics. If males invest according to the value of their brood relative to their expected future reproduction, we expect that females will have evolved to take advantage of this behaviour. For example, if a female has the opportunity to mate with one of two males, the first of which already has eggs in his nest, and the second of which does not, I predict that she will choose to mate with the first male. Assuming all else is equal, the female can expect that eggs in the first male's nest will receive more care (and therefore have greater survivorship) than eggs spawned alone in the second nest, because the larger number of eggs in the first nest will be of more value to the male. Secondly, females may choose older males or those with less probability of future breeding cycles because they will invest more in present reproduction. In this way, the parental investment decision rule may have broad influences on mating system dynamics.

Finally, do animals commit the Concorde fallacy? The original idea of the Concorde fallacy was that an animal should not behave so as to minimize wastage of past investment, rather it should maximize expected future benefits. This idea gave rise to the hypothesis that if an animal was found to base present investment on past investment, then it must be committing the Concorde fallacy (e.g. Weatherhead 1979, 1982; Dawkins and Brockmann 1980). For this reason, Carlisle (1985) recently concluded that some animals do commit the Concorde fallacy and others do not. However, it is clear when we incorporate life history theory into parental investment models that past investment is likely to be an important component of the parental investment decision rule, as this study shows for bluegill sunfish, and thus the above hypothesis is incorrect. Moreover, to commit the Concorde fallacy an animal would have to behave so as to minimize wastage of past investment while being fully capable of greater lifetime reproductive success by not doing so. Natural selection cannot favour such sub-optimal behaviour. Therefore, just as we assume that animals behave optimally (sensu Maynard Smith 1978), we assume that they do not commit the Concorde fallacy.

# SUMMARY

I have reviewed parental investment decision theory and provided an experimental test of the decision rule used by male bluegill sunfish (Lepomis macrochirus) in allocating parental investment to their young. The alternative decision rules tested were: (1) invest according to brood size (number) only; (2) invest according to past investment only; (3) invest according to both brood size and past investment; and (4) invest according to neither brood size nor past investment. By manipulating brood size independently of a male's cumulative investment in the brood, and by measuring each male's defensive behaviour against a model predator, I found that male bluegill invest according to both brood size and past investment. This result is consistent with recent theory that past parental investment devalues adult future reproductive value, and that animals should therefore invest according to the value of their brood relative to that of their own expected future reproduction.

# PART D

# PARENTAL INVESTMENT THROUGH THE BROOD CYCLE

# INTRODUCTION

To maximize lifetime reproductive success, a parent must resolve the tradeoff between investment into present versus future reproduction. Recent theory (Andersson et al. 1980; Pressley 1981; Carlisle 1982; Sargent and Gross 1985) predicts that a parent may resolve the tradeoff by investing according to the value of its brood relative to the parent's own expected future reproduction. From this we can predict that parameters affecting the relationship between present and future reproduction will be incorporated by a parent into its parental investment decision making process.

Sargent and Gross (in press) have recently applied their theory of parental investment to a variety of parental care situations. One of these is parental investment through the brood cycle. According to their relative value rule, which I tested and confirmed in Part C, accumulation of parental investment through the brood cycle should result in the parent increasing its level of parental care with time. However, the return on investment will likely decrease at some point after the eggs hatch as the fry start to obtain resources for themselves and increase in their ability to survive without the parent. Therefore, the pattern of parental investment through the brood cycle should include an increasing phase, followed by a decreasing phase as the fry gain independence.

