Intrafamilial conflict and parental investment: a synthesis

Geoff A. Parker^{1*}, Nick J. Royle^{2†} and Ian R. Hartley²

¹*Population & Evolutionary Biology Research Group, Nicholson Building, School of Biological Sciences, University of Liverpool, Liverpool L69 3GS, UK*

²*School of Biological Sciences, Institute of Environmental and Natural Sciences, University of Lancaster, Lancaster LA1 4YQ, UK*

We outline and develop current theory on how inherent genetic conflicts of interest between the various family members can affect the flow of parental investment from parents to offspring, and discuss the problems for empirical testing that this generates. The parental investment pattern realized in nature reflects the simultaneous resolution of all the conflicts between the family players. This depends on the genetic mechanism, the mating system and reproductive constraints, on whether extra demand by progeny affects current or future sibs, and particularly on the behavioural mechanisms underlying demand (begging or solicitation) and supply (provision of parental investment by parents). The direction of deviation from the optimal parental investment for the parent(s) depends on the slope of what we term the 'effect of supply on demand', the mechanism that determines how changes in food supply affect begging levels. If increasing food increases begging (positive slope), less parental investment is supplied than the parental optimum and if increasing food decreases begging (negative slope), more parental investment is supplied. The magnitude of deviation depends on both the 'effect of supply on demand' and on the 'effect of demand on supply' (the mechanism determining how changes in begging affect food supply, which always has a positive slope). We conclude that it will often be impossible to deduce the extent of underlying conflict by establishing the amount of parental investment given relative to the ideal optimum for the parent. Some possible directions for future research are discussed.

Keywords: evolutionarily stable strategy; begging behaviour; parent–offspring conflict; parental investment; sib competition

1. INTRODUCTION

Our aim is to summarize and further develop the theory of how the various conflicts between family members interact to affect the flow of parental investment (Trivers 1972) from parent(s) to offspring, and to stress that the parental investment realized in nature depends on the simultaneous resolution of the interests of all interactors in the family game. Much of the theoretical base is given in greater detail in the source articles and in Mock & Parker (1997), but we extend analysis of how parental investment deviates from parental optima at the ESS. Because the topic is complex, we hope that the present synthesis, by relegating most of the formal mathematics to appendices, will generate discussion, development and empirical testing of the major issues.

The past quarter of a century saw radical changes in the concept of families and parental care. The 'classical' view saw the family as harmoniously bound to maximize the number of surviving young (Lack 1947, 1954). This era ended when Trivers (1974), foreshadowed by Hamilton

(1964), stressed the conflict between parents and offspring over parental investment. The current view is one of conflict of interests between all family members (figure 1; Mock & Parker 1997).

There is potential conflict between the male and female parents over how much parental investment each should give; either may profit if the other provides more care. Offspring compete for resources associated with parental investment, unless there is parental control of allocation. Sib competition thus forms a second component of intrafamilial strife. Finally, conflict over parental investment allocation spans across generations, usually between parents and offspring but also between sibs in current and future broods. Actual parental investment reflects the simultaneous ESS (Maynard Smith 1982) resolution of all three games (Parker 1985). A lack of overt conflict does not necessarily imply that evolutionary conflict is absent. One player may have 'won' evolutionarily, because others can do nothing strategically to further their own interests.

Behavioural conflict implies underlying evolutionary conflict. This may be between loci expressed in different phenotypes (e.g. between parents and offspring), generating strategies conditional on phenotype, or intralocus (e.g. where genes at a locus determine the extent of parental investment in both parents), resulting in a weighted-average strategy.

* Author for correspondence (gap@liverpool.ac.uk).

† Present address: Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK.

One contribution of 15 to a special Theme Issue on parental care.

Figure 1. Intrafamilial conflict over parental investment. Siblings compete over the investment from parents (sib competition). Offspring have different interests from their parent(s) over investment (parent-offspring conflict). Where both parents invest, they are in conflict over the amount each should give (sexual conflict).

2. CONFLICTS OF INTEREST

Godfray (1995) has called the 'battleground' the parental investment zone between the ideal parental investment levels for each player if other aspects of the game (figure 1) are absent.

We assume that an offspring's 'fitness', f , (viability $\times$ expected future reproductive success) increases with the amount, m , of parental investment it receives. Furthermore, we assume that low levels of parental investment result in a zero fitness for offspring because they need a threshold amount to survive, and that fitness reaches an asymptote at high levels of parental investment because offspring could not make full use of excess resources (the function $f(m)$; figure 2a). Parker & Macnair (1978) assumed that each parent has a fixed total lifetime parental investment, M , to allocate to its progeny, so that the expected number of progeny is M/m . This is therefore a strict application of the definition of Trivers (1972) of parental investment as the cost of investment on present offspring measured in units of future offspring lost because of that investment. Thus, M is the lifetime expectation of offspring units that can be expended and m is a current expenditure. With some caution, m can be seen more specifically, either as a time spent on an offspring (or brood) in a lifetime of continuous breeding of average length equivalent to M , or as an expenditure, such that death occurs when lifetime energy resources, M , expire. Several alternative models exist (for example, Charnov (1982); Godfray (1991); Lessells (2002)) that generate somewhat varied but often qualitatively similar predictions. Parental investment and the assumptions surrounding it are notoriously hard to measure or test empirically.

We now examine the 'battleground' by defining the offspring's ESS in the absence of retaliation by the parent,

and then the parent's ESS in the absence of retaliation by the offspring.

(a) *Sib conflict and offspring optima*

Biologically, there are two extremes for how extra parental investment demand by an offspring may affect its siblings. If the parent fixes the parental investment supply to a nest, any extra demand by given chicks may affect only other brood mates ('intra-brood' conflict; Macnair & Parker (1978)). Or, if the parent responds to extra demand by increasing food input to the more demanding chicks at no loss to the others, brood mates will be unaffected but prospects for future broods reduced ('inter-brood' conflict (Parker & Macnair 1979)). Most systems may involve combinations of both components, e.g. they show sib competition for food input and also increased parental foraging under increased offspring demand. For simplicity, we consider intra- and interbrood conflict separately.

(i) *Intra-brood sib competition*

Here, the parent is assumed to fix the total amount of parental investment per brood; consequently, any extra demand affects only contemporary sibs. The fixed amount of parental investment given can change over evolutionary time, but not within a parent's lifetime.

What share of food input should a sib take under intra-brood conflict? In a brood of two equal full sibs, A and B, from Hamilton's (1964) rule, A should continue to take resources until its marginal gains drop to half those of B, who gets the remainder (Parker *et al.* 1989). For half sibs, marginal gains drop to a quarter. B's interests, however, are best served by an exact reversal, so A and B's interests cannot be satisfied simultaneously and, with larger broods, the same principle applies. For full sibs in a brood of equal offspring, a given offspring J would do best by taking resources until its marginal gains drop to half the marginal gains of each of its sibs, which (ideally for J's interests) would take equal shares of the remainder. The same applies for the other sibs K, L, ..., and cannot be achieved simultaneously, defining the conflict.

