PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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H. C. J. Godfray, G. A. Parker and D. Haig

Phil. Trans. R. Soc. Lond. B 1991 **332**, 67-79
doi: 10.1098/rstb.1991.0034

Clutch size, fecundity and parent–offspring conflict

H. C. J. GODFRAY[1] AND G. A. PARKER[2]

[1] *Department of Biology & NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.*
[2] *Department of Environmental and Evolutionary Biology, University of Liverpool, Liverpool L69 3BX, U.K.*

SUMMARY

Selection often acts in different ways on genes expressed in parents and offspring leading to parent–offspring conflict. The effect of parent–offspring conflict on the evolution of reproductive strategies is explored. Models are constructed using kin-selection techniques and it is argued that these are frequently more useful than techniques from classical population genetics. Parent and offspring optima are compared in models of (1) the trade-off between the number and size of offspring, (2) clutch size and (3) the evolution of reproductive effort with age structure. Parent–offspring conflict over clutch size is examined in more detail. Models of sibling competition are reviewed and it is suggested that the reduction in parental fitness caused by sibling competition may lead to selection on clutch size. The possibility that the parent may be selected to produce a hierarchy of sizes of young in order to reduce sibling conflict is investigated. The preliminary results give little support for this hypothesis. An extreme form of sibling conflict, siblicide, is also discussed. In some cases, the kin-selection approach fails in the analysis of siblicide and classical population genetic models are required. The paper concludes that parent–offspring conflict is a potentially significant, and often overlooked, factor influencing the evolution of reproductive strategies.

> Birds in their little nests agree
> And 'tis a shameful sight,
> When children of one family
> Fall out, and chide, and fight
> Isaac Watts, *Love between Brothers & Sisters*, 1721.
>
> Birds in their little nests agree
> With Chinamen, but not with me.
> Hilaire Belloc, *On Food.*

1. INTRODUCTION

It is a truism to state that family life is seldom unmoderated bliss. Yet biologists analysing life-history strategies have classically assumed harmony of purpose between family members. An obvious case concerns Lack's (1947) pioneering theory of clutch size. Lack assumed that selection would favour the behaviour that generates the maximum number of surviving offspring from a given clutch. This can be optimal for a single parent, but it need not be so for two parents, nor for the offspring.

Although field workers had long and variously described the sometimes quite dramatic manifestations of sib competition, theorists in general ignored such facts when constructing models. The major theoretical development came from Hamilton (1964). Although he was primarily concerned with the problem of altruism between siblings (and other relatives), Hamilton's now-famous rule applies in reverse, to describe the limits of sibling-selfishness. Hamilton also realized that in an evolutionary sense, parent and offspring interests need not coincide. In a remarkable paper, Trivers (1974) used Hamilton's rule to formulate a theory of parent–offspring conflict for sexually reproducing species: offspring should demand more parental investment than serves parental interests.

A backlash against the idea of parent–offspring conflict came swiftly from Alexander (1974); he argued that a gene that causes the summed fitness of a brood to be reduced would be quickly eliminated, in effect because offspring that conflict become parents that produce conflicting offspring. The parent should therefore always win. However, this argument treats parental fitness as paramount and, as Dawkins (1976) pointed out, rephrasing the argument giving primacy to offspring fitness leads to the conclusion that the offspring always wins. The essential consideration is whether a gene that causes offspring to conflict can spread against its alternative allele (for not conflicting). Whereas Alexander's argument is correct for asexuality, the translation of parental to offspring characteristics is imperfect in sexual species; carriers of a mutant conflictor gene can therefore profit at the expense of their non-conflicting sibs. Alexander's paper had the useful effect of stimulating a series of studies based on explicit population genetics (Stamps *et al.* 1978; Parker & Macnair 1978, 1979; Macnair & Parker 1978, 1979; Charnov 1982; Parker 1985). These showed unequivocally that such 'conflictor genes' could spread. Alexander (1974) also argued that parent–offspring conflict is implausible as the parent will always be in a position to impose its optimum.

Despite the controversy, parent–offspring conflict has not been a popular subject with empiricists, perhaps because tests of parent–offspring conflict theory often do not easily lend themselves to the dominant manipulative–experimental research programme of field behavioural ecology. One notable exception concerns parent–offspring conflict over sex ratio in social Hymenoptera (Trivers 1974). Trivers & Hare (1976) produced evidence – from the ratio of investment in males and females – that workers (offspring) control sex ratio in defiance of the parental optimum. This conclusion was quickly challenged by Alexander & Sherman (1977) and is still the subject of active research (Nonacs 1986; Boomsma 1989; Boomsma & Grafen 1990). Much of the other evidence for parent–offspring conflict comes from qualitative and even anecdotal evidence on behavioural interactions such as conflict over the time of weaning and over the amount of food provisioning during parental care, which often does not greatly extend Trivers' (1974) own comments (see Clutton-Brock (1991) for a recent review).

Theoretical studies of parent–offspring conflict have been concentrated in a few quite well circumscribed areas. Perhaps the most attention has been paid to competition between nestling birds (see below) though other active have included conflict over the sex ratio (Hamilton 1967; Trivers & Hare 1976; Charnov 1982), over infanticide (O'Connor 1978; Hausfater *et al.* 1982), and over the allocation of resources to different reproductive tissues in plants (Haig 1987). However, parent–offspring conflict is potentially significant whenever offspring and parents are both able to influence the realization of a life-history trait. The primary aim of this paper is to explore the consequences of parent–offspring conflict for some of the classic problems of life-history theory. The next section discusses techniques for the analysis of models of parent–offspring conflict and then the following three sections treat (i) the trade-off between number and size of offspring, (ii) clutch size and sibling conflict, and (iii) age-specific reproductive effort. We dwell longer on clutch size and sibling conflict as this area has received much theoretical attention. A subsidiary aim of this paper is to provide a non-mathematical review and summary of this work.

2. A NOTE ON METHODOLOGY

Initial concern about the population genetic underpinning of the subject led to the proleptic incorporation of explicit genetics in many models of parent–offpsring conflict (Parker & Macnair 1978, 1979; Macnair & Parker 1978, 1979; Parker 1985; Stamps *et al.* 1978; Feldman & Eshel 1982; Harper 1986). In comparison with phenotypic models, explicitly genetic models are more rigorous and allow the study of evolutionary dynamics, as well as end points. However, genetic models are normally complicated to analyse and the added realism of explicit genetics is rather spurious as seldom if ever is the actual genetic basis of the trait known. A related problem is the uncertainty about the degree to which the results of the analysis depend on the specific underlying genetic assumptions.

An alternative to genetic models is the use of phenotypic models. As parent–offspring conflict concerns interactions between relatives, models must be couched in terms of inclusive fitness. Hamilton's rule provides the easiest technique for studying parent–offspring conflict (Trivers 1974). The rule states that a trait will spread if the sum of the weighted changes in the fitness of self and relatives brought about by the trait are positive. The weights used in comparing fitnesses are the coefficients of relatedness of self to relatives. Hamilton's rule provides conditions for the spread of a trait and, for non-competitive problems, also defines the evolutionary equilibrium. Thus, if an older chick completely determines the division of food between itself and a younger sibling, the optimum resource division for the older chick is found by a simple application of Hamilton's rule.

