



REVIEW

Parent–offspring conflict and the genetics of offspring solicitation and parental response

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Solicitation displays by offspring and responses by parents are commonly regarded as phenotypic expressions of the conflict over parental investment between genes expressed in offspring and their parents. Models for the resolution of the parent–offspring conflict have assumed genetic variation for levels of both offspring solicitation and parental response in order to allow offspring and parental strategies to coevolve and the conflict to be evolutionarily resolved. Empirical research has focused on the phenotypic predictions of these models, and little is known about the genetics of parent–offspring interactions. We review the existing evidence for genetic variation in offspring solicitation behaviours and parental responses from a variety of animal species. This evidence confirms the fundamental assumption of genetic variation in offspring solicitation and parental response, indicating that offspring and parental strategies can (co-) evolve. We discuss potential reasons for the maintenance of genetic variation in offspring solicitation and parental response, and the implications genetic variation and covariation and/or parental effects may have for the resolution of the parent–offspring conflict. Further research on the genetic bases of parent–offspring interactions may be crucial for understanding the resolution of parent–offspring conflict and the coevolution of the behaviours involved.

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The evolution of parental care for dependent offspring originally required an increase in the energy, time and protection parents devoted to rearing offspring. At an initial evolutionary stage, being attentive to signs of need or quality by offspring may have evolved because of the mutual benefit of efficient parental investment in relation to the short-term requirements of the young (Trivers 1974; Parker & Macnair 1979; Harper 1986; Davis et al. 1999). Once parental attentiveness to offspring signs of need has evolved, however, the coevolution between offspring demand and parental response in sexually reproducing organisms starts to be driven by the unequal genetic interests of parents and offspring (Trivers 1974; Godfray 1995a; Mock & Parker 1997). This parent–offspring conflict over parental investment is thought to be the crucial ultimate factor for the evolution of elaborate and costly begging displays by offspring from

subtle signs of need (Mock & Parker 1997). The conflict arises because any gene expressed in offspring, with the potential to influence parental investment, achieves highest inclusive fitness through survival and reproduction of the individual offspring bearing the gene. Conversely, a gene expressed in parents, affecting the parental response to offspring solicitation, has similar chances of being transmitted into future generations through any of its offspring (all else being equal; Trivers 1974). Thus, genes expressed in offspring are often selected to sequester more resources than a parent should invest.

A number of resolution models have been used to seek the probable evolutionary outcome of this arms race between genes expressed in offspring and genes expressed in parents, assuming that parental and offspring strategies are at least partly genetically variable and can (co-) evolve (e.g. Parker & Macnair 1979; Parker 1985; Harper 1986; Godfray 1991, 1995b; reviewed in Godfray 1995a; Mock & Parker 1997). Depending on assumptions made concerning the behavioural interaction between parents and offspring, and the genetic bases of offspring solicitation and parental response, the models predict

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conflict resolutions (evolutionarily stable strategies, ESS) ranging from offspring manipulation of parental investment ('offspring wins' ESS: Parker & Macnair 1978; Parker 1985) to parental control ('parent wins' ESS: Parker & Macnair 1979; Parker 1985) and/or honest signalling of 'need' by the offspring (Godfray 1991, 1995b; Johnstone 1996).

Detailed information about the behavioural interaction between parents and offspring on a phenotypic level is accumulating (Kilner & Johnstone 1996; Mock & Parker 1997; Kölliker et al. 1998; Kölliker 1999). A nutritional component to the level of solicitation by offspring is now experimentally well established for a wide range of species (especially birds; Kilner & Johnstone 1996). A recent suggestion is that nestling birds may also learn to modify their solicitation behaviour according to their parents' feeding style to achieve maximal rewards. They may learn to approach the most profitable positions in the nest (Slagsvold 1997; Kölliker et al. 1998; Budden & Wright 2001) and to beg at the most rewarding begging intensity (Stamps et al. 1989; Kedar et al. 2000; Budden & Wright 2001).

However, only rarely has the genetic basis of offspring solicitation and parental response been investigated, although the genetics of both may strongly influence the phenotypic outcome of the parent-offspring conflict. For example, the resolution of the parent-offspring conflict may be influenced by a genetic covariation of offspring solicitation and parental response (West-Eberhard 1983; Cheverud & Moore 1994; Pagel 1994; Queller 1994; Kölliker et al. 2000), or a parental effect before birth or hatching (Schwabl 1993; Kölliker et al. 2000). These suggestions and the potential consequences of such covariation for the resolution of parent-offspring conflict, for example through a runaway process (West-Eberhard 1983; Pagel 1994; Queller 1994), have not, however, been explicitly addressed in parent-offspring conflict theory.

