TRIVERS' PARENT-OFFSPRING CONFLICT THEORY: PROBLEMS AND SOLUTIONS TO TESTING IN THE FIELD

by

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Like many sociobiological theories, the original parent-offspring conflict theory as proposed by Robert Trivers (1974) was widely criticized as being vague and untestable. However, since its original proposal, many advances have been made in the modeling of the theory. In this paper, the more contemporary models of parent-offspring conflict will be analyzed, and, using the most recent developments, an approach to quantitatively testing the theory in the field will be proposed.

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CHAPTER I

INTRODUCTION

The Role of the Mathematical Model in Sociobiology

Sociobiologists, scientists who study the evolutionary basis of behavior, have been criticized for producing conclusions that are not scientifically valid. They have been criticized for producing conclusions that are "adaptationist" (assume all aspects of behavior are optimal solutions to specific problems) (Lewontin, 1979), utilize "arbitrary agglomeration" (use phenotypic units of evolution that are not justified) (Lewontin, 1979) and exhibit "conflation" (apply animal behaviors to humans without considering human cultural and historic influences) (Lewontin, 1979) amongst other problems. These criticisms, however, have been largely directed at the sociobiologists when they should, in fact, be directed at the subject the sociobiologists study. Sociobiology is an inherently difficult subject to study that contains several barriers to direct experimentation. The major ones are:

1. There are no ancestral organisms with which to work. The genetic precursors to behavioral evolution,

therefore, cannot be observed directly.

2. There are no ancestral environments with which to work. The environmental causes of behavioral evolution, therefore, cannot be observed directly.

3. There is not a great expanse of time with which to work. The process of behavioral evolution, therefore, cannot be observed directly.

With these fundamental barriers to direct investigation of behavioral evolution, an indirect approach has to be taken instead.

One method used today to investigate behavioral evolution is mathematical modeling. When using mathematical models, one can simulate conditions that cannot be observed directly. One can represent the ancestral genotypes and environments of prehistoric organisms artificially and one can condense huge expanses of evolutionary time into seconds. Two major dangers still exist with using a mathematical model as a substitute for direct observation, however. One is the danger of oversimplifying the model. Models, unfortunately, must ignore some potentially relevant facts since the "real world" is too complex to model exactly. A challenge exists in eliminating conditions without compromising accuracy. A second danger is of making false assumptions. It is all too easy to make assumptions that are not true. In fact, few models have had their

assumptions independently tested for accuracy (Andersson, 1987), and many of a model's assumptions are often known to be oversimplifications (Levins, 1966).

For a model to have value in the field, its assumptions and oversimplifications should be shown not to affect the accuracy of its predictions adversely. This requires careful selection and testing of the models before they are applied.

The Goal of the Thesis

The goal of this thesis is to find a method of testing Trivers' (1974) sociobiological parent-offspring conflict theory empirically in the field. This will be done in a series of steps. First, a suitable model for field testing the theory will be found. The modeling criteria of Levins (1966) and Andersson (1987) as well as recent parent-offspring (P.O.) papers, will be used to do this. Then an outline of a method for applying the model to the field will be described. Methods of testing the model's parameters will be outlined, along with qualities necessary in a suitable test species. Then, finally, field predictions will be made and sources of error pointed out. This will be done by researching the predictions of the suitable model and pointing out areas where the model's predictions may differ from results in the field. Difficulties encountered

developing the experimentation techniques of this paper will also be mentioned.

Why Study Parent-Offspring Conflict?

Trivers' sociobiological theory of parent-offspring conflict has been chosen as a candidate for empirical testing for several reasons. One is its controversial nature. There have been several papers criticizing specific aspects of the theory (Alexander, 1974; Feldman & Eshel, 1982; Hartung, 1980), and some criticizing the basis of the theory itself (Alexander, 1974). A need exists for empirical evidence to investigate these arguments.

A second reason is the large volume of information about modeling the theory. It would be impossible to choose a suitable sociobiological model for testing without sufficient knowledge of the modeling techniques. Parent-offspring conflict theory has an abundance of literature on it discussing the past problems and solutions encountered in making models of it.

A third reason Trivers' theory has been chosen is its potential for application. Once it can be shown to be empirically valid then it can be applied to almost every organism on earth as almost every organism is either a parent or an offspring at some point in its life. Theoretically, almost every organism should be affected by

the theory's implications, including humans. Everyday actions such as parent-initiated discipline, offspring-initiated temper tantrums, parental abandonment and offspring begging can be potentially explained by P.O. conflict theory. This would seem reason enough for a paper developing the theory's potential for application and is a major factor initiating this thesis topic.

CHAPTER II

INTRODUCTION TO TRIVERS' PARENT-OFFSPRING CONFLICT THEORY

Before the publication of Trivers' parent-offspring conflict theory, it had always been assumed that the interests of parents and offsprings were similar. Parents would nurture their offspring to insure the survival of their genes and offspring would accept the nurturing for their own survival. Trivers challenged this assumption in his paper entitled, "Parent-Offspring Conflict," published in The American Zoologist, in 1974. In this paper, Trivers stated that offspring are selected to take more parental investment than parents are selected to give. Parents are selected to distribute investment evenly to their offspring while offspring are selected to take more investment than is their share.

Trivers' (1974) theory was based on Hamilton's (1964) idea of inclusive fitness. In Hamilton's definition, fitness is not only defined by the number of offspring produced by an individual, but also by the number offspring produced by its relatives. Hamilton argued that because an individual is selected to reproduce as many of its own genes

as possible, an individual should be selected to help the reproduction of relatives because they share a fraction of the individual's genes. The degree to which an individual is expected to help the reproduction of relatives is proportional to the fraction of genes (r) (degree of relatedness), that the relative shares with it.

Trivers' parent-offspring conflict theory is based on the differing degrees of relatedness an offspring has as compared to its parent. An individual is related to its parents by a fraction of shared genes of 0.5 and to itself on an r of 1.0. As an individual is completely related to itself, but only half as related to its parent, then the individual should be selected to take twice as much of the parent's resources as the parent is selected to give (the individual has twice as many of its own genes as has its parent). There is, as a result of this difference, a genetic conflict of interests between parents and offspring.

Trivers quantified his theory in units of benefit and cost of an act by the parent or offspring. Benefit is measured in units of increased reproductive success of the offspring, and cost is measured in units of decreased future reproductive success of the parent. When an offspring is born, the offspring incurs cost to the parent. As the parent utilizes some of its energy resources and time, the offspring incurs a cost by reducing the parent's ability to

produce future offspring. Initially, Trivers stated, this cost would be small because the offspring would not utilize as much resource because of its small size. The initial benefit to the offspring, however, would be large because it would be dependent in its helpless, newborn state. However, with time, Trivers stated, the offspring would become increasingly capable of fending for itself, and the benefit it would derive from its parents' resources would decrease. At the same time, the cost to the parent would increase because the growing offspring would become larger, more hungry and less manageable. If the cost and the benefit are measured in the same units, then at some point the cost to the parent of giving the offspring investment would exceed the benefit the offspring receives. The parent would try to halt the giving of investment while the offspring would try to elicit it. Because the offspring is related to itself by an r of 1.0 and to its future siblings by an r of 0.5, then the offspring should try to obtain resources until the cost to the parent is more than twice the benefit to itself. As long as a benefit to cost ratio of a parental act changes continuously from some large number to some very small number near zero, then there will occur a period of time during which $1/2 < \text{benefit/cost} < 1$ (see Figure 1). This is the period where conflict between parent and offspring is expected to occur.

