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The selection of social actions in families: II. Parental investment

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ABSTRACT

One of the most widely used applications of kin selection concerns the investment that parents provide to their young. In particular, Trivers' concept of parent–offspring conflict was enthusiastically adopted by biologists and applied to many aspects of parent–offspring interactions, including reproductive effort, clutch size, brood reduction, sex ratios, and dispersal and germination strategies. In this paper, parental and offspring strategies are examined with regard to the amount of resources that parents invest in each offspring; this determines the size and average fitness of the newly independent young. Parental investment is used here as a model system to compare the results of genetic models of social actions with those of autonomous gene models, and to examine the relative merits of using measures of inclusive or collective fitness. To this end, the extent of conflicts over parental investment is derived for two kinds of families, which differ in the way that the young compete with each other (equal versus unequal competition). Finally, the ways in which conflicts are resolved and the relative importance of conflict and cooperation in raising young are discussed.

Keywords: collective fitness, inclusive fitness, kin selection, parent–offspring conflict.

INTRODUCTION

One of the most widely used applications of kin selection concerns the investment that parents provide in their young up to the time when they become independent. In 1974, Robert Trivers introduced one of the key ideas of evolutionary ecology, parent–offspring conflict. Combining kin selection with a cost–benefit analysis of parental investment, Trivers (1974) observed that a parent is equally related to all its offspring and hence it should favour giving resources to one rather than another whenever the benefit to the favoured progeny (1) exceeds the cost to the disfavoured one (2) (i.e. $b_1 > c_2$). An offspring, however, is more closely related to itself ($r_{aa} = 1$) than to a full sib ($r_{at} = \frac{1}{2}$), and thus by the inclusive fitness rule for selfish behaviour, offspring 1 should seek food whenever $b_1 r_{11} > c_2 r_{12}$, or $b_1 > \frac{1}{2} c_2$. Trivers brilliantly explored the conflict between parents and their offspring over the length of the period of parental investment, the amount of parental investment and the preferred sex of potential offspring.

The concept of parent–offspring conflict was adopted enthusiastically by biologists and applied to many aspects of parent–offspring interactions, including reproductive effort, clutch size, brood reduction, sex ratios, and dispersal and germination strategies (Comins *et al.*, 1980; Charnov, 1982; Ellner, 1986; Parker and Mock, 1987; Marks and Redmond, 1987). Theoretical studies have confirmed the basic concept of a conflict of interests between parents and offspring in many but not all circumstances, and they have also shown that kin selection formulations do not always agree exactly with full genetic models (e.g. Feldman and Eshel, 1982).

In this paper, parental and offspring strategies are examined for the central topic of parent–offspring interactions, the amount of resources that parents invest in each offspring; this determines the size and average fitness that the newly independent young attain. A number of factors are known to influence the parental investment strategies of parents and their young (reviewed in Harper, 1986). Parental investment is used here as a model system to compare the results of genetic models of social actions with those of autonomous gene models, and to examine the relative merits of using measures of inclusive or collective fitness.

Parental investment involves a communication system in which the parents and offspring possess different information and play contrasting roles. The young are more able to assess their own needs and how much they would benefit from further investment. Hence they signal to parents for resources; juvenile animals beg and seeds produce hormones that induce the mother plant to treat them as a resource sink (Lee, 1984). Parents assess the signals and respond by either feeding or not feeding an offspring. In addition, in some species of plants and animals, some offspring can kill others or interfere with their feeding. The strategies of the two generations together determine the pattern of parental investment. I seek to discover the nature and size of discrepancies between the two components of the system and how they are resolved. The extent of conflicts over parental investment is derived for two kinds of families, which differ in the way that the young compete with each other. Finally, I discuss the ways in which conflicts are resolved and the relative importance of conflict and cooperation in raising young.

PARENTAL STRATEGIES

The way in which a parent optimally disburses its limited resources to various offspring is considered in collective fitness and inclusive fitness models of selection. I examine families with many (m) offspring. This provides more general results and enables one to consider unequal numbers of offspring that benefit and suffer from a change in the disbursement of parental resources. The results for many offspring can be adapted with minimal modifications to families with few offspring, which were described by Maynard Smith (1989). I assume the offspring in a family consist of two subfamilies, which differ in the consequences of their being fed. These are described for convenience as the older (o) and younger (y) subfamilies, although size, status or position may be more important than age in some species. The older and younger subfamilies, respectively, constitute proportions p_o and p_y of the family ($p_o + p_y = 1$). The members of the two subfamilies may or may not receive the same parental care.