Without knowledge of the genetic basis of parental and offspring behavioural strategies, theoretical models have to make assumptions about the genetic parameters underlying offspring begging behaviour and the parental responses (Mock & Parker 1997). In addition, empirical studies might risk concluding prematurely that observed variation among individuals in parental and offspring behaviours purely reflects environmental variation, for example variation in food availability or the individuals' health. Thus, one may tacitly accept the assumption that all individuals in the population play the same genetically based strategy (i.e. no genetic variation is maintained), and that the parent-offspring conflict was resolved in the past.

Genetic variability of both offspring begging and parental response is an important, as yet not well-confirmed, assumption in parent-offspring conflict theory (Kölliker et al. 2000). One could argue that genetic variability should have vanished because the conflict was resolved in the past, as expected by resolution models that predict single strategy pairs of offspring solicitation and parental response at evolutionary equilibrium (Parker & Macnair 1979; Harper 1986; Godfray 1991, 1995b). However, the observed variation between broods/litters

in offspring begging and parental response is often substantial and may often have a genetic component (Kölliker et al. 2000). Such evidence requires explanations for the maintenance of genetic variation.

We review the theoretical issues concerning the maintenance of genetic variation underlying offspring solicitation and parental response, the implications of genetic covariation among genes expressed in offspring and parents for conflict resolution and the hypothesis that the coevolution of offspring solicitation and parental response may differ between the maternal and paternal lines. We also review the existing empirical evidence for supporting the presence of genetic variation in offspring and parental behaviours. Since most of these studies were carried out in a psychological or developmental framework (and were published in corresponding scientific journals), our review may also help incorporate this literature into research on parent-offspring conflict.

We define solicitation/begging displays from a functional perspective, that is, as behaviours of the offspring that elicit and regulate parental investment. From a proximate perspective, these can include displays that influence parental food provisioning (e.g. begging of passerine nestlings: Kilner & Johnstone 1996; Kölliker et al. 1998), induce parental brooding (e.g. embryonic squawks of American white pelicans, *Pelecanus erythrorhynchos*: Evans 1992), or regulate parental proximity and shelter (e.g. ultrasonic vocalizations of rodent pups, often interpreted as signals of 'fear': Brunelli et al. 1997).

MAINTENANCE OF GENETIC VARIATION

In the following, we discuss reasons for the maintenance of genetic variation in offspring solicitation and parental response. We do not intend to provide a complete list of all forces capable of maintaining genetic variation in natural populations (for recent accounts see: Falconer & Mackay 1996; Roff 1997). Rather, we concentrate on those factors that from a theoretical viewpoint may have the greatest potential to be relevant in the coevolution of genes expressed in offspring and in parents.

Environmental Variation

Fitness costs to parents of providing a given amount of resources to the offspring are central to the evolutionary conflict between genes expressed in parents and offspring. Without a cost of reproduction there can be no conflict (Trivers 1974), and conflict resolution depends on these costs. Fitness costs of parental investment are likely to vary because of environmental factors (e.g. availability of food, presence/absence of predators, or variation in parental condition) and influence differentially the success of various offspring and parental strategies and thus conflict resolution (Parker & Macnair 1978; Mock & Parker 1997; Davis et al. 1999). As a result, environmental variability may lead to the maintenance of genetic variation because no single strategy does best under all environmental conditions (Parker & Macnair

1978). Alternatively, selection may favour phenotypically plastic strategies, which would allow individuals to cope optimally with changing environments (e.g. Roff 1997). Learning mechanisms (see Introduction) may be considered an example of such phenotypic plasticity.

Life History Variation

The coevolution between levels of offspring solicitation and parental response is embedded in the overall life history of the interacting individuals. Between species, and even at the level of populations among individuals, there is commonly ample variation in parental condition, mating behaviour, predation pressure, investment trade-offs of current versus future reproduction, brood size and parental and offspring survival probabilities, etc. (Lindén & Møller 1989; Roff 1992; Stearns 1992; Kilner 1999). In theory, the evolutionarily stable levels of offspring solicitation and parental responses often depend on variation in such variables, for example the degree of promiscuity (Parker 1985; Godfray 1995b), the relative begging costs from predation versus energy usage (Parker 1985; Godfray 1995b), the relative importance of within-versus between-brood conflict (Parker 1985; Godfray 1995b) and variation in brood size (Harper 1986). Because life history traits are variable in nature and affect, in theory, the coevolution of offspring solicitation and parental response, the variation in life history traits in a population may maintain genetic variation in offspring and parental strategies.