Many problems in parent–offspring conflict concern competition between different family members necessitating an evolutionarily stable strategy (ESS) approach. The standard technique for the analysis of these problems is to assume single-locus genetics. However, simpler and more general results can be obtained using a modified form of Hamilton's rule (Godfray & Parker 1991). Assume that the population is at the ESS and that a mutant arises with a deviant behaviour. At the ESS the costs and benefits of an arbitrarily small change of behaviour should be equal. The ESS can thus be found by assessing the costs and benefits of deviant behaviour using Hamilton's rule, and then taking the limit as the magnitude of the deviance approaches zero. This approach can be viewed as a simple extension of that adopted by Trivers (1974) as it uses kin-selection methodology rather than classical population genetics. The 'Marginal' Hamilton's rule works for continuous behaviour strategies with weak selection and additive phenotypic effects.

The assumptions of weak selection and additivity will be violated in some cases of parent–offspring conflict. For example, the effects of siblicide and infanticide are obviously non-additive. In these circumstances, it can be essential to use explicit population genetic models.

The study of parent–offspring conflict can be divided into two stages. Initially the optimum strategies for both the parent and young are calculated and compared. Any discrepancy between the two optima defines the battleground within which the conflict is waged. The second stage is to study the resolution of the conflict and this tends to involve a second series of assumptions. In the simplest case, the offspring or the parent are assumed to have complete control over the

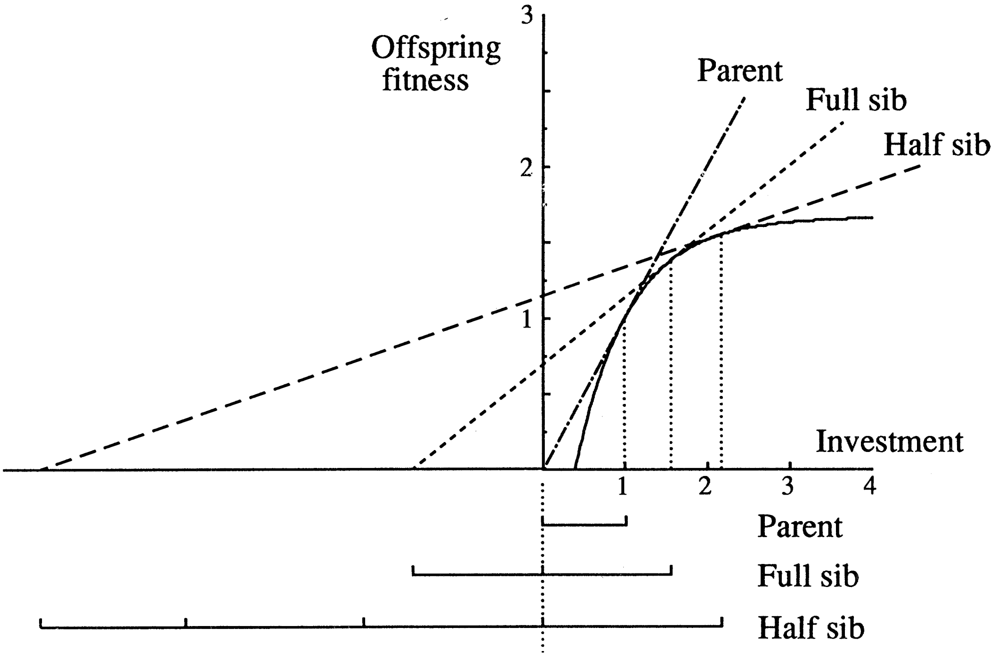

Figure 1. Graphical illustration of the Smith & Fretwell model and its extension to calculating the offspring optima. The solid curve describes offspring fitness as a function of investment. The parental optimum is defined as the point where a tangent rooted at the origin touches the curve. The optimum for full and half sibs can also be defined as the point where a rooted tangent touches the curve. In the case full sibs, the tangent is rooted at a distance to the left of the origin equal to the optimum investment. In the case of half sibs, the root of the tangent is at a distance three times the optimum investment to the left of the origin.

realization of the trait in question and thus one side unconditionally 'wins'; we shall give examples of both parental and offspring triumphs below. Alternatively, both sides may have partial control over the realization of the trait and the predicted strategy is the stimultaneous parent–offspring ESS (which can be calculated using the marginal Hamilton's rule). In this paper we are chiefly concerned with the first of these stages, although in some cases we discuss the likely resolution of the conflict.

3. INVESTMENT PER OFFSPRING

Consider a parent with a fixed amount of resource that it shares between an indeterminate number of offspring. The evolution of this decision will be influenced by the trade-off between the number and quality of young. As a specific example of this trade-off, consider an invertebrate whose only investment in its young is the resources (e.g. yolk) that make up the egg. The animal will experience a trade-off between the size and the number of the eggs it produces (Smith & Fretwell 1974; Parker & Begon 1986; Lloyd 1987). Alternatively, consider an animal, perhaps a mammal, that has a finite amount of resources that it can allocate to a series of successive young (we shall discuss more sophisticated models below). The animal will again experience a trade-off, this time between the number of young it produces, and the amount of resources it allocates to individual offspring (Parker & Macnair 1978; Macnair & Parker 1978; Winkler & Wallin 1987).

Smith & Fretwell (1974) first showed that the optimal investment per offspring could be found using a simple graphical model (figure 1). In words, the optimal investment occurs at the point when the marginal gain in offspring fitness, brought about by an arbitrarily small increase in investment, is exactly counterbalanced by the reduction in the number of offspring consequent on this resource redistribution. The parent balances the benefits of fitter offspring against the reduction in number of offspring: note, as the parent is equally related to all her offspring, she weights all offspring identically.

Smith & Fretwell calculated the optimum investment per offspring from the point of view of the parent. We can now investigate the scope for parent–offspring conflict by calculating the optimum investment per offspring from the point of view of the offspring. Consider the case where all investment is made by a single parent (Parker (1985) explains why assumptions about whether one or two parents invest in the young are important). Again, the optimum will be set by the balance between fitter offspring and the number of offspring. However, whereas the parent valued all offspring identically, any particular offspring devalues other offspring by the coefficient of relatedness between siblings. At the offspring ESS, the marginal gain in offspring fitness with resources is thus less than at the parental ESS and hence investment per offspring is larger and parental fecundity is smaller (Parker & Macnair 1978; Macnair & Parker 1978; Lazarus & Inglis 1986, Clutton-Brock & Godfray 1991). This result can also be shown graphically (figure 1).

