Behav Ecol Sociobiol (1985) 18:59–66

Behavioral Ecology and Sociobiology

Parental investment decision rules: a test in bluegill sunfish

Ronald M. Coleman, Mart R. Gross[1], and Robert Craig Sargent[2]
Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. Canada V5A 1S6

Received January 22, 1985 / Accepted May 28, 1985

Summary. We review parental investment decision theory and provide 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 are: (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 behavior against a model predator, we 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.

Introduction

The theory of life history evolution (Williams 1966; Stearns 1980; Charlesworth 1984) proposes that natural selection will favor behaviors which maximize lifetime reproductive success. However, it is not always clear which of many possible alternative behaviors 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? After a brief review of the theory on how parents adjust their investment into present progeny, we provide an experimental test of parental investment in a fish which has solitary male parental care of its young, the bluegill sunfish (*Lepomis macrochirus*).

Parental investment decision theory

During the last 3 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 behavior 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 be-

---

[1] To whom offprint requests should be sent

[2] Present address: T.H. Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506-0225, USA

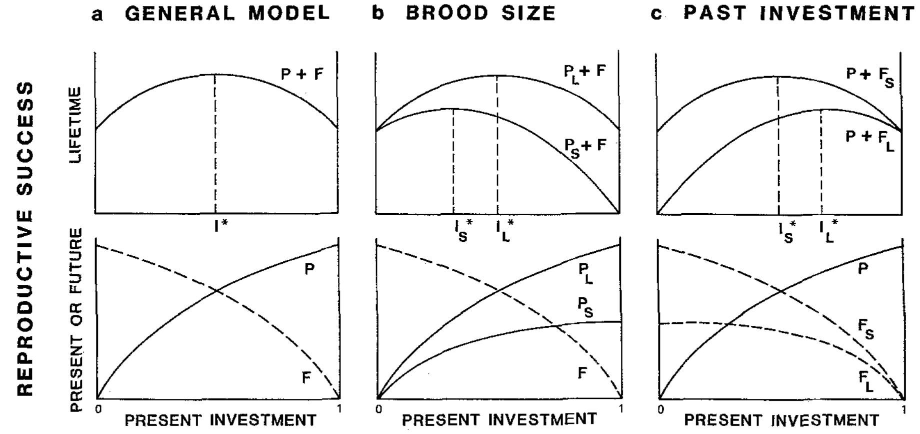

Fig. 1. **a** The effect of present investment on reproductive success. Present reproductive success (P) is assumed to increase with diminishing returns with present investment, while future reproductive success (F) is assumed to be a decreasing function of present investment. Lifetime reproductive success ($P+F$) 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*. **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 ($I_S{}^*$)

havior. 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 (Concorde fallacy: Dawkins 1976; Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977). Several authors have suggested that animals do in fact commit this 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 we 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 strategy.

Recently, 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 – 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 (see below), 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 paper we provide an empirical test of two parameters, namely brood size and past investment. From Sargent and Gross (1985) we derive that the optimal level of present investment maximizes the sum of present and future reproductive success (Fig. 1a). 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. 1b). 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. 1c). More precisely, animals could use either past investment per se, or present condition – the direct result of past investment – as a predictor of expected future reproduction. Separating these two is beyond the scope of this paper, and for simplicity and consistency with the literature we 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 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. We emphasize that to do this does not necessarily constitute committing the Concorde fallacy (although one could argue that it is consistent with committing the Concorde fallacy).

3. Invest according to both brood size and past investment. We 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 we 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 parental 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 3 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 the second brood reduction is characterized by parental behaviors that increase in intensity or frequency with brood size (cf. incubation in birds [Biebach 1981], fanning in fishes [van Iersel 1953]), parents with larger broods will make a greater investment into the brood than those with small broods. When the 3 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 behavior that does not increase by necessity with brood size, the alternative decision rules make distinct predictions about how parental investment will compare among the 3 samples. These are:

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

Parental investment in bluegill sunfish

Bluegill sunfish are a colonial breeding centrarchid with male nest building and exclusive male parental care (Avila 1976; Dominey 1981; Gross and MacMillan 1981). Males aggregate at traditional spawning locations where they sweep nests in the substrate using their caudal fins. Gravid females arrive as a school at the colony and enter the nests to spawn. Spawning activity in the colony lasts for several hours and then the females depart, leaving only the males to care for the fertilized eggs. The eggs are guarded against predators and fanned for 2 to 3 days until hatch. The fry are guarded (but not fanned) an additional 3 to 4 days, after which they and then the adult males leave the colony to forage. Adults may have 2 to 5 brood cycles per season, and breed for 2 to 3 years.

