

PARENTAL INVESTMENT IN THREESPINE STICKLEBACK,

GASTEROSTEUS ACULEATUS

by

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## Abstract

Parental investment, defined as any parental activity that increases the survival of offspring at a cost to the parent, is a useful concept for examining the selective bases of parental behavior. To maximize its lifetime production of surviving offspring, a parent should adjust its level of risk in a parental investment depending on the value of its future "prospects" in relation to its present young. As present young increase in value, either by number or age, a parent should expend more risk in a parental investment so long as the effectiveness of its behavior does not diminish. This will often be the case for a parent that defends a nest containing eggs.

The prediction of an increase in parental risk for more eggs or older eggs has been tested using two natural populations of threespine stickleback, Gasterosteus aculeatus L. Male sticklebacks that were guarding nests were presented with a dummy predator, the prickly sculpin Cottus asper, and their responses were measured. Those males that remained within their nest area and attacked the dummy sculpin had a larger number of eggs or older eggs than those males that deserted their nests and never attacked the dummy. In the population that is sympatric with sculpins, males that initially attacked the sculpin's head had older eggs than those which avoided the head but attacked the tail area.

The level of the male's responsiveness, and associated risk, was recorded in a series of quantitative measures. The time it took a male to return to its nest, as well as the time to attack the sculpin dummy, was shorter for males with a larger number of eggs or older eggs. The number of bites at the dummy in the first minute after the initial attack increased as the egg number and egg age increased. Changes in male risk were in the predicted direction and none of the responses could be associated with any single biological or environmental factor other than the number or age of the eggs.

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## CHAPTER I. INTRODUCTION

"The pervasive role of natural selection in shaping all classes of traits in organisms can be fairly called the central dogma of evolutionary biology." In this statement E. O. Wilson (1975) points out the emphasis biologists place on discerning the adaptive features of biological phenomena. By outlining the selective basis of biological patterns, evolutionary studies seek to develop principles of adaptation. Principles that generate testable hypotheses not only provide an understanding of nature, but can be used to evaluate the precision of natural selection. In this thesis I attempt to produce and test some hypotheses that explain certain behavioral traits involved in parental care. The primary focus is on the ultimate rather than the proximate factors that regulate the expression of parental behavior.

An evolutionary interpretation of parental care has begun to emerge within a general theory of social behavior (Alexander 1974; West Eberhard 1975; Wilson 1975). The period of parental care is usually viewed as a composite of responses selected to maximize the individual parent's contribution to the gene pool of subsequent generations. Theoretical work primarily focuses on the genetic consequences of a parent's "altruistic" behavior, following an outline provided by Hamilton (1964). The self-sacrificing nature of parental care is emphasized in the concept of parental investment introduced by Trivers (1972, 1974). Parental investment is defined as any

behavior toward offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring. Any parental investment, such as feeding or guarding the young, will be adjusted by natural selection to maximize the parent's lifetime production of surviving offspring.

A consideration of the changes that occur in developing offspring suggests that the expression of a parental investment might vary throughout the period of parental care. The probability of the offspring surviving to reproduce will generally increase as they get older. One would expect selection to favor a parent increasing its risk of mortality as long as this increase in the "value" of the offspring is not accompanied by an increase in the offspring's ability to survive without the parent's assistance. This would be the case when the developing offspring are eggs and remain completely dependent on parental protection until hatching. As the offspring become increasingly independent after hatching, the increase in their survival resulting from a given level of parental risk will often decline. This decrease in the effectiveness of a parental response will often favor a curtailment of the parent's investment in the offspring, as observed in the weaning process in some species.

The level of risk displayed by a parent will also depend on the number of offspring receiving the benefit of the parent's assistance. For a parental investment that enhances the survival of all the offspring equally, such as the defense

of a nest, the intensity of the parent's commitment will be proportional to the number of offspring involved. The parent's response will also be influenced by its capability of acquiring more offspring in the future. Thus the level of risk displayed in a parental investment will be a function of (1) the present number of offspring compared to the parent's expectation of future offspring, (2) the potential increase in offspring survival resulting from any given level of risk, and (3) the probability that the offspring will survive to reproduce irrespective of the parental investment.

In the next chapter I formally develop these predictions in a model that considers the evolution of parental investment within the framework of life history theory. The model assesses the expression of a parental investment in terms of the fundamental demographic parameters of populations, thus generating a wide range of predictions for organisms with parental care. Chapter III describes a field test of some of these predictions in natural populations of threespine stickleback, Gasterosteus aculeatus L. The last chapter gives a general discussion of the test results and reviews some other studies of parental care that are relevant to the model of parental investment. The reader more interested in the field experiment with sticklebacks, and satisfied with the arguments presented so far, may turn directly to Chapter III and skip the more general theory.

## CHAPTER II. NATURAL SELECTION AND PARENTAL INVESTMENT

### 1. Introduction

In recent years there has been an increasing interest in the evolution of life history phenomena (for an extensive review see Stearns 1976). Biologists are attempting to explain how natural selection interacts with the environment to mold an organism's survival, age at first reproduction, fecundity, and reproductive lifespan. The evolution of any component of an organism's life history is assumed to depend on its effect on the individual's fitness, defined as its genetic contribution to future generations. Theoretical work is primarily focused on non-social life history traits, as these are analytically more tractable in mathematical models of evolution. A common approach is to consider the existing demographic structure of a population as a major influence on the selection of a specified trait. Here I extend this approach to consider the maintenance and evolution of certain aspects of parental care.

### 2. Reproductive Effort and Parental Investment

R. A. Fisher (1930) first called attention to the problem of determining how natural selection will influence an organism's allocation of resources to reproductive versus non-reproductive activities. His insight led to the notion of reproductive effort, which has been a central concept in

recent studies of life history evolution (Williams 1966a, 1966b; Tinkle 1969; Goodman 1974; Hirshfield and Tinkle 1975; Pianka and Parker 1975). Reproductive effort is defined as the fraction of the total amount of time and energy available to an individual that is devoted to reproduction (Gadgil and Bossert 1970), and is usually quantified by some measure of reproductive to nonreproductive tissues (Hirshfield and Tinkle 1975).

Reproductive effort is difficult to quantify when reproductive activities include parental care. Furthermore when considering the evolution of parental behavior, time and energy may not be a relevant measure of effort. A parental activity that requires little expenditure of time and energy, yet involves a high risk of mortality for the parent, is under stronger selective pressure than would be implied by a corresponding measure of reproductive effort based only on time and energy expended. Any meaningful measure of the reproductive effort involved in parental care should incorporate the risk of mortality to the parent (Hirshfield and Tinkle 1975; Pianka and Parker 1975).

Parental investment (Trivers 1972, 1974) is a useful concept for evaluating the risk involved in parental activities. A parental investment is defined as any parental act that increases an offspring's chance of surviving while decreasing the parent's ability to invest in other offspring. The period of parental care is composed of numerous parental investments, the size of each being measured by its effect on

the parent's ability to produce other offspring (Trivers 1972). The decrease in a parent's probability of future offspring gives a better measure of the importance of a parental activity than reproductive effort. The concept of parental investment may allow one to determine how natural selection will adjust parental activities to increase a parent's contribution to future generations.

### 3. Reproductive Value and Reproductive Success

Fisher (1930) also introduced the notion of reproductive value, which has been widely used in evolutionary theory (Williams 1957, 1966b; Medawar 1957; MacArthur and Wilson 1967; Emlen 1970; Cody 1971). In a stable population, reproductive value ( $V_x$ ) is defined as an organism's age-specific expectation of future offspring (Pianka 1974) and is given by the equation:

$$V_x = \int_x^{\infty} \frac{l_t}{l_x} m_t dt$$

The term  $l_t/l_x$  represents the probability of living from age  $x$  to age  $t$ , and  $m_t$  is the expected number of female offspring produced in the time interval  $t$  to  $(t+dt)$  per female aged  $t$  (or an equivalent measure for males, Warner 1975). In a population changing in size, the equation includes exponential terms that weight the relative importance of future offspring by the population's intrinsic rate of increase (Fisher 1930).



Because it represents an organism's expected production of offspring throughout the remainder of its life, reproductive value is often used as a measure of fitness in theories of life history evolution (Williams 1966b; Hamilton 1966; Pianka and Parker 1975). Taylor et al. (1974) have mathematically demonstrated that maximizing the reproductive value at age zero is equivalent to maximizing the ultimate rate of increase, another common measure of fitness (Mertz 1971; Charlesworth 1973; Bell 1976). Since most theory considers the evolutionary trade-off between survival ( $l_t$ ) and fecundity ( $m_t$ ) at each instant in an organism's lifetime, natural selection is assumed to favor the partitioning of resources so that reproductive value is maximized at every age (Williams 1966b; Schaffer 1974a; Taylor et al. 1974).

However, as first pointed out by Fisher (1930), reproductive value is not an adequate measure of fitness for organisms with parental care. A parent can devalue its expectation of future offspring while increasing its genetic contribution to future generations. Consider the origin of a parental response that involves a "sacrifice" for the young (aged  $y$ ) such that the parent (aged  $x$ ) decreases its chance of survival (i.e. a parental investment). The response increases the offspring's survival at that age ( $l_y$ ), and will be incorporated into the population if the genotype that displays the response has a larger ultimate rate of increase (reproductive value at age zero) than the other genotypes in the population (Mertz 1971). Since the response increases the

survival of offspring born in the past it will not be accounted for by an increase in the measure of the parent's present production of offspring,  $m_t$ . Therefore, the decrease in the parent's age-specific survival ( $l_t$ ) will result in a lower reproductive value ( $V_x$ ) for the parent at that age. Thus, natural selection can favor parental activities that decrease a parent's reproductive value.

Because a parent can influence the survival of its young, any measure of fitness for a parent should include the potential contribution to future generations by offspring still under its care, as well as any contribution by its expected future offspring. I define a parent's reproductive success,  $S$ , as its expectation of future grandchildren. The reproductive success of a parent includes the number of grandchildren that will be produced by the parent's future offspring as well as the offspring presently under its influence. Following Williams (1966b), reproductive success ( $S$ ) can be partitioned into present ( $P$ ) and future ( $F$ ) components such that:

$$S = P + F$$

The present component,  $P$ , is equal to the sum of the reproductive values of each of the offspring presently under parental care. This is equivalent to the number of present young times their average expectation of future offspring. The future component,  $F$ , is determined by the sum of the parent's grandchildren that will be produced by its future offspring. In a population with a stable age distribution the

future component is equal to the parent's reproductive value ( $V_x$ ), since the equation for reproductive value accounts for the contribution by future offspring to subsequent generations (Leslie 1948).

#### 4. Parental Investment and Reproductive Success

The period of parental care can now be considered as a composite of parental investments, each adjusted by natural selection to maximize the parent's reproductive success ( $S$ ). For any specified parental investment, I determine its effect on the present ( $P$ ) and future ( $F$ ) portions of the parent's reproductive success by isolating it from the rest of the parent's life history. In this way the maintenance and evolution of a parental investment is influenced by demographic factors that are independent of the investment.