Thus, if offspring have their way, parental investment is higher and overall parental fecundity is lower. To quantify this statement, it is necessary to specify a particular form for the relation between

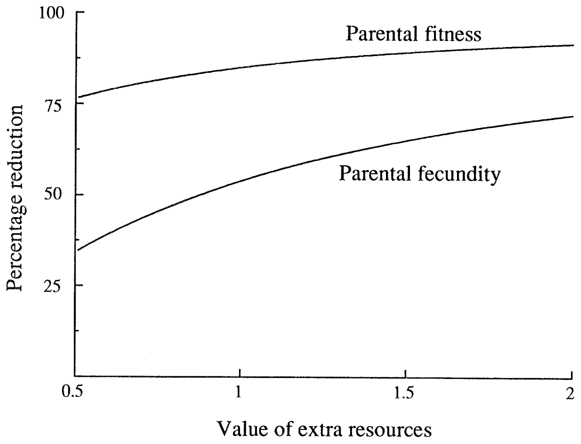

Figure 2. Parental fitness and fecundity (expressed as a percentage of the maximum) when the offspring determine the trade-off between the number and fitness of young. These results were obtained using a specific relation between offspring fitness and resources described in Parker & Macnair (1978). The rate at which offspring fitness increases with additional resources beyond the parental optimum is determined by a single parameter which is plotted on the x axis. Low values imply a rapid gain of fitness and hence greater benefits for conflict.

offspring fitness and parental investment (i.e. the shape of the curve in figure 1). The most important feature of this relation is the rate at which offspring fitness increases with extra resources beyond the parental optimum: more conflict is expected when the profits are greater. Figure 2 illustrates the decline that can occur in parental fecundity. Depending on the shape of the offspring fitness curve, quite considerable reductions can be predicted. Note that although parental fecundity can drop quite spectacularly, the reduction in parental fitness is less impressive. Although the parent has fewer offspring, at least they are fitter, and this acts in partial recompense.

How likely are offspring to be able to influence resource allocation by parents? It seems unlikely that a single ovum could prevail upon the mother to increase expenditure beyond her optimum, although it is perhaps unwise to underestimate potential 'biochemical conflict' between mother and young. However, the Smith & Fretwell model also works as a model, admittedly only very approximate, of mammals and birds with sequential offspring. If birds and mammals monitor their young to assess resource needs (see also below) there is great potential for guile and misinformation by the young. Thus this framework offers a rough guide to the potential life-history consequences of such manifestations of parent–offspring conflict as weaning conflict.

4. CLUTCH SIZE

We now turn to the evolution of clutch size. As the number of individuals in a clutch increases, the average fitness of individual offspring decreases. This decline in offspring fitness is normally caused by competition between members of the clutch for limiting resources (Lack 1947) but may be the result of many other factors. For example, the risk of predation may increase with clutch size if predators are attracted by the total size or noise output of a brood of animals (Skutch 1949). Clutch size will also be influenced by trade-offs between the size of the clutch and the future reproductive success of the parent (Charnov & Krebs 1974, Godfray 1987*b*). However, in this section we will assume that clutch size is determined solely by the first trade-off, between number and fitness of offspring. In these circumstances, a parent will be selected to produce the clutch size that maximizes the fitness returns for that clutch. In the simplest case, when all offspring have identical fitness, this reduces to the problem of maximizing the product of the number of offspring and average fitness. It has become customary to refer to this result as the 'Lack clutch size' as it is a general vision of the explanation given by Lack (1947) for avian clutch sizes.

Consider a bird that a produces a Lack clutch of eggs. Ideally, the parent would prefer each of its offspring to take its fair share of resources and certainly not to engage in any form of 'intrabrood' competition that may reduce their fitness. In the first part of this section we examine how competition between offspring in a brood may frustrate the parental desideratum. We suppose that the young can garner a greater than fair share of resources by increasing their intensity of competition, for example by begging more loudly than their siblings. We show that when there are fitness penalties attached to increased competition, the ESS level of competition among the young can lead to a marked decrease in parental fitness. In the second part of this section we show that competition between siblings can lead to selection on the parent to reduce its clutch size. Although we have used sibling birds as an illustrative example, we have so far ignored a major feature of bird biology, that nestlings typically form a hierarchy of sizes and competitive abilities. In the third part of this section we examine how this assumption affects our conclusions and ask whether the chick hierarchy has arisen as an adaptation to reduce harmful sibling conflict. In the final part of the section, we examine perhaps the most extreme form of sibling conflict, siblicide: the deliberate destruction of one sibling by another.

(*a*) *Sibling conflict and the fitness of the clutch*

The evolution of sibling conflict has most often been studied in the context of competition between sibling birds and the evolution of begging. We shall continue in this tradition though discuss other examples later. Our account here attempts to synthesize the theoretical studies of Stamps *et al.* (1978), Macnair & Parker (1979), Parker & Macnair (1979), Lazarus & Inglis (1986), Harper (1986) and Godfray & Parker (1991). Note, we are concerned here with what Parker & Macnair (1978) called intrabrood competition: competition between members of the same brood. This is in contrast to interbrood competition, competition for resources between broods, obviously mediated through the parents.

To study the evolution of begging it is necessary to state how increased begging translates into increased resources. In fact, all workers have adopted a mechanism that might be called *mean matching* where the share of resources obtained by an individual is influenced by the *relative* intensity of its begging in comparison with the average for the brood (note Harper (1986) is incorrect in saying that the absolute, rather than the relative, begging intensity is important in the models of Parker & Macnair). The mechanism of mean matching implicitly incorporates two biologically important features. First, it implies that increased begging is more efficient in large broods. The reason for this is that in small broods a change in behaviour by one individual has a marked effect on the mean and so lessens the contrast between that individual and the brood average. We have referred to this as the dilution effect. Second, the efficiency of increased begging declines as the background level of begging increases. Begging at an extra decibel is more impressive if the background begging is one decibel than if it is ten decibels. The analysis here is restricted to mean matching though other mechanisms are possible. A possible alternative mechanism suggested to us by M. R. Macnair is that the parent compares the begging intensity of an individual with the begging intensity of the rest of the brood.

As we have assumed that all chicks in a brood are identical, at the ESS all chicks will beg at the same rate. Suppose there are no costs to begging, the ESS can never be stable as small unilateral increases in begging will always be rewarded and never punished. In reality, begging will, at least at some level, incur costs. The manner in which the costs are distributed across the brood members is crucial in predicting the ESS level of begging. Godfray & Parker (1991) distinguish three exemplar forms of cost:

1. Individual costs: all costs of begging are experienced by the individual. This might occur when the costs of begging are exclusively metabolic.
2. Shared costs: the costs experienced by an individual are proportional to the average begging in the brood. Some predators may respond to the mean level of begging emanating from a brood.
3. Summed costs: the costs experienced by an individual are proportional to the sum of all individual's begging. Some predators may respond to the total level of begging emanating from a brood.

(The series of papers by Parker & Macnair used cost forms (1) and (2) while Harper (1986) used cost forms (1) and (3).) The fitness of the young is thus influenced by two components, their share of the limiting resource, and the costs of begging. Different workers have combined these two components in different ways to obtain overall fitness (for example multiplicatively or additively). However, the qualitative results of the model seem robust to this detail.

The ESS level of begging can be found by using the marginal form of Hamilton's rule. At the ESS, the personal benefits of a microscopic increase in resources are exactly balanced by the costs to relatives of reduced resource share and the costs to self and, in the case of most forms (2) and (3), to relatives of increased begging. Of course, costs and benefits to relatives are weighted by the coefficient of relatedness.