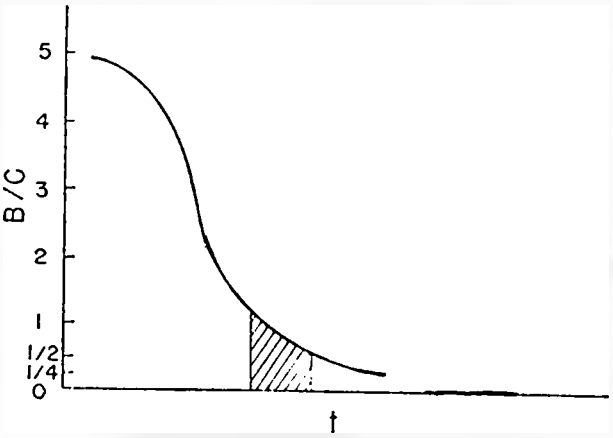

FIGURE 1. The benefit/cost ratio (B/C) of a parental act toward an offspring as a function of time where B is benefit measured in units of reproductive success of offspring and C is cost in comparable units of reproductive success of the parent's future offspring. Shaded area indicates time during which parent-offspring conflict is expected: $1/2 < B/C < 1$.

CHAPTER III

BACKGROUND ON PARENT-OFFSPRING CONFLICT THEORY: THE OTHER MODELS

Introduction

Soon after Trivers' theory was published in 1974 elements of it became widely criticized. Alexander (1974) argued that alleles causing selfish behavior in offspring would not spread because they would lower the reproductive success of the selfish offspring when it became a parent. A selfish allele that helped an offspring obtain extra resources from its parent would be present in a higher proportion in its own offspring. Its own offspring would then act even more selfishly to the individual. This would incur even more cost in terms of reproductive success to the individual than the individual originally gained by being selfish itself. To paraphrase Alexander, selfish genes would not spread because a selfish individual would have lower reproductive success than a non-selfish individual. Alexander (1974) also argued that offspring could never successfully conflict with a parent even if selfish genes could spread. A parent would always be larger, stronger,

and more experienced than the offspring and, therefore, would always "win." Conflict behavior would never be favorably selected.

Trivers' benefit and cost model could not refute Alexander's (1974) qualitative genetic arguments. To defend Trivers' theory, a new class of model was needed. Stamps, Metcalf, and Krishnan (1978) formulated such a model.

The Stamps Model

Unlike Trivers' model, the Stamps model made detailed, genetic assumptions. This allowed it to make more detailed predictions than Trivers' model. Stamps et al. (1978) used a single locus genetic model. This model:

1. described increases in gene frequency from zero (Trivers' model did not show gene frequencies);

2. assumed offspring bore a cost when performing a selfish act in terms of a decrease in its own, reproductive success (Trivers' model only considered cost in terms of the parent's decreased reproductive success);

3. considered the possible effects of behavioral differences in species on P.O. conflict such as simultaneous versus sequential offspring production (Trivers only considered sequential offspring production in single parent species).

The Stamps model successfully refuted Alexander's

(1974) criticisms. It showed that selfish alleles could still spread to fixation in a population even though the selfish alleles reduce the reproductive success of its carriers. The Stamps model implied that offspring should be selected to successfully conflict with "larger," "more experienced" parents despite Alexander's (1974) assertion that they should not.

Aside from refuting Alexander's criticisms of P.O. conflict theory, the model made some other important predictions. It found that the offspring would most likely "win" P.O. conflict [obtain a level of investment closer to their optimal ESS (evolutionary stable strategy; Maynard Smith, 1974)] when the cost to the offspring's behavior is small and parent's behavior is large. It found that the parent would most likely "win" when the cost to the parent's behavior is small and the offspring's behavior is large. Either parent or offspring would "win" (or a compromise solution reached) when the cost to the parent's and offspring's behaviors are both large or the costs are both small.

As well as finding conditions where offspring or parent would "win" in P.O. conflict the Stamps model also found that Trivers' relationship $1/2 < B/C < 1$ defining the period where P.O. conflict would occur was inaccurate. The Stamps model found that this relationship would not define the

period of P.O. conflict when the performance of a selfish act involved a cost to the offspring's own reproductive success. (As mentioned before, Trivers' model only considered cost to a parent's reproductive success not cost to an offspring's reproductive success, therefore, was less realistic). The Stamps model found that in monogomous families that produce offspring simultaneously, P.O. conflict would occur (selfish alleles could spread) even when the cost of a behavior was greater than the benefit (the B/C ratio is less than one). It found that if a selfish offspring could obtain extra parental investment and not suffer from the selfishness of siblings, P.O. conflict could occur even when cost was infinitely greater than benefit (the B/C ratio approaches zero). The Stamps model was the first model to thoroughly investigate these expanded possibilities.

The Hartung Model

The Stamps model allowed Trivers' theory to be taken more seriously. However, the accuracy of Trivers' model as a vehicle for predicting levels of P.O. conflict began to be questioned. Hartung (1980) criticized Trivers' model on the basis of his formulation of inclusive fitness. While Trivers' (1974) assumed the value of a relative to an individual was the fraction of shared genes (r) between

them, Hartung (1980) decided that the value of a relative to an individual was the fraction of shared genes between their potential offspring. Hartung's assumptional change altered the benefit and cost weights in the Trivers' model. Trivers defined benefit as units of increased reproductive success of offspring and cost as units of decreased reproductive success of parents' future offspring. While Trivers (1974) saw an offspring valuing itself twice as much as its parent because it is twice as related to itself (r = 1) as to its parent (r = 1/2), Hartung (1980) saw an offspring valuing itself equally to its parent because its own offspring are as related to itself (r = 1/2) as are its parent's offspring (r = 1/2). Trivers' model predicted the conflict is over cost not benefit. The parent wants half as much cost (C/2) as the offspring (C) but parent and offspring agree on the benefit (B). Hartung's model predicted that conflict is over benefit not cost. The offspring wants twice as much benefit (2B) as the parent (B) and the parent and offspring agree on the amount of cost (C). Lazarus and Inglis (1986) produced a diagram in their paper on P.O. conflict illustrating the differences between the models (see Figure 2).

It should be noted that while some researchers consider Hartung's model an advancement (Lazarus & Inglis (1986), others do not (Bull, 1985). There is no real consensus

which model, Trivers' or Hartung's, is the most "realistic." However, because Trivers' model is the most widely publicized model of parent-offspring conflict, Trivers cost benefit assumptions will be preferred over Hartung's in this thesis, for convenience.

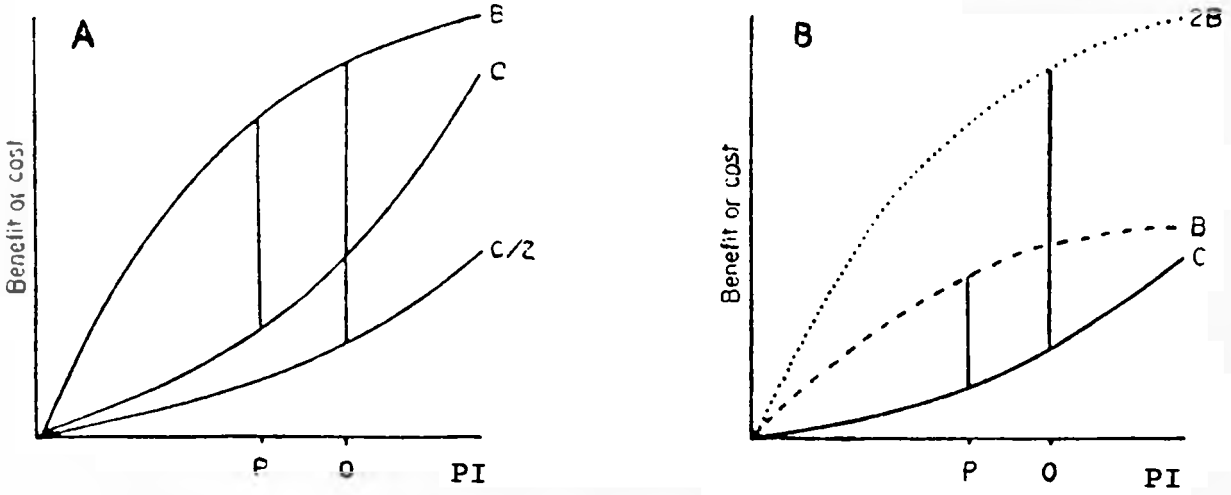

FIGURE 2. Parental investment (PI)

Figure 2 (from Lazarus & Inglis, 1986)
(A) Trivers' (1974) formulation showing the benefit and cost of a parental act toward an offspring at one moment in time as a function of parental investment where net benefit is maximized for parent (P) and offspring (O). B = benefit to parent and offspring; C = cost to parent; C/2 = cost to offspring.
(B) Hartung's (1980) reformulation. B = benefit to parent; 2B = benefit to offspring; C = cost to both parent and offspring. Parental benefit is shown as a dashed line and offspring benefit as a dotted line.

