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Parental investment and family dynamics: interactions between theory and empirical tests

Received: 14 May 2004 / Accepted: 24 August 2004 / Published online: 23 September 2004
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Abstract The pattern of parental investment (PI) seen in nature is a product of the simultaneous resolution of conflicts of interest between the members of a family. How these conflicts are resolved depends upon the mating system, the genetic mechanism, on whether extra PI affects current or future offspring, and the behavioural mechanisms underlying supply and demand of PI. Until recently very little empirical work has been done to underpin these key determinants of conflict resolution. This review examines recent empirical progress in understanding both (1) how conflict is resolved and (2) its evolutionary consequences. How offspring demand interacts with parental supply of resources determines how conflict is resolved. Two extremes are: passive parental choice of competing offspring, relating to offspring control of resource allocation, and active parental choice relating to parental control. Although most previous empirical work has tended to conclude or assume that parents primarily control resource allocation decisions, recent studies explicitly examining predictions from theoretical

analyses have shown that offspring control of resource allocation is more important than previously realised. The amount of PI supplied at resolution depends not on who controls food allocation, however, but on the nature of the supply and demand mechanisms. These have yet to be established experimentally, but a recent regression model illustrates how this could be achieved in the field. Determination of the effect of supply on demand (ESD) and the effect of demand on supply (EDS) mechanisms is critical to parent–offspring conflict theory, which has not been adequately tested empirically. There is an underlying, and until recently untested, assumption of models of intrafamilial conflict that there is genetic variation for both offspring demand and parental supply behaviours, so that the behaviours can coevolve. Recent studies on great tits, burrower bugs and mice all found evidence for genetic variation in supply and demand behaviours, but the predicted negative correlation between genes expressed in mothers and their offspring (i.e. parent–offspring coevolution), was found only for burrower bugs. The lack of a negative relationship for great tits and mice may have been a consequence of antagonistic coevolution between the sexes (sexual conflict). These studies illustrate the importance of the underlying genetics and mating system in determining conflict resolution, and point to the need for new models (especially of inter-brood competition) taking differences in the genetics and the co-evolution of the ESD and EDS mechanisms into account. We also discuss the importance of the comparative approach in determining evolutionary consequences of conflicts, and use the recent work on growth costs of begging to illustrate the difficulties of measuring costs of conflict in an evolutionary currency. The recent growth in empirical work on conflicts in families illustrates an increasing, and increasingly productive, integration between theoreticians and empiricists.

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This special feature is based on Session 1, “Conflict among related individuals”, at the 21st Symposium of the Society of Population Ecology (Tsukuba, October 2003). Edited by E. Kasuya.

Keywords Scramble · Signalling · Parent–offspring conflict · Sexual conflict · Sibling conflict

Introduction

The aim of this review is to outline some recent developments in empirical tests of intrafamilial conflict theory, with a view to highlighting areas of progress and areas still ripe for exploration. Since our review of the current theory of how conflicts between close family members can affect the flow of parental investment (PI) from parents to their young was written (Parker et al. 2002a) there have been a wealth of new empirical studies, covering a wide spread of issues under the broad banner of intrafamilial conflict. Parker et al. (2002a) stressed that the pattern of PI seen in nature is a product of the simultaneous resolution of all the conflicts between the family members, and that this depends upon the genetic mechanism, the mating system, on whether extra investment affects current or future offspring, and particularly on the behavioural mechanisms underlying supply and demand of PI. Consequently there are two fundamental questions associated with intrafamilial conflict:

1. How are the conflicts resolved, and under what circumstances? and
2. What are the evolutionary consequences of the outcomes of conflict resolution?

Much of the difficulty in linking family conflict theory with empirical tests lies in the problems associated with the measurement of parental investment. The currency of PI is its cost in terms of the parent's ability to invest in other offspring (Trivers 1972). PI is perhaps most often seen as parents provisioning young with food, but also includes a variety of other behaviours, such as nest defence or vigilance. Short-term proxies for PI used by empiricists for reasons of tractability, such as energetic expenditure, or feeding rates, may not provide an accurate reflection of this opportunity cost, making it hard to measure in the field. Notwithstanding these problems, empirical work on family conflicts is an expanding and diverse field of research.

Conflict battleground

The conflict battleground is generated by the difference between the optimal level of PI for each family member and the level of PI actually received (Godfray 1995). When considering this battleground it is assumed that the fitness of an offspring, f (survival \times expected future reproductive success), is an increasing function of the amount, m , of PI it receives. Furthermore, each parent can be envisaged as having a fixed total amount of PI, M , that it can allocate to offspring during its lifetime, such that the total number of offspring it can produce is M/m (Parker and Macnair 1978; Fig. 1). From the point of view of the offspring, extra demand of PI may affect its siblings in one of two, non-mutually exclusive ways. If parents provide a fixed total amount of PI to the