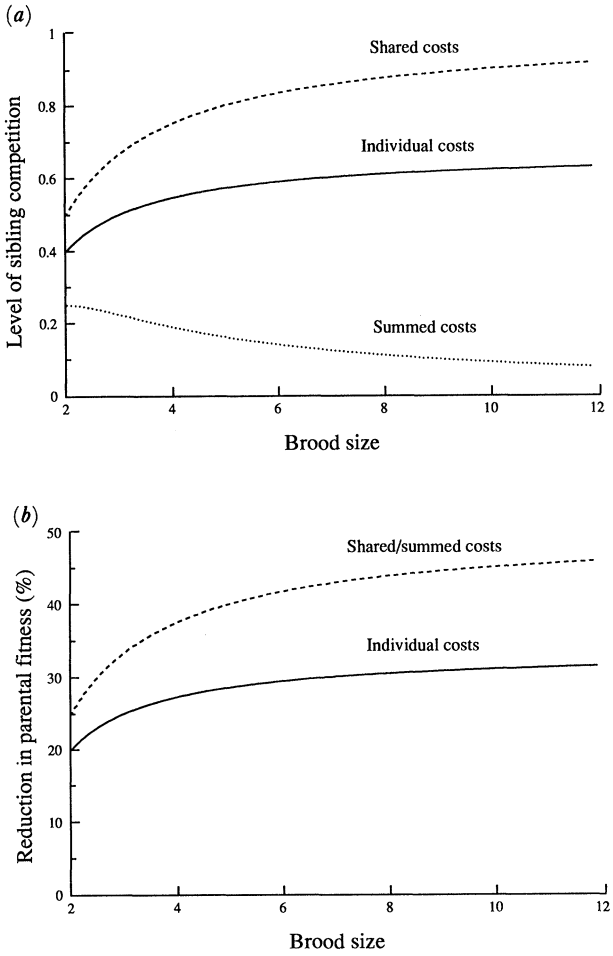

Figure 3. (*a*). The relation between the ESS levels of begging and brood size for three different forms of costs. (*b*) The reduction in parental fitness as a consequence of ESS levels of begging at different clutch sizes and with different forms of costs. (After Godfray & Parker 1991.)

Some typical predictions of ESS begging levels are shown in figure 3 (after Godfray & Parker 1991). The graphs show the level of sibling competition and the reduction in parental fitness as a function of brood size for the three forms of costs described above. Levels of begging are higher for shared costs than for individual costs (Macnair & Parker 1978) but higher for individual costs than summed costs (Harper 1986). Begging increases with brood size in the case of individual costs (Harper 1986) and shared costs (Godfray & Parker 1991) but the reverse occurs with summed costs (Harper 1986). The reduction in parental fitness mirrors these changes except in the case of summed cost which, perhaps counter-intuitively, are the same as those for shared costs (Godfray & Parker 1991). To draw figure 3, we assumed the coefficient of relatedness among siblings was $\frac{1}{2}$. The models predict begging intensity to be inversely related to the coefficient of relatedness (Macnair & Parker 1979).

Lazarus & Inglis (1986) also discuss the relation between parent–offspring conflict and clutch size. Unlike the other studies discussed in this section, they assumed that the total investment in a brood was subject to parent–offspring conflict while intrabrood conflict was either absent or represented by a static dependence of offspring fitness on clutch size. Further work is needed to examine models incorporating both intrabrood and interbrood conflict.

To understand these results, consider the case of individual costs. Because of the dilution effect (see above), the net benefits of relatively louder begging increase with brood size (rapidly at first, but then approaching a plateau) while the costs to the individual remain constant. The trade-off between these two factors gives rise to louder ESS level of begging in large clutches. The dilution effect also occurs in the case of summed and shared costs. However, in these cases the cost term is also influenced by clutch size. With shared costs, the negative consequences of increased begging are divided between all members of the brood and thus become less important as clutch size increases. The reverse happens with summed costs where the harmful effects of individual begging are magnified by clutch size. The change in costs with brood size interacts with the dilution effect to accentuate the increase in begging with brood size in the case of shared costs but to reverse the trend in the case of summed costs. Finally, the reduction in parental fitness is proportional to begging levels in the case of individual and shared costs. In the case of summed costs, the reduction is proportional to the product of begging intensity and clutch size. In the particular model analysed here, this results in the same reduction of parental fitness for summed and shared costs.

To summarize this section, competition between siblings can lead to marked reductions in the fitness of clutches of animals. The exact reduction will depend both on clutch size and on how the costs of competition are spread amongst the brood. Although we have exclusively talked about begging in birds, we could have easily analysed other forms of sibling competition. For example, Godfray & Parker (1991) discuss a model of feeding in gregarious caterpillars. Instead of begging, caterpillars are allowed to alter their rate of food intake. Faster feeding gives an individual a competitive edge but leads to costs, either to the individual (metabolic costs or costs associated with reduction in the efficiency of assimilation) or to the brood (increased consumption of plant material may reduce plant growth and thus the total amount of resource available to the brood).

There is thus a wide battleground in which parent–offspring conflict can occur. Who wins the conflict? Alexander (1974) argued that the parent always wins as it determines resource share. This argument has some force for birds and other species where resources are doled out by the parent, but it does not apply to the gregarious caterpillars discussed above where resource share is determined solely by competition between siblings. In the latter case, the offspring always wins. Dawkins (1976) argued that even in species with parental control of resource share, parent–offspring conflict can still occur as efficient resource distribution requires the parent to monitor offspring needs and this allows the offspring to misrepresent their requirements. In an elegant model, Harper (1986) showed that parents will be selected to adjust their resource share to begging level, as long as some of the variance in begging reflects true need. Parker & Macnair (1979) also argue that the strategy of 'ignore solicitation' may be unstable when there are costs to ignoring offspring begging. The same authors modelled the evolution of parental retaliation by assuming that the extent to which the parent responds to increased begging is controlled by natural selection. They predicted that the joint ESS will be intermediate between the parent and offspring optima.

To test the models discussed in this section, two types of study are needed. First, experimental studies of the relation between begging level and resource share, and of the distribution of costs among individual broods are required. There is already some information on this subject in the ornithological literature (see, for example, Ryden & Bengtsson 1980; Bengtsson & Ryden 1981) but there has yet been no systematic attempt to verify the assumptions of begging models. The second type of study needed is direct tests of the model predictions. The relation between begging levels and clutch size can be tested both intraspecifically and interspecifically. Harper (1986) has discussed interspecific patterns that support the predictions of begging models but a more formal comparative study is required. The predictions of the models might also be tested by relating begging levels to the type and severity of the costs associated with begging. For example, birds nesting in holes suffer lower predation rates than those with open nests (Ricklefs 1969) and tend to beg more noisily (Harper 1986). Finally, the dependence of begging levels on relatedness within broods may offer opportunities to test theory. Harper (1986) suggested that the reason why brood parasites such as cuckoos and cowbirds beg so loudly is that they are unconcerned with the costs experienced by their nest-mates. Studies of brood parasites are to some extent confounded by interspecific differences. However, one might predict that species of birds where intraspecific brood parasitism is common should have higher levels of begging. More speculatively, a particular nestling, hatched from an egg laid in a stranger's nest, might beg more loudly if it was able to recognize its condition.

(*b*) ***Effects on evolution of clutch size***

We began this section by noting that in broods of identical offspring, the Lack clutch size is defined as the clutch size that maximizes the product of clutch size and average offspring fitness. However, we argued in the last section that sibling conflict may reduce offspring fitness. Sibling conflict will thus act as a selection pressure tending to lead to a reduction in clutch size. This occurs because a reduction in clutch size results in greater resource share per head and increased solicitation is less rewarding for a well-fed chick (recall the fitness of a chick rises with increasing resources but at a decelerating rate).