There are a number of data sets in the literature on the pattern of fanning effort through the brood cycle (Table 5a), and these generally agree with the predictions of the theory, showing an inverted V shape peaking around hatching. However, as Sargent and Gross (in press) have pointed out, there is an alternative explanation for this pattern in fanning effort: the oxygen consumption of eggs is known to increase dramatically through the brood cycle (Hayes et al. 1951; Jones 1966; Zoran and Ward 1983). Thus, parents may be adjusting their fanning effort to the increasing oxygen requirements of the eggs, or they may be incorporating both past investment and the oxygen requirements into their decisions about fanning. The increase in oxygen consumption continues after hatching, but at hatching the egg loses its spherical shape and the newly hatched larvae has a much greater surface/volume ratio than the egg from which it came (Hayes et al. 1951). Furthermore, once the larvae can move, it can actively influence its oxygen acquisition. Experiments have shown that when Atlantic salmon (<u>Salmo salar</u>) eggs which are artificially hatched are compared to eggs just about to hatch, the larvae of the hatched eggs are able to withstand an oxygen tension 61% of that required at the egg stage (Hayes et al. 1951). This has been attributed to the greater oxygen acquiring abilities of the larvae. Thus although oxygen consumption continues to increase from the egg through the fry stage, the value of fanning decreases and fanning effort should therefore decline.

Table 5: Changes in parental investment through the brood cycle. The following data sets were obtained from the literature. For measures of fanning effort I have reported duration data where possible, although some authors present other measures as well. Similarly, for brood defense, I used bites/time where possible. A Λ in the trend column indicates effort peaked in the middle of the brood cycle, whereas a V indicates the opposite. In the Max/min column (-) hatch means the max/min occurred a day or two before hatch, whereas (+) hatch means a day or two after hatch.

| | Species | Measure | Trend | Points[1] | Max/min | Reference |
|---|---|---|---|---|---|---|
| a. FANNING | | | | | | |
| 1. | Three-spined stickleback[2] | duration | Λ | 4 | (-) hatch | Sargent & Gross (in press) |
| 2. | Three-spined stickleback | duration[3] | Λ | 12 | (-) hatch | Wootton 1984 |
| 3. | Three-spined stickleback | duration[3] | Λ | 11 | (-) hatch | van Iersel 1953 |
| 4. | Three-spined stickleback | duration | Λ | 9 | (-) hatch | Segaar 1961 |
| 5. | Three-spined stickleback | duration[3] | Λ | 12 | (-) hatch | Wootton 1971 |
| 6. | Three-spined stickleback | duration[3] | Λ | 13 | (-) hatch | Black 1971 |
| 7. | Brook stickleback[4] | duration[3] | Λ | 9 | (-) hatch | McKenzie 1974 |
| 8. | Ninespine stickleback[5] | duration | Λ | 11 | (-) hatch | McKenzie & Keenleyside 1970 |
| 9. | Ten-spined stickleback[6] | duration[3] | Λ | 7 | (-) hatch | Morris 1958 |
| 10. | *Padogobius martensi* | duration[3] | Λ | 11 | hatch | Torricelli et al. 1985 |
| 11. | Blackspotted stickleback[7] | bout length | Λ | 10 | (-) hatch | McInerney 1969 |
| 12. | *Badis badis* | duration[3] | Λ | 6 | (+) hatch | Barlow 1964 |

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(cont'd)

| | Species | Measure | Trend | Points[1] | Max/min | Reference |
|---|---|---|---|---|---|---|
| b. BROOD DEFENSE (AGGRESSION) | | | | | | |
| 1. | Three-spined stickleback | bites/time | ∧ | 4 | (-) hatch | Sargent & Gross (in press) |
| 2. | Three-spined stickleback | bites/time | ∨ | 9 | hatch | Segaar 1961 |
| 3. | Three-spined stickleback | bites/time[3] | ∨ | 11 | hatch | Black 1971 |
| 4. | Three-spined stickleback | bites/time[3] | ∨ | 12 | hatch | Wootton 1971 |

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[1] I include only the data points when the parent is caring for eggs or larvae. The brood cycle data of some authors (e.g. Huntingford 1977; Colgan and Gross 1977; Smith-Grayton and Keenleyside 1978) are not presented because it contains too few data points in the brood cycle to discern a trend.