The Parker and MacNair Model

As of 1978, all the models of parent-offspring conflict had been based on Trivers' (1974) cost and benefit terms using inclusive fitness. Even Hartung (1980) had defined

the cost or benefit of an action by the loss or gain it causes in the reproductive success of the individual plus a fraction (r) of the reproductive success of the actor's relatives. Though Stamps et al. (1978) had modified Trivers' (1974) cost term and Hartung (1980) had altered the method of inclusive fitness allocation, both researchers used models where the P.O. conflict behavior was measured using reproductive success exclusively, instead of by some more observable behavioral unit such as the solicitation level of offspring or volume of food given by a parent. As more researchers began to take an interest in testing P.O. conflict theory empirically, it became apparent that Trivers' (1974) cost-benefit units were too tedious and impractical to measure in the field. Inclusive fitness was a fine concept for a theoretical model, but the use of the idea as a measurement device in the field was not optimal.

Because of the difficulties inherent in Trivers' cost and benefit parameters, Parker and MacNair (1978; 1979) and Parker (1985) produced an entirely different model using different fitness units. First, Parker and MacNair abandoned Trivers' (1974) cost and benefit terms to use more directly measurable terms of parental investment level (m) and offspring solicitation level (x) as behavioral units between parents and offspring. This made the measurement of an action simpler because the model directly employed more

measurable quantities of parental investment and offspring solicitation in its calculations.

Second, the Parker and MacNair model (1978; 1979), (Parker; 1985) used more measurable forms of fitness than the other models. In the Parker and MacNair model, loss of fitness is defined only by the loss of an individual's reproductive success (RS), not by the loss of the individual's RS plus a fractional loss of its relatives' RS. This makes measurement of fitness in the field considerably easier. One simply needs to count the number of offspring an individual produces, not the number of offspring produced by particular relatives.

Third, the Parker and MacNair model included many more parameters accounting for in-the-field differences between species than the other models. In a series of five papers published from 1978 to 1985 (MacNair & Parker, 1978; MacNair & Parker, 1979; Parker, 1985; Parker & MacNair, 1978; Parker & MacNair, 1979), Parker and MacNair modeled the possible effects of monogamy, promiscuity, intra-brood conflict, inter-brood conflict, sequential offspring, simultaneous offspring, shared solicitation cost, unshared solicitation cost, shared parental investment, and unshared parental investment. No other previous model could make P.O. conflict predictions on as many species types and combinations of species types as the Parker and MacNair

model. The Parker and MacNair model was the best model for representing species-specific situations.

Despite the obvious advantages the Parker and MacNair model had over Trivers' (1974) in terms of field testability, it was still created as a theoretical model, not as a model for field testing. It still included some of Trivers' theoretical assumptions that are not necessarily easy to measure in the field. The fitness of an offspring, for example, obeys a law of diminishing returns as a function of parental investment, m (see f(m), page 39), where parental investment, just as in Trivers' model, is measured in terms of a parent's reduced ability to produce future offspring rather than in directly observable units such as the weight of food given. This parental investment unit is not necessarily easy to measure directly in the field. Discussion in a later section, "Inherent Problems with Application" will deal with problems and solutions to applying Trivers' parental investment measure to the field.

The Feldman and Eshel Model

Feldman and Eshel (1982) realized no P.O. conflict model had yet answered the question of whether a parental interference allele could evolve to counter the effects of an offspring selfish allele. They developed a two-locus genetic model to answer this question.

Their model produced two interesting results. One is that although a parental interference allele can succeed against an offspring's selfish allele, this can only occur in cases where a lack of selfish alleles in offspring is already in a stable state of equilibrium. In other words, a parental interference allele cannot itself cause a reduction in offspring selfishness. If a selfish allele is already in a stable equilibrium state, then the parental interference allele cannot actually reduce the selfish allele frequency (i.e., parental interference alleles cannot eliminate past P.O. conflict evolution).

Second, Feldman and Eshel found that, not only is Trivers' (1974) inclusive fitness method of measuring the costs and benefits of behavior impractical, it is also inaccurate. The model found that the inclusive fitness of an individual is not increased by P.O. conflict. Trivers' model assumed that it was. Since many prior models of P.O. conflict (Hartung, 1980; Stamps et al., 1978) used Trivers' cost and benefit terms, it can only be deduced that these models are prone to produce inaccurate empirical predictions in the field along with Trivers' model.

The Bull Model

Bull (1985) was unsatisfied with the fact that no model of P.O. conflict had taken into account the effects of

environment on P.O. conflict level. He, therefore, produced a model specifically designed to account for environmental effects. Like Parker and MacNair (1978), he avoided the use of Trivers' (1974) cost and benefit terms. He did not define an individual's own reproductive success by the reproductive success of the individual's relatives. Bull (1985) used a very specific model. He simulated an annual plant that produces its seeds sequentially from stored resources. The number of offspring per plant is limited by the resource, and the offspring are produced sequentially during brief time intervals. All surviving offspring breed in the generation following birth.

Bull's model produced some important results. First, it showed that the optimal (ESS) level of parental investment may be influenced by properties of the environment (maybe temperature, soil, water, light levels). Second, it showed that the nature of P.O. conflict could depend on properties of the environment (maybe conflict is over water at some times and minerals at other times). Third, it showed that parent and offspring ESS values can be similar enough under certain environmental conditions that P.O. conflict is not measurable in the field (for example, it may not benefit the offspring to extract more PI than the parental optimum because it may kill the parent). All these findings establish the necessity of

environmental variance parameter, a parameter that measures investment from non-genetic causes . A model needs an environmental variance parameter if it is going to predict P.O. conflict levels in the field accurately.

Summary

The P.O. conflict literature has been researched and some qualities necessary for a field testable model have been found. These qualities are that the model:

1. Should avoid the use of inclusive fitness as a fitness measurement;

2. Shall use quantifiable measurements of parent-offspring conflict other than Trivers' (1974) cost and benefit terms;

3. Should account for differences in family type (monogamous, polygamous, sequential offspring, simultaneous offspring, etc.);

4. Should include a parameter for environmental variance.

Because a goal in this project is to find a suitable model for empirical field testing, these qualities will be utilized when evaluating P.O. conflict models in the next section.

CHAPTER IV

DETERMINING A MODEL'S SUITABILITY TO FIELD TESTING

Preface

While it is a goal of this section to rate the various P.O. conflict models empirically on their relative suitabilities to field testing, the rating of models using an empirical measurement can be a presumptuous, inaccurate process at best (Andersson, 1987). Because of this, the goal of this section to rate models quantitatively accuracy cannot be achieved with satisfaction. It is hoped, however, the rating scores derived from this section can be justified to be qualitatively accurate (put the models in the correct order of suitability to the field), even if they are not quantitatively accurate (measure models relative suitability to the field in accurate units). The more realistic purpose of this analysis is not to rate the various P.O. conflict models on an accurate scale (this would be desirable but it is unrealistic); rather, it is to produce an "educated guess" about which of the present P.O. conflict models is best suited to field testing.

Introduction: Background on Method

A goal of this chapter is to find a testable model of P.O. conflict theory. However, the criteria for empirical suitability need to be established before the optimal model can be found. A method of deriving these criteria is to look at the evaluative methods used by other researchers. The two methods that will be used here are those of Levins (1966) and Andersson (1987) because they have proven to be applicable to a wide variety of models.