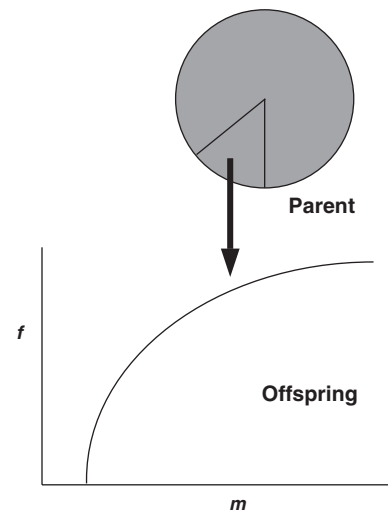


Fig. 1 The parental supply of resources to offspring. If parents allocate a large portion, m , of the total amount of PI, M , to a single offspring, the offspring will have high personal fitness, f , but parents will be able to produce fewer offspring in total. The $f(m)$ curve is generally assumed to be, as illustrated here, monotonically increasing with diminishing returns, such that there is no further increase in fitness associated with supplying beyond a certain value of PI. Although this makes intuitive sense, and seems to generally comply with the available empirical data, the exact shape of this curve has never been explicitly determined empirically for any species. This is important, as the outcome of predictions from models of intrafamilial conflict may be affected if the $f(m)$ curve is substantially different in form from a monotonically increasing function with diminishing returns. Figure redrawn from Fig. 3.2 in Mock and Parker (1997)

current brood, any extra demand by a given offspring will affect only their current brood mates ('intra-brood' competition; Macnair and Parker 1979). On the other hand, if parents respond to an increase in demand by increasing the total amount of PI to the current brood, only future broods will be affected ('inter-brood' competition; Parker and Macnair 1979).

Under intra-brood competition, a given offspring would do best by taking sufficient parental resources until its marginal gains fall to half the marginal gains of its (full) siblings, which are left with the remainder (Parker et al. 1989). Conflict occurs because its brood mates would also do best by following this strategy, but they cannot all achieve it simultaneously. The magnitude of the conflict will depend upon relatedness of brood mates (greater conflict with lower relatedness), total amount of available parental resources, the number of competitors (brood mates) for the fixed amount of parental resource, and whether or not offspring are equally competitive. Empirical evidence for intra-brood competition is abundant, not least as shown by the negative effect of increasing brood size on growth, size and survival of offspring (Mock and Parker 1997).

The amount of conflict under inter-brood competition is dependent primarily on the mating system and on gene expression (e.g. genomic imprinting). If only one sex provides PI (say females), but the male's reproductive

success is completely bound up with that of his partner (e.g. 'true monogamy'; Parker 1985), then conflict will be lower than in situations where the male mates with a different female each time he breeds (e.g. promiscuity). This is because, with promiscuity, the male does not pay a cost, in terms of reduced future prospects, from his mate's increased PI in the current brood (Lessells and Parker 1999). With genomic imprinting gene expression is dependent upon which parent the gene is inherited from. This can potentially lead to severe interbrood conflict, as the promiscuous male's best strategy under genomic imprinting when the 'demand gene' is paternally inherited is to take all currently available female investment (Haig 1992; Mock and Parker 1997).

In contrast to intrabrood competition, evidence for interbrood competition, that an increase in current investment decreases either the size or number of subsequent broods, is less abundant (Mock and Parker 1997). Gustafsson and Sutherland (1988) experimentally modified clutch size of collared flycatchers *Ficedula albicollis* in the field and showed that parents raising enlarged clutches had reduced subsequent fecundity. In addition the fecundity of offspring raised in enlarged broods was also adversely affected. More recently Royle et al. (2002a) found that zebra finch *Taeniopygia guttata* females providing more PI in the current brood, as a consequence of controlling for sexual conflict, had reduced investment (in terms of both the size and number of eggs) in their subsequent clutch. Both studies provide support for models of interbrood competition. However, Charalambous et al. (2003) manipulated in utero growth rate, and thus first-litter parental investment, using mice lacking the growth promoting insulin-like growth factor 2 (*Igf2*) gene. They found that females with low investment in first litters also had low investment in second litters, indicating that females were somehow 'primed' by their first litter size (Charalambous et al. 2003). Even though this result does not disprove the existence of interbrood competition, as the experiment was not broad enough in scope to test this, it does suggest a more complex situation than current interbrood models predict.

The importance of the mating system is also paramount in determining the ideal investment levels from the parents' perspective. When the cost of each parent's PI is felt equally by both parents or when there is uniparental care in the absence of sexual conflict (e.g. 'true monogamy' where a parent cannot gain a new mate if the first mate dies), the amount of PI given per parent to offspring is expected to be greater than that when there is biparental care but when PI costs are only felt by one parent (i.e. when a new mate can be found without cost; e.g. Chase 1980; Houston and Davies 1985; Parker 1985; Lessells 2002; McNamara et al. 2003). This is because each parent would do better if the other provides more PI (Trivers 1972). Royle et al. (2002a) found evidence for fitness costs to offspring of sexual conflict between parents in zebra finches. When the potential workload (number of offspring per parent) was kept constant,

offspring received greater per capita PI from single females than when both parents provided care together. This was due to a reduction in care provided by females in pairs, rather than laziness by males. As a consequence male offspring reared by single mothers were more sexually attractive as adults than their siblings reared by both parents, which provides evidence for the suggestion that biparental care increases the number, and reduces the quality, of offspring raised (Royle et al. 2002a).

Parent-offspring conflict is predicted to occur because the optimal amount of PI that parents should supply is less than the optimum that offspring should demand (Trivers 1974), with the magnitude of the conflict determined by the mating system (as, for example, in Fig. 2, which illustrates the zone of parent-offspring conflict expected under different mating systems (sexual conflict) and interbrood competition with uniparental care). Nevertheless, empirical evidence for parent-offspring conflict is weak (Mock and Forbes 1992).