[2] Gasterosteus aculeatus

[3] other measures (e.g. bouts/time) are also provided in the reference

[4] Culaea inconstans

[5] Pungitius pungitius

[6] Pygosteus pungitius

[7] Gasterosteus wheatlandi

Unlike fanning, brood defense may not necessarily increase before hatching. After the eggs hatch the fry may have an increasing ability to defend themselves (even if this involves such simple movements as wriggling between particles of gravel) so as with fanning effort, we expect brood defense to decline towards the end of the brood cycle. Sargent and Gross (in press) present data on the change in brood defense through the brood cycle of parental male three-spined sticklebacks (<u>Gasterosteus</u> <u>aculeatus</u>). Their data show an inverted V shape of the type predicted by the theory. However, an examination of the literature reveals three other data sets on changes in parental investment through the brood cycle, and none of these are consistent with the theory (Table 5b). Furthermore, all of the existing data come from laboratory experiments on the three-spined stickleback.

The purpose of the present experiment was to examine the pattern of parental investment in the bluegill sunfish, and to determine whether the pattern is explicable by the parental investment theory of Sargent and Gross (1985).

## METHODS

### Colony Site

The study was performed on a bluegill colony located 0.8m deep in Big Rocky Bay, Lake Opinicon (see Fig. 1). The substrate is a mixture of sand and woody debris (mostly pine needles and birch leaves), and supports considerable aquatic plant growth.

Bluegill nest building was first seen on 1 July 1985 and spawning occurred early the next morning. Spawning continued throughout 2 July (until at least 1900 h) but did not resume the following day. The spawning was characterized by moderate levels of cuckoldry (due to the large number of plants, which serve as hiding places). The day after spawning each nest was marked with a small (5 cm x 7 cm) numbered tile. There were 45 male bluegill plus 2 *L. macrochirus* x *L. gibbosus* hybrid males in the colony. Water temperatures at mid-afternoons remained between 23.5 and 25.5 °C and hatching occurred rapidly -- some hatching had occurred by 1400 h on 4 July, and all fertile eggs had hatched by noon 5 July. Several males abandoned their nests during the brood cycle (as is typical for bluegill) and these were excluded from the analyses as were the hybrids.

## Data Collection and Analysis

In order to determine how parental investment changes through the brood cycle, it is necessary to evaluate the amount of parental investment at several points in time. However, it is possible that the evaluation technique will cause some effect on subsequent behaviour, thus it is necessary to have a control for the evaluation technique.

In this study, parental investment was quantified using a parent's willingness to defend its brood against a model predator. To control for the testing procedure, males were assigned to one of two samples: Control or Delayed. The Control males were tested every day while the Delayed males were not tested for the first two days of the brood cycle (July 3 and 4), but were tested every day thereafter. By comparing the defense scores of the two samples on the third day of the cycle, it is possible to determine whether the testing technique had any significant effect on subsequent defense scores.

Parental defense was tested by scoring each male's aggression to the same potential brood predator, a model of an adult bluegill. This technique had proved useful in previous studies and is described in Part C.

For each test, the observer (wearing a mask and snorkel) moved the model in a figure-8 pattern for 30 s at the edge of a nest and recorded the number of bites it received from the nest owner. The presence of the observer did not appear to affect the behaviour of the male being tested. The bites were tabulated using push button counters, then recorded on underwater tablets at the end of each trial. After the 30 s test, the observer removed the model from the nest area, waited 30 s and then repeated the test on the same male. After all males had been tested, the whole procedure was repeated. The values from the 4 30 s tests were then summed to provide a daily score for each male. To make the daily scores comparable, all testing was performed between 1330 h and 1630 h on each day.

To ensure that males in the two samples had generally similar phenotypes, on the last day of the brood cycle the remaining males (n=24) were caught by hand-net, weighed (to the nearest g) using a Philips portable electronic balance (Philips Electronics Ltd, Scarborough, Ont.) and measured (total length, to the nearest mm), and 2-3 scales were taken from the "key scale area" for aging (Gross 1982). Males were then returned to their nests. (The last day of the brood cycle was anticipated to be 8 July since the fry had golden eyes and were bouncing along the bottom of the nests, indicative of the last day of the brood cycle). Indeed, all males and fry had left the colony by the next morning (9 July) except for one male which remained an extra day.