Levins (1966) wrote a very general paper on the evaluation of mathematical models. In this paper Levins formulated a general scheme for rating mathematical models. He states that a good mathematical model is general (it can be applied to many situations), precise (its predictions are exact), and realistic (its predictions conform to real world observations). However, he noted that a model that is strong in two of the three areas is usually deficient in the others. A general, realistic model, for example, is usually not very precise; a precise, general model is not very realistic; a realistic, precise model is not very general. He also noted that while the best models for making theoretical predictions are general and realistic but the best models for making empirical predictions are realistic and precise.

Andersson (1987) also wrote a paper on mathematical

models. In his paper he formulated a method of model analysis (in his case he specifically analyzed sexual selection models). He suggested that the number of assumptions and quantities of a model be noted when analyzing a model. He outlined four categories of assumptions and quantities that should be observed:

1. The number of structural and relational assumptions (e.g., non-overlapping generations, sexual reproduction, promiscuity, etc.).

2. The number of factors that must be assigned numerical values for the model to yield quantitative predictions (e.g., allele starting frequencies, selective coefficients).

3. The number of genotypes, variables, and parameters that must be identified or measured for testing the model.

4. The total number of assumptions and quantities that must be checked for a complete empirical test of the model [structural and relational assumptions (1) plus the number of genotypes, variables, and parameters that must be identified or measured (3)].

Although Andersson's method of comparing models does not outline how to rate a model's usefulness, it does serve the purpose of this paper by giving one approach to analyzing models. Andersson's model analysis method (telling what assumptions and quantities to look for in a

model), and Levin's (1966) model evaluation method (telling what an accurate model contains), combined with some of the suitability requirements described earlier in the paper (p. 21), should help form a scheme P.O. conflict model. A grading system will be constructed, therefore, using these criteria as a basis.

General Method to be Used

As Levin (1966) determined that the best models for empirical testing are realistic and precise, realism and precision will count for a major portion of a model's field testability grade in this evaluation. It will be added that realistic qualities should be rather general because P.O. conflict theory applies to so many different types of organisms. What is considered a realistic assumption for testing one organism should also be generally applicable to other organisms. Precision will, therefore, count for one portion of a model's field testability grade; "general"-realism will count for a second portion of a model's field testability grade. It was also shown in this paper (p. 16) that practicality in the field is an important attribute of a field testable model; therefore, practicality will count as a third major portion of a model's grade. A model's testability grade will, therefore, be calculated using three categories of attributes; precise, "general"-realistic and

practical, each weighted approximately equally.

General-Realism

To define a model's general-realism, the structural and relational assumptions (Andersson's first class of assumptions) will be broken down to include two elements:

1. General, realistic structural and relational assumptions (assumptions that are true to the majority of field observations).

2. Unrealistic structural and relational assumptions and realistic structure and relational assumptions that are not general (assumptions that are either overly simplistic or overly specialized).

The general-realism category will be based on (1) the total number of general, realistic assumptions minus (2) the total number of unrealistic or nongeneral, realistic assumptions. More general, realistic models will obviously make more general, realistic assumptions than unrealistic or overly specialized models will and hence will score higher in the general-realism category. The relative realism and generality of an assumption will be determined by how well the assumption correlates with most field observations. For example, a model that assumes both monogamy and promiscuity can occur is clearly more general and realistic than a model that assumes only monogamy or promiscuity can occur. A

model that assumes sexual reproduction can occur is more generally applicable and realistic than a model that assumes only asexual reproduction can occur.

Precision

The score in the precision category will be based on the total number of structural and relational assumptions of a model [general realistic assumptions (a) and unrealistic or nongeneral realistic assumptions (b)] plus the total number of genotypes, variables and parameters that need to be identified or measured for an empirical test of the model (d). This number will then be divided by three so that the maximum precision score will roughly equal the maximum possible weight of the realism and practicality scores (of about 10 points). The more precise models will obviously have a greater number of structural and relational assumptions and genotypes, variables and parameters and so will score higher in the precision category.

Practicality

The third and last grading category will be a model's practicality in the field (c). The score will be based on the number of qualities in a model which make it easy to test in the field. Two essential qualities which make a model easy to test were described earlier (p. 21). These

are that the model:

1. avoids Trivers' (1974) cost and benefit terms; and

2. avoids the use of inclusive fitness as a fitness measurement.

These qualities will, therefore, be used in the practicality score. Five grading points will be given for each of these characteristics so that the maximum possible weight of the practicality score will again roughly equal the maximum possible weight of the precision and general-realism scores (of about 10 points each). Of course, other characteristics that make a P.O. conflict model practical in the field probably exist, but these qualities remain unknown until more theoretical and field research is done on P.O. conflict theory.

The Structural and Relational Assumptions

Andersson (1987) admitted that it was nearly impossible to determine the exact number of structural and relational assumptions hidden beneath the surface of a model. For this reason, any structural and relational assumptional score derived in this analysis will not be exact. Andersson decided in his paper that the best method for counting the number of structural and relational assumptions is to count the assumptions that reveal the significant differences between models. For this reason, the structural and

relational assumptions that reveal differences between the models will be used here. Also, another condition will be added in this analysis, and that is that the structural and relational assumptions potentially affect P.O. conflict predictions specifically. It should be noted, therefore, that the number of structural and relational assumptions counted will only be approximate and will probably err on the low side.

Outline of the Grading System

A. The number of general, realistic structural and relational assumptions.

B. The number of unrealistic and nongeneral-realistic structural and relational assumptions.

C. The number of practical qualities.

D. The number of genotypes, variables and parameters.

General-Realism Score = A - B

Precision Score = 1/3 (A + B + D)

Practicality Score = 5 x C

Final Results

This study clearly showed the Parker and MacNair (1979) model to be the most suitable for empirical field testing. Its final score of 22 was well above that of the other models (Bull, 1985 ; Feldman & Eshel, 1982; Stamps, 1980;

TABLE 1. The Grading of the Models

Model No. (See Key)[a]	(1)	(2)	(3)	(4)	(5)
General-Realistic Assumptions (A)					
Sexual reproduction	X	X	X	X	X
Overlapping generations	X		X	X	
Diploid inheritance	*	X	X	X	X
All mature offspring don't necessarily breed	X			X	
Shared and unshared parental investment		X	X		
Monogamy and Promiscuity		X	X		*
Selfish act incurs cost to the actor		X	X	X	X
Parental investment budget finite	X	X	X	X	X
Sequential and simultaneous offspring		X	X		
Includes an environmental variance term					X
Unrealistic and Nongeneral-realistic Assumptions (B)					
Asexual reproduction					
Generations do not overlap		X			X
Haploid inheritance	*				
All mature offspring breed		X	X		X
Unshared parental investment only	X			X	X
Monogamy or promiscuity only	X			X	*
Selfish act incurs no cost to the actor	X				
Parental investment budget infinite					
Sequential or simultaneous offspring only	X			X	X
Does not include an environmental variance term	X	X	X	X	
Practical Qualities (C)					
Does not use Trivers' cost and benefit terms			X	X	X
Does not use inclusive fitness			X	X	X
Number of Genotypes, Variable and Parameters that Need to be Measured (D)	5	9	8	7	10

*Not specifically defined in model's parameter.

[a] (1) Trivers' (1974)
(2) Stamps, Metcalf, and Krishnan (1978)
(3) Parker and MacNair (1978; 1979), Parker (1985)
(4) Feldman and Eshel (1982)
(5) Bull (1985)

TABLE 2. Chart of the Scores

Model No.	(1)	(2)	(3)	(4)	(5)
General-Realistic Structural and Relational Assumptions (A)	4	7	8	6	5
Unrealistic and Nongeneral-realistic Structural and Relational Assumptions (B)	5	3	2	4	4
Practical Qualities (C)	0	0	2	2	2
Genotypes, Variables and Parameters (D)	5	9	8	7	10
General-Realism Score (A-B)	-1	4	6	2	1
Precision Score 1/3 (A+B+D)	4.7	6.3	6	5.7	6.3
Practicality Score (5 x C)	0	0	10	10	10
Total Score	3.7	10	22	18	17

Trivers', 1974). The next highest scorer was the Feldman and Eshel model with a score of 18, four points lower than that of the Parker and MacNair model. The Trivers model was clearly shown unsuitable for empirical field testing with its score of 3.7, which was no surprise. The next lowest scorer, the Stamps et al. model, was still a far better scorer than the Trivers' model, scoring 6.3 points higher than it did.