A parental phenotype, 1, causes parents to disburse resources to the two subfamilies in such a manner that individuals of the two sets of offspring have fitnesses w_o and w_y. A second type of parent, 2, disburses more resources to the older subfamily, so the fitness of each member increases by a benefit, b, and the fitness of each member of y decreases by a cost spread evenly among the younger sibs. The cost per recipient, therefore, depends on the ratio of older to younger offspring, that is $c(p_o/p_y)$. A parental allele has a 50% chance of being present in any offspring. By the collective fitness rule (Lloyd, 2000), the action allele in the second type of parent has a fitness advantage when the net effect, $\sum e_i g_i > 0$ (eq. 3 in Lloyd, 2000). That is,

$$m[b_o p_o - c_y p_y (p_o/p_y)]/2 > 0$$

or

$$b_o > c_y \qquad (1)$$

The fitness benefits from continuing to feed an offspring generally decrease as the offspring approach independence (Trivers, 1974). Hence, if a parent feeds one offspring to a larger size than another, the gain to the older offspring is less than the loss to the younger one (Fig. 1). Parental fitness, therefore, is maximized by disbursing resources to all offspring equally. The strategy is independent of family size or the proportions of older and younger offspring.

A calculation based on inclusive fitness gives the same result. The inclusive fitness rule for the situation when the actor (parent) is not affected and there are two kinds of recipients (the two subfamilies) becomes $\sum e_t r_{at} > 0$, which gives $mp_o b/2 - mp_y c(p_o/p_y)/2 > 0$, or $b > c$ again. Inclusive and collective fitness calculations give the same answer.

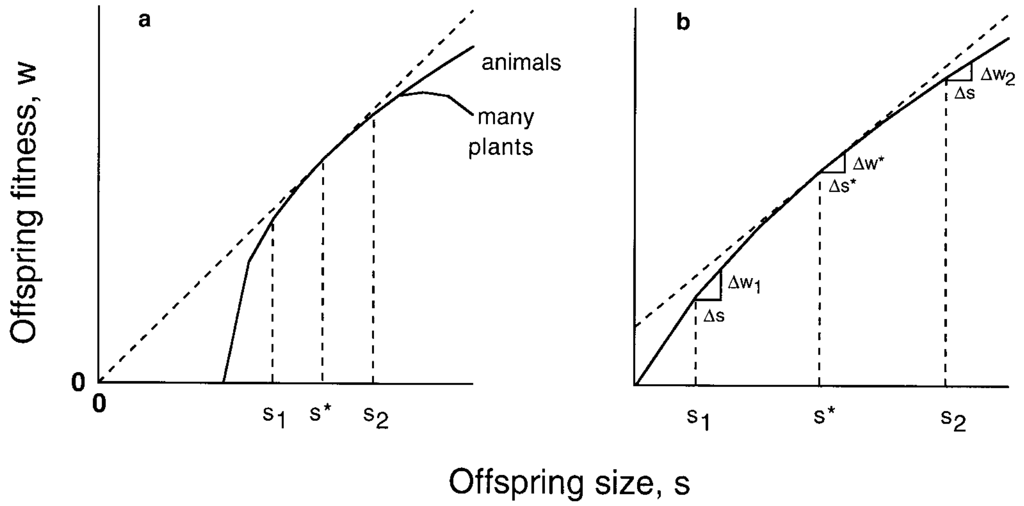

Fig. 1. Optimal sizes for parents and offspring. (a) The optimal size for parents, s^*, is at the point where the fitness curve for single offspring touches the steepest possible straight line from the origin, which represents the highest attainable benefit : cost ratio (Smith and Fretwell, 1974). An offspring's fitness is zero below a minimum threshold size. If offspring can be raised beyond s^*, the parent's strategy is to produce more, not larger, offspring. In many animal species, but not in plant species generally, the offspring would continue to benefit indefinitely if parental investment was to continue beyond the parental ESS. For plants, seed size is a compromise involving many functions, and fitness decelerates rapidly beyond the ESS size. (b) A magnified view of the part of the curve around the parental optimum, s^*. The parental strategy favours an offspring at s_1 being fed rather than one at s^*, since $\Delta w_1 > \Delta w^* (b > c)$. The offspring strategy favours an offspring of size s_2 taking food from one of size s_1 provided $\Delta w_2 > \frac{1}{2}\Delta w_1$ (for monogamous species) or $\Delta w_2 > \frac{1}{4}\Delta w_1$ (for promiscuous species).

STRATEGIES FOR UNEQUALLY COMPETING OFFSPRING

Offspring strategies are more diverse than parental strategies because they are influenced by the relative ability of different offspring to compete with each other. Parker and Macnair (1978, 1979), Craig (1979) and Queller (1984) recognized that the conditions under which offspring are selected to beg depend on whether the costs of extracting more parental resources are borne by current or future sibs. It is useful to make a somewhat broader distinction between families in which all offspring compete for parental resources on equal terms and those in which offspring differ in their competitive abilities. I consider the latter situation first, since the strategies are actually more straightforward.