Consider a parental investment that involves a risk of mortality for the parent, such as the defense of its young against a predator. Following Williams (1966b), the parental investment has a cost,  $C$ , measured as the proportionate decrease in the future component ( $F$ ) of the parent's reproductive success ( $S$ ). If a more intense defense results in a higher risk of mortality for the parent, then the size of the cost will depend on the intensity of the parent's response. The increase in the offspring's survival as a result of the response is the benefit,  $B$ , measured as the proportionate increase in the present component ( $P$ ) of the

parent's reproductive success. The amount of increase in the offspring's survival will often depend on the level of risk taken by the parent. Thus, for a parental investment I consider the benefit as a function of the cost ( $B = B(C)$ ). For any parental investment, I assume there is a limit to the extent that a parent can increase the survival of its offspring (Trivers 1972, 1974; Smith and Fretwell 1974). Figure 1a shows a hypothetical relation between the benefit and cost of a parental investment.

The reproductive success ( $S$ ) of a parent resulting from a parental investment can now be considered as a function of the investment's cost (Figure 1b), such that

$$S(C) = (1 + B(C))P + (1 - C)F \quad (1)$$

The reproductive success ( $S$ ) will be at a maximum where  $S'(C) = 0$  (Figure 2a) and  $S''(C)$  is negative. I define the cost associated with this point as the optimal cost, designated  $C_m$ . Solving from equation (1), the optimal cost for a parental investment is the cost that satisfies the relation

$$B'(C) = \frac{F}{P} \quad (2)$$

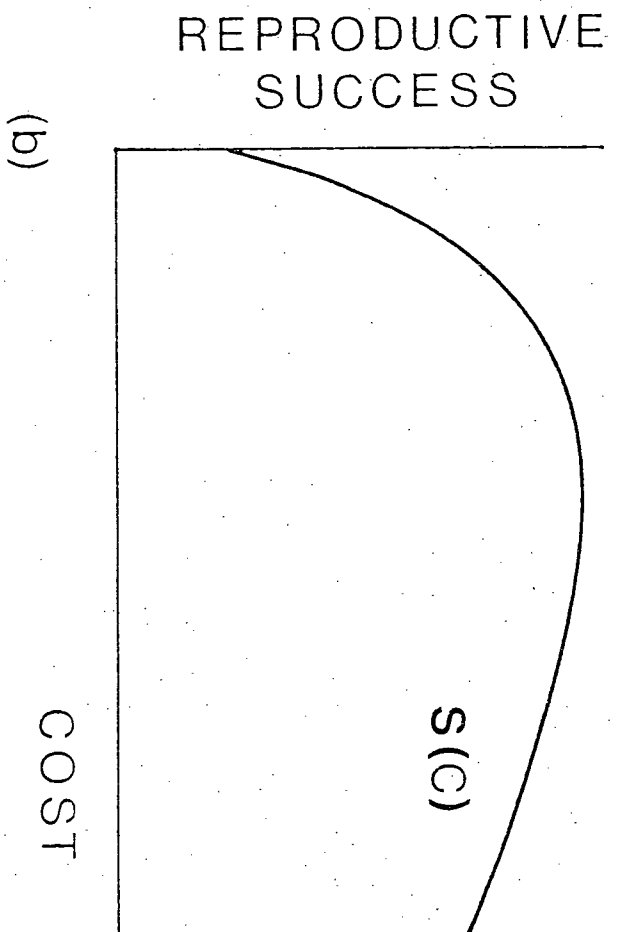
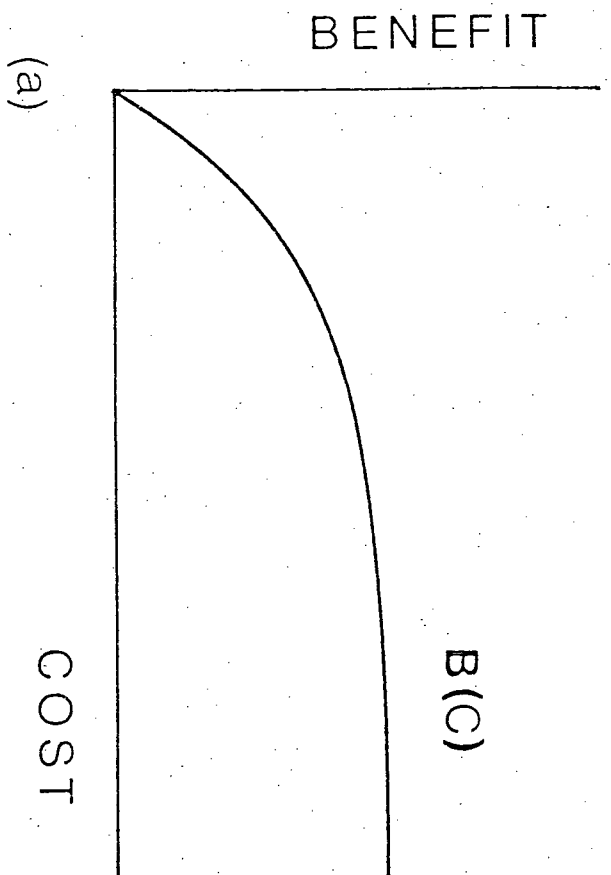
When the benefit is a sigmoidal function of the cost (Brockelman 1975),  $B''(C_m)$  is necessarily negative. Figure 2a shows that  $C_m$  corresponds to the point where the slope equal to  $F/P$  is tangent to the curve for benefit as a function of cost. As  $F/P$  decreases (the tangent line becomes more

## FIGURE 1

## The Influence of the Cost of a Parental Investment

Fig. 1a: A hypothetical relation between the benefit (the proportionate increase in the present component of a parent's reproductive success) and the cost (the proportionate decrease in the future component) of a parental investment. The benefit is considered as a function of the cost,  $B(C)$ , and approaches an asymptote because there is a limit to the extent that a parent can increase the survival of its offspring. In this figure initial increases in cost have the largest effect on the benefit, although the function could also be sigmoidal at low levels of cost.

Fig. 1b: A parent's reproductive success (expectation of future grandchildren) considered as a function of the cost,  $S(C)$ , of a parental investment. The reproductive success is the sum of a present component ( $P$ ), representing the young presently under parental care, and a future component ( $F$ ), which represents the parent's expectation of future offspring. The resulting reproductive success for the relation of benefit and cost shown in Fig. 1a is at a maximum for an intermediate level of cost.

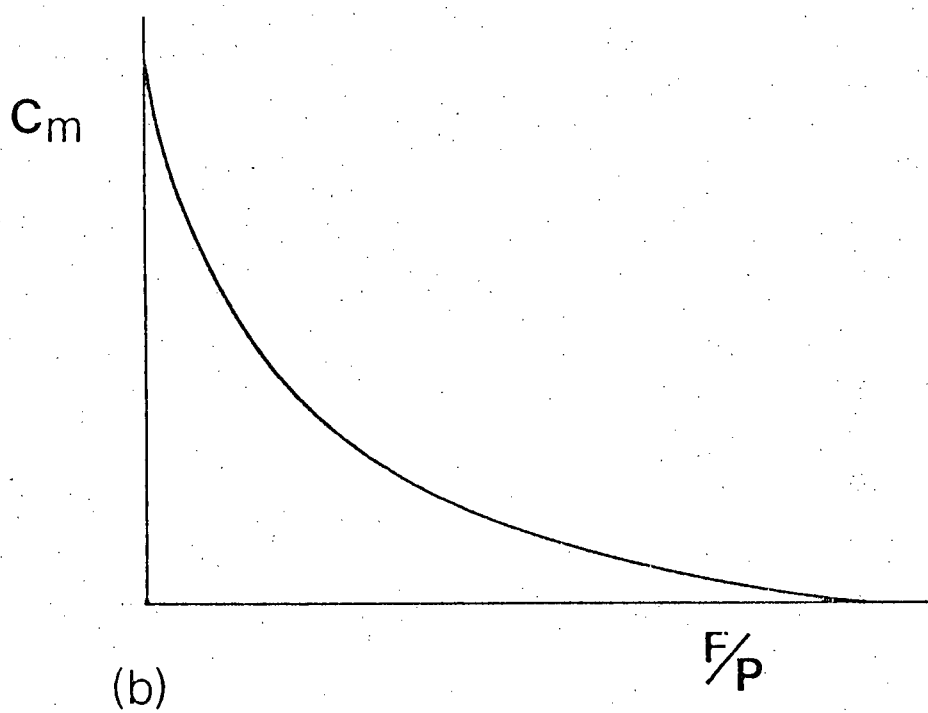
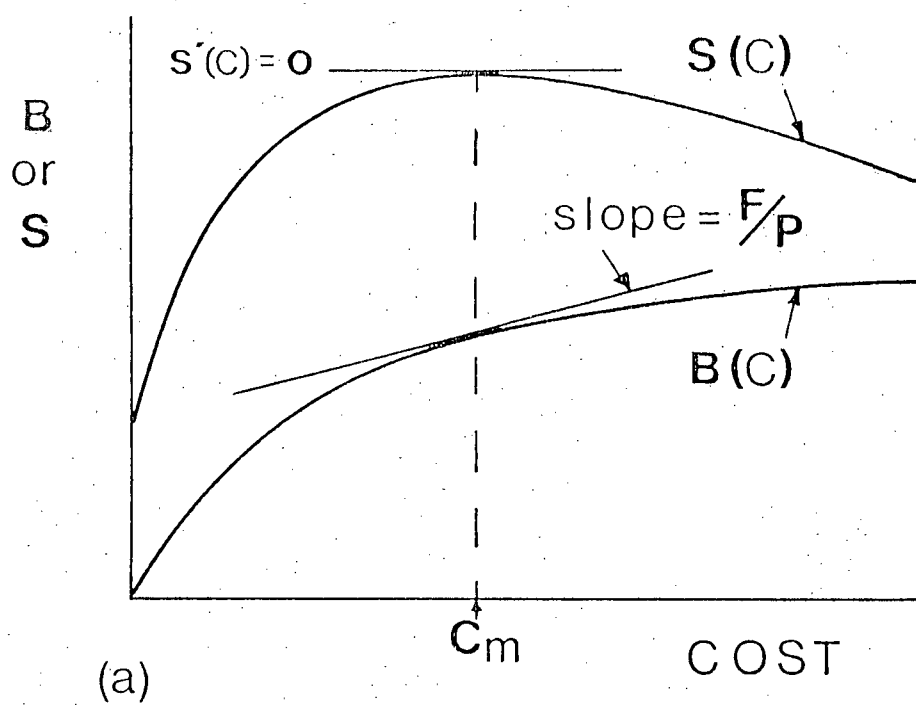


## FIGURE 2

## The Optimal Cost of a Parental Investment

Fig 2a.: The optimal cost,  $C_m$ , is the level of cost at which the parent's reproductive success is at a maximum,  $S'(C)=0$ . This cost corresponds to the point where the slope equal to the ratio of the future (F) to the present (P) component,  $F/P$ , is tangent to the curve for benefit as a function of cost.

Fig 2b: As  $F/P$  decreases (the slope in Fig. 2a becomes more horizontal), either by an increase in the number or reproductive value of the young or by a decrease in the parent's expectation of future offspring, the optimal cost of the parental investment increases.