Often, physical power appears to determine each sib's share of the input. Suppose that the strongest sib can take the first share of the food input, then the next strongest takes the next share, and so on, until the food has been used. The ESS share for the strongest sib, A, depends on what B, C, D, ... etc. will each take in their turn. For the two weakest, say M and N, M should apply the 'half marginal gains' rule to determine what to leave for weakest sib N. This model can generate the pronounced 'runt' effect common in mammals (Mock & Parker 1997): shares for each sib become more disparate down the hierarchy, with the biggest fitness gap between the two weakest sibs (Parker *et al.* 1989), though the extent of runting depends on the form of $f(m)$ (figure 2) (Forbes 1993). Mock & Parker (1997) simulated effects of low food availability in the habitat by reducing the rate at which the fitness function (figure 2) approaches its asymptote, so that the effect on offspring fitness of increasing parental investment was reduced. Note that this is not a dynamic approach to changes in conditions (McNamara *et al.* 1999), but the ESS for a set of habitat states. Comparing habitats with differing food availability as food

Figure 2. (a) Relation between the amount of parental investment received by an offspring (m units), and its 'fitness' (equal to viability $\times$ future reproductive success). (b) Offspring optima for parental investment. Coefficient α determines the range over which the tangent operates in equation (2.1). Note that increasing α decreases m^* , and decreasing α increases m^* . Thus $\alpha = 0.5$ gives a lower ESS m^* than coefficient $\alpha = 0.25$. For $\alpha = 0$ (not shown) the ESS is to take all available parental investment. (c) Parental optima for parental investment. For a single parent (or two parents with true monogamy) $\alpha = 1.0$; for symmetrical biparental care $\alpha = 2.0$, so m^* is lower but this ESS is not continuously stable (McNamara *et al.* 2002).

availability decreases, or when the cost of providing extra parental investment increases, runting is exacerbated until the weakest sib dies. As food availability decreases further, the ESS food shares change somewhat and the progeny

fitnesses decrease until a level of food availability is reached when the next weakest sib dies, and so on, until eventually we reach a habitat where only the strongest sib survives. The direct fitnesses of individual offspring show

big changes viewed across the habitat range, but the inclusive fitnesses of each sib (related to, but not equal to direct fitnesses) show virtually continuous declines. The same is true for the parental fitness. Ideally, the parent does best by allocating equal shares of parental investment to each offspring (assuming they are initially all equally valuable to the parent). However, this ideal parental fitness arising from equal shares does not differ much from the parental fitness realized under the hierarchy model when, as a result of sib competition, offspring become highly unequal. This perhaps explains why parent birds are often so insensitive to the dramas occurring in their nests (see Mock & Parker (1997)). This model generates rather different conclusions from those of O'Connor (1978), who concluded that the threshold for sibicide would usually be significantly lower than that for infanticide.

Offspring may compete against brood mates by increasing their food-gaining effort, e.g. by jostling and jockeying for the best position to gain food, by amplifying begging levels, by increasing rates of suckling, etc. (see Mock & Parker (1997)). These are all forms of scramble competition (*sensu* Nicholson 1954). A model in which each offspring's share of the resource input is determined by its relative scramble effort was also examined by Parker *et al.* (1989). If unequal offspring compete by begging scrambles, stronger sibs usually take most resources, but atypically, they may take less; they always pay lower begging costs and attain higher net fitness.

(ii) *Interbrood competition*

The other extreme of sib competition ('Triversian' or interbrood conflict) occurs when increased demand by a given offspring causes the parent to increase its parental investment to that offspring, but without affecting the current sibs of the demanding offspring. Thus, the parent is forced to invest super-optimally, reducing its prospects of future broods. This is a form of power hierarchy: current offspring can displace future offspring, which represent 'weaker sibs'.

The ideal parental investment for offspring under interbrood sib competition (see Appendix A) is given by the simple marginal value relation (Parker & Macnair 1978; Mock & Parker 1997)

$$f'(m^*) = \alpha \frac{f(m^*)}{m^*}. \quad (2.1)$$

This is a marginal value equation and can be interpreted graphically (see figure 2). The left hand side, $f'(m)$, is the gradient of the fitness curve; at any point it represents the marginal increase in fitness due to a tiny increase in parental investment. The right hand side is also a slope, relating to benefit/cost; it is the slope of fitness achieved with an amount of parental investment expended, or f/m , scaled by a constant, α . The ESS parental investment from a given player's perspective is where this slope touches or forms a tangent to the fitness curve (i.e. equals gradient f'). Coefficient α determines exactly where the slope, $\alpha f/m$, forms a tangent to the fitness curve, and hence defines the ESS value for m^* (the ideal level of parental investment). The lower the value of α , the lower the slope of the tangent line, $\alpha f/m$, so the tangent must touch the curve at a higher value of m to give the ESS. If $\alpha = 0$,

the ESS level of parental investment should be maximal because the tangent touches at the asymptote of the fitness curve.

Coefficient α depends on the mating system and on gene expression. If only one sex invests and expression of a gene for increased demand is the same whichever parent transmits the gene (i.e. no genomic imprinting), α lies between 0.5 and 0.25, seductively resembling Hamiltonian coefficients for full sibs and half sibs, respectively. They cannot be interpreted simplistically in this way (Parker 1985; Lessells & Parker 1999); 0.5 applies only if the costs falling on the investing parent harm the other parent equally. The ways that these costs apply depend on the mating system. Suppose that only the female invests and the male mates with a different female at each breeding attempt. With interbrood sib competition, the male feels no cost from increased female investment since the mother pays the cost in terms of future prospects (which will not affect the mate from the present breeding attempt): then $\alpha = 0.25$. Alternatively, if the male's reproductive success is completely coupled with that of his mate, then $\alpha = 0.5$. An example is 'true monogamy' (Parker 1985), where a male cannot pair again if his partner dies. An α coefficient of 0.25 will apply to most species.

The α coefficients are Hamiltonian only in the sense of future sibs. Inherited from mothers, a demand gene displaces future copies of itself with probability 0.5. Inherited from fathers, it never displaces itself and does best by taking all of its mother's available parental investment (Macnair & Parker 1978). If gene expression is independent of parental sex, $\alpha = 0.25$ (average of 0.5 and 0.0). The phenomenon of genomic imprinting allows gene expression to be dependent on the parent's sex. Haig (1992) realized that $\alpha = 0.5$ then defines the constrained mother's interests, and $\alpha = 0$ those of the unconstrained father; this has some remarkable implications (Haig & Graham 1991; Haig & Westoby 1991). For example, in eutherian mammals the paternal genome appears to be particularly active in the development of the extra-embryonic membranes, possibly at the expense of the mother.

To stress the point that conflict does not depend on average relatedness between sibs, consider a hypothetical species with lifetime pairing, no EPCs and where only females give parental investment. A gene for increased offspring demand transmitted by the mother harms her throughout her life, but when transmitted by the father it never harms him if he can pair again immediately after his mate's death. If the gene is expressed identically, whether it came from the male or the female parent, α is then 0.25 not 0.5, despite the average relatedness between contemporary sibs (which is 0.5) or successive sibs (which is close to 0.5). The point is not whether current young are half sibs or full sibs, but whether the mother's parental investment costs affect the reproductive success of the father (Lessells & Parker 1999). With 'true monogamy' this cost is equal to both sexes, since the male's reproduction ceases with the female's death; α is then 0.5.