Discussion

While the Parker and MacNair (1978; 1979) model was shown to be the most suitable model for empirical testing, it is still not necessarily as optimal a model as possible. There are several reasons for this.

First is the suitability rating is not necessarily accurate (as explained in the preface). Almost all of the quantities that make up the suitability rating are subject to debate. The number of structural and relational assumptions tabulated for a model, the relative realism of the assumptions, the number of parameters that need to be independently measured in a model, they are all characteristics that can be manipulated with a good argument.

Second, the value of the suitability rating is only relative. The Parker and MacNair model was only rated most suitable because it was more suitable than the other models evaluated. A new model not evaluated may well be more suited to empirical testing than the Parker and MacNair model.

Finally, the Parker and MacNair model lacks an environmental variance term, a term that was determined by Bull (1985) to be extremely important for making accurate P.O. conflict predictions. This deficiency is so detrimental to the model's field value that it will be

suggested that any serious field testing of the Parker and MacNair model add an environmental variance term despite the fact it is not present in the original model.

CHAPTER V

APPLICATION OF THE PARENT-OFFSPRING CONFLICT MODEL TO THE FIELD

Inherent Problems with Application

The Parker and MacNair model (1978; 1979), (Parker, 1985) has been found to be the most suitable model for empirical testing of these models evaluated. However, many problems must be overcome before the model can be applied to the field. One problem mentioned in the last chapter was the model's lack of an environmental variance term. Bull (1985) found the lack of any environmental variance term could cause a model to predict P.O. conflict level inaccurately in some situations. The model could predict a false optimum (ESS) level of parental investment and, under certain environmental conditions, predict P.O. conflict when there should not be any (ESS values of parent and offspring would become similar due to environmental conditions). However, adding an environmental variance parameter to the Parker and MacNair model would rectify this modeling deficiency.

A second problem with the Parker and MacNair model is

that it assumes falsely that a parent gives out only whole number ratios of parental investment (M) to a sibship. In families with small sibships this assumption is probably not true (Stamps & Metcalf, 1980). A parent may not always give exactly the whole number ratio of investment corresponding to the number of offspring in the litter. If the parental investment potential is a little more than necessary to produce an even number of offspring this potential is probably not "wasted" (left unused) but probably would go into increasing the whole number ratio allocated to each offspring. Parker (1985) realized this deficiency in the Parker and MacNair model, but pointed out that the whole number ratio of investment (M) was only meant as an average for large sibships. The M value's inaccuracy could be eliminated if species with large sibships were studied.

A third problem with the Parker and MacNair model is that it assumes each parent in a two parent investment case is selected to give just as much parental investment as if it were a single parent. In the field this, again, might not be true. When two parents invest in offspring simultaneously, both parents may not be similarly affected by offspring solicitation levels. One or the other parent may be affected by either P.O. conflict, sibling competition for the parental investment budget, and/or sexual conflict concerning how much each parent should invest.

In the field, two parent investment would likely lower the optimal (ESS) level of parental investment (Parker, 1985). If the model's predictions are going to be valuable in the field, they should be adjusted to show this lower optimal (ESS) level of parental investment. If they are not adjusted, the P.O. conflict level will be higher in the field than the model predicts in the two parent investment case.

A fourth problem with testing the Parker and MacNair model is the difficulty in distinguishing P.O. conflict from brood and sibling competition over investment. For example, it may be difficult to tell whether a chick is begging more loudly to get the mother to give it a larger share of food or to keep the other chicks from getting its share of food. One method of detecting the difference might be to set up specific test experiments. An example of such an experiment might be as follows.

1. Start with a pair of siblings whose begging rates are above the parental optimum and who have similar feeding rates.

2. Replace one of the siblings with another offspring with a lower feeding and begging rate.

3. See if the original sibling decreases its begging rate in response to this weaker competitor.

If the original sibling decreases its begging rate,

then the begging can be said to be at least partially the result of sibling competition. If the original sibling does not decrease its begging rate, then the begging can be said to be the result of P.O. conflict (unrelated to competition from siblings).

A final problem with testing the Parker and MacNair model is the complicated nature of the parental investment units. As mentioned earlier (p. 18), parental investment is not actually measured in direct investment units such as food volume given, but it is measured in units of cost of some direct investment unit (such as food volume given) in terms of the parent's reduced ability to produce future offspring (to concur with Trivers' (1974) initial definition of PI) (see page 18). This may make the model more accurate theoretically, but it makes it less practical to test in the field empirically. Measured quantities of investment such as milk, food and time given, need to be correlated with the decrease in a parent's ability to produce future offspring. However, direct, observable measurements of investment such as food volume given do not always correlate nicely with cost to the parent in reduced ability to produce future offspring. Other factors can be included as cost contributors such as energy and time lost in egg incubation and pregnancy, and risk and energy cost in protecting young from predators. However, independently measuring all the

possible cost contributors involved in raising an offspring would be a tedious, inaccurate task at best. The most feasible way to measure a value for cost of parental investment is simply to find a measurable act of parental investment that represents the major cause of cost to a parent's future ability to produce offspring. The fact this value is going to be lower than the true cost must be unfortunately accepted. A possible way to reduce this error is to use a species where the investment form measured (such as food weight given) represents the only main form of investment given by a parent. Milk weight given might be a good candidate in a species where milk is the primary form of investment (i.e., offspring does not need teaching time, socialization by parents, protection from predators).

Measuring the Parameters

In order to apply the Parker and MacNair model to the field the parameters for the studied species would need to be found. Values such as optimal parental investment level (m), optimal solicitation level (x), maximum offspring fitness and Bull's (1985) environmental variance parameter would need to be determined from the field before the model could make P.O. conflict predictions. Outlined below are some of the primary terms and equations used in the Parker and MacNair model (1978; 1979), (Parker, 1985) that would

need to be measured.

Some Important Terms Used in the Parker and MacNair Model

PI: Parental investment as a cost to parent in reduced ability to produce future offspring.

m: Number of times more PI given than the parental optimum, which also happens to be the minimum amount of investment required for an offspring to survive to maturity (m = 1 is the parental optimum: m < 1 the offspring dies).

M: Total investment budget of a parent (amount of investment times the number of offspring the parent can produce).

x: Number of times more PI demanded by offspring than m units it is given. (x = 1 is the parental optimum; x < 1 the offspring dies.)

K: Fitness level when m is maximized.

c: Positive constant determining the increase in offspring fitness achieved by raising m.

b: Constant determining the slope of the function R(x) where R(x) represents the proportional reduction in fitness R of an offspring as a function of its solicitation level.

Some Important Equations from the Parker and MacNair Model

Equation 1: $f(m) = K\,[1 - \exp(-cm)]$

f(m): relative fitness 'f' (reproductive success) of an offspring as a function of the m units of PI it has gained. A fitness value of 1 corresponds to 2 offspring produced.

Equation 2: $R(x > 1) = 1 - b(x - 1)$

R(x): proportionate reduction in fitness R of an

offspring as a function of its solicitation level x.

Equation 3: $S(x) = d. \exp(-x); d = \exp(1)$

S(x): survival probability of an offspring or brood of offspring as a function of solicitation level x.

Outlined below are some approaches that might be taken experimentally to determine the parameters for a species.