Evolutionarily Unstable Arms Race

Unstable cycling arms races among parental and offspring strategies, rather than evolutionarily stable resolutions, have been proposed repeatedly as a possible 'outcome' of parent-offspring conflict (Stamps et al. 1978; Dawkins & Krebs 1979; Parker & Macnair 1979; Bull 1985). Such an arms race scenario can emerge if (1) responsive parents with demanding offspring are selected to become less responsive in order to prevent exploitation by the offspring, (2) offspring in turn are selected to become less demanding because the cost of exaggerated begging outweighs the benefit with unresponsive parents, (3) more responsive parents are then favoured because of the cost to unresponsive parents of ignoring real needs of the young (Parker & Macnair 1979), and (4) more demanding offspring are selected in turn because the benefit of exaggerated begging outweighs the cost with responsive parents (Parker & Macnair 1979; Bull 1985). Since, in an unstable arms race, several genetic variants of offspring solicitation and parental response strategies occur at any given moment, unstable cycling is a potential source of genetic variation. The direct empirical demonstration of arms races in parent-offspring communication may be difficult because cycles may 'turn' very slowly, that is, over many generations (Parker & Macnair 1979).

An unstable arms race may be expected only if begging is costly. If begging carries insubstantial costs, as certain

signalling models predict (Bergstrom & Lachmann 1998), the arms race may not cycle. Selection on parents to respond less to begging would be followed by offspring maintaining or even escalating their begging. The arms race would thereby at some point become stable.

GENETIC COVARIATION AND CONFLICT RESOLUTION

Genetic covariation between offspring solicitation and parental response may have an important impact on the resolution of parent-offspring conflict, but such covariation has not yet been explicitly included in theoretical models. Nevertheless, possible implications have been put forward in the evolutionary literature (West-Eberhard 1983; Lynch 1987; Cheverud & Moore 1994). In the presence of genetic covariation, external environmental influences on the system can lead to fast evolutionary divergence in parent-offspring communication among populations because of the indirect selection on the correlated trait, as supposed by a general quantitative genetic model of intrafamilial interactions (Lynch 1987). A positive genetic relationship between offspring solicitation and parental response may also result in a runaway process leading to more exaggerated begging displays and higher parental response levels than selection would favour in the absence of genetic covariation (West-Eberhard 1983; Lynch 1987; Cheverud & Moore 1994; Wade 1998). Two scenarios for a runaway process may be relevant. First, the parental response to offspring solicitation in terms of feeding effort may be the driving force for the runaway process. The probable significant fitness costs to parents of increased parental effort may limit the extent to which a runaway process can drive the evolutionary escalation of solicitation levels. The scope for a runaway process may be enhanced, however, if the increase in parental effort caused by offspring solicitation (the begging-dependent parental effort) is associated with a reduction in the baseline, begging-independent, parental effort. The second scenario involves parental preference for offspring begging at higher levels within broods or litters. As total parental effort here does not depend on solicitation, the cost of parental response may be less significant in limiting a runaway process.

Alternatively to the runaway hypothesis, covariation between offspring solicitation and parental response may reflect the underlying variation in genetic 'quality' if variation in both of these is genetically related to 'quality'. This would suggest that parents, by preferentially provisioning offspring begging at higher levels, may select not only for signals of 'need', but also for signals of offspring genetic quality (Queller 1994), for example parasite resistance (Møller 1990), or viability (Lyon et al. 1994; Lumma et al. 1998). However, no explicit models for a runaway process, or parental selection of offspring genetic quality, currently exist for parent-offspring communication (Queller 1994).

With a genetic correlation between levels of offspring solicitation and parental response, Hamilton's rule (Hamilton 1964), on which current resolution models of parent-offspring conflict are based, does not correctly

define the conditions for the spread of genes affecting offspring solicitation and parental responses (Lynch 1987; Eshel & Feldman 1991; Cheverud & Moore 1994). For example, a population genetic model of parent-offspring conflict predicted that exaggerated begging is less likely to evolve when linkage with the locus for parental response is tight (Eshel & Feldman 1991). In a general quantitative genetic model of altruistic behaviour, Cheverud & Moore (1994) predicted that positive genetic covariances between donor behaviour (e.g. parental response) and recipient behaviour (e.g. offspring solicitation) tend to favour higher levels of altruism (e.g. parental response) than would be predicted from Hamilton's rule alone. On the other hand, negative covariances may lead to lower than expected levels of parental response (Cheverud & Moore 1994).

COEVOLUTION OF PARENTAL AND OFFSPRING GENES

Selection pressures on female and male behavioural strategies during reproduction can differ widely (Hrdy 1999), and differences between the sexes in their reproductive roles are common (Clutton-Brock 1991). Such sex differences in parental behaviour may be further enhanced by the sexual conflict over parental investment (Trivers 1972). Thus, one may expect coevolution between genes expressed in offspring (affecting their begging level) and genes expressed in mothers and fathers (affecting their responses to begging) to follow different trajectories in the maternal and paternal lines (Godfray 1995b; Kölliker et al. 2000).

In mammals, the conflict of interest between genes expressed in the mother and the offspring may select for overexploitation of maternal resources by offspring while still in the uterus (Haig 1992, 1993). Thus, both offspring solicitation after birth and the maternal response are potentially influenced by the outcome of the parent-offspring conflict in the uterus. In birds, the development of the embryo starts mainly after all the maternal resources have been allocated to the egg (Winkler 1993; Williams 1994). Thus, chick begging after hatching cannot be directly influenced by the offspring itself before hatching through extraction of maternal resources during egg formation. Bird mothers may therefore have more control over resource allocation before birth than mammalian mothers, although selection on bird embryos might modulate the sensitivity of embryonic tissues to maternal hormones or nutrients in the offspring's favour (Winkler 1993).