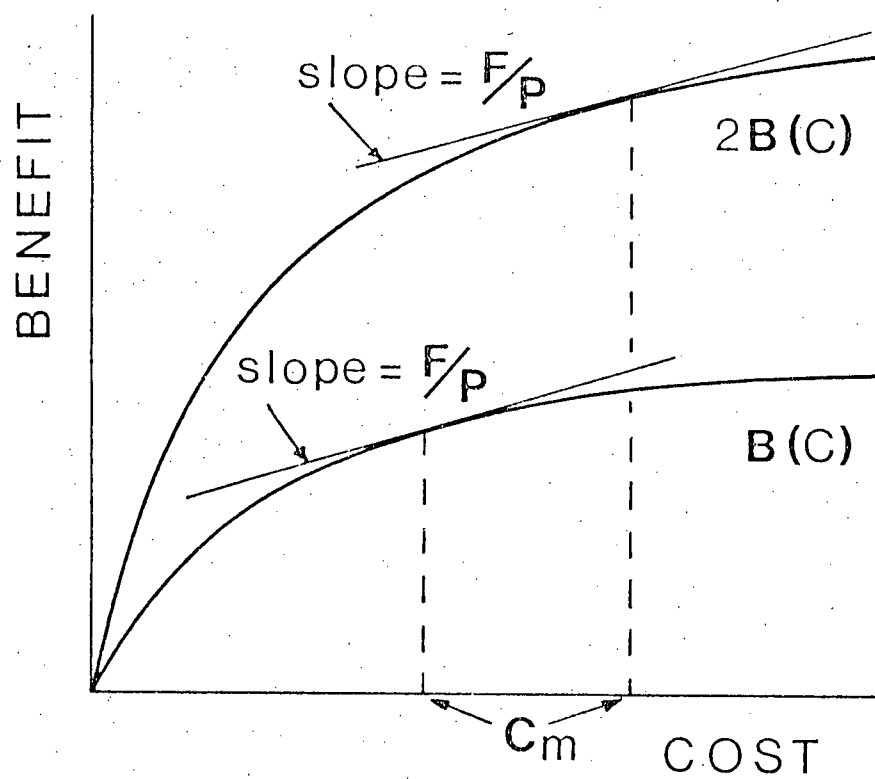




## FIGURE 3

## The Effectiveness of a Parental Investment

For a parental investment that results in more benefit for a given level of cost, the optimal cost ( $C_m$ ) will be higher for a given value of  $F/P$ . Similarly, any decrease in the effectiveness of a parental investment (e. g. if the young become less dependent on the parent's assistance) will favor a lower cost.



horizontal),  $C_m$  increases (Figure 2b). Thus, as the value of the present component ( $P$ ) increases ( $F/P$  decreases), the response that maximizes a parent's reproductive success ( $S$ ) has a higher cost. A decrease in a parent's expectation of future offspring (lower  $F$ ) also favors a parental response involving a higher risk to the parent.

During the period of parental care, the ability of a parent to effect the survival of its young may change (for example, as the young become independent). The benefit of a parental investment may vary for any given level of cost (Figure 3). As the benefit increases, the optimal cost ( $C_m$ ) of a response increases (for parents with equal values of  $F/P$ ). Similarly, a decrease in a parent's effectiveness favors less parental risk.

So far I have considered parental investments that vary in the intensity of the parent's response. For a parental investment that involves an all-or-none response (such as whether the parent defends its young at all), the problem is to determine at what point the response becomes justified (Williams 1966b). An all-or-none response increases a parent's reproductive success if  $S(C)$ , the reproductive success resulting from the response, is greater than  $S(0)$ , the reproductive success in the absence of the response (zero cost). Combining  $S(C) > S(0)$  with equation (1) gives

$$\frac{B}{C} > \frac{F}{P} \quad (3)$$

The benefit in relation to the cost of an all-or-none response must be greater than a parent's future prospects (F) divided by its present prospects (P) for it to increase the parent's reproductive success (S). During the period of parental care, an all-or-none response will not be justified until F/P is exceeded by the benefit-cost ratio of the response (Williams 1966b; Goodman 1974).

### 5. Predictions

The model of parental investment and reproductive success leads to a number of predictions for parental activities. For any parental investment, circumstances in the parent's life history and environment that are independent of the investment will determine the intensity of the parent's response. A number of factors can be considered that will influence the pattern of parental investment throughout the period of parental care. The model also predicts trends in parental investment for various parents within the same population as well as differences between separate populations and species.

The components of a parent's reproductive success (S) are major determinants of a parent's behavior. For any parental investment the ratio of future to present prospects, F/P, will influence the intensity of a parent's response (Figure 2b). During the period of parental care the following may

change the value of  $F/P$  and affect the optimal cost of a parental investment. (1) As the offspring get older their probability of surviving to reproduce increases, resulting in a larger average reproductive value for the offspring (larger  $P$ ). Increases in the age of the young will generally favor parental responses that involve a higher risk. (2) The number of offspring under parental care can increase (due to subsequent breeding) or decrease (due to mortality or fledging). A gain (larger  $P$ ) or loss (smaller  $P$ ) of young will favor a corresponding increase or decrease in parental risk for a given level of  $F$ . (3) As the parent ages its reproductive value will often decrease, especially in seasonal breeders (Pianka and Parker 1975). A decrease in a parent's expectation of future offspring during the period of parental care will favor the parent increasing its risk for the young.

In addition to influencing the optimal cost of a parental investment, the value of  $F/P$  will determine the timing of an all-or-none response during the period of parental care (equation 3). Thus, as the offspring get older (larger  $P$ ), the value of  $F/P$  will decrease to a point where a "risky" all-or-none response will become justified. The rate at which the optimal cost of a parental investment changes will also depend on the rate of change in the value of  $F/P$ .

For any comparison of parents within a population, the age and number of young as well as the reproductive value of the parent will influence the optimal cost for a parental investment. In addition, the sex of the parent may be

important in species where both sexes take part in parental activities, since the age-specific expectation of future offspring may differ between sexes.

Variation in adult and juvenile survival, as well as adult fecundity, will result in different patterns of parental investment for different populations and species. The effect of resource availability, predation, and competition on the present (P) and future (F) components of a parent's reproductive success (S) will favor different levels of parental risk. For any prediction of an environment's effect on the optimal cost of a parental investment it will be necessary to delimit the environment's effect on offspring survival (P) separately from its effect on parent survival (F).

Another major determinant of parental investment is the effectiveness of a parent's response, which is the benefit resulting from a given level of cost (Figure 3). During the period of parental care, the ability of a parent to influence the survival of its young may decrease as the offspring become independent. The resulting decrease in the benefit of a parental investment will favor a lower parental risk (Figure 3). A circumstance that alters the effectiveness of a response, such as the offspring becoming older and more independent, may simultaneously affect the value of  $F/P$ . The influence of the change in  $F/P$  on the optimal cost may act counter to the influence of the change in the effectiveness of a response, making it difficult to predict the final outcome.

Any prediction of a pattern of parental investment will have to account for changes in the effectiveness of a response, as well as changes in F/P. This will be especially true for comparisons of different populations where, for example, the benefit-cost function of a parental investment might vary due to the presence of different predators.

## 6.Changing Environments

Fisher's equation for reproductive value ( $V_x$ ) assumes that age-specific survivorship ( $l_t$ ) and fecundity ( $m_t$ ) are invariant over time and that the age distribution within the population is stable (Caughley 1970). In most natural situations, environmental fluctuations will cause survival and fecundity to vary, resulting in different measures of age-specific reproductive value at any one time. When considering the reproductive value of a parent and its offspring as a major determinant of parental investment, the simplest solution is to assume that any pattern of parental investment is a result of selection acting on the long-term average reproductive values. However, if environmental fluctuations affect offspring survival differently than parent survival, then selection may favor changes in parental investment to compensate for the difference. A fluctuating environment that has its major impact on juvenile mortality will favor decreases in the optimal cost of a parental investment, while fluctuations that primarily affect a parent's survival will

select for increases in parental risk (Murphy 1968; Schaffer 1974b).

Seasonal fluctuations that affect age-specific survival and fecundity, such as seasonal variation in offspring survival, may result in a corresponding pattern of parental investment. Thus, for a population in a seasonal environment, the pattern of parental investment might be best determined by considering the time of year as well as the age of the parent and its offspring. The seasonal change in survival could be incorporated into the measure of reproductive value by including a variable specifying the time of year. This would be similar to the "organism state variable" introduced by Taylor et al. (1974), and would be useful for predicting changes in parental investment that result from seasonal changes in survival and fecundity.

The evolution of any pattern of parental investment in a changing environment may also be influenced by the parent's ability to predict the quality of a given year for juvenile and adult survival (Cohen 1967; Hirshfield and Tinkle 1975). A parent that can correlate environmental cues with a favorable year for offspring will be selected to increase its risk in a parental activity. A parental response may also depend on the parent's ability to predict a change in the effectiveness of a parental investment, which might result from different resource or predation levels. The demographic determinants of a parental investment will lie between the long-term average values of the components of a parent's



reproductive success ( $S$ ) and the actual values that would be known by a parent with "perfect knowledge".

### 7.A Re-examination of the Initial Model

So far I have considered the optimal response of a parental investment as a result of demographic circumstances that are independent of the investment. However, once a pattern of parental investment is incorporated into a population, the investment will in turn mold the population's demography. Although circumstances that are independent of a parental investment will maintain it at a certain level, a parental investment will not evolve in isolation from the remainder of an organism's life history. Considering this interaction may be useful for evaluating the feasibility of the initial model.

The effect of a parental investment being incorporated into a population will be to increase  $P$  and decrease  $F$  (equation 1). This decrease in  $F/P$  will favor a larger optimal cost ( $C_m$ ) for the investment (Figure 2b), which will in turn decrease  $F/P$ . This interaction will result in continual selection for higher levels of cost. However, one would not expect the optimal cost to increase indefinitely but to approach some stable level. To determine if the initial model leads to a final optimal cost, I simulated the interaction between  $C_m$  and  $F/P$ .

Beginning with initial values of the present ( $P_0$ ) and future ( $F_0$ ) components of the parent's reproductive success ( $S$ ), I determined the optimal cost (equation 2) of the benefit-cost relation shown in Figure 1a. This optimal cost ( $C_1$ ) then modified the present and future components such that

$$F_1 = (1 - (C_1 - C_0)) F_0 \quad \text{and} \quad P_1 = (1 - (B_1 - B_0)) P_0$$

where  $C_0 = 0$  and  $B_0 = 0$ , since the interaction represents the first appearance of the parental investment. This was repeated a number ( $n$ ) of times such that the resulting optimal cost,  $C_n$ , satisfies the relation

$$B'(C_n) = \frac{F_{n-1}}{P_{n-1}} = \frac{(1 - (C_{n-1} - C_{n-2})) F_{n-2}}{(1 - (B_{n-1} - B_{n-2})) P_{n-2}}$$

Figure 4a shows that  $C_n$  approaches an asymptote, demonstrating that the optimal cost does not increase indefinitely. In a natural population, the rate at which  $C_n$  increases will depend on the biological circumstance. The purpose of the exercise was merely to determine if the evolution of a new parental investment might lead to a stable response level.