How is the conflict resolved?

An understanding of the ideal levels of PI for the various members of the family (the 'battleground') is required in order to gauge the magnitude of underlying evolutionary conflict. However, to establish how the conflict is resolved requires an understanding of the mechanisms of supply and demand (Mock and Parker 1997; Parker et al. 2002a). Offspring compete for PI, m , using a costly means of communication, x , for example, strenuous begging. An increase in x leads to the offspring gaining more PI, m , but at some cost (e.g. cost to survival,

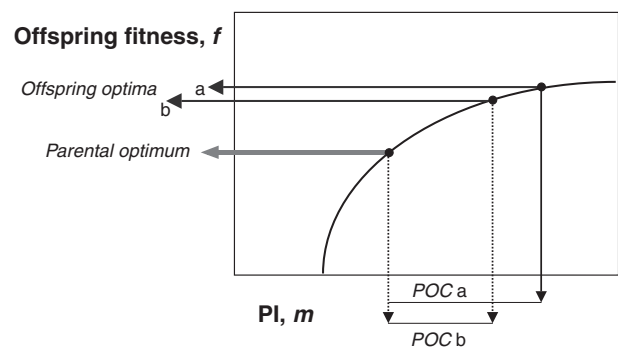


Fig. 2 Zones of parent-offspring conflict (POC) over parental investment (PI) under interbrood competition and uniparental care in which only the female provisions the offspring. Offspring optima are shown under sexual conflict (a) and without sexual conflict between parents (b). With no sexual conflict (e.g. true monogamy, such that neither parent can find a new mate after the first mate dies), the offspring optimum (b) is lower than the optimum (a) under sexual conflict (e.g. promiscuity, or monogamy where a parent find a new mate without cost after the first mate dies). The difference between parent and offspring optima gives the zone of POC. This is greater under sexual conflict (POC a), than when there is no sexual conflict (POC b). For details and derivations of these optima see Parker et al. (2002a)

Haskell 2002; or energetic cost, Chappell and Bachman 2002). The way in which x and m interact determines how conflict is resolved (Mock and Parker 1997; Parker et al. 2002a), which depends upon a continuum of power over the allocation of parental resources.

The power continuum and parent–offspring conflict

At one end of the continuum offspring control food allocation and parents simply passively feed the competing offspring presenting the largest overall stimulus ('scramble' mechanism; Stamps et al. 1978; Macnair and Parker 1979). At the other end of the continuum parents control food allocation and actively choose between competing offspring begging signals ('honest signalling' mechanism; Godfray 1991, 1995). With passive parental food allocation, escalation of begging levels occurs as a consequence of competition between offspring; offspring presenting the greatest overall stimulus gain a disproportionate share of food. With active parent food allocation parents feed young in direct relation to offspring 'need', as signalled by their intensity of begging, discounting amplification of begging stimuli due to competitive ability. 'Need' can be defined as a measure of the increase in the personal fitness of offspring as a result of receiving a unit of food (Royle et al. 2002b).

Under both active and passive feeding mechanisms begging is 'honest' in that any escalation in solicitation by offspring is balanced by costs to the offspring (Parker et al. 2002b). Begging under honest signalling is a direct (one-to-one) indication of true need, and parents should increase food allocation in relation to need. Under scramble competition, however, this is not necessarily the case as a consequence of competitive differences between sibs: begging will relate directly to true need only if all offspring are equally competitive. Under scramble, begging levels will still correlate with true need because the costs that can be 'afforded' by the offspring increase with the potential rewards of escalated begging (Rodríguez-Gironés et al. 2001a; Parker et al. 2002a; Royle et al. 2002b).

Most empirical measures of 'need' tend to use short-term measures such as hunger or condition of offspring as synonymous with need. This assumes that there is a negative relationship between need and condition, because offspring in good condition should require less food (Godfray 1991, 1995; Rodríguez-Gironés et al. 2001a). As already argued, under both active and passive food allocation offspring are likely to achieve increased food input with greater need. Under the honest signalling model this is only likely to hold when the difference in need among offspring is sufficiently large. If offspring differ only slightly in condition, the highest marginal gains to the parent may be obtained by feeding the strongest offspring because they are of higher value (Parker et al. 2002b). Thus, the discounting of the amplification of begging due to competitive asymmetries under the honest signalling approach will be a complex

issue. Consequently, empiricists face considerable difficulties in differentiating not just between scramble and honest signalling (Royle et al. 2002b), but in establishing the honesty of communication between parents and their offspring. However, control of food allocation is likely to be a dynamic process (Royle et al. 2002b), and despite the difficulties outlined above there are notable differences in predictions between the different modelling approaches. In particular, scramble models predict that competitive asymmetries between offspring will primarily determine the outcome, whilst signalling models predict the outcome will be primarily determined by relative need (Parker et al. 2002b).