Figure 4 illustrates the interaction between sibling conflict and clutch size. We plot parental fitness as a function of brood size in three circumstances. To obtain curve (a), we assume that the young do not complete at all and that the parent thus 'wins' the

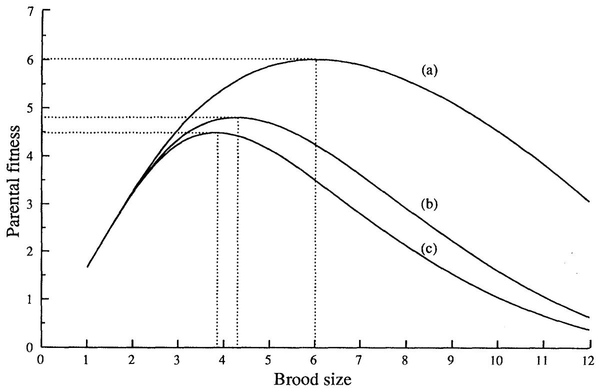

Figure 4. The relation between parental fitness and clutch size. (a) No sibling conflict, the optimum brood size is in this case 6. (b & c) The same relation but assuming that the young compete among themselves for resources and facultatively adjust their level of competition to clutch size; (b) summed or shared costs, (c) individual costs. (After Godfray & Parker 1991.)

conflict. To obtain the other two relations, we assume that the young compete among themselves at a rate appropriate to the size of the clutch in which they find themselves. Note, we are assuming a facultative response by offspring and parents to each other's strategies. Curves (b) and (c) differ as to how the costs of increased competition are spread among the brood members.

Several conclusions can be drawn from figure 4 (a full description and justification of the model is given by Godfray & Parker (1991). Sibling conflict reduces maximum parental fitness (the maxima of (b) and (c) are less than that of (a)) and leads to a reduction in the 'Lack clutch size'. The magnitude of the reduction depends on the nature of the distribution of costs: our results show that greater reductions occur with individual costs in comparison with summed or shared costs. Finally we note that the reduction in clutch, at least in this model, is quite large, of the order of 25–30 %.

In figure 3, we illustrated the relation between sibling conflict and brood size although assuming a fixed clutch size. The same relation can be calculated assuming that the observed clutch is the optimum *after* the parent has modulated its clutch size. It transpires (Godfray & Parker 1991) that the qualitative relation described in figure 3 is unaltered although the absolute level of sibling conflict is reduced.

We suggest that parent–offspring conflict reduces clutch size. Perhaps the best way to test this idea is to look for a relation between clutch size and within-clutch relatedness as the latter will influence the expected level of conflict. Higher levels of sibling conflict should result in selection pressures for greater reductions in clutch size. Thus one would predict that a within-species comparison of populations differing in the degree of intraspecific brood parasitism should reveal an inverse relation between the frequency of brood parasitism and clutch size.

Another test of the predictions is offered by some haplodiploid species that lay clutches of eggs that are either all male or all female. Parasitoid wasps in the genus *Achrysocharoides* (Chalcidoidea, Eulophidae) lay small clutches of eggs in the larvae of leaf-mining moths (Askew & Ruse 1974; Bryan 1983). For reasons that are not understood, four species in the genus lay either all-male or all-female broods (other species are either thelytokous (1), lay mixed broods (1) or are imperfectly studied (a number)). The average relatedness within all-male broods is $\frac{1}{2}$ while the average relatedness within all-female broods is $\frac{3}{4}$. After oviposition, the mother abandons her young and thus any sibling conflict will evolve to the offspring optimum. We thus predict greater conflict, and hence smaller clutch sizes in all male broods. The data for all four species support this prediction (table 1). Other parasitoid wasps also lay broods of one sex although by laying a single egg that divides asexually to produce a clutch of genetically identical individuals (polyembryonic reproduction). In these species, there should be no sibling conflict over resource share. It may be no coincidence that the largest clutches of any parasitoid wasp, by a factor of two, are found in polyembryonic species (Clausen 1940).

Table 1. *Brood size in the parasitoid genus* Achrysocharoides. *Data from Bryan* (*1981*)

	male broods		female broods	
	no.	size	no.	size
A. latreilli	112	1.0	111	2.0
A. zwoelferi	103	1.0	152	2.0
A. niveipes	432	1.0	344	2.2
A. cilla	406	1.2	445	1.9

(*c*) *Sibling conflict and offspring hierarchies*

Our discussion of sibling conflict, at least in birds, has been flawed by the assumption that all offspring have identical competitive abilities and experience the same costs of competition. In fact, birds normally begin to incubate their eggs before completing their clutches and this leads to a hierarchy in chick sizes. It is highly likely that different size chicks have different competitive abilities and suffer different costs to begging. We first ask how these asymmetries may affect sibling competition and then go on to enquire whether the hierarchy itself may have arisen as an adaptation to reduce sibling conflict.

The most straightforward situation to analyse is the case where the largest chick has complete freedom to take as much resource as it wants; the second chick then takes as much as it wants of the remainder and so on down the size hierarchy. Parker *et al.* (1989) analysed a model incorporating these assumptions. Unlike the competitive resource division discussed above, this method of 'pre-emptive' resource division results in an evolutionarily stable distribution of resources between offspring without the need to invoke costs to the mechanism of division. In the two-chick case, the division of resource is determined solely by the behaviour of the elder chick. Its decision is based on the trade-off between using resources to increase its own

Table 2. *Division of resources between great egret chicks. A is the largest and C is the smallest chick. Data from Parker* et al. (*1989*)

	resource share	
	mean	s.d.
chick A	43.2%	6.5%
chick B	37.0%	3.6%
chick C	19.8%	5.8%

fitness against using the same resources to increase the fitness of its sibling. As the elder chick weights the fitness of its sibling by the coefficient of relatedness, the equilibrium resource share is biased in its favour. The process of division is fundamentally the same in larger broods except that now the calculations are more complicated as the optimal decision for the eldest chick will depend on the decisions made by smaller chicks: a set of simultaneous equations have to be solved to obtain the ESS.

One prediction of the model, that resource share should be related to the position in the hierarchy, is supported by data. Table 2 shows data collected by D. W. Mock and his colleagues on food share among chicks of the great egret (*Casmeroidius albus*). Not only does resource share decrease for smaller chicks, but the greatest discrepancy is between the second and third chicks, a feature also predicted by the model.

In reality, older chicks probably have an advantage, but not a hegemony, over resource division. We have explored a number of two-chick models of competitive resource division incorporating either (i) asymmetries in competitive abilities (see also Parker *et al.* 1989) or (ii) asymmetries in the costs of solicitation. Because of lack of space, we only summarize the results here and will present the full models elsewhere. We assume that the resource share obtained by an individual is a function of the difference between a measure of its begging efficiency and the average begging in the nest (i.e. mean matching). To study asymmetries in competitive ability, we weight the begging intensity of each chick by a factor related to its position in the hierarchy. Increased begging is more rewarding for large chicks than for small chicks. To study asymmetries in the costs of solicitation, we assume that the costs of begging are multiplied by a factor related to the position of the chick in the hierarchy. Smaller chicks suffer more from an increase in solicitation than do larger chicks.