Figure 2*b* shows these offspring optima under interbrood conflict and demonstrates how coefficient $\alpha = 0.5$ means that the offspring's ESS parental investment level is less than for $\alpha = 0.25$.

So far we have dealt only with parental investment units. Conversion of parental investment into offspring fitness is usually indirect (Evans 1990): the parent pays a parental investment cost for providing food to offspring, which increases offspring fitness. Suppose that offspring fitness f is a function of the amount, y , of some resource (say food) gained from the parent. Provisioning an amount of food, y , costs the parent $m(y)$ units of parental investment. Thus the function $f(y)$ tells us how an offspring's fitness increases with the amount, y , of food it eats, and $m(y)$ tells us how a parent's parental investment costs increase with amount, y , of food it provides. These now replace the single function $f(m)$. An ESS equation analogous to equation (2.1) can be derived (see Appendix A), which we can call the 'food ESS' to distinguish it from the 'parental investment ESS' in equation (2.1). It also contains α , which takes the same values as before, depending on the assumptions. Mock & Parker (1997) used a simple power function to describe the relation between the parental investment cost m of providing y food units: $m(y) = by^h$, where b and h are constants. Biologically, it is most probable that the costs of providing food escalate as the amount of food increases. This can be modelled by increasing power h above 1.0, which causes increasing concavity of the $m(y)$ curve (see figure 3a). This gives the food ESS:

$$f'(y^*) = \alpha h \frac{f(y^*)}{y^*} \quad (2.2)$$

(Appendix A), which is exactly equivalent to the parental investment ESS in equation (2.1) if the costs of food rise linearly ($h = 1.0$; see figure 3a). But as the $m(y)$ curve becomes increasingly bowed (as h increases above 1, see figure 3a), the effect is to scale up the value of coefficient α , making the tangent line steeper and reducing the amount of food supplied (figure 3b).

Note that the parental investment and food ESSs are really two alternative ways of saying the same thing. The food ESS looks most useful to empiricists because it appears that parental investment need not be measured directly. Unfortunately this is not so, because h can only be estimated by knowing $m(y)$, i.e. how parental investment increases with food provisioning.

(b) The parental optima and sexual conflict

The same ESS framework applies to the parent(s); we can define the ideal parental investment in terms of α in equation (2.1), i.e. in terms of the mating system.

(i) Uniparental care

The ESS amount of parental investment (m^*) for a single parent to allocate to each of a set of equal offspring in the absence of parent-offspring conflict (the 'uniparental optimum') is given again by equation (2.1), with $\alpha = 1.0$, and the food ESS is equation (2.2) with $\alpha = 1.0$ (Appendix B). This can be shown graphically (figure 2c) by drawing the tangent to the curve of $f(m)$ from the origin (Smith & Fretwell 1974). If offspring are unequal in value to the parent, the single parent's best strategy is to equalize the marginal gains across all offspring (Temme 1986), rather as in the marginal value theorem of optimal foraging where habitat patches differ (Charnov 1976).

(ii) Biparental care with parental investment cost to one parent felt equally by the other

The same optimum ($\alpha = 1.0$) applies for biparental care if the costs of parental investment to one parent are felt equally by the other (e.g. true monogamy), but each parent then provides $m^*/2$ units and twice as many offspring can be produced ($2M/m$). Such strong constraints as true monogamy are likely to be very rare, and probably best regarded as a hypothetical limit.

(iii) Biparental care with parental investment cost to one parent not felt at all by the other

The other limit in this axis is where a new mate is found without cost. Then each parent is more successful if the other provides more parental investment, a problem first discussed by Trivers (1972). There have been many approaches to this problem since Maynard Smith's pioneering 'prospective analysis' in 1977. Chase (1980) and Houston & Davies (1985) sought the ESS in terms of 'reaction curve' models. Each curve shows the best parental investment reply to the parental investment from the other parent. This is a game in evolutionary time, not (as was thought) an ESS negotiation rule between two parents during a behavioural interaction, in which each uses the reaction curve to choose its next parental investment level (McNamara *et al.* 1999).

The $f(m)$ relation has been used to deduce the ESS parental investment under 'symmetric' biparental care (Parker 1985). This is also a game where parental investment adjusts over evolutionary time, not a negotiation game in behavioural time. It assumes that parents have equal roles, with parental investment having equal effects on each parent (i.e. hence 'symmetrical'). The ESS has $\alpha = 2.0$, which implies—rather counter-intuitively—that offspring in such a biparental species should receive *less* total parental investment than those of a similar, uniparental species (figure 2c), if we simply compare the parental optima. Effectively, when there are two parents in conflict, each holds back some parental investment compared with the level they would provide if each were caring alone.

However, it has recently been shown that this ESS is not continuously stable—when perturbed away from the ESS, it does not converge back, but diverges to a uniparental care ESS (McNamara *et al.* 2002). An earlier version of the present paper derived parental investment and food ESSs for asymmetric biparental care under Parker's model, and showed that at the parental ESS, the marginal food benefits to offspring equal the marginal food cost to each parent, each scaled by its absolute cost. Though this result is not continuously stable, an equivalent result is obtained by Lessells (2002) using a different model, so this form of solution may be a general property of biparental care ESSs.

(c) Parent-offspring conflict

For intrabrood sib competition, parent-offspring conflict can be measured as the difference between the equal amounts of parental investment per offspring that is optimal for the parent and the skews introduced by sib competition. For interbrood sib competition, parent-offspring conflict can be measured by the difference in the parental investment optima defined by α for parents and offspring (figure 2c). Following Trivers (1974), the optimal parental

Figure 3. (a) Cost of y units of food, in terms of units, m , of parental investment, where $m(y) = by^h$. The curves are for $h = 1.0, 2.0$ and 5.0 with b held at 1.0 . (b) ESS parental food input (y^*) for uniparental care in relation to h for the investing parents. The curve shows the ESS food inputs, y^* , solutions iterated for the case where $f(y) = (1 - \exp[-k(y - y_{\min})])$; k is a shape constant ($= 0.1$) and $y_{\min}$ ($= 5.0$) is the minimum amount of food for the offspring to survive.

investment for a parent to supply is less than that optimal for offspring to demand (figure 2b). The magnitude of conflict depends on the mating system—disagreement is probably least under true monogamy and greatest when both parents give equal parental investment and are equally unconstrained by the effect of demand on the other parent (Parker 1985).

Note that the solutions in this section have defined the ‘battleground’, but do not tell us the parental investment that will be realized after sib competition and parent–offspring conflict are taken into account.

3. CONFLICT RESOLUTION

The battleground having been outlined, how is the conflict resolved? There have been various analyses (reviewed in Godfray 1995; Mock & Parker 1997). We now apply the approach of § 2 to investigate the resolution of intrafamilial conflict.