Parental care has a large cost to males in terms of their survivorship or ability to participate in future brood cycles. For example, in the related pumpkinseed sunfish (*L. gibbosus*) males lose 9% of their body weight during the egg and fry stage. About 74% of this weight is lost while the eggs are being fanned (Gross 1980). 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 infection which decreases adult survivorship.

During the brood cycle the eggs and fry are under constant predation threat by conspecifics as well as other species. Guarding by the parental male is necessary for the survival of the brood (Gross and MacMillan 1981; Bain and Helfrich 1983), but 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). Therefore, brood defense can be used as a measure, functionally independent of brood size, of a parent's parental investment into its brood. In contrast, larger broods receive more fanning effort by the parent than do small broods, presumably because of the greater oxygen demands in the nest environment (e.g. van Iersel 1953; Gross 1980).

Methods

Study site. Lake Opinicon, a 900 ha mesotrophic lake in southern Ontario (Canada), holds a large native population of bluegill sunfish (Keast 1978). Our 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 60 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 July 1. After the spawning, we 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 × 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 July 1 (Fig. 2). Approximately 50% of the brood (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 July 5, 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

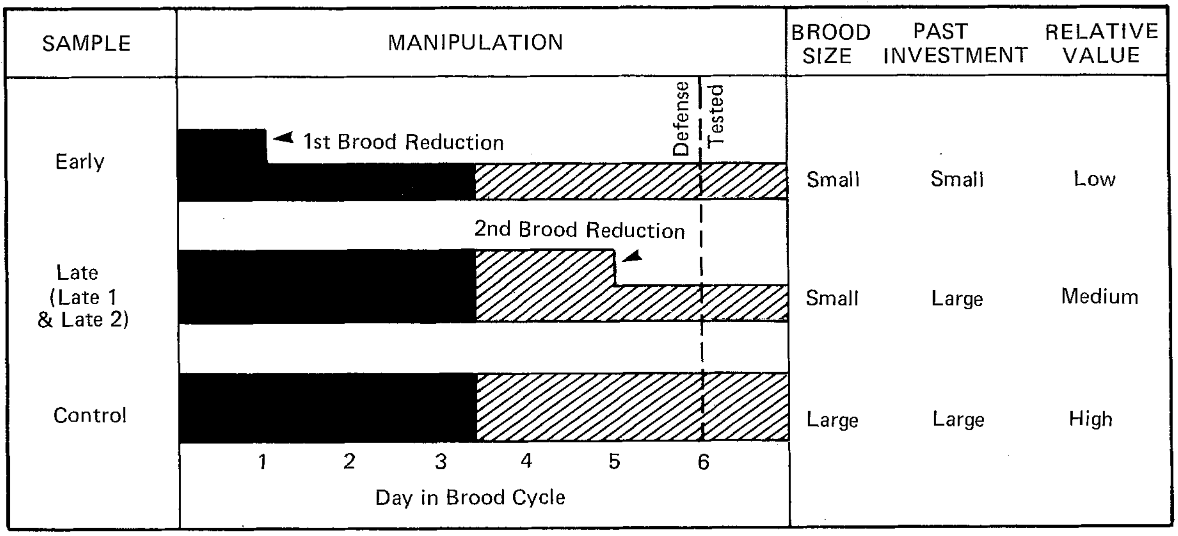

Fig. 2. The experimental design. Parents fan and guard their brood before hatching (solid bars), but only guard after hatching (hatched bars). The day in the brood cycle corresponds coincidentally to the date in July when the experiment was conducted. The chart of the size of the brood, parent's past investment, and relative value of the brood to the parent's future are for day 6, when the parent's brood defense was tested (see text)

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, we 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 predacious 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 30s 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 behavior 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 1,100 and again at 1,500 hours (EST). Immediately after the second defense test, males were caught, weighed using a 300 g Pesola spring balance (2 gram divisions), measured (total length, 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 $\times 10^5$/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 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 1, 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 *t*-test, $t_{46}=0.54$, $P=0.59$). We 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 (Table 1, $F_{2,47}=6.62$, $P<0.003$). Furthermore, one-tailed planned non-orthogonal contrasts 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 stat-