The Parker and MacNair Model
Determining m

The parameter m is defined as the number of times more PI given to an offspring than the parental optimum (the parental optimum being the minimum amount of PI required for the offspring to survive to maturity). For the m value to be derived one would first need to determine the PI value at which m equals 1 (the minimum amount of PI for an offspring to grow to maturity, the parental optimum). Then one would be able to convert all other PI values observed into values of m by dividing them by this minimum amount of PI:

PI observed ÷ PI at m=1 = m

To do this experimentally one might set up a situation where several offspring of the species are given decreasing amounts of PI through their growth stage. The least amount of accumulative PI necessary for an offspring to reach maturity is the PI that correlates with the value at which m = 1. The PI quantity would need to be measured in terms

of some observable unit that closely represents the true cost of the PI to a parent (in terms of reduced ability to produce future offspring). Food weight given by a parent may or may not correlate nicely with the true parental investment allocated. To help make the derived m value more accurate, a species should be chosen that does not allocate parental investment in a large variety of ways as this would make parental investment level difficult to quantify.

Determining x

The parameter x is defined as the number of times more solicitation the offspring produces than the parent "wants" to satisfy (i.e., the parental optimal solicitation level--the minimum level that allows the offspring's survival and the solicitation level that gets the offspring a PI of m = 1). Determining x for a species would take two steps. First one would find how solicitation level correlates with PI begged for. Then one would correlate PI begged for with x. This could be done experimentally by first giving an offspring with a given tendency for solicitation increasing amounts of parental investment (once again food weight may be the most practical form of measure). The level of PI which satisfies the offspring (stops the offspring from soliciting for more) would correlate with the PI that particular solicitation level. (The procedure could be

repeated for offspring with different solicitation levels, so that a wide variety of solicitation levels could be correlated with PI begged for). Then one would divide the observed parental investment solicited for by the parental investment level at which m = 1. This would convert all PI levels solicited for into units of x [as PI solicited for divided by PI where x = 1 or m = 1 equals x. The solicitation level that correlates with the PI at m = 1, determined earlier, is x = 1, by definition.]

Determining M

M is the total PI budget for the average parent of the species. It is the maximum level of investment a parent can devote to offspring. It is defined as a whole number ratio of m, the maximum number of offspring a parent can produce. To find the M value for a species, one would need to have first found that parental optimum investment level for the species (level where m = 1). Then one would need to determine how many offspring a parent can raise when offspring are allowed no more than the parental optimum level of PI each. One would probably need to redistribute investment increments given by the parent artificially (such as food volume) so that each offspring gets only his share (m = 1) of investment. It is assumed again that units such as food accurately represent true PI given. Also, it is

assumed that saving the parent the hassle of distributing the food does not significantly raise the parent's PI potential. The maximum number of mature offspring the parent can produce when each offspring is only raised on the parental optimal level of investment (m = 1) is the whole number of m equalling the total PI budget for the species. In other words, the number of offspring produced times the parental optimum level of investment (m) equals the species' M value.

Determining K

The parameter K is the fitness level of an offspring when m is maximized. In other words, it is the maximum reproductive success an offspring can have after it has been given all the PI it can use during infancy. To find K one would need to count the maximum number of offspring a mature offspring produces after it has been given more than enough PI. To find K experimentally one would set up a situation where offspring are given more PI than they can use (maybe in the form of excess food--once again a species where food correlates well with PI needs to be used). Then, after the offspring have reached maturity, they are all allowed to reproduce as they would in their natural environment. The average number of young that each of these mature "spoiled" offspring has produced corresponds to the fitness level when

m is maximized, the value of K for their species.

Determining c

The parameter c is the positive constant in the fitness function: f (m) = K [1 - exp (-cm)] determining the increase in offspring fitness achieved by raising m. To find c for a species one would first need to have found K. Because $K = \frac{1}{[1 - \exp(-c)]}$ when an offspring's fitness is 1 according to Parker and MacNair's (1978; 1979) definition, all one would need to do to find c is to plug the K value into the equation when m = 1. c can then be easily derived algebraically.

Determining b

The parameter b is the constant determining the slope of the R(x) function: R(x > 1) = 1 - b (x-1), representing the proportionate reduction in fitness R of an offspring as a function of its solicitation level x. To determine the value of b for a species, the fitness of the offspring would need to be plotted against varying values of solicitation intensity (x) and the slope of the line found. One method of doing this might be to use a species where solicitation intensity can be controlled. Different offspring would be artificially induced to beg at different intensities (maybe by controlling the number of begging calls a parent hears).

The reproductive success of the offspring would be monitored and the decrease in fitness would be plotted against the decrease in solicitation intensity. The slope of this line would equal the constant b.

The Environmental Variance Parameter

Bull (1985), in his P.O. conflict model, produced two different forms of the environmental variance parameter, one to be used in cases where there is variation of parental genotype, and the other to be used in cases where there is variation in the offspring genotype. He used the equation $x_i = y + \delta_i$ to represent the first case (where x is parental investment received by offspring; y is the average investment given by a parent to offspring of a particular family, and δ is investment variation around the mean due to environmental causes). He used the equation $x_i = Z + \eta_i$ to represent the second case (where x again is parental investment received by offspring; of a particular family, Z is the average level of investment taken by offspring, and η is investment variation around the mean due to environmental causes). However, the Parker and MacNair model (1978; 1979), (Parker, 1985) does not represent the genetic variance of parent and offspring as two different cases as as the Bull (1985) model does. The Parker and MacNair model represents genetic variance of parents and offspring

jointly. If an equation is to be applied to the Parker and MacNair model, it would, therefore, need to represent this joint genetic variation of parents and offspring.

Creating an equation that fulfills this requirement could be done by combining Bull's (1985) equations. First one would combine the y term (genetic variation among parents) from Bull's first equation, and the Z-term (genetic variation among offspring) from Bull's second equation to form a new term, g, representing genetic variation among both parents and offspring. Then one would combine the δ term (environmental variation around the mean for parents) from Bull's first equation with the η term (environmental variation around the mean for offspring) from Bull's second equation to form a new term, e, representing environmental variation around the mean for both parents and offspring. Finally, one would combine Bull's parental investment term x with Parker and MacNair's (1978; 1979) investment term, PI, to translate Bull's (1985) modeling language into that of Parker and MacNair's (1978; 1979). These changes would produce a revised equation which theoretically could be applied to the Parker and MacNair model:

$$PI_i = g + e_i$$

where PI is the parental investment received by offspring i, g is the average parental investment received by an offspring of the family, and e is the variance in investment

received by offspring i, resulting from environmental causes.

The environmental variance term could be calculated from this equation. This would be done using the same basic method as in Bull's (1985) model. First, the environmental variations around the mean would be found and squared, then these values would be averaged. The only procedure change from Bull's method would be that the δ and η terms he uses would be replaced by e.

$E[\delta_i^2] = \theta_\delta^2 [\eta_i^2] = \theta^2$ (Bull's model; 1985)

$E[e_i^2] = \theta^2$ (Revised model)

To determine the environmental variance parameter for a family in a particular changeable environment four, steps would be required:

1. The individual PI values received by individual offspring (PI_i) of a family would need to be found.

2. The average PI value (g) received by offspring of a family would need to be found.

3. The differences between the average PI value received and the individual PI values received (e) would need to be found.

4. These differences (e_i) would then be squared then averaged to produce the environmental variance parameter, θ^2.

Step 1: Determining PI Received by Offspring

To determine the actual PI received by offspring, one would need to use a species where the PI received is easily measurable. If milk given by a parent correlates fairly well with true parental investment (cost to a parent's future reproductive ability), then maybe a species that lactates could be studied and the different offspring could be weighed (after lactating a certain amount of time) to determine the true amount of milk received. The various milk volumes received per unit lactating time would represent the various PI values received for offspring under changeable environmental conditions. As an example of an environmental effect one might suspect everyday outside events such as social scuffles, predator presence and weather conditions to affect the volume of milk transferred per unit lactating time.

Step 2: Determining g

To determine g, the average PI received by offspring, one would simply find the average of the individual PI; values found for the offspring of a family. This would be done by adding the PI values together and dividing by the total number of offspring, i, in the family.