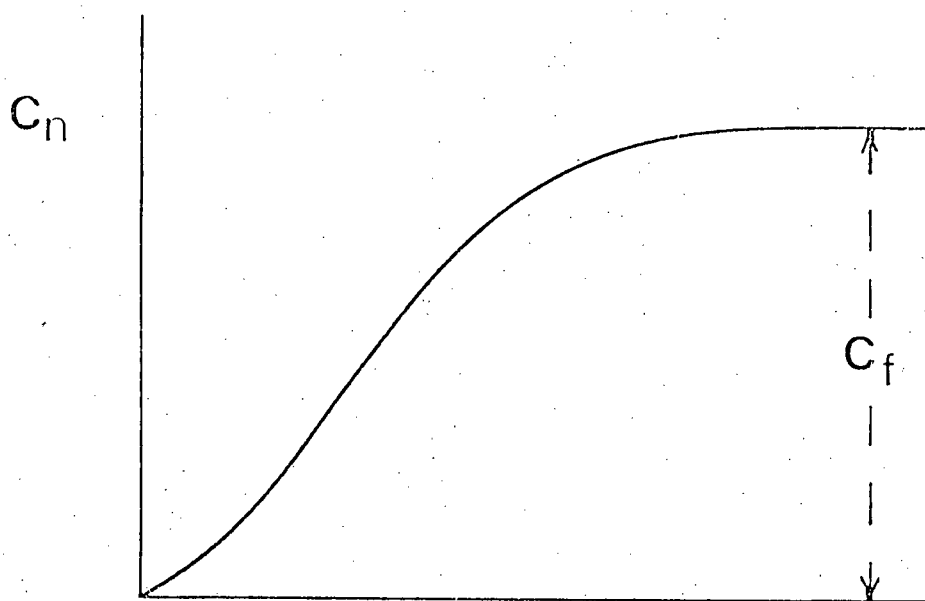
The influence of the initial values,  $F_0$  and  $P_0$ , on the final optimal cost, designated  $C_f$ , was also considered. The value of  $C_f$  was determined by setting it equal to  $C_n$  when the difference,  $C_n - C_{n-1}$ , was less than a specified value at which the optimal cost was considered to no longer be appreciably changing. The results are shown in Figure 4b. The final optimal cost ( $C_f$ ) is lower for a higher initial ratio of future to present prospects ( $F_0/P_0$ ). In addition, as the

## FIGURE 4

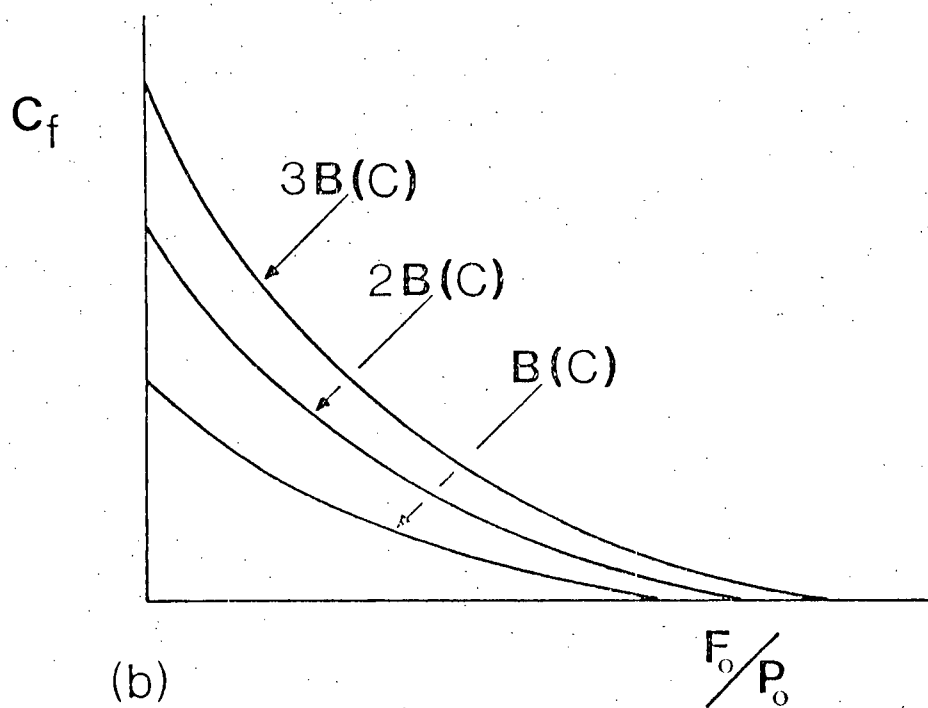
## The Incorporation of a Parental Investment into a Population

Fig. 4a: The results of a simulation representing the change in the optimal cost,  $C_n$ , as a parental investment with a benefit-cost function similar to Fig. 1a becomes established in a population. The optimal cost at each reiteration,  $n$ , remolds the population's demography, by increasing the value of the present component ( $P$ ) and decreasing the value of the future component ( $F$ ), resulting in a new level of cost being favored. The rate of increase in the optimal cost gradually declines and reaches a stable level, designated the final optimal cost ( $C_f$ ).

Fig. 4b: The final optimal cost,  $C_f$ , for a number of simulations starting with different initial values of the present ( $P_0$ ) and future ( $F_0$ ) components. When the benefit for a given level of cost increases, or when the value of  $F_0/P_0$  decreases, the final optimal cost is higher, which is the same qualitative result predicted by the initial model shown in Fig. 2 and Fig. 3.



(a)



(b)

effectiveness of a response increases (larger benefit for a given cost),  $C_f$  increases. These results are qualitatively the same as those predicted from the initial model.

## 8. Discussion

Rather than trying to specify a minimum number of biological and environmental conditions that determine parental care, I have attempted to predict how the expression of a parental investment will be influenced by the demography of a population. A parent's response is considered a result of natural selection acting on a range of parental behaviors, selecting the optimal response for a particular circumstance. Thus I have primarily focused on how the pattern of parental investment in a population is maintained and how it will evolve in different circumstances, rather than the origin of the investment.

The cost of a parental investment serves as a measure of reproductive effort for a parental activity. By stressing the risk of mortality, the concept of parental investment can be used to determine the selective bases of parental behavior. To understand the evolution of any reproductive activity, the measure of reproductive effort should incorporate the risk of mortality (Hirshfield and Tinkle 1975; Pianka and Parker 1975).

In addition, the benefit of a parental investment is considered a major determinant of a parent's response. The

benefit is the proportionate increase in the present component (P) resulting from the parent's response. For a parental response that affects the survival of offspring differentially, such as feeding some young while starving others, the benefit is measured by the average increase in offspring survival. The model only considers parent-offspring relations from the standpoint of the parent. Trivers (1974) has discussed in detail circumstances in which the offspring can elicit more benefit than the parent should optimally give.

The optimal cost of a parental investment corresponds to the parental response that maximizes a parent's contribution to future generations. Thus, I have considered the expression of a parental investment as a function of selection acting to maximize future "profits" rather than as a function of cumulative or past investment (Trivers 1972; Barash 1975).

The notion of reproductive success (S) was introduced as a fitness measure because the equation for reproductive value does not account for parental care. Hamilton (1966) suggested redefining the measure of fecundity ( $m_t$ ) in species with parental care so that "birth" is the time when the offspring become independent of the parent. However, this is not the usual method of calculating fecundity and would lead to complications in species with extended periods of parental care. Schaffer (1974a, 1974b) considers fecundity as the number of offspring that survive to first breeding. While this accounts for the effects of parental care on the population's ultimate rate of increase, it provides no insight

into how a parent might adjust its behavior throughout the period of parental care. By defining reproductive success and partitioning it into present and future components, different patterns of parental investment can be predicted. The future component (F) is comparable to an organism's residual reproductive value (Williams 1966), which is useful in predicting the allocation of energy to reproductive tissues up to the time of birth (Pianka and Parker 1975). The present component (P) allows one to consider a parent's influence on the survival of its offspring, which would not be accounted for in the usual measure of age-specific fecundity.

The concept of reproductive success (S) shares the same problems as any other available measure of fitness (Kempthorne and Pollak 1970). The assumptions of a stable age distribution and invariant survival and fecundity lead to difficulties in making precise predictions for natural populations. The usefulness of the model presented here is in making qualitative predictions that can be tested in field situations. Its main value lies in accounting for differences or predicting changes in parental behavior based on known biological circumstances. For example, an increase in the number of offspring in a nest can lead to a prediction of an increase in parental risk, without requiring exact measures of all the demographic parameters of the population. Some biological circumstances will lead to more general predictions than others. When changes in F/P are not confounded by simultaneous changes in the effectiveness of a response, the

change in parental investment will be more predictable. For example, as eggs in a nest get older the value of F/P will decrease, but the effect of a parent's defense on increasing the eggs' survival will remain constant. Thus a more general prediction of increased parental care with increasing age of offspring can be made for situations where the offspring are eggs than in situations where the offspring have hatched and are becoming more independent as they age. In this latter situation, the benefit of a parental defense may decrease over time favoring less parental risk. The model of parental investment and reproductive success will be most useful when applied to particular circumstances.



## CHAPTER III. NEST DEFENSE BY MALE STICKLEBACKS

1. Introduction

The concept of parental investment leads to a number of hypotheses, some which are more testable than others. Parental activities that alleviate a serious threat to the young while constituting considerable risk for the parent are obvious examples of parental investment and can be used to test these hypotheses. The circumstance in which a parent defends its young against a predator that is a threat to both the young and the parent, provides a useful starting point for evaluating the influence of the offspring on the level of risk undertaken by the parent. To eliminate any effect of the age or number of young on the effectiveness of the parent's defense, it is necessary to choose a situation in which the parent's ability to defend its offspring is independent of their abundance or age. This is often the case when a parent defends eggs in a nest. The parent's ability to chase a predator away from the nest will usually be independent of the number of offspring if they are all concealed within the nest. If the offspring are eggs, they will generally remain dependent on the parent's assistance until hatching, and their age will not affect the benefit resulting from any given level of parental risk. Thus I chose the circumstance of a parent defending a nest with eggs to examine the influence of the offspring on the intensity of the parent's defense. My

operational hypothesis was that the parent would increase its risk for a larger number or older average age of eggs in the nest.

## 2. The Parent - *Gasterosteus aculeatus*

A variety of organisms that exhibit parental care offer potential opportunities for testing hypotheses of parental investment. To test the parental defense hypothesis in this study I have used the threespine stickleback, *Gasterosteus aculeatus*. In this fish species, females enter breeding areas only to spawn and males assume parental responsibilities, defending the eggs and newly hatched fry. The reproductive behavior of male sticklebacks in laboratory situations has been described in detail (Tinbergen 1952; van Iersel 1958; van den Assem 1967). Here I will only add some observations of male sticklebacks in their natural environment that may be relevant to the field experiment.

For this study two isolated populations were chosen on Sechelt Peninsula north of Vancouver, British Columbia. Both were in low elevation lakes, Trout Lake and Garden Bay Lake, which have clear waters suitable for observations from shore. In the springtime male sticklebacks move into shallow areas along the lake shores, where they establish territories and build nests of algae and other plant debris. Baggerman (1957) found that breeding in *G. aculeatus* is triggered by increasing temperatures and longer day lengths. Males entering breeding

condition can usually be identified by their characteristic development of bright red throats and blue irises. In 1975, the first breeding males in Trout Lake were observed in the second week of May. These were tending nests in shallow areas where the water temperature had climbed to 16° C. Males gradually began to settle in shore areas adjacent to deeper parts of the lake as the main lake temperature increased. In Garden Bay Lake, males with breeding coloration were also first observed in the middle of May.