Suppose a fraction of the young of a family are older than the others and by virtue of their greater age are able to signal more strongly for parental resources. Offspring may engage in unequal scramble competitions. Earlier-hatching chicks, or fruit that are initiated in an inflorescence before others, or ovules in a fruit that are fertilized earlier, may all have a competitive advantage. Moreover, the positions of some fruit in an inflorescence or of some seeds in a fruit may give them precedence over others (Stephenson, 1981). Disparities between offspring also arise when a whole clutch of eggs or a crop of seeds is produced before another, either in the same year or in different years. In some species, older offspring may directly prevent parents from feeding their younger sibs or even cause their death. Direct interference of this kind is well known in birds with obligate brood reduction (Mock *et al.*, 1990). It also occurs when seeds produce a hormone that causes later-initiated fruits and seeds to abort (Lee, 1984).

In all these situations, some offspring are able to take a disproportionate share of the parental resources at the expense of their current or future sibs, who are unable to influence events. I examine the extent to which such selfishness is advantageous and causes departures from the parental strategy of even feeding. The advantaged and disadvantaged offspring will again be referred to as older and younger subfamilies. Moreover, the means of competition is described as the intensity of begging signals; where it occurs, direct interference with younger sibs will have parallel fitness effects.

Genetic ESS models of the invasion and fixation of signalling genes are examined first to establish whether the mode of inheritance or the frequencies of alleles affect the signalling strategies of older offspring. Subsequently, I compare autonomous gene models that use inclusive fitness or collective fitness to integrate the effects on actors and recipients.

Suppose a dominant allele, H, causes older sibs to produce a *higher* intensity of begging signals than those produced by the homozygous recessive hh. In a population that consists only of residents with the low-signalling allele, the fitness of older offspring is 1 and that of younger offspring is k, where $k < 1$. The average fitness of the recessive allele in families with low-signalling older sibs is

$$\bar{w}_{\mathrm{h}} = \bar{w}_{\mathrm{hh}} = p_{\mathrm{o}} \cdot 1 + p_{\mathrm{y}} \cdot k = p_{\mathrm{o}} + p_{\mathrm{y}} k$$

A dominant allele that appears as a rare mutant will occur predominantly as a heterozygous parent that mates with a recessive homozygote in the cross Hh × hh. The family segregates in the ratio $\frac{1}{2}$Hh : $\frac{1}{2}$hh. When they are older sibs, the heterozygous high-signallers take a larger share of resources from their younger sibs *of either genotype* and gain a fitness benefit b. The disadvantaged younger sibs suffer a fitness cost, $-c$, for every older high-signalling sib. The cost per younger sib depends on the ratio of older high-signallers to younger sibs (actors to recipients). In the rare segregating families, half of the older sibs are high signallers but all the younger sibs experience the cost. Hence the cost to each younger sib is $-cp_o/2p_y$. Assuming that the whole family is derived from the same cross (mating is monogamous), the average fitness of the rare dominant allele in the family is

$$w_{HH} = w_{Hh} = p_o(1+b) + p_y\left(k - \frac{cp_o}{2p_y}\right)$$

Thus, the fitness advantage of the dominant allele is

$$\bar{w}_H - \bar{w}_h = p_o\left(b - \frac{c}{2}\right)$$

A dominant allele that causes older sibs to signal at a higher intensity can invade a population when

$$b > \frac{c}{2} \tag{2}$$

Suppose a dominant strong-signalling allele invades under these conditions. To examine whether the allele will be fixed if it becomes prevalent, consider the reinvasion of the *recessive* allele, h, into a population of HH residents. Thus, the average fitness of a resident H allele, in HH × HH crosses giving all HH progeny, is

$$\begin{aligned}\bar{w}_H = \bar{w}_{HH} &= p_o(1+b) + p_y(k - cp_o/p_y)\\ &= p_o(1+b-c) + p_y k\end{aligned}$$

A rare h allele in an HH population will be expressed almost invariably in Hh × Hh crosses which yield progeny in the ratio $\tfrac{1}{2}$HH : $\tfrac{1}{4}$Hh : $\tfrac{1}{2}$hh. The h allele occurs in the progeny in equal numbers of copies as a heterozygote and a homozygote, and fractions p_o, p_y of each genotype are in older and younger sibs. In the whole family, the number of higher signallers ($\tfrac{1}{2}$Hh and $\tfrac{1}{4}$HH older sibs) is $(\tfrac{3}{4})(p_o/p_y)$ that of the total number of younger sibs. Hence the average (collective) fitness of a rare recessive allele is

$$\begin{aligned}\bar{w}_h = \tfrac{1}{2}\bar{w}_{Hh} + \tfrac{1}{2}\bar{w}_{hh} &= p_o[\tfrac{1}{2}(1+b) + \tfrac{1}{2}] + p_y\left(k - \frac{3cp_o}{4p_y}\right)\\ &= p_o(1 + \tfrac{1}{2}b - \tfrac{3}{4}c) + p_y k\end{aligned}$$

The fitness advantage of the resident higher-signalling allele is

$$\bar{w}_H - \bar{w}_h = \tfrac{1}{2}p_o(b - \tfrac{1}{2}c)$$

The higher-signalling allele cannot be reinvaded and is therefore fixed when

$$b > \frac{c}{2} \tag{3}$$

The conditions for invasion and fixation of a dominant allele are identical.