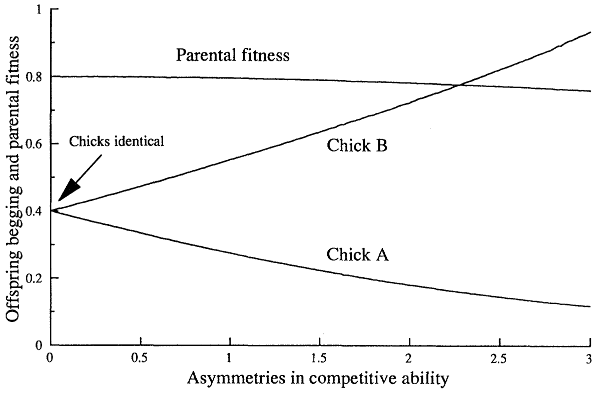

Figure 5. ESS levels of sibling begging with competitive asymmetry. Chick A has a competitive advantage over Chick B. In the absence of any asymmetry, the predicted level of begging (0.4) is identical to the two chick case of figure 3. As the asymmetry increases, the superior chick begs less and the inferior chick begs more. Parental fitness declines slowly from a figure about 0.8 times the value that could be achieved in the absence of sibling conflict.

Figure 5 illustrates some typical result from a model incorporating asymmetric competitive abilities[†]. As the asymmetries increase, the larger chick begs less. However, because of its competitive advantage, its fitness actually increases. In contrast, the rate of begging by the smaller chick increases as the asymmetries widen while its fitness declines. Even when begging by the small chick is very inefficient, quite high levels of begging are still selected. To obtain figure 6, we assumed that there was no difference in competitive ability between the chicks but that the smaller chick suffered greater fitness penalties than the larger chick: apart from this the models are identical. The greater costs experienced by the small chick select for lower begging levels. The reduction in competition from its sibling allows the larger chicks also to reduce its level of begging.

The presence of sibling hierarchies can thus have important effects on resource distribution and on competitive solicitation. The evolution of sibling hierarchies has become a major preoccupation of experimental ornithologists and no less than eight separate hypotheses have been advanced as explanations (Lessells & Avery 1989; Slagsvold & Lifjeld 1989). One suggestion, its origins discernible in Hamilton (1964) but developed by Hahn (1981) and Mock & Ploger (1987), is that the hierarchy is an adaptation by the parent to reduce sibling competition.

We can explore this explanation using the models discussed in this paper. Consider the reduction in parental fitness which is caused by competitive begging in broods of identical siblings. In the particular model we used to obtain figure 3, the parent of a two-chick brood suffered a 20% drop in fitness owing to sibling competition. Suppose that the imposition by the parent of a hierarchy in chick sizes results in complete dominance of larger over smaller chicks, the pre-emptive form of resource division discussed above. The abnegation of resource division by the parent has a cost that depends on the rate at which offspring fitness increases when the offspring obtains extra resources above the parental optimum. By using a model exactly equivalent to that in figure 3, one can calculate that the reduction in parental fitness caused by pre-emptive resource division by the young is somewhere between 0% and 14% with values in the range 4–12% being perhaps the most realistic biologically. These figures,

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[†] This model is a modification of the symmetric model in Godfray & Parker (1991) which was used to obtain figure 3. We have assumed individual costs and that the benefits of increased resources and the costs of solicitation combine multiplicatively. An additive model with individual costs (Parker *et al.* 1979) gives qualitatively very similar results as do multiplicative models with summed and shared costs (H. C. J. Godfray & G. A. Parker, unpublished results).

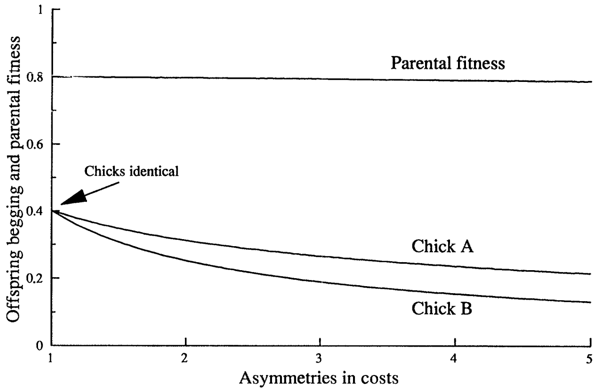

Figure 6. ESS levels of begging with asymmetric costs. As in figure 5 but increasing the asymmetry decreases begging by both chicks. Parental fitness again declines slightly with increasing asymmetry.

which should be compared with the 20% reduction caused by competitive solicitation, suggest an advantage to the parent of a hierarchy of chick sizes.

However, this conclusion is strongly contingent on the absence of any competitive solicitation. Consider the asymmetric solicitation models illustrated in figures 5 and 6. These models are again directly comparable with the symmetric model of figure 3. In both cases, parental fitness *declines* as the asymmetries between the young increase. We have explored several related models and have found a decline in parental fitness to the normal outcome though in some cases there may be a very small rise in parental fitness with increasing offspring asymmetry (Parker *et al.* 1989).

In conclusion, asymmetries among offspring affect the outcome of sibling competition. The parent may be selected to produce a hierarchy of chick sizes if this leads to pre-emptive resource division. However, we found little evidence that the introduction of asymmetries into models of resource division by competitive solicitation decreased the scope for parent–offspring conflict. To evaluate the importance of sibling competition in the evolution of chick hierarchies, further work is needed to discover exactly how resources are divided in nests of different sized chicks. In addition, the comparison of offspring and parent optima needs to be extended to inquire how the presence of a hierarchy affects the resolution of the conflict.

(*d*) *Siblicide*

We conclude this section by a discussion of the most direct way an offspring can affect clutch size: by killing one of its siblings. It has been known for some time that siblicide occurs in a number of bird groups and this phenomenon was referred to as 'Cain & Abel Conflict' by Gordon (1927). Siblicide is perhaps most frequent in large raptors although it also occurs in pelicans, gannets, cranes, skuas, penguins and herons (Lack 1968; O'Connor 1978; Drummond *et al.* 1986; Mock 1987; Anderson 1990). 83% and 76% of clutches of the lesser spotted eagle (*Aquila pomarina*) and the black eagle (*A. verreauxii*) contain two eggs yet in no case has a lesser spotted eagle been observed to rear two young (Mayburg 1973) and there is only a single possible case of twin fledging in the black eagle (Gargett 1970). In both cases siblicide is responsible for the reduction in clutch size. In a more typical eagle, the golden eagle (*A. chrysaetos*), sibling aggression always occurs although brood reduction only occurs in 80% of cases (Brown 1976). Siblicide also occurs in a number of invertebrate groups (Polis 1981) where it is frequently, although by no means always, associated with cannibalism.

Lack (1966) suggested that siblicide was an adaptation to allow the parent to respond to varying environmental conditions. In years of good food supply all chicks are reared whereas in poor years both the parent and the young benefit from a reduction in brood size through siblicide. In species with obligate, or near obligate siblicide, a parent may lay a second egg as an insurance against the infertility of the first egg (Dorward 1962; Anderson 1990).