Smiseth et al. (2003a) approached the challenge of distinguishing between scramble and honest signalling outcomes by testing whether food allocation is under offspring or parental control using burying beetles, *Nicrophorus vespilloides*, which are 'partially begging' species; offspring feed themselves in addition to begging for food from parents. Consequently, burying beetles offer insights into the evolution of offspring begging strategies from simple, non-signalling foraging strategies, as partial begging represents an evolutionary transition, rather than just a developmental change associated with ontogeny (Smiseth et al. 2003a). Beetle larvae cease begging when the efficiency of self-feeding is such that growth can be maintained at a rate at least as good as that when receiving food from parents. Smiseth et al. (2003a) tested whether this transition to nutritional independence was under offspring or parental control. They conducted behavioural observations of the time the female spent near the larvae, and the time spent begging by the larvae when they were close to the female. Although the parent showed no change in behaviour towards larvae over time, larvae reduced the time spent begging in the presence of the parent, suggesting the transition to nutritional independence was under offspring control (Smiseth et al. 2003a). Interestingly, this provides support for recent theoretical work which suggests that honest signalling has evolved from scramble competition (Rodríguez-Gironés 1999; Godfray and Johnstone 2000), reflecting the mechanistic simplicity of passive feeding and scramble competition compared to active feeding and honest signalling (Royle et al. 2002b).

One of the fundamental differences between scramble models and honest signalling models for parent–offspring communication is that, whereas in scramble models begging strategies are determined by escalated competition among brood members (Macnair and Parker 1979; Parker et al. 2002b), this does not happen under honest signalling. Neuenschwander et al. (2003) tested whether begging behaviour of great tits *Parus major* comprised a significant scramble component, through cross-fostering and experimentally altering brood size. If parents compensate, so that feeding rate remains constant across brood sizes, honest signalling models predict that begging intensity should remain constant, or decrease, whereas scramble models predict

that begging intensity should increase as brood size increases (Neuenschwander et al. 2003). It was found that, although parents compensated for the change in brood size by maintaining the same feeding rates, begging increased with experimental brood size, strongly suggesting offspring primarily controlled food allocation and that scramble competition is important in parent–offspring communication in great tits, at least when they are near fledging age. In addition, nestlings in larger broods suffered deterioration in their body condition, presumably as a consequence of the elevated begging levels, supporting results from theory that under certain circumstances scramble competition is more costly than honest signalling (Parker et al. 2002b). It would be interesting to repeat the experiments when chicks were younger, as the mismatch between demand and supply is likely to be smaller, so the influence of scramble competition would also be expected to be less great (Royle et al. 2002b). Nevertheless, this study provides clear evidence for the potential importance of scramble competition in begging displays, and the passive allocation of food by parents.

Another recent study by Smiseth et al. (2003b) on bluethroats *Luscinia svecica*, which have biparental care, also provides some insights into parental food allocation mechanisms. The amount of food available was manipulated downwards through the temporary removal of males, using a pair-wise experimental design, so that the same broods experience both food limitation (one parent) and normal feeding conditions (both parents). When food availability was reduced food distribution was found to be further skewed in favour of the largest, oldest chicks at the expense of their junior nestmates (Smiseth et al. 2003b). However, this was not due to any significant change in behaviour, in terms of begging postures or nest position, by the largest chicks. The authors interpret this as evidence that (the largest) offspring do not control food allocation, and cite the fact that nestling rank had a greater effect on food distribution within the brood under conditions of food limitation compared to normal conditions, as support for this interpretation. Whilst it is certainly possible that parents do actively allocate food under food limitation, their results are also consistent with a scramble outcome. Honest signalling models (i.e. active food allocation and parental control) do not predict that competitive asymmetries between chicks dominate food gains, as found in their study, as food is predicted to be allocated primarily according to need, discounting differences in competitive ability (Parker et al. 2002b). In contrast, in scramble models competitive asymmetries modify the overall begging stimulus that each chick presents, so that begging does not necessarily relate directly to need (Parker et al. 2002b). Passive parent feeding (offspring control) involves a preferential response to the greatest overall begging stimulus, which can include the effects of age and size, so an increased skew in provisioning the largest chicks under conditions of food limitation (Smiseth et al. 2003b) is entirely consistent with food being passively

delivered by parents, even if there is no active change in chick behaviour. If parents allocate food actively to broods, differences in size or competitive ability within the brood may confound the ability of parents to read their offspring's signals if the cost of signalling is different (e.g. Kilner 2001) for chicks with identical needs. If only the begging signal can be read, then honesty can be corrupted, as larger chicks are more likely to be able to bear the costs of begging (Parker et al. 1989).

These studies illustrate the problems empiricists face in trying to distinguish between scramble and honest signal solutions. Some of this, at least, is likely to be a consequence of the dynamics of the parent–offspring power continuum (Royle et al. 2002b). However, it also highlights the need for more studies looking at the honesty and accuracy of begging signals, particularly in relation to changes in resource availability over both the short and longer terms.

Demand and supply mechanisms

Although there are consequences for the resolution of parent–offspring conflict which are dependent upon the mechanism of food allocation involved, the amount of PI achieved by an offspring at resolution depends not so much on the continuum of power between parents and offspring, but on the nature of the mechanisms of supply and demand (Mock and Parker 1997; Parker et al. 2002a). Resolution of conflict in families depends upon how a change in the supply of PI affects demand by offspring [Effect of supply on demand (ESD) mechanism], and how a change in offspring demand effects the supply of PI [Effect of demand on supply (EDS) mechanism].