The battle concerns parental investment—from whom, to whom, and how much. First, we specify the strategies that can be adopted by the various family members. The par-

ental strategy is simply to vary (in evolutionary time) the continuous parental investment level, m . Offspring compete against each other, and also extract parental investment from their parents, by costly begging or some equivalent activity that can increase the actor’s share of parental investment resources. Specifically, imagine a continuous, costly offspring strategy, x , plausibly a begging level, a scramble effort played against brood mates for access to food (e.g. a tussle level for teats), or a costly signal of an offspring’s true need to a parent. Increasing x by a given offspring must both increase its gain, m , and its costs. Costs may be in terms of survival (figure 4a): an offspring’s survival probability, S , decreases with its begging level, x (Macnair & Parker 1978). The payoff to the offspring is the product, benefit $f(m(x))$ times survival $S(x)$. An alternative additive approach treats payoffs as energy benefits minus energy costs (Parker *et al.* 1989; Godfray 1991). The way that these two strategies, m for the parent and x for the offspring, interact to determine payoffs generates the ESS resolution of the conflict. We are particularly concerned with how the ideal parental investment levels of § 2 compare with those likely to be realized at conflict resolution.

Figure 4. (a) Survival probability, S , of offspring in relation to its begging level, x . (b) Possible forms for the ESD mechanism, $X(m)$: $X'(m) > 0$; $X'(m) = 0$; $X'(m) < 0$. (c) Direction of the deviations from the parent's optimum (for uniparental care) generated by the positive ESD ($X'(m) > 0$) and negative ESD ($X'(m) < 0$) (see § 3).

(a) *The power continuum in parent-offspring conflict*

Precisely how the two strategies, m and x , interact is likely to depend on a continuum of biological power; all points on this continuum seem possible in nature. At one extreme—control by offspring—parents cannot regulate parental investment allocation to individual offspring, so that an offspring begging more gains more by some simple physical rule. For example, it is hard to see how a female mammal can regulate exactly the flow of milk to individual offspring; rather, offspring that struggle hardest to gain the best teats and suckle most actively will gain the biggest share of the milk. Typically, such scrambles are modelled so that the gains to an individual offspring match that offspring's begging level relative to the mean begging level (Macnair & Parker 1979; Parker & Macnair 1979; Parker 1985), often termed 'mean matching' (Harper 1986;

Godfray & Parker 1992). Thus begging to level x_i yields a share proportional to $x_i/(\text{mean } x \text{ for the brood})$. Mean matching assumes a fixed scramble mechanism determined by offspring behaviour, with no parental control over parental investment allocation. The ESS (we will call it the 'scramble ESS') is given by the pair of strategies, m^* for the parent, and x^* for the offspring (Parker & Macnair 1979).

The alternative extreme—control by the parent—allows the parent to monitor offspring behaviour and to allocate parental investment in accordance with parental interests. This is the 'honest signalling' approach pioneered by Godfray (1991, 1995), founded on the theory of Grafen (1990) for biological signals. Instead of the parental investment allocated (m) being fixed by the offspring behaviour (x), the parental investment allocation mechanism adapts to the variation in condition (the 'true need')

of offspring: i.e. $m(x)$ evolves, rather than being a by-product of competition between siblings. Godfray (1991) argued that offspring in poorer condition have more to benefit from parental investment than offspring in good condition, and that the parent can assess an offspring's begging level, but not its condition. Signal (x) and response (m) then coevolve to generate a parental investment allocation pattern related to the offspring's true need (which is 'honest signalling' *sensu* Zahavi (1987)). An offspring's condition, c , is assumed to vary from $c_{\min}$ (lowest) to $c_{\max}$ (highest). The ESS (we will call it the 'signalling ESS' for comparison with the 'scramble ESS') now consists of two functions: $m^*(x)$, the ESS parental investment given to an offspring begging at level x , and $x^*(c)$, the ESS begging level at condition c . The parental investment allocated increases with an offspring's begging level x^* , which in turn declines with its condition c . At the signalling ESS, offspring in maximum condition $c_{\max}$ do not beg at all. If an offspring cheats by begging to level $x > x^*$, it gains more food, but its benefits are offset by its higher costs, exactly as in the scramble ESS.

Although they represent two ends of a continuum, the scramble and signal approaches have a great deal in common. A conclusion of both models, rather than an assumption, is that begging must be costly; costs must increase with begging for an ESS to be achieved. Both have essentially the same form of ESS: m^* for the parent and x^* for the offspring. In both, offspring that beg more are predicted to receive more food. Empirically, it will often be difficult to distinguish between them (Parker *et al.* 2002). For example, demonstrations that hungrier offspring gain more food are commonly claimed to support the signalling hypothesis. However, very similar results are obtained from the scramble model when condition is included (Parker *et al.* 2002). Begging levels would correlate with need, because the costs that can be 'afforded' will increase with the offspring's potential gains. This is not then equivalent to a signalling ESS, because the underlying mechanism for parental investment allocation, $m(x)$, is fixed by the scramble mechanism rather than evolving as a result of signalling. The scramble model has been investigated to include effects of sibling strength asymmetries (Parker *et al.* 1989); unsurprisingly, stronger sibs achieve higher net gains because they can signal strongly for less cost. Competitive asymmetries between sibs have not yet been incorporated into the signalling model, though they could be. However, at the ESS, it seems probable that the parent should compensate for the strength of the offspring if this amplifies its signal, and respond only to true need. So the observation that, in many birds, the strongest chicks gain most food does not support the signal ESS: even when parents are in a good position to control food allocation, they are not always doing so (Mock & Parker 1997).

Though not originally apparent, a further similarity between the two approaches is that the parental investment realized at resolution relates to the ideal parental investment (§ 2) in a qualitatively similar fashion depending on the mechanisms relating to supply and demand. Therefore, the realized parental investment depends not so much on the power continuum as on the nature of these mechanisms. We now summarize how this occurs.

(b) Demand and supply mechanisms

Hussell (1988) was the first to recognize the importance of what he termed 'supply' and 'demand' functions in modelling parent-offspring interactions. Resolution of intrafamilial conflict depends critically on two mechanisms (termed mechanism 1 and 2 respectively by Mock & Parker (1997)): (i) how changes in parental investment supply affect begging demand (the ESD mechanism), and (ii) how changes in demand affect parental investment supply (the EDS mechanism). The scramble and signalling approaches made similar qualitative assumptions about EDS, but very different assumptions about the critically important ESD.

ESS solutions are found by formulating fitness payoffs of mutants that deviate in strategy from the ESS. We know from field experiments that changes in expected food levels can change begging levels (Mock & Parker 1997). Thus, a mutant mother who deviates from the ESS (by playing m instead of m^*) may precipitate an immediate change in her offspring begging levels, which will affect her fitness. Suppose that the offspring are playing the ESS strategy, which is x^* if the mother plays the ESS m^* . The shift in the typical supply level to m by the mother causes them to alter their begging behaviour from x^* to a level we shall call X (their evolved strategy is x^* , but the mother's deviation causes them to now show X). Now, ESD defines how this altered begging level, X , relates to mutant deviations in the mother's parental investment supply level around the ESS, m^* . Similarly, a mutant offspring that deviates from the ESS (by playing $x \neq x^*$), may promote a change in the parent's parental investment allocation, which will affect the fitness of the mutant offspring. EDS defines how the altered parental investment gain, termed μ , to distinguish it from the parent's evolved parental investment strategy, m^* , changes with mutant deviations in offspring demand around the ESS, x^* .

