PARENT-OFFSPRING CONFLICT: CAN A GENETIC MECHANISM OVER-RIDE AN ADAPTIVE LEVEL?

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Received 20 August 1987, 20 May 1987

ABSTRACT: When parents care for offspring in protecting them from predators and providing food, their behaviour consists of a number of characters, and these characters could be regulated at the level that is adaptive for the parents. But this level will not in general be the level that is optimum for the offspring. Hence conflict of interest may arise. Current theory finds that in some circumstances parents are not able to entirely ignore offspring demands, for example when offspring begging reflects fluctuations in hunger. In these circumstances theory shows that the best way for the parents to answer the demands of their offspring is to respond not completely, but partially. But what transforms offspring behaviour into demands on the parents? Parents can only regulate their behaviour according to the information available, including season and abundance of food as well as offspring behaviour. Comparison between parents naturally selects the parents' characters that perceive and interpret this information to levels that are adaptive for the parents. Parents do not need to interpret offspring begging in some sort of proportionate way, they can do so in a permissive way. If it is begging the parent may feed it, otherwise not. In contrast to the conflictor genes of current theory, the adaptive level approach predicts that offspring will beg only in broods typically greater than one, when a parent that is present is likely to have food.

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Parent-offspring conflict, a topic introduced by Trivers (1974), was described by Parker (1985, p519) as, "the allocation of a parent's reproductive expenditure (investment) between its progeny (Trivers 1974). Essentially there are two optima, one for the parent and one for the offspring. In sexually reproducing species, these optima do not coincide, and offspring will be selected to demand more investment than the parent is selected to supply."

Using games theory, Parker (ibid, p519) studied the consequences of a genetic mechanism, a conflictor gene, that determines such conflict. He found that, "The conflict is likely to be resolved by an ESS in which intermediate (compromise) levels of investment are paid out to offspring which nevertheless continue to make costly demands (on the parents) for yet more investment."

This note examines parent-offspring conflict from the Darwinian standpoint of characters and adaptive level, where the adaptive level of a character is that level from which any deviation incurs reduced fitness as measured by net reproductive value (Fisher 1958); and finds that, contra Parker, parent-offspring conflict is resolved in favour of the parent. Birds with altricial young are used to illustrate the argument.

The relevant characters of the offspring include the size and markings of the gape, rate of digestion, and manner of presenting the gape and producing a pattern of calls. These characters are shaped during phylogeny by comparison with other offspring where the criterion is inclusive fitness (Hamilton 1964). Any change in these characters that increases inclusive fitness will spread throughout the population. Conversely when these characters are already at the adaptive level, change will not spread.

The offspring is concerned by the consequences to the parent only insofar as they affect its inclusive fitness. Otherwise it is indifferent as to whether or not its begging behaviour and the markings of its gape do act as super-releasers that manipulate or deceive the parent. The offspring is selected to regulate its behaviour (e.g. begging behaviour) at the level that is adaptive for itself. Whether or not the offspring does manipulate or deceive the parent is another matter.

Information concerns those variables in the animal's environment that it could use to help regulate its behaviour at the adaptive level. The single criterion that distinguishes such variables is that they bear a relation to the adaptive level. For example the red spot on a yellow background on a Herring Gull's bill

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The editors thank G.A. Parker and another referee for help in evaluating this paper.

(Larus argentatus) bears a relation to the adaptive direction and occasion for a chick to peck (Tingergen & Perdeck 1950). One can term the general assembly of these variables as biological information because the animal could perceive and interpret these variables so as to regulate its behaviour at adaptive levels. In other words it could infer adaptive levels of behaviour from these variables. In addition to the array of variables presented by the offspring and mentioned above, the parent also perceives other relevant variables such as availability of food, time of season, and weather conditions. This array of information is enough for the parent to be able to regulate its behaviour at the level that is adaptive for the parent, and natural selection ensures that it does so.

Current theory assumes that parents may not be able to entirely ignore offspring demands, for example when offspring begging reflects fluctuations in hunger. And that where parents do respond to offspring demands then the best solution is to provide investment in some proportion to these demands (Parker & MacNair 1979, Parker 1985). But parents could also interpret offspring begging in a permissive way, i.e. when offspring are begging you can feed them otherwise not. Besides, what is an offspring 'demand'? Offspring can gape and squawk. They cannot say, 'I really need 40 grams of food today', and even if they could, the parent can still interpret this statement in any way that suits it. Selection is about parents who once did interpret offspring behaviour in a variety of ways, and which of these ways has survived in the animals we see today. If this is not the adaptive level then surely one must identify some constraint that prevents it, such as the physiological problem being too complex.

How could a parent invest in some proportion of offspring 'demands'? But first, what magic transforms offspring behaviour into 'demands' on the parent? There is neither magic nor transformation. Beauty lies in the eye of the beholder, and the impact of the offspring's markings and behaviour lies solely in the eye of interpretation, i.e. the inference of the parent. If one is unable to measure the level of offspring behaviour on some 'demand' scale, how can one invest in a proportion of it?

All the characters of an organism evolve to the level that is adaptive for that organism (Darwin 1859). But could the genetic mechanism suggested by Parker (ibid) make the parents act non-adaptively? Parker's genetic mechanism implies that these characters of perception and interpretation of the parent are fixed so that the parent 'pays out' at some specified proportion to offspring demand (see Parker's Fig. 4) whereas the entirely different characters of the offspring's begging behaviour are allowed to evolve. Why should these characters of the parent remain fixed? Even if some genetic mechanism could ensure this, what prevents a mutant gene (or series of mutant genes) from arising that does allow these parental characters to evolve? And why would they not evolve to the level that is adaptive for the parent? Could it be that some ontogenetic or phylogenetic restraint prevents the parent from modifying its behaviour to match the changing circumstances (in ontogeny or phylogeny) of developing offspring, food availability and time of year? For example the parent could find that the complexity of perceiving this array of information and interpreting it adaptively is a physiological task so formidable as to be beyond its capability. Alternatively the cost of such a complex physiological mechanism could be more than the advantage gained in rearing more offspring. However it remains to be shown that such a restrain does exist. Until then some such assumption is an important part of the framework supporting the conflictor-gene solution. Another possible restraint is that selection might not be able to operate on a behavioural character until it had reached 'selection value'. But Fisher (1958) showed that 'selection value' is a false concept and does not restrain the evolution of morphological characters. There is no reason why 'selection value' will restrain a behavioural character.

Why then do offspring beg? Darwin (1859 ed. Burrow p117) states '... as more individuals are produced than can possibly survive, there must in every case be a struggle for existence ... one individual with another ...'. This statement does not merely suggest that offspring beg to increase their share of food from their parents in comparison to their siblings, but that they certainly will do so. But this jockeying for position between siblings will not in any way affect the effort expended by the parent.

What experimental evidence would support one or other of the two hypotheses, conflictor gene and adaptive level? The adaptive level hypothesis predicts that offspring ought to beg only when there is a likelihood of a parent being present with food and when the brood size is typically greater than one, whereas the conflictor gene hypothesis predicts that offspring ought to beg whenever a parent is present no matter what the typical brood size. So evidence could be obtained to favour one or other of these hypotheses.

The conflict of interest between parent and offspring is of course important, (as indeed are the conflicts arising in other relations) and will give rise to numerous interesting phenomena (e.g. regression, Trivers 1974). However this note suggests that the resolution will normally follow the adaptive level for the parent.

Comments by David Croft and Bryan Nelson on an earlier draft have greatly improved this communication, it is a pleasure to thank them.

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