Step 3: Determining e_i

To determine the investment variations around the mean, e_i, one would subtract the parental investment amounts received by each offspring (PI_i) from the average investment amount received by offspring of the family (g).

Step 4: Determining θ^2

To determine the environmental variance parameter (θ^2) for the family, one would square each of the e values, add them together, then divide by the number of offspring in the family, i. $E[e^2] = \theta^2$

CHAPTER VI

PARENT-OFFSPRING CONFLICT FIELD PREDICTIONS

Introduction

The Parker and MacNair model (1978; 1979), (Parker, 1985) with an environmental variance term needs to predict P.O. conflict level in diverse field situations successfully if the model is to be a support to P.O. conflict theory. Unfortunately, the predictions combining the Parker and MacNair model with the Bull (1985) environmental variance term have not yet been calculated quantitatively. As it is not a goal of this paper to make these detailed calculations (this would warrant an entirely new thesis), only the P.O. conflict predictions made from the Parker and MacNair model already calculated will be considered here. These calculations still should be fairly good indicators of the P.O. conflict levels expected in the field. The only effect adding the environmental variance parameter should have on these predictions are that:

1. Joint investment levels (ESS values) might be possible when there is a small initial difference in parent and offspring ESS level.

2. The mean fitness of the family at ESS might be lowered.

The Predictions

True Monogamy vs. Untrue Monogamy

One of the predictions made by the Parker and MacNair model is that the relationship between fitness of an offspring and the amount of investment it receives differs between cases where there is true monogamy and untrue monogomy. True monogomy is defined as when parents pair for life and do not find a new mate after one partner dies. Untrue monogamy is defined as when parents stay together only to the production of the next brood or parents stay together to rear successive broods but the death of one partner does not prevent the other from finding a new mate. In the true monogamy case, the model found the ESS values of selfishness to be globally stable (see Figure 3, case a), while in the untrue monogamy case the model found the ESS values to be only locally stable (see Figure 3, case b).

One Parent vs. Two Parent Investment

The Parker and MacNair model found that whether one or two parents invest in either the true monogamy or untrue monogamy case affects the optimal investment levels for

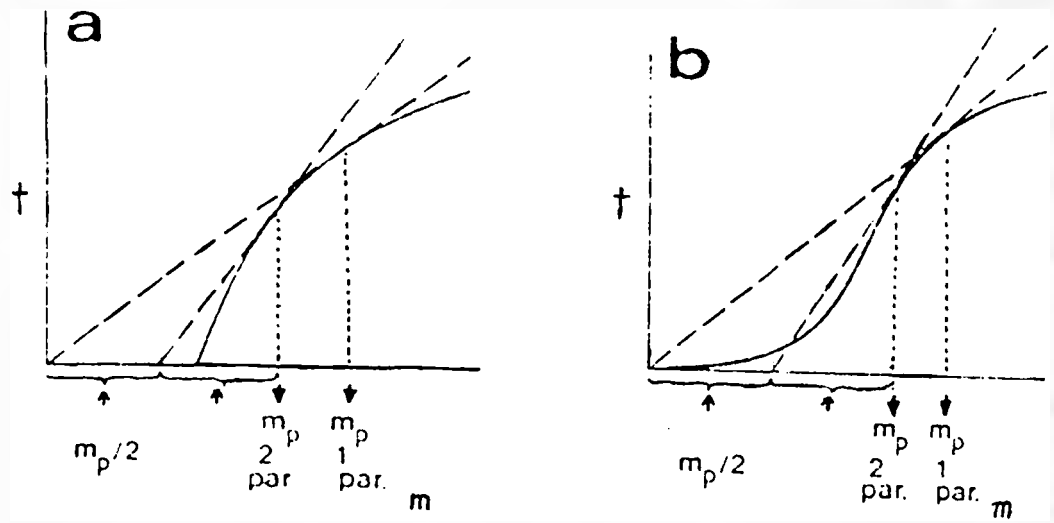

FIGURE 3. (Parker 1985). Fitness of an offspring (f) as a function of parental investment (m) that it receives. The tangents show the optimum investment levels for the one and two parent investment cases (m_p; 1 par.; 2 par.) for situations where there is true monogamy (a) and untrue monogamy (b). The ESS values for the true monogamy cases (a) are globally stable while the ESS values for the untrue monogamy cases (b) are only locally stable. In both true and untrue monogamy situations the optimum investment level for the parent (m) is higher when one parent invests than when two parents invest.

parents. The model found that when only one parent invests, the optimal parental investment budget is greater than when two parents invest (see Figure 3, cases a and b).

<u>One Parent vs. Two Parents Constrained</u>

The Parker and MacNair model predicted that there would be a difference in P.O. conflict level in cases where both parents are constrained by offspring selfishness (suffer

reduced future reproductive success), and cases where only one parent is constrained by offspring selfishness. The model found that P.O. conflict level is higher when one parent is constrained by offspring selfishness than in cases where both parents are constrained by offspring selfishness (see Table 3).

TABLE 3. Scale of Increasing Conflict for the Case Where Only One Parent Invests in the Offspring or There is True Monogamy (Parker 1985)

α	β	Type of Conflict	Breeding Constraint	Type of Solicitation Cost
3/4	1/4	Inter-brood	Both parents constrained	Individual
2/3	1/3	Inter-brood	Both parents constrained	Shared
		Inter-brood	Full siblings	Individual
5/8	3/8	Inter-brood	One parent constrained	Individual
4/7	3/7	Intra-brood	Half siblings, maximum	Individual
1/2	1/2	Inter-brood	One parent constrained	Shared
		Intra-brood	Full siblings	Shared
1/4	3/4	Intra-brood	Half siblings, maximum	Shared

Parent-offspring conflict increases going down the table, where $\alpha = m \frac{f'(m)}{f(m)}$ and $\beta = -x \frac{S'(x)}{S(x)}$ (see pp. 39 and 40 for def. of $f(m)$ and $S(x)$). The parental optimum in the absence of parent-offspring conflict is $\alpha = 1$; the offspring optimum in the absence of parent-offspring conflict is $\beta = 1$.

Shared vs. Unshared Offspring Solicitation Costs

The Parker and MacNair model predicted there would be a difference in P.O. conflict level in cases where offspring share the cost of solicitation among siblings (e.g., increase their risk of predation), and cases where they carry the solicitation cost themselves. The model found that in cases where offspring share the cost of solicitation amongst siblings, there is an increased P.O. conflict level over cases where offspring carry the cost of solicitation themselves (see Tables 3 and 4).

TABLE 4. Scale of Increasing Conflict for the Case Where Both Parents Invest Equally in the Offspring (Parker 1985)

α	β	Type of Conflict	Type of Solicitation Cost
1-1/3	2/3	Intra-brood	Individual
1-1/4	3/4	Inter-brood	Individual
1	1	Intra-brood	Shared
		Inter-brood	Shared

Parent-offspring conflict increases going down the table. The parental optimum in the absence of parent-offspring conflict is $\alpha = 2$. The offspring optimum in the absence of parent-offspring conflict is $\beta = 2$.

Simultaneous vs. Sequential Offspring

The Parker and MacNair model found that whether

offspring are produced simultaneously or sequentially affects the level of P.O. conflict. When there is one parent investment and true monogomy, simultaneous offspring would be expected to show more P.O. conflict than sequential offspring. When there is two parent investment and untrue monogomy, simultaneous offspring would be expected to show less P.O. conflict than sequential offspring (see Tables 3 and 4).

Low Solicitation Costs/Low Cost of Increasing Investment vs. High Solicitation Costs/High Cost of Increasing Investment

The Parker and MacNair model predicted that the costs of solicitation and increasing investment could affect the level of P.O. conflict. When solicitation costs and low and/or the costs of increasing investment are low, then P.O. conflict level would be higher than when solicitation costs are high and/or the costs of increasing investment are high (see Tables 3 and 4).