The male stickleback collects plant debris and constructs a cylindrical nest that lies flat on the lake bottom. Most of the nests observed in Trout Lake (n=103) and Garden Bay Lake (n=66) were in well exposed areas open to the main body of the lake. Nests were not uniformly distributed along the shore; some areas had a larger concentration of males than others. The mean distance to its nearest neighbor's nest was 1.61 m (standard error (SE) =.095) for Trout Lake males and 1.26 m (SE=.088) for males from Garden Bay Lake.

Nests were generally close to shore, except where shallow areas extended far out into the lakes. The mean distance of nests from shore was less in Trout Lake ( $\bar{x}$ =.86 m, SE=.050) than in Garden Bay Lake ( $\bar{x}$ =1.85 m, SE=.164), which has more gradual sloping shallows than Trout Lake. The mean depth of water over the nests ( $\bar{x}$ =.38 m, SE=.015) in Trout Lake did not vary until the last part of the breeding season. By mid July water temperatures had climbed to 25° C. (measured at .4 m depth) and most sticklebacks had stopped breeding. In

contrast, males in Garden Bay Lake continued to breed through July, when water temperatures exceeded 25° C., until the first week of August when the water temperature had dropped back to 22° C. The mean depth of nests in Garden Bay Lake increased during this period, with a mean nest depth of .39 m (SE=.012) in the first week of July and a mean depth of .70 m (SE=.190) at the end of July.

Laboratory studies of threespine sticklebacks have characterized males as being highly active in territorial defense (van den Assem 1967) and courtship of females (van Iersel 1953). However males in Trout Lake were strikingly passive in defending their nest areas and seldom displayed the well known zig-zag dance, in which the male courts a female by abruptly jumping from side to side. In addition, males in the early stages of the reproductive cycle were often lacking bright throat coloration, which appears to function in aggression between males and in the courtship of females (ter Pelkwijk and Tinbergen 1937). In contrast, males in Garden Bay Lake vigorously defended territories, actively courted females, and displayed bright red throats throughout the reproductive cycle.

Many of the differences in reproductive behavior between Trout Lake males and males from Garden Bay Lake may be the result of a difference in the availability of gravid females. Gravid females were frequently observed along the shores of Trout Lake, but were seldom seen in Garden Bay Lake. This disparity in female availability is reflected by the number of

eggs found in males' nests. In Trout Lake 79 per cent of the nests collected contained eggs compared to 55 per cent in Garden Bay Lake. Of those nests containing eggs, the mean number of eggs per nest in Trout Lake was 349.9 (SE=34.42, n=58). This represents approximately six successive spawnings by different females, whose mean fecundity in Trout Lake was 58.1 eggs per spawning (SE=5.29, n=21). The mean number of eggs per nest in Garden Bay Lake was less than half the mean in Trout Lake ( $\bar{x}$ =151.7, SE=13.94, n=26).

This difference in the mean number of eggs per nest might be attributed to egg production by females. Trout Lake develops a summer algal bloom and has a mud bottom in contrast to the clearer waters and gravel bottom of Garden Bay Lake. If this affects the availability of food it might account for a higher production of eggs by Trout Lake females, since food levels influence the number of eggs per spawning and the length of the inter-spawning interval in G. aculeatus (Wootton 1973).

My main purpose in pointing out this variation between sticklebacks from Trout Lake and Garden Bay Lake has been to give some specific information on the populations used to test the parental defense hypothesis, while providing a general background on male reproductive behavior. Some of these differences will also be useful for interpreting the results of the field experiment.

### 3. The Threat - Cottus asper

To test the parental defense hypothesis it was necessary to find a common predator of both the male stickleback and its eggs. The prickly sculpin, Cottus asper, is a benthic fish commonly found in low elevation lakes and streams along the coast of British Columbia. Sculpins are abundant in Garden Bay Lake and absent from Trout Lake. Moodie (1972) found stickleback eggs in over 30 per cent of the adult prickly sculpins he examined from Mayer Lake in the Queen Charlotte Islands. In a study of Harewood Lake on Vancouver Island, Murray (unpublished data) found that sculpins were preying intensely on both adult sticklebacks and their eggs. In addition, 7 out of 12 sculpins collected at the beginning of the stickleback breeding season in Mixal Lake, one half mile from Garden Bay Lake, contained remains of adult sticklebacks.

The interaction of sticklebacks and sculpins collected from Garden Bay Lake was observed in the laboratory. In a 40 liter aquarium a sculpin as small as 98.4 mm (standard length) could successfully capture and ingest an adult stickleback 61.5 mm in length. Sculpins were ambush predators of sticklebacks; they were never observed to chase their prey. A sculpin would typically lie in wait on the bottom until a stickleback swam within the area surrounding its head, at which point the sculpin would lunge at the stickleback by utilizing its large pectoral fins. Sculpins never attacked a stickleback over their tail area, but would turn to face the

stickleback before striking. Similar predatory behavior has been reported for other species of Cottus (Hikita and Nagasawa 1960; Phillips and Claire 1966; Patten 1975).

The method by which sculpins prey on stickleback eggs in nature is unknown. Predation was observed in the laboratory by introducing a sculpin to an aquarium containing a male stickleback with its nest. When the male returned to fanning after the initial disturbance, the sculpin began to approach the nest in a series of jumps along the bottom. With each forward movement of the sculpin, the male would leave the nest and approach the sculpin. The male would occasionally attack the sculpin, driving it away from the nest, and sometimes the sculpin would strike at the male. Eventually the sculpin lunged for the nest, and in a rocking motion repeatedly seized and spat out the nest contents. All the eggs were ingested before the male was able to drive the sculpin from the nest area.

A number of field observations were made of stickleback and sculpin interactions in Garden Bay Lake. Males frequently chased sculpins out of their nest areas. If the sculpin was a potential predator of the male (larger than 100 mm), the male would often approach the sculpin from behind and bite it on the tail. In one instance a male at the start of nest building successively chased five sculpins, all less than 100 mm, from its territory. Predation by sculpins was never directly observed, although a male and female stickleback swimming toward a nest during courtship were both struck at by

a large sculpin.

#### 4. Fight or Flight - Choosing a Field Test

To test the prediction of increased parental risk with a larger number of eggs or older eggs in the nest, I decided to measure a male's response to a choice situation. The objective was to determine the influence of the eggs on the level of risk taken by a male in defending its nest against a sculpin predator.

A dummy sculpin was prepared from a large specimen (138.3 mm standard length) of C. Asper. This was well beyond the size of sculpin that could easily prey on the sticklebacks in Trout Lake and Garden Bay Lake (all males tested were less than 60 mm), thus minimizing any effect of male size on the response. The dummy was preserved in ethanol and glycerine (to prevent drying) and was washed before each test. Transparent fishing line was attached through the head and caudal area so that the dummy could be suspended and controlled from the end of two poles, each 2.5 meters in length.

The experimental procedure was to move quietly along the shore until a male with a nest was observed. If the male was frightened from his nest area by my approach, I waited until it had resumed normal fanning before I began a test. The model was then lowered down over the nest. The disturbance at the water surface often frightened the male from the nest area



and I observed the direction that the male escaped. Since males usually return from the same direction in which they escape, I was able to orient the dummy so that its head was facing the direction from which the male was most likely to return. In this way the test was standardized so that the returning male always faced the mouth end of the sculpin dummy. Upon return the male characteristically stopped at the periphery of its territory where it could view the nest. At this point I would gently bob the dummy in a simulated feeding motion of approximately one bob per second. This motion was similar to the feeding behavior observed in the laboratory, although the amplitude was slightly exaggerated to ensure that the male would spot the dummy. The bobbing motion was continued throughout the test, making it possible to keep the dummy's head oriented to the male if it attempted to swim around to the dummy's tail.

The male's response to the sculpin dummy was recorded as a series of different "risk measures". Responses were categorized into three separate "all-or-none" measures, as either a high risk or low risk response (see Discussion). The prediction was that for each all-or-none measure, males in the high risk category would have more eggs or older eggs than males in the low risk category.

Upon returning to its nest area and spotting the sculpin dummy, the male would usually either desert the nest area again or attack the dummy. This was recorded as an "Attack" or "No Attack", with the attack response representing a higher

risk. Males that re-deserted their nest never returned and attacked the sculpin dummy (tests were terminated after three minutes). Of those males that did attack the dummy, the location on the sculpin's body that was first bitten was recorded, since some males were able to swim around the dummy and attack it from behind before it could be reoriented. If the male first attacked the sculpin's head the response was recorded as "Head", and any attack on the body behind the sculpin's operculum was recorded as "Tail".

Occasionally a male would not desert its nest area when the dummy was first introduced into the water, but would remain within an area approximately one half meter from the nest. This response was recorded as "Remain", in contrast to the more common "Desert" response. Remaining in the nest area was considered a higher risk response than deserting the nest, and every male that remained within its immediate nest area subsequently attacked the dummy.

In addition to the all-or-none measures, a number of "quantitative" risk measures of the male's response were recorded utilizing two stopwatches. Each quantitative measure accounted for a range of intensity in the male's response, and the prediction was that the level of risk displayed would be higher for males with larger numbers of eggs or older eggs in their nests.

The initial time it took a male to return to a location where it could view its nest was designated the "Return Time", and a quicker return time was considered a higher risk

response. If the male then attacked the dummy, the "Time to Attack" was recorded as the time between the male's return to a stationary position at the periphery of its territory and its first bite at the dummy. For those males that never deserted the nest area, the Return Time was assigned as one second and the Time to Attack was measured from the time the male had turned and faced the dummy until its first bite. After the initial attack, the number of bites at the dummy in the next 60 seconds was recorded (Bites per Min), and males with a larger number of eggs or older eggs were expected to attack the dummy more fiercely, resulting in a larger number of recorded bites per minute.

The sculpin dummy was also presented to males that were guarding fry, which remain in a swarm over the nest for approximately a week after hatching. The dummy was placed over the remains of the nest if it was visible, or in the midst of the swarm if no nest was spotted. The same male responses were recorded.

At the end of each test the male was captured with a dip net (if possible), measured, and subsequently released. Nests were collected and the eggs were preserved in 10% formalin. After tests on males guarding fry, a small sample of fry was collected. In addition, a number of nest measures were recorded after each test: (1) the depth of water over the nest, (2) the distance from the nest to shore, (3) the temperature of the water at the nest, (4) the distance of the nest from the nearest rock or plant cover that could shelter

the male, (5) the distance to the male's nearest neighbor's nest, (6) the presence of sunlight or shade on the nest during the test, (7) disturbance of the water surface by wind, (8) the date, and (9) the time of day.

The nest contents were transferred to 30% alcohol in the laboratory and the number of eggs in each nest was counted. The eggs were classified by embryological stage and assigned a "physiological age" (Swarup 1958). This age was the time in hours that the eggs used in Swarup's study took to reach each embryological stage at 18° C. The mean physiological age of the eggs was calculated for each nest, as well as the variance in egg age within the nest. An estimate of the mean "chronological age" of the eggs in each nest was determined (see Appendix I), based on water temperatures and the development rate of eggs from a stickleback population on Vancouver Island (McPhail, unpublished data).