In both mammals and birds females generally interact with the offspring earlier before birth, and mostly for a more extended period, than males. Thus, reciprocal selection pressures may in most cases be more important in the maternal line than in the paternal line because of the longer exposure of offspring strategies to mothers and of maternal strategies to offspring.

In an extension of Godfray's (1991) model of honest signalling of 'need', Johnstone (1996) allowed the interaction between a parent and its offspring to be preceded by an a priori and costly parental investment. Contrary to

the original model of honest signalling of 'need' (Godfray 1991), the model predicts that parents are not investing at their own optimal level, but that rather a compromise between parental and offspring interest would be expected at evolutionary equilibrium (Johnstone 1996). The model might be of biological relevance not only as an extension of Godfray's (1991) model and its assumption of independence of successive feeding events, but may also relate to the initial costly investment by female mammals and birds during gestation and egg laying, respectively. Because only females make such a costly initial investment in offspring, the model suggests that the outcome of the conflict between genes expressed in mothers and offspring may tend more towards a compromise resolution than the outcome of the conflict between genes expressed in fathers and offspring. Fathers may have more control over conflict resolution than mothers.

Another asymmetry between the sexes arises through extrapair matings (Birkhead & Møller 1992). Some fathers have to invest in unrelated young (the 'cuckolded' males) and some produce offspring they do not have to care for (the 'cuckolder' males), whereas mothers mostly invest in their own offspring. As a consequence for young competing for parental resources in the same nest or litter, they are less likely to share genes of paternal than maternal origin. In addition, genes expressed in fathers affecting their response to begging have a lower probability of being present in the young in which they invest than the genes expressed in mothers. Thus, selection may favour both a higher equilibrium solicitation level and a lower parental response level in the paternal line than the maternal line.

Asymmetries in reproductive strategies between the sexes may select for inheritance mechanisms where the expression of genes depends on the descent of genes through maternal or paternal lines. Different (sets of) genes affecting the parental response may be expressed in mothers and fathers (i.e. sex-linked gene expression), and the expression of genes in offspring, influencing solicitation levels, may depend on the parental origin of the genes (i.e. genomic imprinting, Haig 1992, 1993).

GENETIC VARIATION IN OFFSPRING SOLICITATION

'Peeping' of Chicks

The precocial young of chickens, *Gallus gallus domesticus*, emit 'peep' vocalizations, and mainly do so when the hen is absent (Bermant 1963). 'Peeping' may thus reflect the chick's solicitation for proximity of the mother (Webster & Hurnik 1987). Genetic variation for the rate of 'peeping' by chicks has been suggested for White Leghorn-like commercial stocks, in experiments using a paternal half-sibling breeding design (two hens artificially inseminated by the sperm of one rooster per replicate). While significant between-dam variation was found, the between-sire component of variance was not significant (Webster & Hurnik 1987; Table 1). The authors explained this discrepancy either by maternal effects, or the lower genetic variation among roosters

Table 1. Evidence for genetic variation in offspring solicitation

Species	Behaviour	Design*	Heritability estimate	Potential confounding effects and problems	Population	Source
Birds						
Domestic hen, <i>Gallus gallus domesticus</i>	'Peep' vocalization rate	HSB	Between sires: 0; Between dams: 0.46†/0.25†/0.21†	Maternal effects in the egg; low genetic between-sire variability; artificial breeding history	Commercial breed (white Leghorn)	1
Barn swallow, <i>Hirundo rustica</i>	Begging call duration	WFC	0.98†	Maternal effects in the egg; common rearing environment	Natural population	2
Cliff swallow, <i>Hirundo pyrrhonota</i>	Begging call duration	WFC	0.54	Maternal effects in the egg; common rearing environment	Natural population	2
Great tit, <i>Parus major</i>	Vocal begging intensity	CF	0.52†/0.40†	Maternal effects in the egg; common rearing environment on 1st day after hatching	Natural population	3
Mammals						
Rat, <i>Rattus norvegicus</i>	Ultrasonic calling rate	CF	(No estimate)†	Maternal effects during gestation; artificial breeding history; small sample size	Artificially bred strain	4
Rat	Ultrasonic calling rate	AS	(No estimate)†	Artificial breeding history; inbreeding	Artificially bred strain	5
Mouse, <i>Mus domesticus</i>	Ultrasonic calling rate	SC; SCB	0.51†	Artificial breeding history; inbreeding	Artificially bred strains	6
Mouse	Ultrasonic calling rate	SC; SCB	(No estimate)†	Artificial breeding history; inbreeding	Artificially bred strains	7
Mouse	Parental handling time received by pups	SC; CF	(No estimate)†	Maternal effects during gestation; inbreeding; artificial breeding history; begging behaviour not measured	Artificially bred strains	8
Mouse	Incidence of receiving spontaneous care	SC; CF	(No estimate)†	Maternal effects during gestation; inbreeding; artificial breeding history; begging behaviour not measured	Wild mice reared in lab; inbred strains	9
Domestic sheep, <i>Ovis</i> spp.	Lamb bleat rate	SC; CF; ET	(No estimate)†	Artificial breeding history	Commercial breeds	10
Human	Cry duration	REP	(No estimate)†	Environmental variation; maternal effects during pregnancy	2–3-day old, bottle-fed healthy babies	11