Except where noted, the probability level for significant differences among samples was set at 0.05.

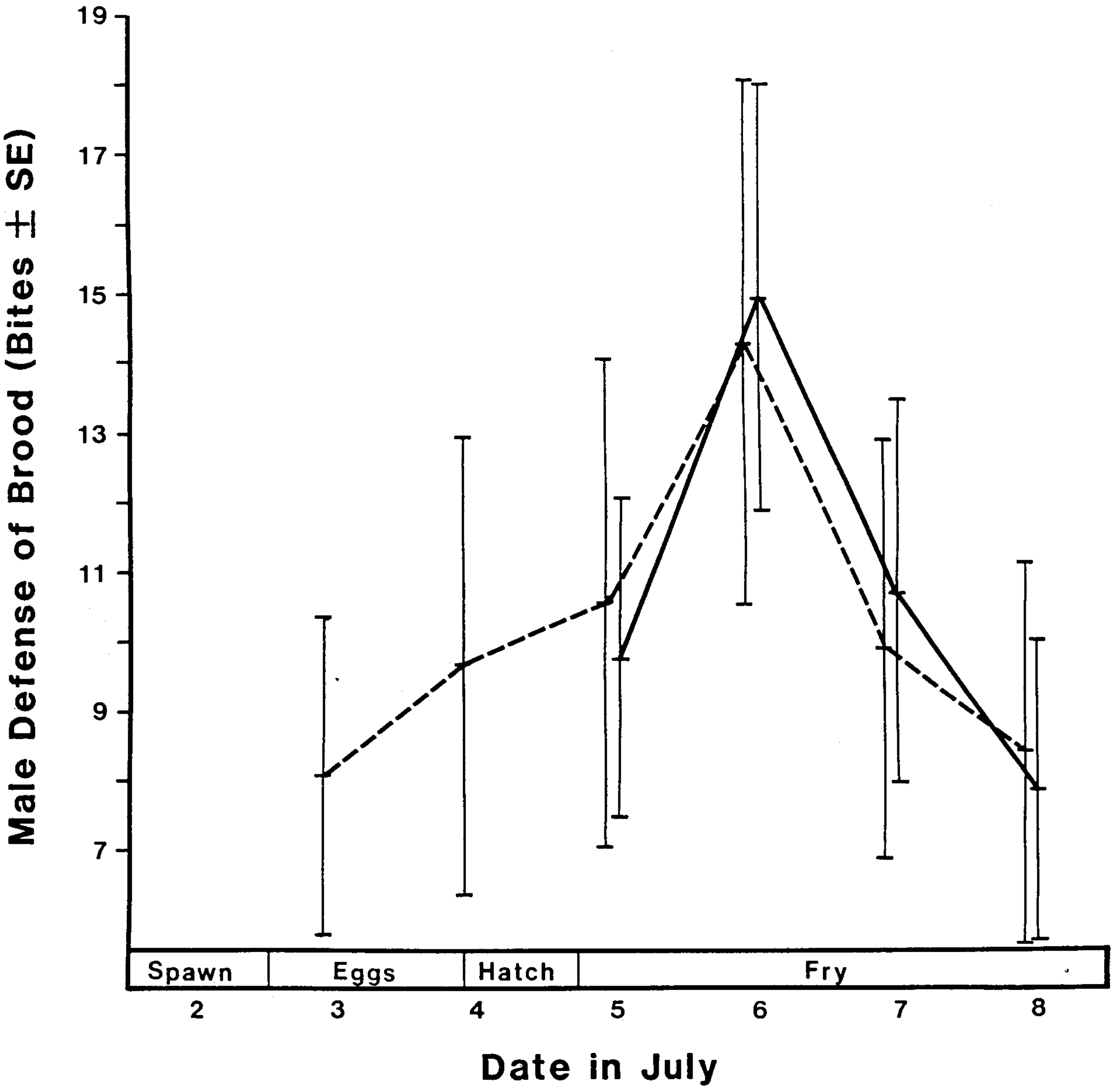
# RESULTS

The males of the two samples were similar with respect to total length (two-tailed t-test, $t_{21}=0.31$, $P=0.76$) and weight (two-tailed t-test, $t_{22}=0.56$, $P=0.58$). Furthermore, the defense scores for the Control and Delayed samples did not differ significantly on any of 5 July through 8 July (two-tailed t-tests; Day 5: $t_{22}=0.34$, $P=0.74$; Day 6: $t_{22}=0.20$, $P=0.84$; Day 7: $t_{22}=0.29$, $P=0.77$; Day 8: $t_{22}=0.25$, $P=0.81$). Therefore, the defense tests had no significant effect on the results of subsequent tests, and the data from the two samples were combined for the analysis of the brood cycle.

The willingness of males to defend changes through their brood cycle (Fig. 5). Comparing the Control samples for 3 July to 8 July (One-way ANOVA with repeated measures, $F_{5,55}=2.53$, $P<0.04$); or all males for 5 July to 8 July (One-way ANOVA with repeated measures, $F_{3,69}=7.97$, $P<0.001$), shows statistically significant changes in male aggression. Defense starts low, increases to a peak on 6 July and then decreases through the rest of the brood cycle.