Males were tested until the end of the breeding season in both lakes. A total of 51 males were tested in Trout Lake and 57 males in Garden Bay Lake. Only males that had nests were tested, and no male was tested more than once, thus eliminating any possibility of habituation to the dummy. Sometimes the contents of the nest were spilled during collection (most often when the eggs were in late stages and less cohesive), so that the number of eggs could not be determined. For these situations the egg number was not counted, but if the remaining sample was large, the eggs were used to estimate the mean egg age. Any other measurements

that were suspected of obvious error (e. g. if I frightened the male by falling into the water) were not included in the analysis.

## 5. Experimental Results

The parental defense hypothesis predicted that males with a larger number of eggs or older eggs would display more risk in defending their nests from the sculpin predator. For each all-or-none measure, the male's response was categorized as either high or low risk, and the prediction was that males in the high risk category would have a significantly ( $p < .05$ ) larger number of eggs, or average egg age per nest, than males in the low risk category. The Attack, Head, or Remain response was considered to constitute higher risk than the corresponding No Attack, Tail, or Desert response.

A comparison of the mean number of eggs in each response category for the three all-or-none risk measures is shown in Table I. The results generally support the hypothesis for both Trout Lake and Garden Bay Lake males. In both lakes, the number of eggs for males that attacked the dummy and remained within their immediate nest area at the beginning of the test is significantly larger (Mann-Whitney U test) than for those males that didn't attack the dummy and deserted their nest area. The mean number of eggs per nest of males that initially attacked the sculpin's head is also larger than the mean for males that swam around to the sculpin's tail, however

the difference is not statistically significant.

The difference in the mean age of eggs for males in each risk category is shown in Table II for the physiological egg age and Table III for the chronological egg age. The results are qualitatively the same for either measure of egg age. Males from both lakes that attacked the dummy had significantly older eggs than males that didn't attack, and males with older eggs generally remained in the nest area more often. In both lakes the mean age of eggs for males that attacked the sculpin's head was greater than the mean egg age for males that attacked the tail area, but the difference was only significant in Garden Bay Lake.

A comparison of the two populations (Table IV) indicates that the mean number of eggs for males that attack the dummy is significantly larger for Trout Lake males than for males from Garden Bay Lake. This difference can not be entirely attributed to the greater frequency of males without any eggs in Garden Bay Lake, as shown by a comparison of means calculated from only those nests that contained eggs. A similar difference was found for the mean age of eggs for males from both lakes. Both the physiological and chronological egg age for males that attacked the sculpin dummy is larger in Trout Lake than Garden Bay Lake, however this difference is only significant for chronological egg age. There were no other significant differences between the two populations for the other all-or-none risk measures. The mean number and age of eggs for these other risk categories,

TABLE I. A comparison between the number of eggs for males in the high and low risk category for each all-or-none response

RISK MEASURE	MEAN	SE	N	PROB <sup>1</sup>
<u>Trout Lake</u>				
Attack	257.3	50.52	21	.001
No Attack	76.2	42.25	16	
Head	217.9	39.07	16	p>.10
Tail	139.7	111.48	3	
Remain	434.7	113.12	6	.002
Desert	126.4	31.04	32	
<u>Garden Bay Lake</u>				
Attack	118.0	17.60	25	.001
No Attack	21.1	12.95	21	
Head	146.4	21.90	14	.05<p<.10
Tail	90.0	26.99	10	
Remain	202.5	18.50	2	.047
Desert	66.7	13.42	43	

1. Mann-Whitney U test

TABLE II. A comparison between the physiological age of the eggs for males in the high and low risk category for each all-or-none response

RISK MEASURE	MEAN	SE	N <sup>1</sup>	PROB <sup>2</sup>
<u>Trout Lake</u>				
Attack	80.4	11.68	25	.001
No Attack	26.2	10.63	17	
Head	93.9	13.20	19	.05<p<.10
Tail	37.0	29.51	3	
Remain	123.1	18.31	8	.001
Desert	43.3	8.83	33	
<u>Garden Bay Lake</u>				
Attack	62.7	11.19	32	.001
No Attack	10.1	6.51	21	
Head	84.0	14.72	20	p<.025
Tail	29.6	12.32	11	
Remain	138.9	19.88	3	.006
Desert	33.9	7.47	48	

1. Sample size for egg age is often larger than egg number (TABLE I.) because estimates of egg age included eggs from spilled nests, which were not used in the analysis of egg number.

2. Mann-Whitney U test



TABLE III. A comparison between the chronological age of the eggs for males in the high and low risk category for each all-or-none response

RISK MEASURE	MEAN	SE	N	PROB <sup>1</sup>
<u>Trout Lake</u>				
Attack	56.7	8.17	25	.001
No Attack	18.0	7.21	17	
Head	65.8	9.24	19	.05<p<.10
Tail	27.0	21.56	3	
Remain	79.7	12.66	8	.001
Desert	30.5	6.21	33	
<u>Garden Bay Lake</u>				
Attack	37.6	6.64	32	.001
No Attack	6.0	3.81	21	
Head	50.4	8.73	20	p<.01
Tail	17.6	7.17	11	
Remain	82.1	10.04	3	.006
Desert	21.8	5.00	48	

1. Mann-Whitney U test

TABLE IV. A comparison between the two populations for the number and egg age of males that attacked the sculpin dummy

NEST MEASURE	TROUT LAKE Mean $\pm$ SE(n)	GARDEN BAY LAKE Mean $\pm$ SE(n)	PROB <sup>1</sup>
<u>Number of Eggs</u>			
All Nests	257.3 $\pm$ 50.52 (21)	118.0 $\pm$ 17.60 (25)	.013
Only with Eggs	286.0 $\pm$ 51.55 (19)	163.9 $\pm$ 12.86 (18)	.025
<u>Physiological Age</u>			
All Nests	80.4 $\pm$ 11.68 (25)	62.7 $\pm$ 11.19 (32)	.112
Only with Eggs	91.4 $\pm$ 11.37 (22)	80.2 $\pm$ 12.18 (25)	.226
<u>Chronological Age</u>			
All Nests	56.7 $\pm$ 8.17 (25)	37.6 $\pm$ 6.64 (32)	.037
Only with Eggs	64.4 $\pm$ 7.94 (22)	48.1 $\pm$ 7.20 (25)	.065

1. Mann-Whitney U test

calculated for only those nests that contained eggs, is given in Appendix II.

The influence of the number and age of eggs on each of the quantitative measures of the male's response was examined by regression analysis. The prediction was that with larger numbers or older eggs in a male's nest, the Return Time and Time to Attack would decrease, and the number of Bites per Min would increase. The slope for each quantitative risk measure as a function of egg number or egg age was calculated and tested for significance.

The relation between the number of eggs per male's nest and each quantitative risk measure is shown in Table V. For both lakes the male's response is in the predicted direction, and all the slopes are significant. The influence of the mean age of eggs per male's nest on each quantitative measure is shown in Table VI for physiological egg age and Table VII for chronological age, both measures of egg age giving the same qualitative results. In the two populations, the return time and the time to attack decreases for males with older eggs in the nest, while the number of bites per minute increases.

There are no significant differences between the two lakes for the slopes or intercepts of any of the regressions. Considering only those males that had eggs in their nests, the changes in the quantitative responses for the combined populations are still in the predicted directions (Table VIII). The results for each separate lake, and more complete regression statistics, are given in Appendix III.

TABLE V. Regression results for each quantitative risk measure as a function of the number of eggs in the nest

RISK MEASURE <sup>1</sup>	PREDICTED SLOPE	OBSERVED SLOPE	SE SLOPE	N	PROB <sup>2</sup>
<u>Trout Lake</u>					
Return Time	-	-.005	.0014	27	.001
Time to Attack	-	-.003	.0011	20	.003
Bites per Min	+	+.027	.0076	22	.001
<u>Garden Bay Lake</u>					
Return Time	-	-.008	.0025	35	.003
Time to Attack	-	-.006	.0026	24	.022
Bites per Min	+	+.043	.0246	23	.046

1. Time measures are log transformed
2. Probability that the slope is not in the predicted direction (one-tailed F test)

TABLE VI. Regression results for each quantitative risk measure as a function of the physiological age of the eggs in the nest

RISK MEASURE <sup>1</sup>	PREDICTED SLOPE	OBSERVED SLOPE	SE SLOPE	N	PROB <sup>2</sup>
<u>Trout Lake</u>					
Return Time	-	-.020	.0050	30	.001
Time to Attack	-	-.014	.0043	23	.002
Bites per Min	+	+.086	.0320	25	.006
<u>Garden Bay Lake</u>					
Return Time	-	-.011	.0034	42	.002
Time to Attack	-	-.011	.0031	31	.001
Bites per Min	+	+.070	.0290	30	.011

1. Time measures are log transformed

2. Probability that the slope is not in the predicted direction (one-tailed F test)

TABLE VII. Regression results for each quantitative risk measure as a function of the chronological age of the eggs in the nest

RISK MEASURE <sup>1</sup>	PREDICTED SLOPE	OBSERVED SLOPE	SE SLOPE	N	PROB <sup>2</sup>
<u>Trout Lake</u>					
Return Time	-	-.030	.0072	30	.001
Time to Attack	-	-.020	.0062	23	.002
Bites per Min	+	+.126	.0453	25	.005
<u>Garden Bay Lake</u>					
Return Time	-	-.018	.0057	42	.002
Time to Attack	-	-.018	.0053	31	.001
Bites per Min	+	+.116	.0492	30	.012

1. Time measures are log transformed
2. Probability that the slope is not in the predicted direction (one-tailed F test)

TABLE VIII. Regression results calculated for the combined populations counting only those males with eggs in their nests. The slope and probability is given for each risk measure as a function of the number or age of the eggs.

RISK MEASURE <sup>1</sup>	NUMBER OF EGGS	PHYS. AGE	CHRON. AGE
Return Time	-.002 p=.046	-.007 p=.038	-.011 p=.038
Time to Attack	-.003 p=.006	-.010 p=.002	-.016 p=.002
Bites per Min	+.023 p=.013	+.059 p=.015	+.092 p=.016

1. Time measures are log transformed

The influence on the male's response of the different nest measures (nest depth, water temperature, etc.), as well as the number of eggs, physiological egg age, male size, and variance in egg age, was examined by multiple regression for those males in which there were no missing values for any of the various measures. For the all-or-none risk measures the influence of the egg and nest measures was determined by discriminant analysis, which is a special case of multiple regression (Gilbert 1973), using only those nest measures that were normally distributed. None of the various measures contributed consistently to the prediction of the male's response besides the number or age of the eggs (Appendix IV). In Trout Lake the distance of the nest from shore contributed significantly to the prediction of the Time to Attack in addition to the egg number, and in Garden Bay Lake the depth of the nest added to the prediction of the Return Time. Although the correlation between egg number and egg age for males that had eggs was low in both Trout Lake ( $r=.1166$ ) and Garden Bay Lake ( $r=-.0711$ ), the number of eggs is sufficient to predict the male's response in all the risk measures except the male's tendency to desert its nest, which is best predicted by the age of the eggs. However this may underestimate the influence of egg age on the male's response, since nests with older eggs had a higher frequency of spillage during collection and were not included in the multiple regression analysis. For all the risk measures, only a small proportion (<55%) of the variance in the male's response is



accounted for ( $R^2$ ) by the egg number or age.