The conditions for invasion and fixation of a *recessive* higher-signalling allele, s, can be obtained in a parallel way by considering the appearance of s or S respectively into a resident population containing the other allele. Without working through the details, it can readily be seen that the rare allele being considered as the action allele experiences all the fitness effects in actors but shares the effects in recipients equally with copies of the no-action allele, as in the case of a dominant higher-signalling allele. Hence the conditions for selection of recessive and dominant alleles are the same, as given by equations (2) and (3).

More generally, we can consider any autonomous gene that causes older sibs to exhibit a higher intensity of signalling. This is appropriate for all modes of inheritance in which an action allele has a constant effect whenever it is expressed, including complete dominance or recessiveness. Using the collective fitness rule derived in Lloyd (2000), an autonomous higher-signalling allele at any frequency is favoured when its net effect on the allele copies in all sibs in a family is positive. Assuming that the alleles segregate similarly in the younger and older subfamilies (for a gene derived from a male parent, this means mating is monogamous), $\sum e_i g_i > 0$ when $m(p_o b - \frac{1}{2} p_y c(p_o/p_y)) > 0$, or $b > \frac{1}{2}c$ again.

We can also consider the selection of a stronger signal in an older sib as a process of kin selection, comparing the inclusive fitnesses of the action and null alleles. The inclusive fitness of the action (higher-signalling) allele is greater than that of the null allele when $\sum e_i r_{ij} < 0$. For full sibs, $e_a = b$, $\sum e_p = -cp_o/p_y$, and $r_{at} = \frac{1}{2}$. The action allele is selected when $\frac{1}{2}m[(p_o b \cdot 1 - p_y(cp_o/p_y)) \cdot \frac{1}{2}] > 0$, or $b > \frac{1}{2}c$ again.

Thus both the collective fitness and inclusive fitness formulations of autonomous genes at any frequency agree with the genetic ESS models that consider the extreme situations where one or other allele is rare. The agreement between the various formulations conforms with the theory presented in Lloyd (2000). Since the older and younger sibs are different subfamilies, the alleles are distributed to both subfamilies independently and randomly, as required for identity by descent (IBD) calculations of relatedness.

Although they agree, the collective and inclusive fitness methods interpret the events from different perspectives. The collective fitness model says $b > \frac{1}{2}c$ because the number of copies of the action allele that receive benefits is twice the number that receive costs. The inclusive fitness model says $b > \frac{1}{2}c$ because the action allele in the actors is identical by descent with an allele in half the sibs (or, more loosely, the recipients share half their genes with the actor). Both interpretations indicate that the discrepancy between parental and offspring strategies is due to the segregation of the two gene copies in one parent into different offspring. This causes the offspring genes to behave selfishly and favour the offspring that carry them at the expense of their sibs. A parent–offspring conflict exists when $c > b > \frac{1}{2}c$, as Trivers (1974) proposed.

THE EFFECT OF BREEDING SYSTEMS

All seed plants are promiscuous; pollinators transfer pollen to a seed parent from many pollen donors. A minority of animals that engage in parental care are also promiscuous or polyandrous. If each male parent fathers a fraction f of the offspring in each family, a proportion $f/2$ of the family will have an action allele for strong signals from a father who carries that allele. A mother with an action allele passes it to half her offspring. On average, parents with action alleles transmit these to a proportion, $(1 + f)/4$, of their offspring. Hence the relative numbers of action alleles in recipients and actors, $g_t : g_a = (1 + f)/4$. A stronger signal is selected when an action allele has a collective fitness advantage, $\sum e_i g_i > 0$, or

$$b > \frac{c(1+f)}{4} \tag{4}$$

For complete monogamy $f = 1$ and equation (4) reduces to $b > c/2$ as derived in equation (2). At the other extreme, each male parent fathers only one offspring. That condition is approached in many seed plants, although it may never be reached entirely. When $f \to 0$,

$$b > \frac{c}{4} \tag{5}$$

A kin selection interpretation of this situation is that offspring are related to their parents on average by $r = \frac{1}{4}$, so $\sum e_i r_{ij}$ gives equation (5). By either argument, offspring in promiscuous or polyandrous families are expected to be more selfish about taking a disproportionate share of resources than offspring in monogamous families.