Examining the defense scores for all the males, one-tailed planned non-orthogonal paired contrasts adjusted to an error probability of 0.017 (see Sokal and Rohlf 1981, p. 242) are significant for all contrasts: Day 5 to 6 ($t_{23}=2.90$, $P<0.004$),

Figure 5: Changes in defense through the brood cycle ($\bar{x}$±SE). The dashed line shows the average daily brood defense scores for Control males (n=12) over the brood cycle, while the solid line shows the brood defense scores for all males (n=24) over the last two-thirds of the brood cycle. The latter data are shifted slightly to the right for clarity of presentation.


19
17
15
13
11
9
7
Male Defense of Brood (Bites ± SE)
Spawn
Eggs
Hatch
Fry
2
3
4
5
6
7
8
Date in July

Day 6 to 7 ($t_{23}=4.51$, $P<0.00008$), and Day 7 to 8 ($t_{23}=2.61$, $P<0.008$). Examining only the Control males over the whole brood cycle shows the same trend (Fig. 5), however, the large number of contrasts adjusts the critical error probability to 0.010, and only the Day 6 to 7 contrast is statistically significant (Day 3 to 4, $t_{11}=0.60$, $P=0.28$; Day 4 to 5, $t_{11}=0.62$, $P=0.27$; Day 5 to 6, $t_{11}=2.30$, $P=0.02$; Day 6 to 7, $t_{11}=2.97$, $P<0.007$; Day 7 to 8, $t_{11}=1.75$, $P=0.05$). Note that adjustment of the critical acceptable error rate is considered a conservative approach to analyzing multiple comparisons (Sokal and Rohlf 1981).