Thus ESD is the function $X(m)$ and EDS is the function $\mu(x)$. The ESS parental investment at resolution of intrafamilial conflict is defined by the gradients of these functions at the ESS: i.e. by gradients $X'(m^*)$ and $\mu'(x^*)$. Exactly the same logic applies for the food ESS, so that ESD becomes $X(y)$, i.e. how deviations in food input affect the begging level, and EDS becomes $Y(x)$, i.e. how begging deviations affect food allocation. The equivalent gradients are $X'(y^*)$ and $Y'(x^*)$.

Note that these gradients are expressed quite generally—they are not dependent on assumptions about the power continuum, from scramble to signal. What they do is define the magnitude of coefficient α in equations (2.1) and (2.2) that we have shown in § 2 to determine where the ESS amount of parental investment or food input will occur. A set of α values expressed in terms of these gradients, for different mating system assumptions, and for parental investment and food ESSs, are given in table 1 (derived in Appendix C). Note that the two gradients always appear as a product, which we shall call $v(= X'(m^*)\mu'(x^*)$ for the parental investment ESS, or $X'(y^*)Y'(x^*)$ for the food ESS); neither gradient ever appears singly. We can now compare the ideal parental investment for the players, defined by the α values in § 2, with the α solutions for conflict resolution in table 1. It is easy to calculate that the offspring's ideal α is always smaller than its equivalent α at conflict resolution. From

Table 1. Ideal and conflict resolution values of coefficient α , under various assumptions about sib competition and mating systems. (v is the product of the two gradients, i.e. $X'(m^*)\mu'(x^*)$ for the parental investment ESS, or $X'(y^*)Y'(x^*)$ for the food ESS.)

mating system	parent's ideal α	offspring's ideal α	conflict resolution values for α
<i>uniparental care</i>			
intra-brood conflict	1.0	(see § 2a(i))	$\left[\frac{1}{1-v} \right]$
inter-brood conflict where only one parent invests directly, but both parents are equally affected by this investment (e.g. true monogamy)	1.0	0.5	$\left[\frac{1-0.5v}{1-v} \right]$
inter-brood conflict where investment by one parent has no cost to the other parent	1.0	0.25	$\left[\frac{1-0.25v}{1-v} \right]$
<i>symmetrical biparental care</i>			
inter-brood conflict where both parents are equally affected by the investment costs of the other parent (e.g. true monogamy)	1.0	0.5	$\left[\frac{1-0.5v}{1-v} \right]$

§ 2 and figure 2*b,c*, we know that this means that the offspring's ideal parental investment will always be less than the parental investment realized at the conflict resolution. What these solutions imply about parental interests depends on whether the product of the two gradients (v) is positive or negative. To examine this, we consider EDS and ESD separately.

(i) *EDS: the effect of change in demand on supply level*

Interpretation of EDS is simple: if offspring beg more, they gain more food. This assumption is made by both scramble and signal approaches and conforms with the biological data (Teather 1992; Kacelnik *et al.* 1995; Leonard & Horn 1998; Rauter & Moore 1999). So gradient $\mu'(x^*)$ or $Y'(x^*)$ is positive.

Exactly how deviations in an offspring's begging level affect its gains depends on the assumptions of the model. With honest signalling, if a chick deviates by begging at a higher level than the ESS for its condition, the parent supplies the food that would be given to an offspring in greater need, giving the amount appropriate to the condition corresponding to the higher demand level at the ESS (Godfray 1991). In scramble models, with inter-brood conflict, increased begging is assumed to increase an offspring's gains in proportion to its begging relative to the ESS level (Parker & Macnair 1979). Thus a chick begging to level x in the ESS population (x^*) simply gains $\mu = m^*(x/x^*)$. For intra-brood conflict, a chick begging to level x in the ESS population gains a share of the resources for the brood (m^* per chick) equal to its begging level relative to the mean level for the brood. So for a rare dominant demand gene, $\mu = m^*(x/0.5[x + x^*])$.

The fact that EDS is always positive means that, at the ESS, we will generally see costly begging across the scramble-signal power continuum and the explicit form of the EDS determines how much overt begging we expect. This also depends on ESD.

(ii) *ESD: the effect of change in supply on demand level*

ESD is the crucial determinant of how realized parental investment will deviate from the ideal parental investment of the parent.

Unlike EDS, there is no obvious *a priori* assumption about how changes in supply affect demand levels. A parent deviating by increasing parental investment above the ESS level might increase, decrease, or have no effect on the begging levels of its offspring (figure 4*b*). In fact, food supplementation experiments on nestlings suggest that all three forms of ESD are possible. Negative ESD is probably commonest (Cash & Evans 1986; Redondo 1991; Bustamente *et al.* 1992; Redondo & Castro 1992; Mondloch 1995), but positive ESD also occurs (Hofstetter & Ritchison 1998; Stamps *et al.* 1985).

It is the slope of the ESD relation (figure 4*b*) that will determine the direction of deviation in parental investment from the parental optimum. The easiest way to see this is from table 1, by comparing α values for the ideal parental investment with those predicted at conflict resolution. In all cases, if the gradient of ESD is positive (more food means more begging), v will be positive, because we know the gradient of EDS is positive (see § 3*b(i)*). Thus, from the formulae in table 1, α at conflict resolution will be greater than the α ideal for the parent. The ESS parental investment (or food) level at resolution is therefore *less than* the ideal parental optimum (figure 2). If the gradient of ESD is negative (more food means less begging), then v is negative and α at conflict resolution will be less than 1.0. Thus the parental investment at resolution is *greater than* the α ideal for the parent (figure 2). If a deviation in food level does not affect begging, then $v = 0$, $\alpha = 1.0$ and parental investment stays the same as the parental ESS. This is summarized in figure 4*b*.

It is interesting that the scramble and signal approaches made different implicit assumptions about ESD, so that initially it was thought that they generated fundamentally

Figure 5. Deviations from the parental optimum at the food ESS. Total food supplied at the ESS, y^* , is plotted against the product, v , of the gradients of the ESD and EDS mechanisms. Offspring benefits were taken explicitly as $f(y) = (1 - \exp[-k(y - y_{\min})])$, with $k = 0.1$ and $y_{\min} = 5.0$. Parental investment costs were linear: $m(y) = by$. intra, intrabrood conflict with uniparental care; uni, uniparental care where non-investing parent is unaffected by its mate's parental investment; tm, true monogamy. The parental optimum for the three curves is shown by the horizontal line—above this, more food is supplied than the parental optimum, below it, less is supplied.

different predictions about parental investment at the ESS. In the initial scramble model, Parker & Macnair (1979) envisaged a negative ESD, simulating relief of hunger. Thus, their resolution parental investment level is higher than the parental ideal. In the initial signal model (Godfray 1991), the ESD was implicitly assumed to be zero. Hence, the parent retains its ideal parental investment. A modification by Johnstone (1996) transformed this into a negative ESD, leading to super-optimal parental investment at resolution from the parental perspective.