Models of scramble and honest signalling make similar qualitative assumptions about the EDS, supported by empirical data (e.g. Teather 1992; Kacelnik

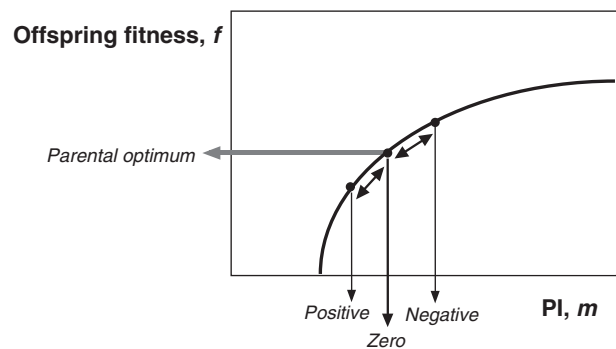


Fig. 3 Direction of deviation away from the parental optimum parental investment, in the absence of sexual conflict. Outcomes are shown for a positive ESD (more food leads to more begging) and a negative ESD (more food leads to less begging; as assumed in early scramble models). For honest signalling models it is assumed that there is no deviation from the parental optimum, such that provision of more food has no effect on begging. For further details see Parker et al. (2002a)

et al. 1995; Leonard and Horn 1998; Rauter and Moore 1999), that if offspring beg more they get more food. However, the two different modelling approaches make different assumptions about the ESD. This is the primary determinant of how much the realised PI deviates from the ideal PI of the parent (Fig. 3, Parker et al. 2002a). In initial scramble models the slope of the ESD relation (demand on y -axis and supply on x -axis) was assumed to be negative, so that increased supply of food resulted in reduced begging, and consequently generated the prediction that the amount of PI supplied at resolution will be higher than the parents' ideal (Parker and Macnair 1979). In contrast Godfray (1991) made the implicit assumption that the slope of ESD was zero, generating the prediction that the amount of PI supplied at resolution in the initial honest signalling model remained at the ideal amount from the (female) parent's perspective (Mock and Parker 1997; Parker et al. 2002). Empirical work, providing food supplements to chicks, indicates that the slope of the ESD may be negative, positive or zero. A negative ESD has been found for pelicans (Cash and Evans 1986), penguins (Bustamente et al. 1992), magpies (Redondo and Castro 1992) and pigeons (Mondloch 1995). A positive ESD has been recorded for budgies (Stamps et al. 1985) and screech owls (Hofstetter and Ritchison 1998). The sign of the ESD slope indicates the direction of deviation from the parents ideal PI (Fig. 3), whilst the magnitude of this deviation is a product of both the ESD and EDS slopes, and the type of conflict (intra- or interbrood) and mating system (Parker et al. 2002a).

Although these mechanisms have yet to be elucidated empirically, Kölliker (2003) has recently produced a regression model which formalises the original supply-demand model of Hussell (1988), and suggests a method for empirically estimating the relative effects of the EDS and ESD mechanisms, using nestling begging call playback (EDS) and supplementary provisioning experiments (ESD). A requirement of the experimental design is that the provisioning effort measured in the EDS experiment and manipulated in the ESD experiment are made in equal units, as is the begging measured in the ESD experiment and manipulated in the EDS experiment. This would allow a quantitative estimate of the mechanisms involved and the equilibria for offspring begging and parental provisioning, and it could also be used to translate units of offspring demand into units of parental supply, and vice versa, which may allow testing of any deviations from the amount demanded by offspring and the amount actually provided by parents (Kölliker 2003). Kölliker (2003) also makes the point that the timescale over which the equilibria are measured is likely to be of critical importance, with the short-term equilibria not necessarily reflective of long-term equilibria. Timescale will also be of critical importance if the mechanism of food allocation is context-dependent (Royle et al. 2002b). This regression technique makes the possibility of empirical measures of the EDS and ESD, and thus

an estimate of the amount of conflict between parents and offspring, an achievable aim.

Heritability and the genetics underlying intrafamilial conflict

Most theoretical studies of intrafamilial conflict utilise game theoretical models, which typically are phenotypic rather than explicitly genetic in framework. Strategies are modelled as the phenotypic outcome of conflict over PI amongst genes expressed in parents and their offspring (Mock and Parker 1997). There is an underlying assumption that there is genetic variation for the co-evolving behaviours of offspring begging and parental provisioning (Mock and Parker 1997). Until recently, virtually nothing was known about the genetic basis of intrafamilial conflict, although three recent studies from diverse taxa have now helped to shed some light on the issue.

All three studies found evidence for genetic variation in both offspring demand and parental supply behaviours, but the nature of the relationships between parents and offspring differed considerably. Using a combination of cross-fostering of chicks and begging playback experiments, Kölliker et al. (2000) showed that, in great tits *Parus major*, offspring begging intensity was primarily dependent upon their common origin, suggesting a genetic basis to offspring solicitation. However, only mothers responded to an increase in offspring demand by increasing supply, and the magnitude of the supply response was positively related to the intensity of offspring demand only in the maternal line, not the paternal line (Kölliker et al. 2000). This suggests that there is differentially expressed genetic covariation of the parent-offspring relationship, relating to parental origin (Kölliker et al. 2000). Models of maternal-offspring coadaptation predict that there should be a negative correlation between the effects of genes expressed in mothers and their offspring (Wolf and Brodie 1998; Wolf 2000). This was not found to be the case for great tits, where there was positive covariation between offspring demand and parental supply response (Kölliker et al. 2000) or mice, where the predicted negative association was absent (Hagar and Johnstone 2003). However, in both cases this was most likely a consequence of antagonistic coevolution between the sexes (i.e. sexual conflict; Hagar and Johnstone 2003).

