Models of Parent-Offspring Conflict

Ethology and Behavioral Ecology

A. In this section we will look the nearly universal conflict that will eventually arise in any species where there is some form of parental care.

1. When parental care is given, there are always periods of time when the evolutionary interests of the parents and the offspring coincide. Thus, there are times, especially early in life when parental care (PC) will usually be in the interest of both the parents and the offspring. If PC is withheld, the young of these species do very poorly or die. Thus, selection should have operated to produce mechanisms whereby the young demand care. Here, we have a classic cooperative signal where both parties benefit from the signal.

a. Notice that at this stage there is a very powerful selective pressure for a communication system between parent and offspring.

b. The offspring are selected to be able to produce signals that induce the parents to provide aid; there is selection on the parents to respond to these signals.

? Under what circumstances would it not be in the interest of the parents to provide aid to very young offspring? Assume that aid is normally given in this species -- we are not asking whether or not parental aid has evolved in general but whether it should always be given even to very young individuals.

2. However, there will eventually come a time when the interest of the parents and offspring will start to diverge.

a. Generally, the **offspring will be able to benefit from large amounts of aid over a long period of time**. This should be obvious.

b. **On the other hand, if the parents continue to provide aid the point eventually will be reached where it is hurting them. There are two obvious reasons for this:**

i. Any type of parental aid involves sacrifice on the part of the parent -- parents have less food and more risk and are weakened as a result of giving aid. If the species is likely to breed again (review notes on life history strategies), it is normal to need some time to regain strength after one bout of reproduction prior to entering the next.

ii. As the offspring get larger, if they continue to rely on the parents for all of their needs as when they were young, they will need more and more resources, This obviously will tax the parents more and more, making it more and more difficult for them to meet these demands and to recover from these demands and reproduce again.

c. Thus, a time will come when it is no longer in the interest of the parents to continue to invest in their present young -- however, it may well not seem that way to the offspring who will benefit from increased parental gifts (up to a point). When this happens (when the parents wish to terminate aid and the offspring do not agree, we have **Parent-Offspring Conflict.** Such conflict will continue until such time as conditions now result in an agreement to end care (or continue it).

d. It was an important task to evolutionary theorists to explain the conditions under which parent-offspring conflict would arise and when it would be terminated.

B. The Modeling of Parent-Offspring Conflict

1. Optimality theory is used and usually currency is INCLUSIVE FITNESS UNITS (# of offspring * relatedness). There are two general questions involving parent-offspring conflict.

a. **Questions of how long to provide aid** -- what is generally referred to as **weaning conflict** even though the concept is applicable to all types of parental care, not just mammals.

b. If aid is given, questions as to the amount of aid.

c. Obviously, these are partially related -- it should be evident that the more time parents invest, likely the greater amount of materials they will invest. Nevertheless, parental time is also a separable variable from parental energy investment.

2. **Weaning Conflict**:

a. **How the parents see it:**

i. Assumptions:

a. The parents will reproduce again

b. All offspring cost the same to produce

c. All offspring are healthy

d. The parents are all related to them in the same manner (usually $r = 0.5$)

ii. We will measure the parents' gains and costs only in terms of their direct fitness. This is because we have assumed that they are presently capable of reproduction. We assume no indirect gains or costs since we are looking only at the immediate effect of the actions of the parents on the present offspring and their effects on the parent's future reproduction. Thus $W_{I,\ parents} = W_{D,\ parents}$

b. The parents are expected to provide care to the offspring so long as the cost of the care (in terms of reduction of their own direct fitness -- their future offspring) does not exceed the benefit (in terms of fitness gain for the present offspring. Since the decision is between present and future offspring, all of which have the same relatedness to the parents, then the parents will chose to aid their young if:

$$\frac{C}{B} < 1.0$$

(The immediate benefits in terms of the survival of these offspring are greater than the costs in future offspring to these parents).

b. **How the offspring see it:**

i. The success of the offspring in demanding more resources from the parents has two effects on the offspring's' fitness.

a. There are direct fitness gains that come from benefits bestowed on them by their parents.

b. There are indirect gains if they forgo some parental care and it is now available to their *future sibs*.

ii. Assumptions:

a. Sibs all cost the same for parents to produce

b. Sibs are all healthy

c. Parents will reproduce again

d. Unlike the parents, there is an asymmetry of relatedness:

i. The offspring are 100% related to themselves.