The experimental results for males that were guarding fry are given in Table IX. Only six males were tested but there is a clear trend of decreasing risk with larger fry. The mean length of fry represents the time since hatching, and this relation is probably similar in both populations, since the mean diameter of eggs in Trout Lake ( $\bar{x}=16.9$ ,  $SE=.307$ ,  $n=20$ ) is approximately the same as in Garden Bay Lake ( $\bar{x}=17.0$ ,  $SE=.162$ ,  $n=20$ ). Those males that attacked the dummy sculpin had significantly smaller fry than those that didn't, and the time to attack increased for males with older fry, while the number of bites per minute decreased.

TABLE IX. Responses of males guarding fry

MEAN LENGTH OF FRY	5.7	6.7 <sup>1</sup>	6.8	7.5	9.2	10.0
MALE RESPONSE	Attack	Attack	Attack	No Attack	No Attack	No Attack
Time to Attack	1.2	3.0	8.0	--	--	--
Bites per Min	36	23	19	--	--	--

<u>ATTACK</u> Mean Fry Length $\pm$ SE	<u>NO ATTACK</u> Mean Fry Length $\pm$ SE	<u>PROBABILITY</u> U Test
6.4 $\pm$ .35	8.9 $\pm$ 1.63	.05

1. Male from Garden Bay Lake

## CHAPTER IV. DISCUSSION

The results of the field experiment demonstrate an increase in the intensity of a male's defense for a larger number or older eggs in the nest. The underlying motivation and responsiveness influencing the strength of a parent's response to a nest predator has been discussed in detail by Curio (1975), who also found a temporal change during the breeding cycle in the mobbing intensity of pied flycatchers. Other studies have described similar changes in the intensity of distraction displays by nesting birds (Armstrong 1956; Simmons 1955; Stephens 1963, Gramza 1967), but have primarily focused on the proximate factors influencing the behavior (however see Barash 1975). Many of these anti-predator responses are difficult to assess in terms of their cost to the parent, and evaluations based on time or energy expended make the implicit assumption that these "currencies" are limiting. In this study I have attempted to measure responses which involve an increased risk of mortality to the parent for an increase in the intensity of its defense.

Each of the all-or-none risk measures categorizes the male's response to the sculpin dummy as constituting either a high or low risk for the male, based on observations of the predatory behavior of sculpins. Those males that attack the sculpin are assumed to take more risk than males which never approach the dummy, since sculpins never pursue their prey and only attack when a stickleback is in close proximity. A male

that attacks the sculpin's head has entered a critical strike area, and should have a higher probability of being captured than a male which actively avoids the sculpin's head and attacks its tail. Similarly, males which remain in their immediate nest area after the sculpin is first introduced are in close proximity to the sculpin, and would have a higher probability of being captured than males which instantly desert their nest area after a disturbance.

The quantitative measures of the male's response reflect the intensity of its defense, and would also involve an increased risk of mortality for the male with a live sculpin predator. Although the decrease in the Return Time and the Time to Attack mostly represent an increased readiness to defend the nest, the probability of being captured by a nest predator increases with a shorter time away from the nest. A larger number of Bites per Min represents repeated contacts with the sculpin's head, which was kept oriented to the male throughout the test, and would result in a higher probability of capture by a live sculpin.

The mechanism by which a male recognizes the number and age of the eggs in its nest was not examined. Males frequently have direct contact with the eggs, often poking and rearranging the egg mass in the nest. A number of laboratory studies indicate that parental behavior in G. aculeatus is directly influenced by stimuli from the eggs. The proportion of time a male spends fanning the eggs increases with egg number and age, and nest switching experiments have

demonstrated that this behavior is directly influenced by the eggs, rather than the sequence or number of past fertilizations (van Iersel 1953; Beune, unpublished MS). Increases in fanning are stimulated by an increase in the carbon dioxide concentration of the water surrounding the nest (Sevenster 1961), and the changes in fanning through the developmental period correlate with changes in the metabolism of the eggs (Jones 1966). In this study both the physiological and chronological age of the eggs were equally significant predictors of a male's response. Experiments with eggs developing at different rates indicate that a male's fanning behavior is a response to the embryological stage of the eggs rather than the time since fertilization (van Iersel 1953). Thus it is most likely that males are responding to the physiological age of the eggs, rather than their chronological age.

The results of this and other studies of parental care correspond to many of the predictions generated by the model of parental investment and reproductive success. For each of the quantitative risk measures, there was an increase in the intensity, and associated risk, of the male's defense as the number or age of the eggs increased. During the incubation period of many bird species a similar increase occurs in the conspicuousness of the distraction displays by parents (Stephens 1963; Gramza 1967; Barash 1975), and in the intensity of the mobbing response to nest predators (Smith and Hosking 1955; Curio 1963, 1975; Curio et. al. 1969). These

increases in the intensity of parental defense can be associated with the larger reproductive value of older eggs, which favors a parent taking a higher risk in a parental investment (Figure 2).

Each of the all-or-none risk measures categorizes the male's response to the sculpin dummy as constituting either a high or low risk for the male. However only the Attack-No Attack measure actually represents an all-or-none response; the Head-Tail and Remain-Desert measures were developed as a means of quantifying responses that are variable in intensity, but difficult to measure. The significantly larger number and age of the eggs for males that attacked the dummy represents an increased probability of this response occurring as the "value" of the eggs in the nest increases. This corresponds qualitatively to the model's prediction of certain high risk responses not becoming "justified" until the value of the present young (in relation to the parent's future prospects) exceeds a threshold (equation 3). This has also been observed for the attack response of willow warblers to a predatory cuckoo (Edwards et. al. 1950), and for the ontogeny of the distraction displays of different birds, which follow a sequential pattern from less to more conspicuous as the age of the eggs increases (Simmons 1955; Barash 1975). Similarly, N. G. Smith (pers. com.) has observed that oropendulas do not enter their nests at night to incubate until later stages of egg development, a behavioral pattern which primarily appears to be a response to nest predation rather than increased

energy demands of the eggs (Ricklefs 1969).

Males increased their risk in nest defense until the eggs hatched, after which the frequency of attacking the sculpin dummy, as well as the intensity of the male's defense, declined. The decrease in parental risk after hatching, even though the value of the young continued to increase, can be associated with the decrease in the effectiveness of the male's defense (Figure 3). As the fry develop, their swimming ability increases and they become less dependent on parental assistance in avoiding nest predators. The benefit resulting from a given level of parental risk rapidly declines, and outweighs the advantage to the parent of increasing its risk for older young. Barash (1975) has given a similar interpretation for the difference in the timing of the most conspicuous distraction displays of precocial birds, which occur shortly after hatching, and the maximum displays of altricial birds, which don't reach a peak until several days after hatching. This corresponds to the increased independence of precocial young shortly after hatching, while altricial young remain completely dependent on the parent's assistance until just before fledging. Thus the different pattern of parental risk for the two groups can be associated with temporal changes in the effectiveness of parental defense, although the influence of the renesting capabilities of each group should also be considered.

It is interesting to note that the inverted U-shaped trend over the breeding cycle in the intensity of the male's response to the sculpin dummy is directly opposite to the temporal pattern of "aggression" to conspecifics found in many laboratory studies of G. aculeatus (Segaar 1961; Symons 1965; Black 1971; Wootton 1971). In these studies the frequency of biting at a conspecific intruder (usually another male behind glass or a model) decreases as the eggs near hatching, and then subsequently increases as the fry develop. Thus the pattern of male response to the dummy predator in this study suggests discrimination of the dummy sculpin from other sticklebacks, an expected result based on other studies of stimulus recognition in G. aculeatus (ter Pelkwijk and Tinbergen 1937; Tinbergen 1952). Although sculpins are absent from Trout Lake, the pattern of response to the sculpin dummy in this population was similar to the response pattern of males in Garden Bay Lake, where sculpins are present. Curio (1963, 1969) also found a similarity in the response to a model predator by Darwin's finches on islands where the predator was absent and on islands where the finches were sympatric with the predator.

A larger proportion of males from Garden Bay Lake than Trout Lake avoided the sculpin's head, and the increased tendency to attack the head area with more or older eggs was significant only in Garden Bay Lake, which implies that males in this population recognize the sculpin's strike zone. Thrushes have a similar tendency to avoid the front of a



stuffed jay predator, and try to attack it from behind (Goodwin 1953). This specific response to the sculpin by males in Garden Bay Lake may be influenced by experience or could be a population characteristic. Seghers (1970, 1973) found a similar variation between populations of the guppy Poecilia reticulata in their anti-predator behavior, and showed that this may have evolved as a response to the presence of different predators.

The number of eggs for males that attacked the sculpin dummy in Garden Bay Lake was significantly lower than the number for males in Trout Lake. The increased probability of a male in Garden Bay Lake attacking the sculpin when there is a small number of eggs in the nest may be a result of the lower number of eggs usually received by males in this population. Thus in relation to the male's future prospects, a given number of eggs in the nest may be worth more in Garden Bay Lake than in Trout Lake and will favor a higher parental risk (equation 3), although the absence of sculpins from Trout Lake could also influence this variation in the attack response threshold.

None of the nest measures other than the number or age of the eggs added consistently to the prediction of the male's response. The size of the male did not significantly influence its response to the sculpin dummy, although male size might be important with a smaller sculpin that would have difficulty handling a large stickleback. After an initial consideration one might expect there to be a significant

increase in male risk as the breeding season progresses, since seasonal breeders often show a rapid decline in reproductive value (Pianka and Parker 1975) which would favor an increase in parental risk for a given value of present young (Figure 2). However the model predicts that risk will be proportional to the ratio of future to present prospects ( $F/P$ ), and a corresponding decline over the summer in the reproductive value (probability of survival) of the eggs would counteract the influence of the decline in parental reproductive value. Kynard (1972) found that 76.8 per cent ( $n=34$ ) of the stickleback males in Wapato Lake, Washington were able to rear eggs in May, but the success rate of males in August was only 2.4 per cent ( $n=82$ ), which suggests that egg survival is generally lower at the end of the breeding season. The reproductive value of sticklebacks hatched in late summer may also be lower if a small size decreases the probability of surviving through the winter. Furthermore males appear to have been selected to avoid breeding in the early fall, even though there are often secondary rises in water temperature similar to increases in the springtime, by an additional breeding requirement of increasing daylengths (Baggerman 1972).

There was a large degree of variability in the response of males to the dummy for any given number or age of eggs in the nest. Thus many possible differences between the two populations in the level of risk undertaken by males could not be statistically resolved. The cause of this variability in

the response levels is difficult to determine. The variability in the lake environment, as well as the nature of the experiment, made it difficult to standardize the stimulus, and this may have influenced the strength of a male's response (Curio 1975). The male's past experience, especially in Garden Bay Lake where sculpins are present, may have also affected the male's response at the time of the test. In addition, loss of the eggs shortly before the test (e. g. from predation by other sticklebacks) could have resulted in a higher risk response than would have been predicted by the number of eggs in the nest, since a male's responsiveness may slowly wane after egg loss. These and other possible factors, such as basic behavioral differences among individual males (Black 1971), will have to be examined before it can be determined whether the variability in response is a result of adaptation, or just a lack of precision in the system.