(c) *How much parental investment deviation at the resolution of the conflict?*

While the *direction* of deviation from the parental optimum depends on the sign of the ESD gradient, the *magnitude* of deviation depends on the magnitude of v , i.e. on the magnitude of both ESD and EDS gradients. These magnitudes also depend on the conflict (inter- or intrabrood) and the mating system (uniparental or biparental care; whether costs to one parent can be felt by the other).

To demonstrate this, we examined ESS food levels for numerical examples (using similar $f(y)$ and $m(y)$, as used in figure 3b). Figure 5 shows the total food supplied (y^*) at the ESS for conflict resolution. The product of the two gradients: $v = X'(y)Y'(x)$, was varied between -0.5 and $+0.5$ (i.e. from negative ESD through zero to positive ESD). The ideal parental optimum occurs when $v = 0$ (shown as a horizontal line), so the difference between the curves and this line gives the deviation from the ideal parental y^* . For uniparental care, intrabrood conflict gives most deviation from the parent's optimum, followed by

interbrood conflict in which the non-investing parent feels no costs due to the investment of its mate. The opposite extreme, where the costs of investment are incurred equally by both partners (e.g. true monogamy) shows least deviation.

These deviations in parental investment or food supply match conclusions about the overt begging level (Parker 1985): the greater the deviation from the ideal parental ESS the greater the amount of begging shown at the ESS. However, it is possible (at least theoretically, for the scramble model) for one or other party to 'win' outright (achieve the ideal α value) if the gradient of the ESD is so steep as to preclude any begging or any deviation in parental investment or food level from the current state (Parker 1985; Mock & Parker 1997).

4. FUTURE PROSPECTS

Until recently there has been relatively little interplay between theoretical and empirical researchers in intrafamilial conflict, and one of our aims is to encourage greater interaction. Below, we highlight some potentially productive areas.

Whilst we can witness overt conflict, or its absence, in nature, it is a real problem to establish whether parental investment given and received is above or below the parental optimum. Trivers & Hare (1976) deduced this by looking at investment ratios in social insects. Nevertheless, evidence for parent-offspring conflict is weak (Bateson 1994; Mock & Forbes 1992). Little data exist on how current expenditure affects future reproductive success. For species with family interactions resembling supply and demand games, we stress that whatever the parental investment level observed (whether the same as, more than or less than the parental optimum), this tells us little about the magnitude of underlying evolutionary conflict. This can be understood only in terms of the ideal levels of parental investment for the players in the family, by the supply and demand mechanisms and particularly by the sign of ESD (how change in supply affects demand).

Does ESD evolve? There are certain plausible adaptive possibilities. If offspring cannot measure environmental food abundance other than by parental food input, it might pay them to beg more when input increases, generating positive $X'(m)$. Alternatively, negative $X'(m)$ may result if each successive food unit becomes less valuable to offspring through digestion efficiency and/or mortality risks decreasing with increased food input, reducing begging.

Whatever its form, the ESD response itself becomes a game between parents and offspring, suggesting that it must form part of the ESS solution. In principle, the same applies to EDS, though the signalling model incorporates this by assuming parental control and the scramble model by assuming offspring control.

How can we differentiate empirically between signalling versus scramble solutions? Demonstrating that offspring beg more and receive more when hungry is commonly claimed as evidence for honest signalling. However, as discussed, this finding is equally well interpreted in terms of scramble (Parker *et al.* 2002). Tests require details of exactly how parents allocate food. With scramble begging, the parent responds to the nearest most-intense stimulus,

which one can imagine as a series of unequal, overlapping hemispheres, one for each chick, each with its intensity falling away from the centre of its base (the gape of the begging chick) towards its periphery. With signalling, one would expect some form of comparison of the hemispheres, then a return to the largest after compensation for the effect of size of the offspring. Empirical discrimination between the two cases will not be easy.

More understanding of heritability of begging and its interaction with parental sex and environmental conditions is required (Kölliker *et al.* 2000). This would allow further development of interbrood competition models, which have, so far, been largely ignored by empiricists. Theoretical models are needed that take account of recent work on chick learning and begging intensity (Kedar *et al.* 2000), which suggests that begging may be more plastic than previously thought. Surprisingly, to our knowledge, no studies have demonstrated parental decision-making processes relating to begging, and although parental feeding effort increases with begging (evidence reviewed by Kilner & Johnstone (1997)), the distinction between scramble and signalling remains unclear.

The comparative approach offers one way to test such models (Royle *et al.* 1999), though finding a common currency for parental investment or reproductive success across species is a real problem. The same applies for within-species studies; for example, when comparing chick-provisioning effort between parents when the male also has a territory to defend. Although measurement of the energetic costs of various behaviours has recently proven useful, the challenge of their translation into an evolutionary currency such as lifetime reproductive success still remains.

We are, therefore, far from understanding intrafamilial conflict. The recent increase in interest nevertheless gives cause for optimism.

The authors thank Yoh Iwasa, Kate Lessells and John McNamara for discussions, and Sigal Balshine-Earn, Bart Kempenaers and Tamas Székely for organizing a fascinating workshop. We are indebted to Kate and Tamas for comments on the manuscript, and especially to Kate for her considerable efforts that we hope eventually made this paper much more accessible than its original version. This work was supported by National Environmental Research Council (NERC) grant GR3/11794.

APPENDIX A: OFFSPRING OPTIMA UNDER INTERBROOD CONFLICT

Consider a promiscuous species where only the female cares for offspring and dies after expending her total parental investment of M units. The optimal parental investment for an offspring depends on whether the gene comes from its mother or its father. If the mutant gene is from the mother, then half her offspring will be carriers taking $m \neq m^*$ units (where m^* is the ESS). Thus the mutant offspring success (for a dominant mutant gene) is

$$W(m, m^*) = \frac{M}{0.5(m + m^*)} f(m). \quad (\text{A } 1)$$

With an adult sex ratio of s males per female, each male mates on average M/sm^* times, and we assume it is with a different female each time. Thus, from the father, the mutant offspring success is simply

$$W(m, m^*) = \frac{sM}{sm^*} f(m), \quad (\text{A } 2)$$

so that s cancels out (Parker 1985). We find the ESS, m^* , by differentiating W with respect to m and evaluating at m^* . Where gene expression independent of parental sex, W is half the sum of equations (A 1) and (A 2) (Macnair & Parker 1978; Parker 1985), giving equation (2.1) with $\alpha = 0.25$. Under true monogamy male fitness is given by equation (A 1) instead of equation (A 2), giving equation (2.1) with $\alpha = 0.5$. Under genomic imprinting, we solve each equation separately, giving $\alpha = 0.5$ for a maternal gene and $\alpha = 0$ for a paternal gene (Haig 1992).