Offspring "Wins" vs. Parent "Wins" Cases

The Parker and MacNair model predicted the conditions under which the parent or offspring would most likely "win" P.O. conflict (be selected to obtain an ESS level of investment closest to its optimal level). The model

predicted that parents would most likely "win" when the costs of solicitation are borne only by the offspring. Offspring would most likely "win" when there are shared costs of solicitation amongst the brood, and when both parents are constrained by solicitation (for details, see Table 5). The Parker and MacNair model also found that "who plays what first" also helps predict the "winner" of P.O. conflict. If the parent supplies a fixed level of investment per brood, and the level selected for has reached equilibrium before a selfish gene arises in the brood, then the "parent wins" solution can also occur. If the fixed level of investment has not reached an evolutionary equilibrium when a selfish gene arises, then offspring may still "win" the conflict. Offspring and parents will reach a compromise situation when there is shared investment by both parents (neither party clearly "wins").

TABLE 5. Conditions Necessary to Maintain a "Parent Wins" or "Offspring Wins" Solution (Parker, 1985)

Model	Maximum Starting Gradient for S(x) to Keep Parent at Offspring's Optimum (i.e., Offspring wins)	Maximum Starting Gradient for S(x) to Keep Offspring at Parent's Optimum (i.e., Parent wins)
<u>One-Parent Investment</u>		
1. Inter-brood conflict		
(i) One parent constrained		
a. Individual costs (of solicitation)	- 3/4	- 3/4
b. Shared costs	- 3/4	-1-1/2
(ii) Two parents constrained		
a. Individual costs	- 1/2	- 1/2
b. Shared costs	- 1/2	-1
2. Intra-brood conflict		
(i) Full siblings		
a. Individual costs	*	- 1/2
b. Shared costs	*	-1
(ii) Half siblings; maximum		
a. Individual costs	*	- 3/4
b. Shared costs	*	-3

TABLE 5. Continued

Model	Maximum Starting Gradient for S(x) to Keep Parent at Offspring's Optimum (i.e., Offspring wins)	Maximum Starting Gradient for S(x) to Keep Offspring at Parent's Optimum (i.e., Parent wins)
Two-Parent Investment		
1. Inter-brood conflict (both constrained)		
a. Individual costs	-1-1/2	-1-1/2
b. Shared costs	-1-1/2	-3
2. Intra-brood conflict		
a. Individual costs	*	-1
b. Shared costs	*	-2

The parent or offspring can win outright when the amount of m (investment paid out at the ESS) is equal to the parent's or offspring's optimum. This can occur when survival probability S(x) falls so steeply from its initial value of 1.0 at x = 1.0 that it can never pay to have offspring making extra demands (x > 1) on the parent. This table shows the maximum conditions for the starting gradient S' (x = 1) necessary to hold m stable at any level between the parental and offspring optimum (ESS) investment values (m_p and m_o). The solution is stable providing that the starting gradient S' (x = 1) is less than the values indicated. The lower the value, the less likely it will be that the solution is stable.*

* = parent or offspring wins solution, not applicable to the model given.

CHAPTER VII

CONCLUSION

Summary

The literature on P.O. conflict theory has been researched, and a method of testing P.O. conflict theory in the field has been formed. It must be emphasized that this method is intended more as a guideline than as a solution to P.O. conflict testing. A comprehensive solution to testing P.O. conflict theory in the field is still years away. Hopefully, however, the efforts of this paper have made some valuable headway into solving the problems of testing P.O. conflict. The important findings of this paper will be summarized below.

First, some of the characteristics of a field testable P.O. conflict model were found. It was found a testable model should:

1. Avoid Trivers' (1974) cost and benefit units.
2. Avoid inclusive fitness as a unit of fitness measurement.
3. Include an environmental variance term.
4. Account for the effects that differences between

species have on P.O. conflict level (monogamous species vs. polygamous species, sequential offspring producers vs. simultaneous offspring producers, etc.).

Using these characteristics and combining them with some model analysis and evaluation techniques from Levin's (1966) and Andersson's papers (1987) a grading system for P.O. conflict models was developed. Using this system the Parker and MacNair model (1978; 1979),(Parker, 1985) with Bull's (1985) environmental variance term was found to be the best model for field testing. Characteristics necessary in a suitable test species were then described, based on the attribute of the model. It was found that a suitable test species should have:

1. measurable behavior that corresponds fairly well with true parental investment level (cost to a parent's future reproductive success);

2. a measurable solicitation behavior that correlates accurately with true PI sought by an offspring; and

3. large sibships in cases where there are simultaneous offspring.

Experimental techniques for measuring the species specific parameters were then described in detail. Possible sources of error were found. The chief sources of error were as follows.

1. Attributing PI to a behavior that in fact does not

cost the parent any future reproductive success.

2. Assuming a solicitation behavior in seeking a certain level of PI where it is not.

3. Confusing sibling competition behavior with parent-offspring conflict [may include 1. and/or 2.].

4. Assuming a parent in a two-parent investment case is selected to give just as much parental investment as in a one-parent case.

5. Assuming a parent gives only whole number ratios of investment to a sibship.

Predictions on P.O. conflict were then made based on the calculations of the model. These predictions were that P.O. conflict would be increased when:

1. There is untrue monogamy over when there is true monogamy.

2. One parent is vulnerable to offspring solicitation over both parents being vulnerable to offspring solicitation.

3. Solicitation costs are shared by the brood rather than by the individual offspring.

4. Offspring are simultaneously produced, and one parent raises the offspring or offspring are sequentially produced, and two parents raise the offspring.

5. Solicitation costs are low, and/or the cost of increasing investment are low.

Also, the model predicted that parents would most likely "win" P.O. conflict (acquire a level of investment closer to their optimum ESS), when the costs of solicitation are borne only by the offspring. Offspring would most likely "win" when there are shared costs of solicitation amongst the brood and when both parents are constrained by solicitation. Compromise situations would result when there is shared investment by both parents.

Finally, it was warned in this paper that the environment could have an effect on P.O. conflict predictions. It was found through the research of Bull (1985) that:

1. Joint investment levels (ESS's) might be possible when there is a small initial difference in parent and offspring ESS level, and environmental variance is allowed to have an effect.

2. The mean fitness of the family at ESS might be lowered when environmental variance is allowed to have an effect.

Conclusion

Trivers' (1974) parent-offspring conflict theory, like many other sociobiological theories, has been modeled extensively. However, it has not undergone any rigorous empirical testing. Because of the theory's vast potential

for application, and because of the volume of details known about its modeling, it has proven to be a prime subject for this paper outlining a field testing method. However, despite the accomplishments of this paper, researchers may still find P.O. conflict theory difficult to test in the field. This study has attempted to accumulate information that will aid in the theory's experimentation but it must be remembered there is still much to be done. Even if this paper has not successfully surmounted all the problems of P.O. conflict testing,hopefully efforts will not cease here.

It is hoped that future research will show P.O. conflict theory an empirically valid explanation for many of the parent offspring interactions observed in nature.

GLOSSARY

benefit: increase in the reproductive success of offspring resulting from an act.

cost: decrease in the future reproductive success of the parent resulting from an act.

degree of relatedness (r): fraction of shared genes between relatives. The r between parents and offspring is 1/2.

environmental variance: the amount of parental investment on offspring receives from non-genetic causes.

ESS: evolutionary stable strategy.

inclusive fitness: fitness of an individuala plus a fraction (r) of the fitnesses of the individual's relatives.

fitness: number of surviving offspring an individual produces. An individual that produces no surviving offspring has a fitness of zero. An individual that produces four surviving offspring is twice as fit as one that produces only two.

parental investment: a parental act that increases the offspring's chance of survival but decreases the parent's ability to invest in other offspring.

parent-offspring conflict: difference between the level of investment the offspring is selected to take and the level of investment a parent is selected to give. The true degree of parent-offspring conflict present does not necessarily equal the behavioral conflict observed though it should be expected to concur with it.

sibship: group of offspring born to the same parent at the same time. A brood or litter is a sibship.

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