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## APPENDIX I. THE CHRONOLOGICAL EGG AGE

The chronological age of the eggs, the time from fertilization to collection, was estimated by calculating the time the eggs take to reach a given embryological stage for the water temperature in the lake at the date of collection. The average water temperature for each lake throughout the summer was estimated by averaging the early morning (lowest) and late afternoon (highest) water temperatures, measured at the mean nest depth (.4m). This average temperature was combined with information on the development rate of stickleback eggs at different temperatures, calculated from data collected by McPhail (unpublished) on a population from Harewood Lake, Vancouver Island. The time these eggs took to reach each embryological stage, as described by Swarup (1958), had been measured at 15, 20, and 25° C. To determine the development rate, I used regression analysis to calculate the slope for the development time at each temperature as a function of the physiological age of the eggs, which is the time the eggs in Swarup's study took to reach each embryological stage. The following developmental slopes were found at each water temperature:

Temp.	15°	20°	25°
Slope	1.262	.731	.581

The decreasing developmental slope for higher water temperatures indicates that the time to reach a certain stage decreases with higher temperatures. However, the developmental slope is not a linear function of the water temperature. To determine the developmental slope for intermediate temperatures, a quadratic equation was fitted to the above data giving the developmental slope as a function of temperature:

$$\text{Slope} = .0076(\text{temp})^2 - .373(\text{temp}) + 5.15$$

Thus to calculate the chronological age of the eggs in each nest, (1) the average temperature of the lake at the date of collection was estimated, (2) this temperature was used in the above equation to calculate the developmental slope, and (3) the mean physiological age of the eggs was multiplied by the calculated slope, giving the mean chronological age of the eggs.

## APPENDIX II. ALL-OR-NONE RISK MEASURES

Results calculated for only those nests with eggs

	TROUT LAKE			GARDEN BAY LAKE		
RISK MEASURE	MEAN $\pm$ SE (N)	PROB		MEAN $\pm$ SE (N)	PROB	
<u>Number of Eggs</u>						
Attack	286.0 $\pm$ 51.55 (19)	p<.10		163.9 $\pm$ 12.86 (18)	p>.10	
No Attack	165.5 $\pm$ 74.80 ( 8)			111.0 $\pm$ 50.41 ( 4)		
Head	249.0 $\pm$ 37.63 (14)	p>.10		170.8 $\pm$ 16.80 (12)	p>.10	
Tail	209.5 $\pm$ 150.50 ( 2)			150.0 $\pm$ 19.62 ( 6)		
Remain	434.7 $\pm$ 113.12 ( 6)	.025		202.5 $\pm$ 18.50 ( 2)	p>.10	
Desert	205.7 $\pm$ 40.74 (20)			151.1 $\pm$ 15.62 (19)		
<u>Physiological Egg Age</u>						
Attack	91.4 $\pm$ 11.37 (22)	.041		80.2 $\pm$ 12.18 (25)	p>.10	
No Attack	55.6 $\pm$ 17.76 ( 8)			52.9 $\pm$ 26.94 ( 4)		
Head	104.9 $\pm$ 12.11 (17)	p>.10		93.3 $\pm$ 14.76 (18)	p<.10	
Tail	55.4 $\pm$ 39.85 ( 2)			46.5 $\pm$ 16.32 ( 7)		
Remain	123.1 $\pm$ 18.31 ( 8)	.012		152.4 $\pm$ 6.55 ( 3)	.035	
Desert	68.0 $\pm$ 10.57 (21)			65.3 $\pm$ 11.15 (25)		
<u>Chronological Egg Age</u>						
Attack	64.4 $\pm$ 7.94 (22)	.041		48.1 $\pm$ 7.20 (25)	.206	
No Attack	38.4 $\pm$ 11.90 ( 8)			31.7 $\pm$ 15.42 ( 4)		
Head	73.5 $\pm$ 8.48 (17)	p>.10		56.0 $\pm$ 8.74 (18)	.072	
Tail	40.5 $\pm$ 29.11 ( 2)			27.7 $\pm$ 9.38 ( 7)		
Remain	79.7 $\pm$ 12.66 ( 9)	.012		82.1 $\pm$ 10.04 ( 3)	.025	
Desert	47.9 $\pm$ 7.42 (21)			39.4 $\pm$ 6.66 (25)		

## APPENDIX III. QUANTITATIVE RISK MEASURES

## A. Regression results for all nests

RISK MEASURE <sup>1</sup>	CONST	SE	COEFF	SE	r	n	PROB
	A	A	B	B			
<u>Number of Eggs</u>							
Return Time (TL)	3.8	.44	-.005	.0014	.567	27	.001
Time to Attack (TL)	3.5	.37	-.003	.0011	.595	20	.003
Bites per Min (TL)	6.3	2.53	.027	.0076	.625	22	.001
Return Time (GB)	3.3	.28	-.008	.0025	.493	35	.001
Time to Attack (GB)	4.1	.38	-.006	.0026	.464	24	.011
Bites per Min (GB)	4.1	3.62	.043	.0246	.356	23	.046
Return Time (CO)	3.3	.24	-.004	.0010	.476	62	.001
Time to Attack (CO)	3.7	.24	-.004	.0009	.555	44	.001
Bites per Min (CO)	5.7	1.94	.029	.0075	.510	45	.001
<u>Physiological Egg Age</u>							
Return Time (TL)	3.9	.43	-.020	.0050	.599	30	.001
Time to Attack (TL)	3.6	.43	-.014	.0043	.591	23	.002
Bites per Min (TL)	7.2	3.15	.086	.0320	.489	25	.006
Return Time (GB)	3.0	.26	-.011	.0034	.447	42	.002
Time to Attack (GB)	3.7	.28	-.011	.0031	.535	31	.001
Bites per Min (GB)	5.9	2.62	.070	.0290	.416	30	.011
Return Time (CO)	3.3	.23	-.014	.0029	.504	72	.001
Time to Attack (CO)	3.7	.24	-.012	.0025	.569	54	.001
Bites per Min (CO)	6.4	1.98	.079	.0211	.459	55	.001
<u>Chronological Egg Age</u>							
Return Time (TL)	3.9	.43	-.030	.0072	.615	30	.001
Time to Attack (TL)	3.6	.44	-.020	.0062	.586	23	.003
Bites per Min (TL)	7.0	3.14	.126	.0453	.502	25	.005
Return Time (GB)	3.0	.26	-.018	.0057	.440	42	.002
Time to Attack (GB)	3.7	.28	-.018	.0053	.525	31	.001
Bites per Min (GB)	6.0	2.64	.116	.0492	.405	30	.012
Return Time (CO)	3.3	.23	-.022	.0045	.511	72	.001
Time to Attack (CO)	3.7	.24	-.020	.0038	.578	54	.001
Bites per Min (CO)	6.3	1.97	.125	.0322	.470	55	.001

1. Time measures are log transformed

(TL) -Trout Lake; (GBL) -Garden Bay Lake; (CO) -Combined Lakes

## APPENDIX III. QUANTITATIVE RISK MEASURES

## B. Regression results for only those nests with eggs

RISK MEASURE <sup>1</sup>	CONST A	SE A	COEFF B	SE B	r	n	PROB
<u>Number of Eggs</u>							
Return Time (TL)	2.6	.65	-.002	.0017	.296	19	.108
Time to Attack (TL)	3.3	.48	-.003	.0013	.515	17	.016
Bites per Min (TL)	7.5	3.23	.025	.0090	.552	19	.007
Return Time (GB)	4.1	1.07	-.012	.0061	.496	15	.029
Time to Attack (GB)	3.5	1.01	-.003	.0058	.147	17	.289
Bites per Min (GB)	12.3	10.16	-.001	.0576	.000	16	.932
Return Time (CO)	2.6	.45	-.002	.0014	.290	34	.046
Time to Attack (CO)	3.4	.34	-.003	.0012	.426	34	.006
Bites per Min (CO)	8.1	2.88	.023	.0099	.374	35	.013
<u>Physiological Egg Age</u>							
Return Time (TL)	2.6	.68	-.009	.0070	.289	21	.101
Time to Attack (TL)	3.4	.59	-.013	.0050	.487	20	.014
Bites per Min (TL)	9.2	4.15	.070	.0390	.367	22	.045
Return Time (GB)	2.4	.54	-.006	.0051	.254	22	.126
Time to Attack (GB)	3.3	.41	-.007	.0039	.373	24	.035
Bites per Min (GB)	8.5	3.97	.051	.0378	.283	23	.094
Return Time (CO)	2.5	.42	-.007	.0040	.270	43	.038
Time to Attack (CO)	3.3	.34	-.010	.0032	.427	44	.002
Bites per Min (CO)	8.9	2.82	.059	.0268	.322	45	.015
<u>Chronological Egg Age</u>							
Return Time (TL)	2.6	.68	-.014	.0096	.316	21	.080
Time to Attack (TL)	3.4	.60	-.018	.0080	.480	20	.015
Bites per Min (TL)	8.8	4.15	.104	.0561	.384	22	.037
Return Time (GB)	2.3	.55	-.009	.0089	.213	22	.171
Time to Attack (GB)	3.3	.41	-.011	.0068	.341	24	.049
Bites per Min (GB)	9.3	4.04	.072	.0660	.230	23	.145
Return Time (CO)	2.5	.42	-.011	.0064	.271	43	.038
Time to Attack (CO)	3.3	.34	-.016	.0050	.434	44	.002
Bites per Min (CO)	9.0	2.82	.092	.0417	.318	45	.016

1. Time measures are log transformed

(TL) - Trout Lake; (GBL) - Garden Bay Lake; (CO) - Combined Lakes

## APPENDIX IV. MULTIPLE REGRESSION RESULTS

RISK MEASURE	SIG IND VAR	COEFF	SE	N	PROB	R <sup>2</sup>
<u>Trout Lake</u>						
Return Time	egg number	-0.385	.0831	35	.001	.370
	nest depth	-0.427	.9805			
Time to Attack	egg number	-1.424	.1002	23	.018	.236
Bites per Min	egg number	1.110	.9282	22	.046	.181
Remain-Desert	egg age	0.669	.0011	19	.011	.320
Attack-No Attack	egg number	4.492	.0990	20	.001	.493
Head-Tail	no sig var	---	---	17	---	---
<u>Garden Bay Lake</u>						
Return Time	egg number	-0.821	.1026	27	.000	.529
Time to Attack	egg number	-2.565	.1338	19	.015	.409
	shore dist	1.035	.8498			
Bites per Min	egg number	2.680	1.056	20	.015	.282
Remain-Desert	egg number	0.091	.0724	26	.020	.194
Attack-No Attack	no sig var	---	---	26	---	---
Head Tail	no sig var	---	---	16	---	---

SIG IND VAR are those independent variables that contributed significantly ( $p < .05$ ) to the prediction of the risk measure. For the all-or-none risk measures the high risk response was assigned the value 1 and 0 was assigned to the low risk response. Only nests that contained eggs were used in the analysis of the all-or-none measures, and the time measures and egg number are log transformed. PROB is the probability of obtaining a value of  $R^2$  given that there is no association between the dependent and independent variables.