O'Connor (1978) first pointed out that parents and young may differ over the conditions for brood reduction and that the extent of disagreement would depend on clutch size. There is, however, a potential problem in O'Connor's analysis as he used simple inclusive fitness arguments. Inclusive fitness arguments normally require weak selection with the trait having an additive effect on fitness, assumptions that may be violated by siblicide. These considerations suggest that siblicide may have to be analysed using explicitly genetic models. However, the assumption of additivity will remain valid in analyses of siblicide in large broods of animals where elder offspring kill a small number of their younger sibling. This behaviour, which occurs in a number of invertebrate groups such as chrysomelid and coccinelid beetles (Alexander 1974; Banks 1956), was modelled by Parker & Mock (1987) who indeed found disagreement between parent and young over clutch size. They estimated the magnitude of the disagreement by assuming biologically plausible relations between clutch size and fitness and concluded that, in general, the disagreement was likely to be small. In invertebrates with this type of siblicidal behaviour, the parent abandons its eggs after oviposition: it thus seems likely that in the absence of intervention by the parent, the offspring will 'win' the parent–offspring conflict.

Despite the potential problems with O'Connor's analysis, explicit genetic models of sibicide in birds with small clutches confirms his results, although with one important proviso. The victim of siblicide must be a runt, unable to damage its siblings, even if it carries a siblicide gene (Godfray & Harper 1990)†. This is not

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† A single locus analysis of siblicide produces an interesting theoretical curiosity. Over a wide range of parameter space both siblicidal behaviour and pure non-siblicidal behaviour are ESSs. However, only siblicidal behaviour is a continuous stable strategy (CSS, Eshel & Motro 1981; Eshel 1983). By definition, a resident strategy is an ESS if it can resist invasion by all mutant strategies (Maynard Smith 1892). However, suppose the resident strategy varies slightly, perhaps by chance: if this small deviation allows the spread of a mutant then the ESS is not a CSS. In the real world, we should only expect to observe those ESSs that are also CSSs. O'Connor identified a single ESS in his inclusive fitness analysis and this corresponds exactly to the CSS of the genetic analysis.

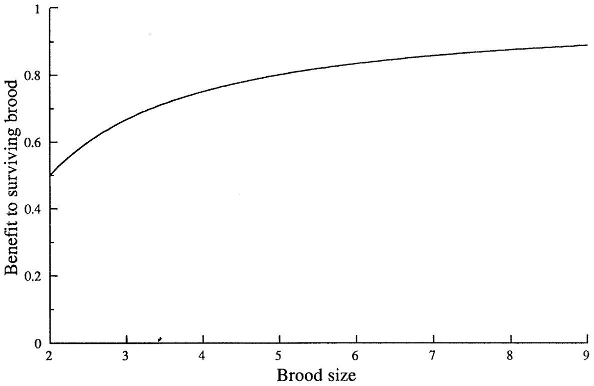

Figure 7. O'Connor's condition for brood reduction. Brood reduction is favoured by the young if the benefit to the surviving brood members is above the line. Benefit is measured in 'offspring equivalents'. Thus siblicide is favoured in a clutch of two if the fitness of the surviving chick increases by a factor of 0.5. The parent will favour siblicide if the benefit to the surviving brood members is greater than one.

an unreasonable assumption in most bird species where there is a hierarchy in chick sizes and an obvious runt. As O'Connor noted, the extent of parent–offspring conflict over the conditions for siblicide is greatest for small clutch sizes (figure 7).

In those cases of siblicide where there is not an identifiable and helpless victim, genetic models suggest that the presence of siblicidal behaviour will often depend on the past history of the population (Godfray 1987*a*; Godfray & Harper 1990). Models of this type probably apply to parasitoid wasps. The young of many parasitoid species have large mandibles which they use to kill all other larvae in the same host. Godfray (1987*a*) argued that the possession of fighting mandibles has some of the properties of an absorbing state, once evolved they are difficult to loose as any mutant, non-siblicidal allele is at a great disadvantage. This might explain why there is a dichotomy rather than a continuum in parasitoid clutch sizes: species tend either to lay single eggs (giving rise to fighting larvae) or clutches of eggs (non-fighting larvae) (Le Masurier 1987). It also suggests that there may be extensive parent–offspring conflict over clutch size. One wasp species, with fighting larvae, may be able to rear one individual from a particular host type, whereas a second a wasp species, of identical size but without fighting larvae, may be able to rear up to about 15 offspring from the same host.

5. PATTERNS IN LIFETIME REPRODUCTIVE SUCCESS

We now more from considerations of parental investment and clutch size to the wider question of the allocation of resources between reproductive and trophic functions over the lifetime of an organism. The trade-off between present and future reproductive success is one of the most fundamental problems of life-history theory and has been the subject of extensive analysis (Williams 1966; Stearns 1976; Sibly & Calow 1983). In this section we elaborate on a short note by Charnov (1982) who pointed out that parents and offspring will disagree about this division of resources, and that this may affect lifetime fertility and mortality schedules. Again our strategy is to locate offspring and parental optima to discover the scope for parent–offspring conflict. We present here a summary of some recent modelling that will be presented and justified in full elsewhere.

Consider an animal that produces one offspring a year throughout its life. The offspring benefits from increased investment by the parent, although with diminishing returns. However, increased investment by the parent in this season's offspring increases the probability of dying over the winter before the next breeding season. To simplify matters, we shall assume a strictly regulated population (by density-dependent recruitment to the breeding population) and that the only consequences of increased investment for the parent is decreased survival the following winter. Under these assumptions, the optimum parental investment can be found by maximizing the sum of present reproductive success and future reproductive success at each breeding season. (Technically, this is done by a process of backward iteration from a time sufficiently far in the future that the assumption can be made that future reproductive success is zero. By the time the process of iteration reaches an age to which the animal might be expected to have survived, the transient effects of any assumptions about the time horizon have disappeared.) The optimal allocation of resources for the offspring differs from that of its parent in that it devalues the future reproductive success of the parent by its coefficient of relatedness to future siblings.

In the simplest case, parental survival at any particular level of investment is constant and it is possible analytically to obtain the parent and offspring optima which are age independent. The amount of parent–offspring conflict depends, as before, on how much an offspring benefits from extra resources beyond the parental optimum. Figure 8 illustrates the drop in parental longevity and expected lifetime reproductive success that may occur if the offspring obtain complete control over resource allocation. The reduction in parental longevity and fitness is greatest when the offspring have most to gain from exceeding the optimum investment for the parent.

In reality, the probability of parental survival will vary with age as will the deleterious effects of increased investment. We have modelled such a situation by assuming an underlying sigmoid survival curve (we assumed a Weibull mortability distribution). In the statistical literature on survival analysis, the effects of extraneous variables on survival are frequently studied using an 'accelerated life model' (see for example, Cox & Oates 1984). High values of the variable increase mortality to a level that would otherwise have been experienced later in life, hence the term accelerated life. We have assumed that increased investment affects survival in this manner. Thus, if a five-year-old animal increases investment by one unit, it experiences a risk of mortality appropriate to (say) a six-year-old animal and, similarly, an eleven-year old animal would experience the risk of a twelve-year-old animal.