(1) Webster & Hurmik 1998; (2) Medvin et al. 1992; (3) Kölliker et al. 2000; (4) Graham & Letz 1979; (5) Brunelli et al. 1997; (6) Hahn et al. 1987; (7) Roubertoux et al. 1996; (8) Ressler 1962; (9) Jakubowski & Terkel 1982; (10) Dwyer et al. 1998; (11) Komer 1974.

*HSB: half-sibling breeding design; WFC: within-family correlation; CF: cross-fostering; AS: artificial selection; SC: strain comparison; SCB: strain cross breeding; REP: repeatability.

†Statistically significant genetic effects.

than among hens. The roosters had previously been subjected to intense artificial selection and inbreeding, while the hens had been randomly bred (Webster & Hurnik 1987).

Begging Calls of Altricial Nestlings

Nestling birds often call vigorously for food during parental visits (Kilner & Johnstone 1996; Kölliker et al. 1998), but also when the parents are absent (Christe et al. 1996; Price et al. 1996; Roulin et al. 2000), and hungry nestlings generally beg at higher intensities (Kilner & Johnstone 1996; Kölliker et al. 1998). Parents mostly respond to the begging calls by increasing their feeding efforts (Ottosson et al. 1997; Burford et al. 1998; Davies et al. 1998; Price 1998; Wright 1998; Kölliker et al. 2000).

Phylogenetic tests of divergent evolution of the intensity of begging displays have been carried out for the predicted negative correlations between (1) the begging intensity of nestlings and average nestmate relatedness, and (2) the begging intensity and predation pressure (Parker & Macnair 1978; Godfray 1995b). In accordance with the first prediction, the nestlings of species with a high incidence of extrapair paternity, where relatedness among nestmates is low, beg more loudly (Briskie et al. 1994) and have redder gapes (limited to species nesting at sites with sufficient light; Kilner 1999) than the nestlings of species with low extrapair paternity. The second prediction was supported by the demonstration of a negative relationship among species between begging call loudness and the estimated predation rate on the nestlings (Briskie et al. 1999). By explaining current variation in begging display levels among independent phylogenetic groups, these studies indirectly suggest genetic variation in the begging call intensity of nestlings in past populations of common ancestors.

In several bird species nestlings resemble their nestmates in call duration and/or intensity (Table 1). However, simple within-brood correlations as means to estimate genetic components of variation are confounded with the rearing environment, which is especially relevant for begging displays where an important environmental component of nestling resource 'need' has been shown repeatedly (Hussel 1988; Kilner & Johnstone 1996; Kölliker et al. 1998). Cross-fostering eggs or newly hatched chicks between broods can greatly reduce this problem, because variation in the rearing environment is randomized before biological siblings are compared. Such a study has recently been carried out in two populations of great tits, *Parus major* (Kölliker et al. 2000; Table 1). Newly hatched chicks were partially cross-fostered between broods. The begging calls of individual nestlings at 10 days old were recorded under controlled laboratory conditions. Between 20 and 26% (depending on the population) of the variation between individual nestlings in their begging call intensity could be attributed to their common origin, suggesting an estimate of genetic variation in the range of 40–52% (Table 1). Because possible parental or environmental effects before the nestlings hatched could not be completely ruled out (see