Table 1. Descriptive data and defense scores for the Early, Late-1, Late-2, and Control samples. The combined data for the two Late samples are also presented. Data are means ±SE, sample sizes are in parentheses

<table>
<tr><th rowspan="2">Variable</th><th colspan="4">Sample</th></tr>
<tr><th>Early</th><th>Late 1</th><th>Late 2</th><th>Control</th></tr>
<tr><td rowspan="2">Age</td><td rowspan="2">8.0 ±0.3 (6)</td><td>8.3 ±0.2 (14)</td><td>7.6 ±0.2 (9)</td><td rowspan="2">7.9 ±0.2 (16)</td></tr>
<tr><td colspan="2">8.0±0.2 (23)</td></tr>
<tr><td rowspan="2">Length</td><td rowspan="2">175.2 ±2.0 (6)</td><td>175.4 ±2.4 (15)</td><td>173.3 ±2.8 (9)</td><td rowspan="2">177.1 ±2.3 (18)</td></tr>
<tr><td colspan="2">174.6±1.8 (24)</td></tr>
<tr><td rowspan="2">Weight</td><td rowspan="2">90.2 ±3.6 (6)</td><td>94.7 ±3.9 (15)</td><td>90.6 ±3.9 (9)</td><td rowspan="2">97.4 ±3.8 (18)</td></tr>
<tr><td colspan="2">93.1±2.8 (24)</td></tr>
<tr><td rowspan="2">Fulton's condition factor</td><td rowspan="2">1.67±0.04 (6)</td><td>1.74±0.03 (15)</td><td>1.73±0.04 (9)</td><td rowspan="2">1.74±0.02 (18)</td></tr>
<tr><td colspan="2">1.74±0.02 (24)</td></tr>
<tr><td rowspan="2">Defense score</td><td rowspan="2">0.58±0.19 (7)</td><td>0.92±0.09 (15)</td><td>1.01±0.13 (10)</td><td rowspan="2">1.20±0.09 (18)</td></tr>
<tr><td colspan="2">0.96±0.08 (25)</td></tr>
</table>

istically as Control > Late > Early, consistent with hypothesis 3: invest 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, we did not measure male weights at the start of the experiment because we 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 ($F_{1,45} = 2.01$, $P = 0.18$).

Discussion

The results of our 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 our 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-spine sticklebacks (*Gasterosteus aculeatus*), and Carlisle (1985) on a cichlid (*Aequidens coeruleopunctatus*) found an increase in parental care behavior with an increase in brood size, which is consistent with our 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 phoenicieus*); 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; others) 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 lower 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 (*Pimephales promelas*) 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 behavior, which will affect future reproductive success, were not evaluated.

In this experiment we 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: that 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 broods and large broods in our 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 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.

Our findings suggest that constraints to animal behavior 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 behavior. 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, we 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 principle 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 favor such sub-optimal behavior. Therefore, just as we assume that animals behave optimally (sensu Maynard Smith 1978), we assume that they do not commit the Concorde fallacy.

Acknowledgements. This study benefited from facilities of the Queen's University Biological Station, Lake Opinicon, Ontario (director Dr. R.J. Robertson). We thank Robin Whittall and Angela Boerger for field assistance; and Ian Fleming, Eric van den Berghe, Hubert Markl and an anonymous referee for helpful suggestions. R.M.C. was supported by an NSERC of Canada Postgraduate Scholarship, M.R.G. by an NSERC University Reserach Fellowship, and R.C.S. by a NATO (NSF) Postdoctoral Fellowship. This research was supported by an NSERC Operating Grant (U0244, M.R.G.) and a grant from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History (R.M.C.).