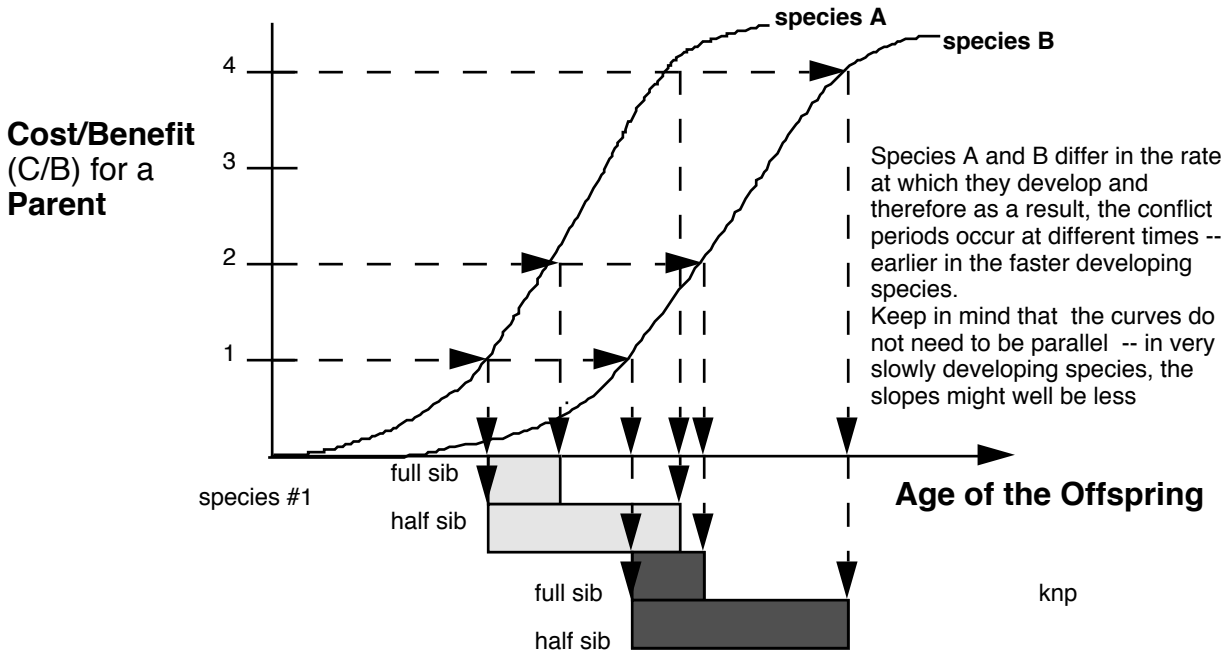
ii. However, offspring are only related to their sibs by ***r***, where the value of ***r*** depends on the mating system and amount of inbreeding.

iii. By contrast, remember that the ***r*** for the parents to their offspring are always 0.5.

iii. There is a conflict. Present offspring will value themselves $\frac{1}{r}$ times as much as they will value future sibs. This is the factor by which they are related to themselves as compared to the next offspring. Thus a present individual is 2 times as related to itself as to future full sibs and 4 times as related to itself as to future half sibs. Accordingly, selection will favor it valuing itself 2 and 4 times more than such sibs

iv. If this is the case, **the offspring will be willing to demand investment from its parents until the cost in future offspring (sibs) becomes $\frac{1}{r}$ times as much as the benefit in direct fitness gain to the present offspring.** For full sibs this is double the benefit cost the parents are willing to accept (next page):

Parent Offspring Conflict -- When should investment be terminated as far as each of the two parties is concerned?



The boxes represent the periods of conflict between parents and offspring for the two species. Note that the conflict starts whenever parental costs/benefits (in fitness) exceed 1.0 -- at this point the offspring will value its future sibs in determining its interests. If they are full sibs, selection will favor the present offspring's agreement in the termination of care when C/B >2.0 for the parents (since r = 0.5); if they are likely to be half sibs, the offspring' s interst is to continue to receive care until C/B to the parent is > 4.0; thus a longer conflict period results.