One situation may engender even stronger selfishness by dependent young. Brood parasites lay their eggs in the nests, colonies or ovaries (in the case of plants) of other species, and the host mother cares for the parasite's offspring. Both the maternally and paternally derived genes of the brood parasite's young are unrelated to the genuine progeny of the host. Most bird species that are brood parasites lay only one egg per nest, and some of them are also promiscuous (Rothschild and Clay, 1957; Lack, 1968; Rothstein, 1990). The beetle, *Atemeles pubicollis*, which is parasitic in ant colonies, lays a number of eggs, but these are cannibalistic and normally only one beetle is raised with a number of ant larvae (Holdobbler, 1971).

By extension of the reasoning for polyandry, a proportion $f/2$ of the family of a brood parasite will have an action allele for strong signals from a father or mother who carries that allele. Stronger-signalling parasitic juveniles are selected ($\sum e_i g_i > 0$) when

$$b > \frac{cf}{2} \tag{6}$$

If the parasite's family constitutes only a small fraction of the host's brood ($f \ll 1$), there is little restraint on the extent to which parasitic young should seek to elicit feeding at the expense of the host's genuine young. If a parasite lays only one egg in a nest or colony and will not lay another there in future, the single progeny has no sibs to compete with and $f \to 0$. Then

$$b > 0 \tag{7}$$

The optimal strategy of the parasitic young is to beg without restraint from sibling considerations (Harper, 1986).

The prediction of suprasignalling by parasitic juveniles is borne out by observations of their behaviour. As expected, the young of bird parasites often destroy the host eggs or chicks or cause them to die of malnourishment. The parasitic young are also notorious for the supranormal begging signals they produce and it is often claimed they receive a disproportionate share of the foster parent's resources. That claim has been disproved in the case of experimental mixed host-plus-parasite clutches of the European cuckoo and reed warbler in warbler nests. Nevertheless, the sole cuckoo fledglings that occur naturally grow to a much greater size than the (usually 3–4) fledglings of a warbler clutch (Brooke and Davies, 1989; Davies and Brooke, 1991). *Atemeles* larvae receive a disproportionate share of the resources of an ant colony (Holdobbler, 1971).

Species of *Ficus* offer a unique opportunity to compare the strategies of offspring of diverse origin that are fed by the same mother. Single ovules, even in the same fig (syconium), may be occupied by the genuine offspring, immature fig seeds (which are numerous in each syconium), offspring of the pollinating fig wasps (brood mutualists which lay fewer eggs after a female wasp enters a syconium), or offspring of fig parasites (brood parasites of figs that characteristically lay still fewer eggs from outside a syconium). The three types of offspring should differ in the degree of selfishness they exhibit. Unfortunately, I have not been able to find any information on the comparative signalling strategies or mature sizes of the various offspring types that mature in fig ovules.

When parents breed asexually, all offspring are identical to each other and to their parent. An action allele in one offspring is present in all its sibs, so each offspring should treat its sibs as an extension of itself. The optimal strategy for offspring, as well as parents, is to feed all young equally (Parker and Macnair, 1978).

IS THE SELECTION OF SOCIAL ACTS THAT OF GENES OR INDIVIDUALS?

Natural selection is a two-level process with indispensable events at the gene and individual levels. Genetic models explicitly incorporate events at both levels. When genes have constant effects, the selection of non-social behaviours involving only lineal fitness effects can be monitored at either the gene or individual level alone. Now we ask whether this is also true of the selection of social acts. These differ in that a controlling (action) allele has two phenotypic effects on its carriers – the lineal effect on the actors and the non-lineal effect on the genetically correlated recipients.

In the case of unequally competing offspring, the events can be described equally accurately by a model of autonomous genes (using collective or inclusive fitness) or by a model of individuals which considers the inclusive fitness of the whole genome rather than just the action allele. But in the case of equally competing offspring, alleles of the action locus are not distributed independently to actors and recipients. To calculate the effects on copies of the action allele in actors and recipients, it is necessary to trace the distribution of alleles to all participants from the source of the correlation, a parent. A gene model using collective fitness can do this, so the selection of social acts can be analysed with a gene model when genes behave as if they operate autonomously. But an individual (phenotypic) model would not incorporate the non-random distribution of alleles to actors and recipients and would fail. In this situation, genes have primacy over individuals as descriptors of the selection process, but not as the cause of selection. The earlier conclusion that both gene and individual events are indispensably involved still holds.

DOES THE SELECTION OF SOCIAL ACTS MAXIMIZE FITNESS?