References

Avila VL (1976) A field study of nesting behavior of male bluegill sunfish (*Lepomis macrochirus* Rafinesque). Am Midl Nat 96:195–206

Bain MB, Helfrich LA (1983) Role of male parental care in survival of larval bluegills. Trans Am Fish Soc 112:47–52

Barash DP (1975) Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bull 87:367–373

Biebach H (1981) Energetic costs of incubation on different clutch sizes in starlings (*Sturnus vulgaris*). Ardea 69:141–142

Boucher DH (1977) On wasting parental investment. Am Nat 111:786–788

Carlander KD (1977) Handbook of freshwater fishery biology, vol 2. Iowa State University Press, Ames

Carlisle TR (1982) Brood success in variable environments: implications for parental care allocation. Anim Behav 30:824–836

Carlisle TR (1985) Parental response to brood size in a cichlid fish. Anim Behav 33:234–238

Charlesworth B (1984) The evolutionary genetics of life histories. In: Shorrocks B (ed) Evolutionary ecology. Blackwell, Oxford, pp 117–134

Colgan PW, Gross MR (1977) Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibbosus*) over the reproductive phase. Z Tierpsychol 43:139–151

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Dawkins R, Brockmann HJ (1980) Do digger wasps commit the Concorde fallacy? Anim Behav 28:892–896

Dawkins R, Carlisle TR (1976) Parental investment, mate desertion and a fallacy. Nature 262:131–133

Dominey WJ (1981) Anti-predator function of bluegill sunfish nesting colonies. Nature 290:586–588

Fagerstrom T (1982) Maternal investment, female rivalry, and a fallacy. Oikos 39:116–118

Grafen A, Sibly R (1978) A model of mate desertion. Anim Behav 26:645–652

Gross MR (1980) Sexual selection and the evolution of reproductive strategies in sunfishes (*Lepomis:* Centrarchidae). PhD thesis, Utah, University Microfilms International, Ann Arbor, Mich

Gross MR (1982) Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Z Tierpsychol 60:1–26

Gross MR, Nowell WA (1980) The reproductive biology of the rock bass, *Ambloplites rupestris* (Centrarchidae), in Lake Opinicon, Ontario. Copeia 1980:482–494

Gross MR, MacMillan AM (1981) Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). Behav Ecol Sociobiol 8:163–174

Hubbs CL, Lagler KF (1958) Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor

Iersel JJA van (1953) An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behav Suppl 3:1–159

Keast A (1978) Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ Biol Fish 3:7–31

Kramer DL, Liley NR (1971) The role of spawning behaviour and stimuli from the eggs in the induction of a parental response in the blue gourami, *Trichogaster trichopterus* (Pisces, Belontiidae). Anim Behav 19:87–92

Kramer DL (1973) Parental behaviour in the blue gourami *Trichogaster trichopterus* (Pisces, Belontiidae) and its induction during exposure to varying numbers of conspecific eggs. Behaviour 47:14–32

Maynard Smith J (1977) Parental investment: a prospective analysis. Anim Behav 25:1–9

Maynard Smith J (1978) Optimization theory in evolution. Annu Rev Ecol Syst 9:31–56

Orians GH (1969) On the evolution of mating systems in birds and mammals. Am Nat 103:589–604

Pressley PH (1981) Parental effort and the evolution of nest-guarding tactics in the threespine stickleback, *Gasterosteus aculeatus* L. Evolution 35:282–295

Robertson RJ, Biermann GC (1979) Parental investment strategies determined by expected benefits. Z Tierpsychol 50:124–128

Rohwer S (1978) Parent cannibalism of offspring and egg raiding as a courtship strategy. Am Nat 112:429–440

Sargent RC (1985) Territoriality and reproductive tradeoffs in the threespine stickleback, *Gasterosteus aculeatus*. Behaviour 93:217–226

Sargent RC, Gross MR (1985) Parental investment decision rules and the Concorde fallacy. Behav Ecol Sociobiol 17:43–45

Sargent RC, Gross MR (in press) Williams' principle: an explanation of parental care in teleost fishes. In: Pitcher T (ed) The behaviour of teleost fishes. Croom Helm, London

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco, Calif

Stearns S (1980) A new view of life-history evolution. Oikos 35:266–281

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, Ill, pp 136–179

Unger LM (1983) Nest defense by deceit in the fathead minnow, *Pimephales promelas*. Behav Ecol Sociobiol 13:125–130

Weatherhead PJ (1979) Do savannah sparrows commit the Concorde fallacy? Behav Ecol Sociobiol 5:373–381

Weatherhead PJ (1982) Risk-taking by red-winged blackbirds and the Concorde fallacy. Z Tierpsychol 60:199–208

Williams GC (1966) Natural selection, costs of reproduction and a refinement of Lack's principle. Am Nat 100:687–690

Williams GC (1975) Sex and evolution. Princeton University Press, Princeton, NJ

Note added in proof:

The assumption that fanning activity of parental male bluegill increases with brood size has now been verified.