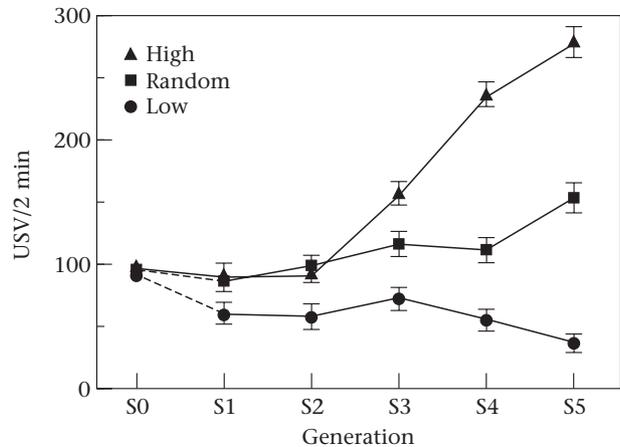


Figure 1. Results from an artificial selection experiment on ultrasonic calling rate of Norway rat pups. S0–S5 refer to the number of generations in the selection experiment (S1=first generation after artificial selection started). The average number of ultrasonic vocalizations (USV)/2 min is shown. The high and low lines were established by selecting in each generation the most deviant individuals from within litters for mating, and the control line was maintained by randomly choosing individuals for breeding. From Brunelli et al. 1997. Five generations of selective breeding for ultrasonic vocalization (USV) responses in *N:NIH* strain rats. *Developmental Psychobiology*, 31, 255–265. Copyright © 1997 John Wiley & Sons, Inc. Reprinted by permission of S. A. Brunelli and John Wiley & Sons, Inc.

Limitations of empirical studies), the estimates refer to upper limits.

Ultrasonic Vocalizations of Rodent Pups

Rodent pups emit ultrasonic begging calls when separated from the parents, in particular at low temperature and when hungry (Noirot 1972; De Gheff 1974; Graham & Letz 1979; Jans & Leon 1983; Brunelli et al. 1997). Parents respond to the calls by approaching, retrieving and nurturing their young (Noirot 1972; De Gheff 1974; Smotherman et al. 1978; Kleese & Hull 1980). In rats, a cross-fostering study (including a sample of three litters), where newly born pups were exchanged between mothers, showed that the common origin, but not the rearing environment, had a significant influence on the rate of ultrasonic calling by pups. This again suggests that genetic variation explains some of the variation in begging calls (Graham & Letz 1979; Table 1).

The only artificial selection experiment on a begging display currently available has been carried out in rats, *Rattus norvegicus*, based on a genetically heterogeneous breeding stock (*N:NIH* strain; Brunelli et al. 1997; Table 1). Three lines were established by selecting individuals for both high and low ultrasonic calling rate of pups, and by maintaining a random-bred control line. The three artificial selection lines diverged quickly (Fig. 1), and highly significant differences between lines in the ultrasonic calling rate of pups were found after only three generations (Brunelli et al. 1997; Fig. 1). The selection lines on average continued to diverge for up to 13 generations (S. A. Brunelli, personal communication). This

study clearly shows that the ultrasonic calling rate of rat pups responds to artificial selection and thus has a heritable component. The selective breeding was based on the most deviant individuals from within litters (Brunelli et al. 1997), implying that the young ending up in different selection lines had on average experienced the same maternal environment. Thus, the observed responses to selection may largely be independent of maternal effects (Falconer & Mackay 1996), assuming no differential investment by rat mothers during gestation according to pup genotype.

In mice, *Mus domesticus*, significant variation among inbred strains in the ultrasonic calling rate of pups has been observed repeatedly (Roubertoux et al. 1990). Two studies used crosses between such strains to test for the presence of a genetic component. Individuals from pairs of different inbred lines (BALB/c × DBA/2J, Hahn et al. 1987; CBA/H × NZB/B1NJ, Roubertoux et al. 1990; Table 1) were measured for their ultrasonic calling rate, cross-bred and their F1 offspring, as well as the offspring of a variety of back-crosses, were tested for their ultrasonic calling behaviour. Both studies showed significant genetic variation for ultrasonic calling rate of pups among strains, and revealed complex genetic backgrounds, such as directional dominance, epistasis and parental effects (Hahn et al. 1987; Roubertoux et al. 1990).

Bleating of Lambs

In sheep, *Ovis* spp., the bleating of newly born lambs has an important function in regulating maternal proximity shortly after birth. Different breeds of sheep vary in the rate of lamb bleating (Dwyer et al. 1998). In an embryo transfer study between Scottish Blackface and Suffolk breeds, the embryos originating from the two breeds were, 6 days after artificial insemination, transferred to ewes from the same and the other breed, respectively (Dwyer et al. 1998; Table 1). The bleat rate of the lambs was then measured shortly after birth. Suffolk lambs had significantly higher bleat rates than Blackface lambs, independent of the ewe's breed (Table 1). As this study controlled for maternal effects during gestation by cross-fostering embryos shortly after fertilization, it shows genetic variation in the rate of lamb bleating between these two breeds of sheep.

Crying of Human Babies

The crying of human babies induces physiological stress responses in their parents (Wiesenfeld & Zander Malatesta 1983), and elicits caring behaviour (Lumma et al. 1998). Measures of the intensity of the crying of human neonates (e.g. duration, rate and frequency) differ significantly between individual neonates (Korner 1974; Barr 1993; Furlow 1997; Table 1). Extensive and persistent crying can be characteristic of certain babies, a phenomenon also known as the 'colic syndrome' (Barr 1999). There is often no medical indication for obvious physical deficiencies or needs of such neonates (Barr 1999). Thus, individual differences in the intensity of baby crying exist

(Table 1), but these may contain not only genetic, but also maternal or nonobvious nutritional, components of variation.