To derive the 'food ESS', we have two functions, $f(y)$ and $m(y)$ instead of the single function $f(m)$. For uniparental care where fathers invest nothing and feel no costs of their mates' parental investment, the analogue of equation (A 1) defines offspring success for a gene inherited from the mother:

$$W(y, y^*) = \frac{M}{0.5[m(y) + m(y^*)]} f(y), \quad (\text{A } 3)$$

where y is the mutant strategy ($y \neq y^*$). Differentiating with respect to y and evaluating at y^* gives

$$f'(y^*) = \alpha \left(\frac{m'(y^*)}{m(y^*)} \right) f(y^*) \quad (\text{A } 4)$$

with $\alpha = 0.5$. The analogue of equation (A 2) gives the fitness for a gene carried by the father, which gives $\alpha = 0$. Without genomic imprinting, therefore, $\alpha = 0.25$, as in the parental investment ESS.

APPENDIX B: OPTIMA FOR PARENTS

Consider the parental investment ESS for uniparental care. The success of an investing parent deviating by playing $m \neq m^*$ is

$$W(m, m^*) = \frac{M}{m} f(m), \quad (\text{B } 1)$$

and the ESS is found in the usual way, giving equation (2.1) with $\alpha = 1.0$. The same applies for true monogamy (Parker 1985). The 'food ESS' for this case maximizes

$$W(y, y^*) = \frac{M}{m(y)} f(y), \quad (\text{B } 2)$$

giving equation (A 4), or (2.2) if $m(y) = by^h$, with $\alpha = 1.0$.

APPENDIX C: CONFLICT RESOLUTION

Here, we let $f(m)$, $f(y)$ be the benefits to an offspring of gaining m units of parental investment or y units of food, and an offspring's survival probability, S , reduce with its begging level, x . The measure of offspring fitness is now $f(m) \cdot S(x)$. For uniparental care without any constraint on the non-investing parent, the parental investment ESS for the investing parent is derived from the function for parental fitness:

$$W(m, m^*) = \frac{M}{m} f(m) S(X(m)). \quad (\text{C } 1)$$

The parallel food function is

$$W(y, y^*) = \frac{M}{m(y)} f(y) S(X(y)), \quad (\text{C } 2)$$

in which X is the begging level of an offspring whose parent deviates from m^* (at which it would beg to level x^*) by playing m . Differentiating by m in equation (C 1) or y in equation (C 2), and remembering that $X(m^*) = x^*$, these give the parent's parental investment ESS as

$$f'(m^*) = \frac{f(m^*)}{m^*} \left[1 - m^* \frac{S'(x^*)}{S(x^*)} X'(m^*) \right] \quad (\text{C } 3)$$

(Mock & Parker 1997), and the food ESS as

$$\frac{f'(y^*)}{f(y^*)} = \frac{m'(y^*)}{m(y^*)} - \frac{S'(x^*)}{S(x^*)} X'(y^*). \quad (\text{C } 4)$$

When $m(y) = by^h$, $m'(y^*)/m(y^*) = h/y^*$. Note that this gives

$$f'(y^*) = \frac{f(y^*)}{y^*} \left[h - y^* \frac{S'(x^*)}{S(x^*)} X'(y^*) \right], \quad (\text{C } 5)$$

which has a parallel form to equation (C 3) and is equivalent if costs are linear ($h = 1.0$), which parallels equation (B 5). The same applies for j and hence equation (2.3) applies again at the ESS.

We next derive the values of $-S'(x^*)/S(x^*)$ for the offspring, which can then be substituted into the above equations to yield the equations in table 1. These values depend on whether conflict is intra- or interbrood. For intrabrood conflict with uniparental care, the offspring cannot change the total parental investment (or food), but can change its own share by begging more. So offspring playing $x > x^*$ do not alter the average gain per offspring, m^* , but gain a greater share $\mu(x) > m^*$. At the ESS, $\mu(x^*) = m^*$. Thus

$$W(x, m^*) = \frac{M}{m^*} f(\mu(x)) S(x);$$

which, after differentiating by x , gives

$$-\frac{S'(x^*)}{S(x^*)} = \mu'(x^*) \frac{f'(m^*)}{f(m^*)}, \quad (\text{C } 6)$$

and for the food ESS, the food realized by begging to level x is $Y(x)$, giving

$$-\frac{S'(x^*)}{S(x^*)} = Y'(x^*) \frac{f'(y^*)}{f(y^*)}, \quad (\text{C } 7)$$

where $Y(x^*) = y^*$ at the ESS. Substituting between equations (C 6) and (C 3) gives the parental investment ESS, and between equations (C 7) and (C 4) gives the food ESS for intrabrood conflict (table 1).

For interbrood conflict, first consider uniparental care without true monogamy. Without genomic imprinting, the offspring success is the mean of the success via each parent, following equations (A 1) and (A 2), which yields the offspring parental investment ESS, where $\mu(x^*) = m^*$,

$$-\frac{S'(x^*)}{S(x^*)} = \mu'(x^*) \left[\frac{f'(m^*)}{f(m^*)} - \frac{1}{km^*} \right], \quad (\text{C } 8)$$

where $k = 4$. For true monogamy, the ESS (obtained from equation (A 1) alone) is the same but with $k = 2$ (see also Mock & Parker 1997). The parallel food ESS, where $Y(x^*) = y^*$, is

$$-\frac{S'(x^*)}{S(x^*)} = Y'(x^*) \left[\frac{f'(y^*)}{f(y^*)} - \frac{m'(y^*)}{k \cdot m^*(y^*)} \right], \quad (\text{C } 9)$$

where k takes the same values (4, 2) depending on the mating constraint.

The parental investment ESS is now found by substituting between equations (C 3), (C 8), and the analogous food ESS by substituting between equations (C 4) and (C 9) (table 1).