It is often claimed that kin selection maximizes the inclusive fitness of individuals. In the case of offspring signals, this claim has been made by Trivers (1974) and others. However, this need not be true; for example, consider that, in the case of self-fertilization, selection can lead to a decrease in average (lineal) fitness. Let us now examine how the average fitness of offspring changes as a stronger-signalling allele spreads under the conditions just derived. The average fitness of *all* offspring (and their genes, including copies of *both* alleles) is the combined average of the older and younger subfamilies. That is,

$$\begin{aligned}\bar{w} &= w_0 + \frac{1}{m}\sum_i e_i = w_0 + p_\mathrm{o} e_\mathrm{o} + p_\mathrm{y} e_\mathrm{y}\\ &= p_\mathrm{o} + p_\mathrm{y} k + p_\mathrm{o} b - p_\mathrm{y} c(p_\mathrm{o}/p_\mathrm{y})\\ &= p_\mathrm{o} + p_\mathrm{y} k + p_\mathrm{o}(b - c) \qquad (8)\end{aligned}$$

The effect of an action allele in the parents or their offspring depends on the sign of the term $(b - c)$. As long as $b > c$, both the parents and offspring are selected to favour more parental investment in each young (Fig. 1). Selection in both generations then increases the average fitness. When offspring exceed the size to which parents are selected to invest in them, $b < c$ (this is beyond s^* in Fig. 1). Then the spread of a stronger-signalling offspring allele causes a progressive decrease in the average fitness of the whole family and of the genes they contain. The same conclusion is reached when the average inclusive fitness of all offspring is considered. This entails counting all offspring $1 + r$.

Thus selection does not always maximize the fitness of individuals (or genes) in social acts. A considerable number of parallel situations are known in which organismic selection with no social (non-lineal) effects causes a decline in average fitness (e.g. selection of self-fertilization, Fisher, 1941; or of sex-driving genes, Hamilton, 1967).

The reason why the average fitness decreases with the spread of a stronger-signalling offspring allele in conflict with the parent's interests is that the *total* costs of the allele exceed the benefits, although *for allele carriers* the benefits exceed the costs. The allele, like others of a parallel nature, is selected because it has a more detrimental effect on carriers of the competing allele than on its own carriers. The competing allele bears proportionally more of the costs and less of the benefits. As always, selection operates by favouring the fitter allele and the individuals that carry it. It is the fitness advantage (or relative fitness, if one compares fitnesses by division rather than subtraction) of genes and their carriers that is invariably maximized, not their average fitness. The maximization of average fitness is a secondary epiphenomenon that applies in some circumstances but not in others. It is not a general property of kin selection (Sahlins, 1976; Harper, 1986) any more than of other types of natural selection (Fisher, 1941).

STRATEGIES FOR EQUALLY COMPETING OFFSPRING

There are many situations in which offspring are initiated together and compete on an equal footing. These include bird and mammal species in which the young are hatched or born in rapid succession, and multiple seeds within a single fruit or within different fruit that are initiated more or less simultaneously (provided no disparities arise from the positions seeds are borne at). In these situations, stronger-signalling young can take resources from their sibs only if the two sets differ in signalling alleles. Consequently, the distribution of action alleles to weaker-signalling recipients is non-random. It is therefore advisable to first examine a genetic model for the selection of signals.

Assume that when all young in a family signal at the same intensity (whether this is high or low), they are fed at the same rate and attain the same fitness, defined as 1. When some young signal more strongly than their competing sibs, they receive more food and attain a higher fitness, $1 + b$. Each stronger-signalling sib reduces the fitness of its weaker-signalling competitors collectively by a total cost, $-c$. In a population with a recessive genotype hh, which causes all progeny to signal weakly,

$$\bar{w}_{\mathrm{h}} = \bar{w}_{\mathrm{hh}} = 1$$

A rare mutant with a dominant allele H that induces stronger signals occurs predominantly as a heterozygote and mates with the resident genotypes, hh. Half the progeny are heterozygous strong signallers. The fitness of the mutant allele is

$$\bar{w}_{\mathrm{H}} = \bar{w}_{\mathrm{Hh}} = 1 + b$$

$$\therefore\ \bar{w}_{\mathrm{H}} = \bar{w}_{\mathrm{h}} = b$$

The mutant has a fitness advantage and invades the population when

$$b > 0 \tag{9}$$

Dependent juveniles should be completely selfish about seeking parental care because they receive only benefits from their begging signals. The costs fall entirely on the weaker-signalling allele.

The same result is readily obtained from the collective selection rule for multiple social actions. Here $e_{\mathrm{a}} = b$ and the total number of copies of action alleles in stronger-signalling progeny $\sum g_{\mathrm{a}} = \frac{1}{2}m$. The weaker-signalling progeny do not possess the action allele, so $\sum g_{\mathrm{t}} = 0$. Thus the stronger-signalling allele has a higher collective fitness when $\sum e_{\mathrm{a}} g_{\mathrm{a}} > 0$; that is, $\frac{1}{2}mb > 0$ or $b > 0$, as in equation (9).