# DISCUSSION

The results of the experiment support the prediction that brood defense by parental male bluegill sunfish has an inverted V shape pattern through the brood cycle. The peak was between 1 and 2 days after the eggs hatched (cf. Table 5). This is consistent with the theory that the value of the brood relative to that of the parent's expected future reproduction determines a parent's investment into its young, i.e. the relative value rule. The increasing investment is explicable as the result of accumulating investment devaluing the parent's expected future reproduction. The decreasing phase is explicable as due to the increasing ability of the fry to fend for themselves towards the end of the brood cycle, although I have not tested this assumption. Several studies have examined the behaviour and survival probabilities of bluegill fry beginning soon after they leave the nest (Brown and Colgan 1984, 1985; Beard 1982), but few data exist on the behaviour of fry in the nest. Morgan (1951) describes the newly hatched larvae as "not capable of much action" due to the large amount of yolk in their yolk sacs. As this yolk is absorbed, the fry's mobility increases. Brown (1983) reports that at the onset of free-swimming (the end of the brood cycle) the eyes, mouth, opercula and pectoral fins of young bluegill are all functioning. This agrees with my own observations on bluegill nests: the newly hatched fry do not move much in the bottom of the nest, but as they grow older their activity increases until on their last day in the nest they are capable of bouncing and swimming short distances. Bain and Helfrich (1983) found that survival of bluegill larvae increased with the proportion of coarse material in the nest substrate, and they observed larval bluegill using the interstitial spaces as hiding places. Gross and Nowell (1980) report that in the closely related rock bass, *Ambloplites rupestris*, the fry actively burrow into the nest gravel when disturbed. Larimore (1957) observed the development of larval warmouth, *Lepomis gulosus*, and found that they increased in mobility during the parental care period, and furthermore, they developed "remarkable ability to avoid a dip net" toward the end of the brood cycle.

As Table 5b indicates, there is some contradiction in the findings of various researchers for the pattern of brood defense through the brood cycle. One likely explanation for the contradictory results is in the length of tests researchers used. From Table 5a, fanning effort peaks near hatching time. Just before hatching, a male three-spined stickleback may spend over half his time fanning (Wootton 1984), and I found in Part B that a bluegill spends approximately 66% of its time fanning a day or two before hatching. If the method of testing brood defense does not allow the male to maintain its fanning effort for long periods of time, and is not perceived as being particularly threatening, then the male may chose to fan versus attack the threat. If this were the case, the defense results would likely be the mirror image of fanning effort (i.e. a V shape), as several researchers have found. Furthermore, Black (1971) reports that male three-spined sticklebacks reduce their territory size from the time of fertilization to when the eggs hatch. If the stimulus for brood defense is presented at a fixed distance from the nest over the brood cycle, (as in the male in a glass jar technique used by Segaar 1981, Black 1971 and Wootton 1971), the defense scores may show a V pattern as a result of changes in territory size alone. The testing procedure used in my experiment is brief, a threat to the brood, and performed at the nest edge; thus, my procedures avoided these problems.

Previous attempts at explaining these patterns of parental investment have either been non-existent or have been only at the proximate level. For example, van Iersel (1953) discussed the changes through the brood cycle in terms of changes in a male stickleback's motivational state. He concluded that the eggs release and prime the fanning drive and that their releasing value increases due to their increasing oxygen consumption as the eggs grow. He did not offer an explicit explanation for the decreasing phase other than to say that it is internally caused and appears to depend on the level of fanning reached before hatching. Segaar (1961) has made extensive surgical operations on the telencephalon of three-spined sticklebacks to determine which parts of the brain control the aggressive, sexual and parental behaviours of guarding males. He concluded that removal of various portions of the brain can affect the allocation of effort to these behaviours, but this does not tell us anything about the adaptive significance of the allocation scheme. This proximate approach to behaviour has been less powerful at explaining the diversity of behaviour observed in the world, and is presently being replaced by an evolutionary or life history approach as advocated in this thesis.

There are three principal time frames of importance to a breeding animal: (1) within a brood cycle, (2) between brood cycles but within one season, and (3) between breeding seasons. This study examined only the first of these, and it is worth briefly mentioning how this relates to the other two time frames. The question of how investment should change between brood cycles within a season is similar to the question of changes within a brood cycle. In both cases, past investment accumulates with time. Within a brood cycle the offspring's chances of survival may increase with time, while the value of offspring produced at different times in the season may be different. For example, offspring produced late in the season may have much lower probability of surviving the winter than earlier offspring, and thus the value of offspring late in the season may be less. Between breeding seasons, the parent's past investment accumulates with each breeding season, and the value of the offspring may differ also. In this context, their value could depend on for example, whether the weather is generally good or bad (which will influence whether the offspring are likely to survive or not).