GENETIC VARIATION IN PARENTAL RESPONSE

Variation in parental behaviour between species, and between individuals of the same species is common (Clutton-Brock 1991). Attempts to disentangle experimentally the common rearing environment from shared genes is more difficult for parental responses than for offspring solicitation behaviours, because mortality and dispersal between birth and breeding in natural populations may often limit the sample of related individuals that can be compared (Kölliker et al. 2000). This may explain why good evidence for genetic variation in parental behaviour, or response to offspring solicitation, is even more scant than in the case of offspring solicitation displays. Thus, there is often only indirect evidence for genetic variation in parental behaviour available, which may not be free of environmental effects. In addition, most studies reporting genetic variation in parental behaviour refer to absolute, begging-independent levels of effort, rather than responses to offspring solicitation behaviours.

Response to Begging Calls in Great Tits

In the cross-fostering experiment on great tits, the response of mothers (determined from begging playback experiments) and the begging call intensity of their offspring reared in foreign nests were significantly correlated (Kölliker et al. 2000; Table 2), suggesting genetic covariation. It could be excluded statistically that the covariation arose indirectly via maternal condition (Kölliker et al. 2000). The covariation can, if truly genetic (early environmental or parental effects may be an alternative explanation: Kölliker et al. 2000), arise only if both begging call intensity and maternal response have a genetic component (Falconer & Mackay 1996; Roff 1997). Because only the former could be estimated, the demonstration of both a genetic component in the begging call intensity of nestlings and a significant origin-related covariation with maternal response indirectly suggests genetic variation in the maternal response to begging calls.

Rodent Care for Pups

In mice, differences between strains in levels of parental care behaviours have been observed repeatedly (e.g. Ressler 1962; Jakubowski & Terkel 1982; Cohen-Salmon et al. 1985; Table 2), suggesting genetic variation among strains. One study used a reciprocal cross-breeding design among house mice from a wild-type and an inbred laboratory stock (CF-1), and measured the incidence of spontaneous care-taking behaviour towards unrelated test pups of the F1 offspring (Perrigo et al. 1993; Table 2). Mice with wild-type mothers overall had lower incidence of care-taking behaviour than mice with CF-1 mothers. The effect of the father's genotype on

Table 2. Evidence for genetic variation in parental (response) behaviour

Species	Behaviour	Design*	Heritability estimate	Potential confounding effects and problems	Population	Source
Birds						
Great tit, <i>Parus major</i>	Mother response to begging playbacks	CF	(No estimate)	Indirect evidence: origin-related covariation with vocal begging intensity of biological offspring (Table 1); maternal effects	Natural population	1
Mammals						
Mouse, <i>Mus domesticus</i>	Parental handling time given to pups	SC; CF	(No estimate)†	Maternal effects during gestation; common rearing environment; inbreeding; artificial breeding history	Artificially inbred laboratory strains	2
Mouse	Lactation activity	HSB; CF	0.30†	Artificial breeding history	Outbred laboratory strain	3
Mouse	Retrieval of pups	SC	(No estimate)†	Inbreeding; artificial breeding history	Inbred strains	4
Mouse	Incidence of spontaneous caretaking	SC; CF	(No estimate)†	Maternal effects during gestation; common rearing environment; inbreeding; artificial breeding history	Wild mice reared in laboratory; inbred strains	5
Mouse	Incidence of spontaneous caretaking	SC; SCB; CF	(No estimate)†	Inbreeding; artificial breeding history	Artificially bred wild mice; inbred strains	6
Domestic sheep, <i>Ovis spp.</i>	Ewe low-pitched bleat rate	SC; ET; CF	(No estimate)†	Maternal effects during gestation; common rearing environment; artificial breeding history	Commercial breeds	7
Domestic sheep	Lamb acceptance; grooming	SC	(No estimate)†	Maternal effects during gestation; common rearing environment; artificial breeding history	Commercial breeds	8
Domestic sheep	Ewe response to lamb bleating playbacks	SC	(No estimate)†	Maternal effects during gestation; common rearing environment; artificial breeding history	Commercial breeds	9

(1) Kölliker et al. 2000; (2) Ressler 1994; (3) Strózik 1989; (4) Cohen-Salmon et al. 1985; (5) Jakubowski & Terkel 1982; (6) Perrigo et al. 1979; (7) Dwyer et al. 1998; (8) Dwyer & Lawrence 1998; (9) Shilito-Walser et al. 1996.

*HSB: half-sibling breeding design; CF: cross-fostering; ET: embryo transfer; SC: strain comparison; SCB: strain cross breeding.