The result cannot be obtained from a kin selection model using an IBD coefficient of relatedness, however. The IBD relatedness of equally competing full sibs is the same as that for sibs that compete unequally, $r = \frac{1}{2}$. Hence, by the kin selection rule for social actions, a high signalling intensity is selected when $\sum e_i r_{ij} > 0$ – that is, when $b - c(\frac{1}{2}) > 0$ or $b > c/2$. The answer is incorrect because the action alleles are not distributed randomly to actors and recipients as required for a relatedness coefficient based on identity by descent.

The conditions for fixation of a dominant stronger-signalling allele can be obtained by examining the conditions under which a recessive weaker-signalling allele cannot invade a population of residents with the dominant allele. Then, the average fitness of identical, equally competing sibs is

$$\bar{w}_{\mathrm{H}} = \bar{w}_{\mathrm{HH}} = 1$$

A rare recessive mutant is most likely to be expressed in a family from a cross Hh × Hh, which gives segregating offspring in the ratio $\frac{1}{4}$HH : $\frac{1}{2}$Hh : $\frac{1}{4}$hh. In such families, the ratio of stronger-signalling actors to weaker-signalling recipients is 3 : 1, so when each actor imposes a total fitness cost, $-c$, on recipients, the cost per recipient from lost resources is $-3c$. Then

$$\bar{w}_{\mathrm{h}} = \tfrac{1}{2}w_{\mathrm{Hh}} + \tfrac{1}{2}w_{\mathrm{hh}} = \tfrac{1}{2}(1 + b) + \tfrac{1}{2}(1 - 3c)$$

$$\therefore\ \bar{w}_{\mathrm{h}} - \bar{w}_{\mathrm{H}} = \tfrac{1}{2}(b - 3c)$$

The recessive allele cannot reinvade unless $b > 3c$, which is most unlikely, especially as the cost exceeds the benefit at sizes beyond that at which parents are selected to cease parental care (Fig. 1). A dominant stronger-signalling allele will therefore be fixed because it is likely that

$$b < 3c \tag{10}$$

The conditions for fixation and invasion are not the same, although both indicate that stronger-signalling alleles are almost invariably selected. Selection is frequency-dependent because the ratio of action alleles bearing the costs and benefits of the stronger signals changes as the allele increases.

The selection of a *recessive* allele causing stronger signals in equally competing sibs is not subject to the same conditions as those for a dominant allele, because the relative number of allele copies experiencing the benefits and costs of the action also depends on the mode of inheritance. When genetic or collective fitness models for the invasion and fixation of a recessive allele are worked through, it is seen that a recessive allele is able to invade if $b > c/3$ and it becomes fixed if $c > 0$. This is a double reversal of the quantitative conditions for a dominant allele, but qualitatively the result is the same. In all realistic combinations of costs and benefits, a stronger-signalling allele is able to invade, spread and become fixed.

Whether the action allele is dominant or recessive, the eventual outcome of selection in equally competing families does not cause a departure from the parental strategy of feeding offspring evenly. When a stronger-signalling allele is fixed, its effects on the disbursement of parental resources *disappear*. Then every family consists of uniformly signalling, and uniformly fed, offspring, as was the case before the allele started to replace the weaker-signalling alternative. The evolution of stronger signals causes only transitory inequalities in the feeding of young while the allele is still spreading and is segregating in some families. At the end of the selection process, the parental and offspring strategies are in complete accord in causing equal disbursement of parental resources to all offspring.

THE RESOLUTION OF PARENT–OFFSPRING CONFLICTS

Whereas parents are always selected to feed their offspring equally, offspring have various strategies, depending on their circumstances. Although I have considered only a few of the major factors involved, the offspring strategies that were obtained vary from complete selfishness for single young of brood parasites to complete egalitarianism for asexually produced young. Among non-parasitic sexual broods, disparities in the feeding rates of different offspring persist with unequally competing sibs but not with equally competing sibs. Competition between siblings will often be a complex combination of equal and unequal contests.