Hagar and Johnstone (2003) compared litter sizes and measured maternal provisioning from crosses within and between two inbred strains of mice *Mus musculus* (CBA and C57/B6), which differed in how family conflict is resolved, probably as a consequence of genomic imprinting. Offspring from B6 strains tend to be larger than those of CBA origin, but B6 litter size tends to be smaller than that of CBA strains (Hagar and Johnstone 2003). Following cross-fostering it was found that, although the natural female's body mass had a positive effect on litter size, the natural female's strain did not

influence litter size. Remarkably, however, the father's strain had a strong effect on litter size, with CBA males having larger litters than B6 males. This means that the father's strain either alters the number of eggs the female produces, or it affects the proportion of embryos that are reabsorbed, following implantation in the female's uterus (Haig 2003). Although the natural mother's strain, the natural father's strain, and the strain of the foster mother's mate did not much influence provisioning, foster mother's strain had a significant effect, with CBA females providing less resources (milk) than B6 females (Hagar and Johnstone 2003). If there was maternal-offspring co-evolution, a negative correlation between the effects of genes expressed in offspring and mothers would be expected, but B6 females, which were better providers than CBA females, did not produce offspring that had lower demand. Reduced provisioning by CBA females is counterbalanced by the larger litter size of CBA males, meaning selection for increased demand by offspring of CBA females will be weak (Hagar and Johnstone 2003).

In contrast, Agrawal et al. 2002 found evidence for a negative correlation between the genetic components expressed by mother and offspring in burrower bugs *Sehirus cinctus*. Using cross-fostering experiments, the authors showed that female bugs not only responded to offspring demand, but increased supply of resources to offspring that were in poorer condition and responded differently to offspring of different genotypes. In addition, a paired split-clutch experimental design, where each clutch was split in half and each half clutch was raised by a different unrelated foster mother allowed comparisons to be made across treatments whilst controlling for the effects of differences in offspring genotype and clutch size (Agrawal et al. 2002). If offspring signal their demands to mothers then any genetic variation in the form of the offspring demand should generate a positive correlation between related individuals. This was exactly what was found for burrower bugs; there was a positive correlation between the amount of food provisioned to each family split across the two treatments, controlling for differences in family size (Agrawal et al. 2002). This demonstrated that offspring varied in their ability to demand resources from parents. There was also a negative correlation between the amount of food supplied by mothers to their foster clutches, and the amount of food offspring from the mother's natural clutch succeeded in demanding from an unrelated foster mother. Since cross-fostering controls for post-hatching environmental variation, any correlation between mothers and offspring should be a consequence of genetic factors, which shows that there is a negative correlation between genetic components of the maternal-offspring coadaptation (Agrawal et al. 2002).

These studies demonstrate how important consideration of the particular life history and genetics of the study species is when attempting to unravel the complexities involved in the resolution of family conflicts.

What are the evolutionary consequences of the outcome of conflict resolution?

Family conflicts and life history characteristics—the comparative approach

The comparative approach identifies patterns in evolutionary events and offers a complementary method to empirical experiments for elucidation of the long-term evolutionary effects of family conflicts on life histories. Although there are general problems in identifying common currencies for comparing PI and reproductive success across species, the use of comparative analyses in the study of intrafamilial conflicts is, nevertheless, a powerful tool.

Briskie et al. (1994) used the relatedness of individuals within broods of passerine bird species, as measured by the amount of extra-pair paternity and incidence of brood parasitism, as a proxy for the amount of expected conflict within broods of different species. Although caution needs to be exercised when predicting the effect of within-brood relatedness of offspring on sibling competition as it only really applies to intrabrood, not interbrood competition (Parker 1985; Lessells and Parker 1999), it has been used with some success in comparative analyses (e.g. Briskie et al. 1994; Royle et al. 1999; Lloyd and Martin 2003). Briskie et al.'s (1994) work showed that, as predicted by models of intrabrood competition (Macnair and Parker 1979; Parker and Macnair 1979), the loudness of nestling begging increased as the within-brood relatedness declined, suggesting that over evolutionary time nestling birds have responded to reductions in the average relatedness of nestmates by elevating their begging levels.

This evidence that offspring selfishness is moderated by relatedness within broods was further supported by a comparative study by Royle et al. (1999), who examined whether sibling competition was an important determinant of a key life-history trait, growth rate, in birds. Selection should favour increased competition in broods of mixed paternity, and the largest chicks within a brood tend to win out in scrambles or contests for food supplied by parents (Mock and Parker 1997). Consequently nestling growth rates, as a result of increased competition among nest-mates, should be highest in those species in which siblings are less closely related to one another. As predicted there was a strong positive association between the rate of multiple paternity within broods and nestling growth rates, even when controlling for potentially confounding variables such as rate of nest predation, adult body size, brood size, mating system and the form of parental care (Royle et al. 1999). The results provide evidence to suggest that competitive interactions among related individuals within families have contributed substantially to the large variation in growth rates exhibited by bird species, above and beyond that influenced by dif-

ferences in proximate ecological and developmental factors between species.