# SUMMARY

The changes in parental investment through the brood cycle are documented for bluegill sunfish, and the result is consistent with the relative value rule of parental investment allocation. The parent's willingness to defend follows an inverted V shape through the cycle, peaking between 1 and 2 days after the eggs hatch. The initial increase in defense is explicable as the effect of accumulating past investment (because it devalues the parent's expected future reproduction) and the declining phase may be the result of the increasing ability of the fry to fend for themselves after hatching.

# PART E

# GENERAL DISCUSSION

This research into parental investment has provided some answers while simultaneously raising a number of new questions. I have performed the critical test of recent models of parental investment theory by showing that for at least one organism, the bluegill sunfish, parental investment is allocated according to the value of the brood at stake relative to the value of the parent's own expected future reproduction. It remains for other researchers to show that other organisms are similarly designed. Presuming that this is in fact a general phenomenon, as we would expect from an adaptationist viewpoint, then we may proceed towards constructing more comprehensive parental investment models. The parameters to incorporate into these models may be suggested by examining natural variation in parental care. For example, when I examined the pattern of parental investment through the brood cycle, it became clear that numerous parameters can affect the value of the brood and/or the value of the parent's expected future reproduction. To fully understand how bluegill allocate their parental effort, it will be necessary to determine which of these possible parameters are important. To do so will require careful experiments into such things as the change in return on parental investment as fry gain independence. It is noteworthy that previous approaches to behaviour encouraged increased investigation of neural mechanisms and other proximate causes of behaviour whereas the life history approach used in this research directs effort at understanding the costs and benefits of behaviours with little or no regard for their proximate causes.

My results suggest several specific avenues for future research. First, there are numerous possible minor extensions and applications of the present theory. For example, one obvious extension for bluegill is to test the effect of cuckoldry, which in effect reduces the value of the brood, on parental willingness to invest. Other possible investigations (see the discussion in Part D) include the effect of parental age on parental investment. A parent's expected future most likely decreases with age since mortality rates seem to increase with age (Gross 1980); however, ability to provide care might also change with age.

Second, the assumptions of Sargent and Gross's (1985) model are few, but they are important. Experiments should be done to see under what conditions the value of investing increases with diminishing returns, and the theory should be extended to cover other possible return curves. The theory should also be examined for its robustness to deviations from these assumptions. For better and for worse, much of our understanding of parental investment in fishes is based on only two species: the three-spined stickleback and the bluegill sunfish. These organisms have proved useful in behaviour research for logistic reasons, as well as because one benefits from working on a species whose basic biology is known. The cost of this narrow range of test subjects, however, is that we risk molding our theory to the specific life histories and environments of these species. I think parental investment research will benefit from consideration of how well current and future models and particularly their assumptions apply to radically different forms of parental investment, such as oral brooding or bubble-nesting, and under different ecological conditions. Some oral brooding cichlids, for example, leave the fry on the substrate for several days before caring for them in their mouths. Given some information on the return on investment into oral brooding versus fanning, it should be possible to predict the point of initiation of the oral phase and how it will change with changes in ecological parameters, such as predation pressure.

As mentioned in Part A, one of the next major steps for parental investment theory will be the development of models for the allocation of care in biparental situations and those involving parent-offspring conflict. The former in particular is devoid of good theory, although several investigators have documented the relative contributions of parents in biparental situations.

It should also be possible to make some predictions about the implications of parental care to other aspects of behaviour (as discussed in Part A). In Part C, I made one such prediction about how a female should chose where to spawn. If the male of a species provides parental care, and if he incorporates brood size into his parental investment decision rule, then a female should spawn with a male that already has eggs in its nest versus one that does not. Similarly, if future research shows that males evaluate the amount of cuckoldry they have experienced and adjust their parental investment accordingly, then it will pay females to detect and avoid cuckolders when spawning. This is an interesting prediction because if the cuckolder and parental strategies are in an Evolutionary Stable State (Gross and Charnov 1980), then were it not for the possible parental investment implications of cuckoldry, females should not care which type of male fertilizes their eggs.