Note that the present offspring are in agreement as to the need to continue parental investment up to some point and as to the need to terminate it after another point. Thus, in the case of full sibs they agree up to (in terms of parental cost and present offspring benefit) $\frac{C}{B} = 1$; they both agree to terminate when $\frac{C}{B} > 2.0$ and t**hey are in conflict when**

$1.0 < \frac{C}{B} < 2.0$.

? Make a similar drawing for half sibs. Is the conflict period different? Explain.

2. Conflict over the amount of investment. An optimality model. For this model:

a. The **<u>y-axis will be benefit or cost in terms of the currency</u>**, inclusive fitness units.

b. The **<u>x-axis is the amount of parental investment</u>** -- say the total number of calories delivered, the total number of or amount of some crucial food item, etc.

c. In hypothesizing a benefits curve, we would expect a classic **diminishing returns curve** -- obviously there is a certain crucial amount of investment that must be delivered to the offspring (the amount of course depends on the species and perhaps also the sex -- females are sometimes more expensive to produce than males for instance).

i. Thus, initial small investments provide little benefit

ii. As the investment increases the benefit increases rapidly but eventually starts to level off.

iii. Finally, a point will be eventually reached where further investment will provide no further benefit in terms of fitness (the animal is strong and perfectly capable of taking care of itself and may even benefit from no longer sitting in a nest (or at home!). thus the curve levels off with further aggregate investment or it may even fall off.

iv. Generally the Benefit curve should be though of as the effect of the parents on the direct fitness of the present offspring. Obviously, to some degree the benefit to the offspring is also to the parents since the goal is grandchildren.

d. In terms of **COST Curves we will need two: one for the offspring and one for the parent.**

i. Parental cost curves: For the reasons outlined above, **costs are initially low but they tend to accelerate (for instance since bigger young need more food and also prevent the parent from engaging in further reproduction)**. Thus the cost curve is usually not a straight line but usually accelerates upward (it is mathematically an exponential equation of the form $Y = aX^b$ where b is a number > 1.0).

a. Since the parents are selected to maximize their lifetime reproduction of surviving offspring, they will want to get on the next reproductive cycle once they have maximized the B-C for any particular individual.

b. Keep in mind that B-C will not be maximized if the offspring doesn't stand a good chance on its own

c. Getting on with the next reproduction cycle can simply mean putting on weight or recovering from the present one.

ii. Offspring cost curves**:**

a. Offspring will tend to **DEVALUE any parental cost** when compared to the benefit the offspring receives.

b. The **reason is that offspring at the moment cannot reproduce or begin a reproductive cycle**. As usual they will view whatever they are able to get their parents to do in terms of their inclusive fitness.

c. Obviously, up to some point any parental aid can be thought of as increasing their direct fitness

d. However, this aid eventually comes at the cost of their indirect fitness (here comes kin selection again) -- *if they induce the parent to continue to feed them, they are doing it at the expense of future sibs or half sibs (unless their parents are not likely to breed again).*

e. Trivers put it this way in his groundbreaking 1974 paper[1] on the subject:

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[1] Trivers, R. L. 1974. Parent-offspring conflict. Am. Zool. 14:249-264.

i. The offspring is 100% related to itself but only 50% related to any future full sib (or 25% to some future half-sib).

ii. Thus, selection will operate to favor behavior in the present offspring where the B/C of its actions are weighed terms of its likely relationship to some future offspring.

iii. Essentially we can view the present offspring as the actor (since it is trying to "decide" the appropriate amount of care to induce from its parents). According to Hamilton:

$$\frac{B}{C} > \frac{1}{r}$$

or, as regards the consequences to the actor

$$B > \frac{C}{r}$$

Thus, the direct benefit to the present offspring (actor seeking parental investment) must be greater than the cost in future sibs (i.e. the value from the parent's cost curve -- see next page) divided by their relationship. In other words, if the present offspring receives additional parental care that say, allows it to increase its reproduction by one, this had better come at less than the cost of two future full sibs. If not, the request for this parental care would actually work against the actor's evolutionary interests.