Lloyd and Martin (2003) investigated the influence of sibling competition on incubation duration, rather than postnatal development rates, in birds. They found a similar effect of multiple paternity on prenatal development rates, which are genetically independent of one another, to that found by Royle et al. (1999) on postnatal development; growth was more rapid as brood relatedness declined. However, Lloyd and Martin (2003) also used two other measures of sibling competition, the extent of brood parasitism and the degree of hatching asynchrony, which did not show similarly significant results, although effects of both measures were in the predicted direction. Whilst the mixed nature of the results may potentially be explicable, at least in part, as a consequence of methodological problems associated with the use of rates of brood parasitism in birds for example, they do raise questions as to whether the relationship between multiple paternity and prenatal development rates is one of cause and effect (Lloyd and Martin 2003); although this is also a general issue for comparative studies of this type. The authors suggest that this relationship may arise indirectly as a consequence of the correlated selection of adult mortality acting on both incubation period (longer incubation being associated with low adult mortality; Ricklefs 1993; Martin 2002), and extra-pair mating (extra-pair copulations may be costly to future survival or reproduction; e.g. Westneat and Rambo 2000). Although it seems a bit unlikely that the survival cost to adults of extra-pair copulations and shorter incubation times should have a greater selective effect on prenatal growth rates than that of sibling competition, the results indicate caution is required when interpreting correlational data.

For their study of the life history consequences of sibling competition in mammals, Stockley and Parker (2002) used a different method for estimating the amount of intrabrood competition for resources. Although the number of nipples per offspring is typically around two for most mammals (Gilbert 1986), there is considerable evidence that milk availability varies substantially at different nipples (Mock and Parker 1997). Individual growth rates within litters vary with success in competing for the most productive nipples; the largest individuals are generally most successful (Stockley and Parker 2002). An evolutionarily stable strategy (ESS) model of scramble competition produced several predictions. First, larger birth mass, through increased prenatal growth rate, should give an advantage to offspring in scramble competition for access to the most productive nipples. If mothers control prenatal growth rates, this should not occur. Second, if the mother controls the total milk supply postnatal growth rates will be lower when competition for nipples is higher, as a result of the higher energy expenditure from scramble competition (Stockley and Parker 2002). These predictions were both supported in comparative analyses of the Carnivora and Insectivora. Species with high post-

natal sibling competition, as measured by the number of offspring per nipple, were found to have relatively high prenatal growth rates for their adult size. This is consistent with previous work indicating that offspring have a degree of control over their prenatal growth (Haig 1992). In addition, for carnivores, although species with high levels of postnatal sibling competition had high prenatal growth rates, they subsequently had low postnatal growth rates in relation to their birth weight. Taken together these results provide evidence that sibling competition is an important selection pressure influencing life history diversity, and particularly the developmental mode, of mammals (Stockley and Parker 2002).

Comparative analyses are only correlative, and cannot directly validate paths of causation, but in conjunction with experimental empirical work (e.g. Royle et al. 2002b) the evolutionary consequences of family conflicts are being increasingly recognised.

The challenge of measuring costs in an evolutionary currency

A good illustration of the problems associated with measuring costs is provided by some recent studies of begging. Both honest signalling and scramble models for the evolution of begging incorporate the concept of costly begging in order to maintain stability (Parker et al. 2002a). Without costs, begging would escalate without bounds. The begging strategy is stabilized by exact balancing of the marginal gains of escalated begging with the marginal costs (Macnair and Parker 1979; Godfray 1991; Parker et al. 2002a). However, a recent review of the energetic cost of begging behaviour concluded that metabolic costs of begging are low and so evidence for substantial fitness costs is poor (Chappell and Bachman 2002). This was primarily because studies of the energetics of begging have mostly utilised measurements of oxygen consumption of individual chicks whilst begging (e.g. Leech and Leonard 1996; McCarty 1996; Bachman and Chappell 1998), which ignores anaerobic aspects of energy metabolism (Weathers et al. 1997). Furthermore, energetic costs are short-term and require translation into a suitable evolutionary currency in order to assess the effect of begging on fitness (Parker et al. 2002a). More recently an attempt has been made to quantify begging costs in a potentially fitness-related currency: growth rate.

Based on the assumption that higher growth rates yield higher fitness Kilner (2001) showed that escalated begging resulted in a depression in growth rate and thus fitness in nestling canaries *Serinus canaria*. Size-matched pairs of siblings were assigned to one of two begging treatments, in which chicks were forced to beg for different periods to receive the same quantity of hand-fed food (Kilner 2001). As a result, chicks forced to beg at excessive levels had retarded growth in both the short term (mass gain over the experimental period) and the long term, and this was more pronounced within pairs of

siblings which had a greater difference in begging intensity between siblings during the experiment. Kilner suggests that this growth cost of begging in canaries is a reasonable approximation of a cost to fitness, because survival to independence is strongly related to daily mass gain [although see Charnov (1993) for an alternative view]. Maynard-Smith and Harper (2003) criticised Kilner's study by pointing out that the relative rate of mass gain appears to have been greater for chicks at 6 days of age compared to that at 8 days, yet chicks at 6 days of age showed no evidence of mass loss when forced to beg for extended periods.