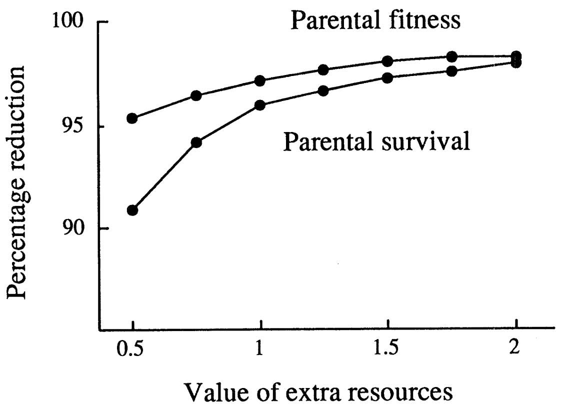

Figure 8. Parental fitness and fecundity (expressed as a percentage of the maximum) when the offspring determine the trade-off between present and future reproductive success. In the absence of changes in parental investment, mortality is constant throughout life. As in figure 2, these results were obtained using a specific relation between offspring fitness and resources described in Parker & Macnair (1978). The rate at which offspring fitness increases with additional resources beyond the parental optimum is determined by a single parameter which is plotted on the *x* axis. Low values imply a rapid gain of fitness and hence greater benefits for conflict.

A typical result of this analysis is shown in figure 9. Annual reproductive investment is initially high but then drops as the animal ages. Only when the animal is very old does it begin to rise again. The extent of parent–offspring conflict appears to be inversely related to the quantity of parental investment. The amount of conflict rises as an animal ages but eventually falls in extreme old age. Note, it is very unlikely that either the rise in parental investment in old age, or the decrease in parent–offspring conflict would ever be observed: very few animals live long enough to manifest this trait.

To understand these results, recall that the effect of increased investment is to 'accelerate life', that is to increase the risk of mortality to that experienced by an older animal. As the risk of mortality when young is low, and remains low for several years, the consequences of increased investment are relatively mild. As the animal grows older and approaches the age when the risks of mortality accelerate, the consequences of increased investment become dire and this leads to a decrease in investment per offspring. When the animal is very old, the chances of surviving until the next breeding season are so small that the optimal investment in the current breeding season again begins to rise. This latter rise is a graded form of terminal investment.

Parent–offspring conflict increases with parental age for two reasons. First, as investment drops, the advantages of inveigling greater investment from the parent increases (recall the relation between offspring fitness and investment is monotonically increasing but with decelerating slope). In addition, the offspring is less concerned than its parents about the reduction in numbers of future siblings and is thus willing to sanction a level of investment that entails a greater risk of mortality for the parent.

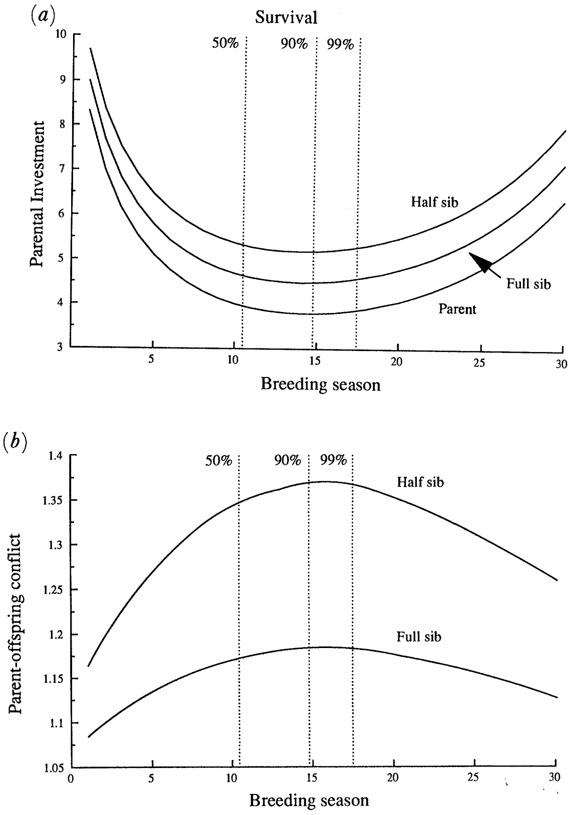

Figure 9. (*a*) Parental investment as a function of age when the background mortality is described by a Weibull distribution and extra parental investment acts to 'accelerate life'. The three curves describe investment when the decision is determined by the parent, a sibling or a half sibling. The times by which 50 %, 90 % and 99 % of an initial cohort will have died are shown by dotted lines. (*b*) The magnitude of parent–offspring conflict (offspring optimum minus parent optimum) as a function of parental age.

6. CONCLUSIONS

Our aim in this paper has been to highlight the potential importance of parent–offspring conflict by comparing offspring and parent optima in a number of the classic problems from life-history theory. We have shown that such effects exist, and may indeed be substantial.

Our efforts will be of no more than technical interest if Alexander (1974) is right in his belief that the parent always succeeds in imposing its will on the offspring. However, this must be untrue in some cases, for example when a parent abandons a clutch of eggs after oviposition and is thus in no position to influence interactions between her young. Even when the parent remains with the clutch, it seems likely that parental attention to variation in the needs of the young will allow the young to demand and obtain more resources than is optimal for the parent. An obvious future step in the analysis of such problems is to follow Harper (1986) in developing sibling conflict models where offspring differ in their resource requirements. Recent developments in the study of animal signalling are also relevant here (Grafen 1990).

We also suggest that selection acting on the parent to avoid parent–offspring conflict may be an important factor in shaping reproductive strategies. We have quantitatively investigated the advantages to the parent of producing hierarchies of chick sizes and have found partial support for the suggestion that it may have evolved to reduce sibling conflict. We also suggest that sibling conflict may act as a selection pressure affecting clutch size. Without wanting to overestimate the importance of parent–offspring conflict, we do suggest that the avoidance of conflict should be considered when attempting to explain any facet of reproductive strategies, from clutch size to honey combs.

Finally, we stress that we are under no illusions that we have been dealing with real birds or insects. The models we have examined are general and tools for thought rather than suitable for immediate application to particular systems. Nevertheless, we do claim that our models generate qualitative predictions that are worth testing against nature. There are real problems (both ethical and practical) in parameterizing parent–offspring conflict models and performing manipulative tests: we believe that ingenuity in overcoming such problems could be richly rewarded. In addition, we believe that the massive literature on the reproductive biology of many animals, in particular birds, offers great prospects for comparative tests of predictions about parent–offspring conflict.

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Discussion

D. Haig (*Department of Plant Sciences, Oxford University, U.K.*). In your paper, you give the relatedness among half sibs as a quarter. This is actually the average of a relatedness of a half for maternal genes in the offspring, and a relatedness of zero for the paternal genes. Whenever there are interactions among half sibs, there is potential for conflict between maternal and paternal genes within offspring, and a possibility that natural selection will result in alleles that display differential gene expression depending on the parent of origin (i.e. 'genomic imprinting'). For example, in eutherian mammals, the paternal genome appears to be particularly active in the development of extraembryonic membranes. If so, the averaging of maternal and paternal relatedness in models of parent–offspring conflict may give misleading quantitative predictions.

H. C. J. Godfray. Our assumption that the relevant measure of relatedness between half sibs is a quarter would be wrong if both (i) maternal and paternal genes were capable of independently influencing the behaviour of offspring and (ii) the outcome of conflict between the two types of genes was the complete, or predominant, control by either the maternal or paternal set. We think that independent action by maternal and paternal genes is most likely to be important at the embryonic stage where gene products still have very direct effects on growth and development. In addition, we think that the most likely outcome of conflict between the two sets of genes is a compromise where the assumption of a coefficient of relatedness of a quarter would still apply, at least approximately. However, this is an extremely interesting point and deserves further exploration.