With this diversity of situations, how important is parent–offspring conflict in causing departures from the even-handed strategy of parents? Three factors reduce the role of such conflicts in many species:

1. It is reasonable to assume, as Trivers (1974) did, that a young animal will often continue to benefit if it is able to obtain resources substantially beyond the amount that its parent is selected to provide. Such an assumption is less appropriate for the seeds of plants, however. At the end of parental investment, mature seeds are physiologically inactive but they must subsequently meet the complex demands involved in their dispersal, landing, burial, dormancy, germination and establishment. Each of these functions imposes its own requirements on a seed, and these may involve divergent optima. In particular, the optimal size for dispersal is often less than that for successful establishment (Stebbins, 1970; Harper, 1977). As a result, there is likely to be a narrow window of favourable seed sizes for any species, and the fitness curve relating seed size and fitness may decelerate rapidly or even have a maximum point not far beyond the ESS size (Fig. 1). Then, the range of sizes for

which $b > c$ ($\Delta w_2 > \Delta w_1$ in Fig. 1) may be close to the range of sizes for which $b > c/4$ ($\Delta w_2 > \frac{1}{4}\Delta w^*$ in Fig. 1). There is then little room for parent–offspring conflict.

2. Alexander (1974) and Michener and Brothers (1974) argued that, in many species, parents are likely to win a feeding conflict because of their greater size and power. While such 'parental manipulation' may sometimes occur, animal young can on occasions subvert the best of parental wills, as every human parent knows. Even seeds growing on the end of the funicle connecting them to their mother can exercise a large influence on seed development through the production of hormones. Parental manipulation may operate sometimes, but it does not always carry the day.

3. Parents have another and possibly more ubiquitous advantage, however. Suppose a stronger signal from an older offspring, such that it would lead to unequal disbursement, is selected. Parents can respond to an escalation of signals by raising the threshold signal strength that elicits a feeding response. 'Parental retaliation' of this nature could engender a further response by the offspring. The cycles of escalation and retaliation are likely to end in the parent's favour because there is an asymmetry of *costs* (not *power* as in parental manipulation). Parental retaliation is virtually costless, whereas offspring escalation carries a physiological cost, and sometimes a predator cost as well (Harper, 1986).

In combination, these three factors may lead to investment strategies in many species that match or closely approach the parental strategy of feeding all offspring so they gain equally despite any competitive disparities among them.

In the past two decades, the concept of parent–offspring conflict has dominated discussions of parental investment. The popularity of conflict interpretations may have arisen in part because of their novelty and dramatic nature (and perhaps also because of our intrinsic fascination with conflicts). But the emphasis also stems in part from observations of apparent *behavioural* conflicts. We should not assume, however, that an interplay of demands and refusals necessarily indicates a conflict of *fitness*. The signal-and-response system is essential to the fitness of both parties. Parents and their young depend absolutely on each other for their reproductive fitnesses. In many instances, behavioural conflict may represent nothing more than the operation of a communication system that is of mutual benefit. A system in which offspring demand according to their needs and parents respond according to their means favours both parties, even if it looks stressful at times.

The signal–response system of parental investment is basically one of cooperation between two parties with disparate roles but with interests that largely coincide. It is easy to exaggerate the evolutionary significance of behavioural conflicts and to ignore the less dramatic aspects of cooperation. Many accounts of parental investment in evolutionary ecology texts are one-sided, giving much more attention to the spectacular elements of conflict than to the routine but essential ones of cooperation. The theme of cooperation between parents and their offspring was mentioned briefly by Trivers (1974) in the first exposition of parent–offspring conflict, but it has received little attention since.

COOPERATION BETWEEN PARENT AND OFFSPRING IN SEED ECOLOGY

To illustrate the importance of cooperation in the interdependence of parents and their progeny, we consider the ecological circumstances of seeds. A weaned mammal or a fledgling bird is essentially a subadult that is able to live in a way that is broadly comparable to that of its parents, even if the two generations have divergent habits or social roles. In contrast, a seed is a propagule – a temporarily quiescent individual suspended between its past embryonic development and future independent life. Moreover, seeds are not just offspring. The true offspring, the embryo, is invariably wrapped in at least one parental tissue, the seed coat, and frequently in one to several more layers – the perisperm within the seed coat and the fruit wall, perianth or even bracts outside it. As mentioned above, a seed performs a succession of functions. The initial functions of release and dispersal are carried out in most if not all species entirely by the parental tissues surrounding the embryo. The wings of a maple samara, the plumes of a thistle fruit, and the flesh and stone of an avocado are all parental structures controlled by parental genes. After their release from their parent, the seeds are separated (in most species) and unable to exploit each other. Hence the superior dispersal characteristics of one seed do not detract from the dispersal of its sibs. Although the process of dispersal is one of unfettered parental manipulation, there is no conflict among sibs or between the offspring and their parents. It is in the interests of genes in both generations for every seed to be dispersed in the most proficient manner possible.

In the later activities of a seed, during its germination and the establishment of a free-living seedling, the parental and offspring tissues continue to operate with complete cooperation. The responsibility for the next generation is frequently shared between physiological processes in parental and offspring tissues during germination, and then passes rapidly to the establishing offspring. The whole sequence of events from release to free-living independence benefits the fitness of the parent and the offspring equally and there is no conflict between the generations.

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