Rodríguez-Gironés et al. (2001b) used a similar procedure to examine the costs of begging in relation to growth in magpies *Pica pica* and ring doves *Streptopelia risoria*. They found a substantial depression of growth in magpie chicks forced to beg for extended period before receiving food over a 3-day period, but no effect on growth of ring dove squabs forced to beg for an extra 70 min/day over a 10-day period. Interpretation of the results in this study is not helped by the different treatments used to stimulate escalated begging for magpies and ring doves. Nonetheless, the difference in the effects of escalated begging does not appear to be just a consequence of methodological differences. As Rodríguez-Gironés et al. (2001b) point out the experimental procedure used for magpies was almost identical to that employed by Kedar et al. (2000) for house sparrows *Passer domesticus*, yet no growth rate depression was recorded for chicks with escalated begging in the latter study.

Another recent paper by Leonard et al. (2003) casts further doubt on the general applicability of growth costs associated with elevated begging levels. Leonard et al. (2003) followed the protocols of Kilner (2001) and Rodríguez-Gironés et al. (2001b) to examine the effect of begging on growth of nestling tree swallows *Tachycineta bicolor*, a species for which metabolic studies suggested the costs of begging were low (Leech and Leonard 1996; McCarty 1996). In line with these energetics studies Leonard et al. (2003) found no evidence of a growth cost of escalated begging in tree swallows. Whilst the equivocal nature of these results may reflect species differences in costs of begging, or show that begging is only costly in terms of growth under certain conditions (Rodríguez-Gironés et al. 2001b), it may also reflect the over-simplicity of the assumption concerning the nature of the relationship between growth and fitness. Fitness may be traded off with other traits other than just growth. As Leonard et al. (2003) highlight, none of the studies mentioned provide any direct evidence that the growth effects of begging have any consequences for fitness (see also Clarke 1998). Nonetheless, the studies by Kilner (2001) and Rodríguez-Gironés et al. (2001b) do indicate that costs of begging relating to traits associated with fitness can occur. Whilst this approach does not provide a suitably rigorous evolutionary currency as yet, it does represent a significant advance on energetic studies, which do not measure begging cost as specified by models

of family conflict (Kilner 2001). The major difficulty is in demonstrating costs to fitness over the relatively short timescale that is feasible for empirical testing.

Prognosis and conclusions

Many parental care behaviours of the sort described in this review are essentially cooperative in outcome, in that the fitness of the family members is increased as a consequence of parental care. However, underlying conflicts of interest can create asymmetries of parental investment within families, which can potentially shape the evolution of species life histories and intrafamilial interactions. The development of mathematical models of intrafamilial conflict has provided a framework for empirical testing of conflicts in the lab and in the field. In recent years there has been a burst of empirical tests of family conflict theory, some of which we have highlighted in this review. There have been real advances in our understanding of how conflicts are resolved, particularly the genetics underlying conflict resolution, and the likely consequences of that conflict resolution. The broad applicability of intrafamilial conflicts in biological processes is also being increasingly recognised. For example, important roles for family conflicts have been implicated in weight gain during early life in humans (Wells 2003), in the evolution of sex determination mechanisms (Werren et al. 2002), milk yield and fat composition in cattle (Sederstrom et al. 2002), and seed mass (Bañuelos and Obeso 2003) and floral traits (Delsalle and Mazer 2002) in plants.

However, there is still much to do. In order to demonstrate an evolutionary conflict it is necessary to experimentally manipulate each side in the conflict, such that one side benefits at the expense of the side whose fitness has been depressed (Mock and Forbes 1992; Royle et al. 2002b). This has not been achieved empirically as yet, but the development of a method for elucidating supply and demand mechanisms suggests this may not be far away. More work is needed on parental decision-making with respect to food allocation strategies (i.e. active or passive), particularly in terms of the context in which these food allocation strategies are made. Although lip service is often paid to the importance of resource availability in moderating conflicts among family members, and it is often recognised that resource availability varies in real time, very little has been done to explicitly link changes in resource availability to changes in food allocation or supply and demand strategies. These are always assumed to be static and not dynamic in nature (Royle et al. 2002b). A related area ripe for further empirical exploration relates to the precision of the communication between parents and offspring: how accurate is this, and how does the accuracy vary with resource availability?

The relationship between empirical work and the development of theory is a two-way process. New models are required that take into account differences in

the underlying genetics of family conflicts of different species/taxa, especially with respect to models of interbrood competition. In addition, to understand the dynamic nature of conflict resolution, we need to develop evolutionary models that allow the EDS and ESD mechanisms to co-evolve (Kölliker 2003).

Nevertheless, as this review shows there is now considerable and productive integration of empirical work and theory. The isolated factions of Mock and Forbes' (1992) review of the application of parent-offspring conflict theory have moved somewhat closer together, with increasingly productive results.

Acknowledgements N.J.R. would like to thank Yukihiro Toquenaga, Koichi Fujii and staff and students at the Institute of Biological Sciences, University of Tsukuba, for organising an excellent and stimulating symposium and for their hospitality during his visit to Japan. The authors would also like to thank two anonymous referees for comments on a previous version of this paper.

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