An important result of this research into parental investment decision rules has been the clarification of the role of past investment, something which has been debated for almost two decades. Although Williams first highlighted the cost of investment in 1966 (Williams' Principle: Sargent and Gross 1985), the incorporation of this idea has been painfully slow. When Trivers (1972) defined parental investment, he explicitly recognized that investment has a cost, and yet his model of investment allocation emphasized minimizing wastage of past investment rather than the cost of investment on future reproduction. As explained at the end of Part C, this led to the idea of the Concorde fallacy and the hypothesis that any animal basing present investment on past investment was committing it. As recently as this year, Carlisle (1985) concluded that some animals do commit the Concorde fallacy, and that others do not. She proposes that we should accept this "fact" and that future research should be directed towards identifying the circumstances under which organisms do or do not commit the Concorde fallacy. However, when we incorporate Williams' Principle into parental investment theory, it becomes clear that this "fact" is false. By incorporating past investment into its parental investment decision rule, an organism is indicating that its future reproduction is important, and that there is a tradeoff between investing in the present and the future, not that it is committing the Concorde fallacy. Thus, the Concorde fallacy is dead, at least in this context.

### *Management Implications*

Parental investment research has seldom been applied to fish management policies, largely because most commercially harvestable species exhibit no post-fertilization investment into their offspring. This is not merely coincidence: commercial fisheries are most viable on species with large recruitments in which the fishery can harvest a large portion of the stock while not exterminating it. Because there is a tradeoff between number of progeny and investment into each progeny, those species with large enough recruitments to support a commercial fishery seldom provide parental care. Similarly, species with substantial parental care are seldom used in aquaculture, although there are exceptions. If such species are cultured, the parental care behaviour is generally viewed as a problem to be surmounted by technology (see Reay [1984] for a discussion of the use of biological information in aquaculture). However, there are some species of economic importance that do provide parental care. These are typically the object of sport fisheries, e.g. largemouth bass, smallmouth bass and black crappie. Others, such as the bluegill, affect sport fisheries in important ways (see below).

There are two general objectives which resource managers strive for: (1) to reduce the numbers/effects of undesirable species; and/or (2) to increase the numbers/quality of desirable ones. Bluegill are occasionally managed for the latter objective as forage fish for bass, but more typically for the former objective. Because of the bluegill's ability to outcompete more 'desirable' sport fishes, in some areas "the reduction of bluegill year classes [is] a desirable management strategy" (Beard 1982). To do this, Beard suggests either pumping the fry out of the nests, or chemically treating selected areas of lakes to kill the bluegill. Although it pains me to think of it, a more environmentally sound and cost effective technique for destroying a year class of bluegill would be to seine over a colony and remove the guarding males during the parental care period. The results of Part D suggest that on the day after hatch the males are especially willing to defend their nests, therefore I suspect they will most easily be caught at that time (thus maximizing catch per unit effort of the management team).

The largemouth bass is the subject of an important fishery in several parts of North America. Like other centrarchids, largemouth bass provide extended parental care for up to one month after spawning (Scott and Crossman 1973), and an important aspect of managing a bass fishery is determining how soon to open the fishery after the bass have spawned. It would be of great benefit to fish managers to know the effects of opening the fishery at various points in the parental care cycle on brood survivorship. Of potentially greater importance is the effect of catch and release fisheries on largemouth populations. In these fisheries it is legal to catch a guarding largemouth bass provided that it is promptly released upon capture. However, in lakes where brood predators are abundant, such as Lake Opinicon, even a brief absence of the parent from the nest may allow most of the fry to be consumed by predators. The management of fish species exhibiting parental care is therefore likely to benefit from further understanding of parental investment dynamics.

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