REFERENCES

- Bateson, P. 1994 The dynamics of parent-offspring relationships in mammals. *Trends Ecol. Evol.* **9**, 399–403.
- Bustamante, J., Castro, J. J. & Moreno, J. 1992 The function of feeding chases in the chinstrap penguin, *Pygoscelis antarctica*. *Anim. Behav.* **44**, 753–759.
- Cash, K. & Evans, R. M. 1986 The occurrence, context and functional significance of aggressive behaviours in young American white pelicans. *Behaviour* **102**, 119–128.
- Charnov, E. L. 1976 Optimal foraging the marginal value theory. *Theor. Popul. Biol.* **9**, 129–136.
- Charnov, E. L. 1982 Parent-offspring conflict over reproductive effort. *Am. Nat.* **119**, 737.
- Chase, I. D. 1980 Cooperative and non-cooperative behaviour in animals. *Am. Nat.* **115**, 827–857.
- Evans, R. M. 1990 The relationship between parental input and investment. *Anim. Behav.* **39**, 797–813.
- Forbes, L. S. 1993 Avian brood reduction and parent-offspring 'conflict'. *Am. Nat.* **142**, 82–117.
- Godfray, H. C. J. 1991 The signalling of need by offspring to their parents. *Nature* **353**, 328–330.
- Godfray, H. C. J. 1995 Evolutionary theory of parent-offspring conflict. *Nature* **376**, 1133–1138.
- Godfray, H. C. J. & Parker, G. A. 1992 Sibling competition, parent-offspring conflict and clutch size. *Anim. Behav.* **43**, 473–490.
- Grafen, A. 1990 Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546.
- Haig, D. 1992 Genomic imprinting and the theory of parent-offspring conflict. *Sem. Devl Biol.* **156**, 401–403.
- Haig, D. & Graham, C. 1991 Genomic imprinting and the strange case of the insulin-like growth factor II receptor. *Cell* **64**, 1045–1046.
- Haig, D. & Westoby, M. 1991 Genomic imprinting in endosperm: its effect on seed development in crosses between species, and between different ploidies of the same species, and its implications for the evolution of apomixis. *Phil. Trans. R. Soc. Lond. B* **333**, 1–13.
- Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52.
- Harper, A. B. 1986 The evolution of begging: sibling competition and parent-offspring conflict. *Am. Nat.* **128**, 99–114.
- Hofstetter, S. H. & Ritchison, G. 1998 The begging behaviour of nestling eastern screech-owls. *Wilson Bull.* **110**, 86–92.
- Houston, A. I. & Davies, N. B. 1985 The evolution of co-operation and life history in the dunnoek, *Prunella modularis*. In *Behavioural ecology: the ecological consequences of adaptive*

- behaviour (ed. R. M. Sibly & R. H. Smith), pp. 471–487. Oxford: Blackwell Scientific.
- Hussell, D. J. T. 1988 Supply and demand in tree swallow broods: a model of parent–offspring food provisioning interactions in birds. *Am. Nat.* **131**, 175–202.
- Johnstone, R. A. 1996 Begging signals and parent–offspring conflict; do parents always win? *Proc. R. Soc. Lond. B* **263**, 1677–1681.
- Kacelnik, A., Cotton, P. A., Stirling, L. & Wright, J. 1995 Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proc. R. Soc. Lond. B* **259**, 259–263.
- Kedar, H., Rodríguez-Gironés, M. A., Yedvab, S., Winkler, D. W. & Lotem, A. 2000 Experimental evidence for offspring learning in parent–offspring communication. *Proc. R. Soc. Lond. B* **267**, 1723–1727. (DOI 10.1098/rspb.2000.1201.)
- Kilner, R. & Johnstone, R. A. 1997 Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**, 11–15.
- Kölliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. S. & Richner, H. 2000 The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proc. R. Soc. Lond. B* **267**, 2127–2132. (DOI 10.1098/rspb.2000.1259.)
- Lack, D. 1947 The significance of clutch size. *Ibis* **89**, 302–352.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Leonard, M. L. & Horn, A. G. 1998 Need and nestmates affect begging in tree swallows. *Behav. Ecol. Sociobiol.* **42**, 431–436.
- Lessells, C. M. 2002 Parentally biased favouritism: why should parents specialize in caring for different offspring? *Phil. Trans. R. Soc. B* **357**, 381–403. (DOI 10.1098/rstb.2001.0928.)
- Lessells, C. M. & Parker, G. A. 1999 Parent–offspring conflict: the full-sib–half-sib fallacy. *Proc. R. Soc. Lond. B* **266**, 1637–1643. (DOI 10.1098/rspb.1999.0826.)
- Macnair, M. R. & Parker, G. A. 1978 Models of parent–offspring conflict. II. Promiscuity. *Anim. Behav.* **26**, 111–122.
- Macnair, M. R. & Parker, G. A. 1979 Models of parent–offspring conflict. III. Intra-brood conflict. *Anim. Behav.* **27**, 1202–1209.
- McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999 Incorporating rules for responding into evolutionary games. *Nature* **401**, 368–371.
- McNamara, J. M., Houston, A. I., Barta, Z. & Osorno, J.-L. 2002 Should young ever be better off with one parent? *Behav. Ecol.* (Submitted.)
- Maynard Smith, J. 1977 Parental investment: a prospective analysis. *Anim. Behav.* **25**, 1–9.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Mock, D. W. & Forbes, L. S. 1992 Parent–offspring conflict: a case of arrested development? *Trends Ecol. Evol.* **7**, 409–413.
- Mock, D. W. & Parker, G. A. 1997 *The evolution of sibling rivalry*. Cambridge University Press.
- Mondloch, C. J. 1995 Chick hunger and begging affect parental allocation of feedings in pigeons. *Anim. Behav.* **49**, 601–603.
- Nicholson, A. J. 1954 An outline of the dynamics of animal populations. *Aust. J. Zool.* **2**, 9–65.
- O'Connor, R. J. 1978 Brood reduction in birds: selection for infanticide, fratricide, and suicide? *Anim. Behav.* **26**, 79–96.
- Parker, G. A. 1985 Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.* **33**, 519–533.
- Parker, G. A. & Macnair, M. R. 1978 Models of parent–offspring conflict. I. Monogamy. *Anim. Behav.* **26**, 97–110.
- Parker, G. A. & Macnair, M. R. 1979 Models of parent–offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim. Behav.* **27**, 1210–1235.
- Parker, G. A., Mock, D. W. & Lamey, T. C. 1989 How selfish should stronger sibs be? *Am. Nat.* **133**, 846–868.
- Parker, G. A., Royle, N. J. & Hartley, I. R. 2002 Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol. Lett.* **5**, 206–215.
- Rauter, C. M. & Moore, A. J. 1999 Do honest signalling models of offspring solicitation apply to insects? *Proc. R. Soc. Lond. B* **266**, 1691–1696. (DOI 10.1098/rspb.1999.0833.)
- Redondo, T. 1991 Early stages of vocal ontogeny in the magpie (*Pica pica*). *J. Ornithol.* **132**, 145–162.
- Redondo, T. & Castro, F. 1992 Signalling of nutritional need by magpie nestlings. *Ethology* **92**, 193–204.
- Royle, N. J., Hartley, I. R., Owens, I. P. F. & Parker, G. A. 1999 Sibling competition and the evolution of growth rates in birds. *Proc. R. Soc. Lond. B* **266**, 923–932. (DOI 10.1098/rspb.1999.0725.)
- Smith, C. C. & Fretwell, S. D. 1974 The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506.
- Stamps, J. A., Clarke, A. B., Arrowood, B. & Kus, B. 1985 Parent–offspring conflict in budgerigars. *Behaviour* **94**, 1–40.
- Teather, K. L. 1992 An experimental study of competition for food resources between male and female nestlings of the red-winged blackbirds. *Behav. Ecol. Sociobiol.* **31**, 81–87.
- Temme, D. H. 1986 Seed size variability: a consequence of variable genetic quality? *Evolution* **40**, 414–417.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine Atherton.
- Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264.
- Trivers, R. L. & Hare, H. 1976 Haplodiploidy and the evolution of the social insects. *Science* **191**, 249–263.
- Zahavi, A. 1987 The theory of signal selection and some of its implications. In *Int. Symp. Biological Evolution* (ed. V. P. Delfino), pp. 305–327. Bari: Adriatica Editrice.