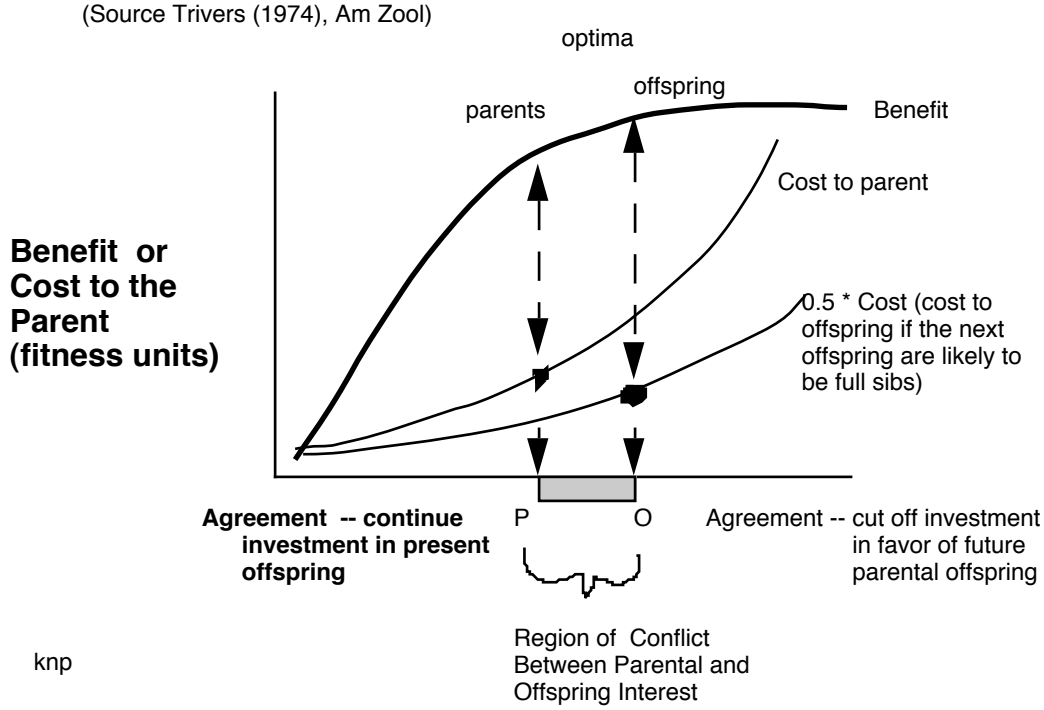
iv. **The offspring will therefore try to maximize difference between their version of the cost curve (the parent's curve devalued by the factor r) and the benefit curve (their direct fitness). This will give them the best possible mix of W_D and W_I benefits.**

! Note that although the parents are related to future and present offspring by some factor ***r***, this does not matter in their calculations. In terms of their own direct fitness, if there is no intermittent inbreeding, they are equally related to all offspring and having offspring is the only way to gain fitness in this situation. Thus, the asymmetry conflict that exists for the offspring does not exist for the parent.
? If all of the offspring were genetically identical (asexual reproducers or totally inbred), would parent/offspring conflict exist according to the assumptions of this theory? Think about what your answer might tell you about the evolution of colonial organisms where each individual is genetically identical -- or for that matter, the early evolution of multicellular organisms.

3. Thus, a conflict will arise when the optima for the parents and offspring's inclusive fitnesses are not the same. A solution to a typical theoretical example of P/O conflict is shown below. In this particular case, the argument is over how much resource to invest:

Parent - Offspring Conflict: How Much Should a Parent Invest in a Particular Offspring?

(Source Trivers (1974), Am Zool)



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Amount of Parental Investment (Arbitrary Units)

! Note that *r* * C, not C/r is used because we are looking at how the offspring view the costs of parental care. Thus, *r* * C is not the actual cost to the parent, it is the way that the offspring views of values the parent's costs and is therefore simply a way to predict when the offspring will finally believe that further investment in its direct fitness by the [parent is no longer in its interest

? What will happen to the length of the conflict period if the next offspring is likely to be a half-sib?

If the parents are not likely to survive to the next year, what does that do this graph?

-- to reiterate from the weaning conflict model:

4. Notice that before the conflict period and after it, both parents and offspring are in agreement:

a. Before -- the offspring is not really ready to be on its own; therefore its fitness is low and the parent has not realized its maximum benefit from the aid it is capable of giving -- better to give more.

b. After the condition where $C * r > B$, the offspring will maximize its inclusive fitness by allowing its parents to breed again. It's direct fitness has gained almost the maximum it could gain (but not all), but this loss is more than made up for by its gain in indirect fitness if its parent's breed again.