†Statistically significant genetic effects.

the occurrence of care-taking behaviour was detectable only in combination with wild-type mothers and in female offspring, suggesting complex inheritance patterns which possibly include dominance (CF-1 dominant over wild-type) and sex-specific gene expression (Perrigo et al. 1993). In another study, several female mice from an outbred laboratory stock were mated with the same male for each replicate (Strózik 1985; Table 2). The offspring (paternal half-siblings) were cross-fostered shortly after birth, and the paternal half-sisters' maternal behaviours were quantified and compared as adults. By comparing the behaviours of paternal half-sisters reared by unrelated foster mothers, this design controlled for environmental and most parental effects (except maternal effects during gestation that depend on the genotype of the male mate). The detected significant between-sire variation for lactation activity (Table 2), that is, the time spent crouching over test pups in the lactation position, strongly suggests heritable variation for this parental behaviour in female mice (Strózik 1985).

Modern molecular techniques have allowed researchers to search for single genes that are causally involved in the expression of maternal care behaviours. The targeted inactivation of the gene *fosB* had the effect that mouse parents stopped retrieving and nurturing their young, which nearly invariably resulted in the neglected pups' early death (Brown et al. 1996). The gene *Mest* (also known as *Peg1*) is imprinted (expressed only when inherited by the father) and its inactivation resulted in a strong reduction in nest-building and pup-retrieval behaviour (Lefebvre et al. 1998). The mothers carrying the inactivated *Mest* gene had pups with low viability. The inactivation of the gene *Peg3* (also known as *Pw1*), another paternally expressed locus (Li et al. 1999), had similar effects on maternal behaviour. Other genes currently known, whose products affect the maternal retrieval response to experimentally separated pups, are the ones encoding for dopamine β -hydroxylase (Dbh) (Thomas & Palmiter 1997), the prolactin receptor (PRL-r) and the oestrogen receptor (see Bridges 1998 and references therein). While these studies show that the expression of a number of single genes is necessary for the development of parental behaviour in female mice, it is not known whether different alleles (i.e. genetic variation) exist for any of these genes.

Ewe Responses to Lamb Bleating

In sheep, breeds differ significantly in the acceptance of, and time spent grooming, newborn lambs (Dwyer & Lawrence 1998; Table 2). In addition, ewes vocalize in response to lamb bleating by emitting low-pitched vocalizations. Variation among ewes in the rate of these vocalizations may be related to maternal ability or willingness to invest in the lamb (Dwyer et al. 1998). Significant between-breed variation in the rate of low-pitched vocalization was demonstrated in a comparison of Blackface and Suffolk ewes (Dwyer et al. 1998; Table 2). In a study on three other breeds of sheep (Border Leicester, Jacob, Soay), significant between-breed

variation in the ewes' response to playbacks of lamb bleating was found (Shillito-Walser et al. 1981; Table 2).

GENETIC COVARIATION

Genetic covariation of offspring solicitation and parental response has rarely been investigated. Indirect empirical evidence for it is provided by one study on mice where pups of two strains were cross-fostered. BALB/c parents cared more for pups than C57BL parents, independent of pup genotype (Table 2), and BALB/c pups received more care independent of the parent's genotype than C57BL pups (Ressler 1962), suggesting positive genetic covariation among strains between the pups' ability to induce and parental inclination to perform care. However, another study found less clear patterns of covariation when comparing other mouse strains with similar experimental designs (Cohen-Salmon et al. 1985). Conversely, ewes from responsive sheep breeds (Scottish Blackface) give birth to lambs bleating at a lower rate than ewes from less responsive breeds (Suffolk), suggesting negative covariation between these two breeds (Dwyer et al. 1998).

More direct evidence for genetic covariation between offspring solicitation and parental response is scant and more experimental work is needed. A recent study has investigated the covariation experimentally in a natural population using a cross-fostering design in great tits (Kölliker et al. 2000). A positive origin-related covariation between the maternal response and the begging call intensity of her genetic offspring reared in foreign nests was found, suggesting positive genetic covariation. Again, given the limitations intrinsic to cross-fostering designs (see Limitations of empirical studies), the study cannot fully rule out environmental or parental effects during egg laying and incubation as an alternative explanation (Kölliker et al. 2000).

PARENTAL EFFECTS

Persistent differential effects of mothers before the birth of offspring, that is, maternal effects, on the expression of offspring solicitation behaviours after birth have been reported in both mammals and birds. Before birth females transfer nutrients (Haig 1993; Williams 1994), hormones (Haig 1993; Schwabl 1993, 1996) and antibodies (Heeb et al. 1998; Roulin & Heeb 1999) to their offspring, which may affect the level of offspring solicitation after hatching or birth either directly or indirectly via the health or condition of the hatched/newborn young. It has been shown experimentally that the begging duration of canary, *Serinus canaria*, chicks shortly after hatching is significantly affected by the amount of testosterone (known to be transferred from canary mothers to the eggs; Schwabl 1993) in the egg yolk (Schwabl 1996). Young hatching from eggs injected with testosterone begged for longer than control young.

The suggestion that the coevolution of offspring begging and parental response to begging may differ between the maternal and paternal lines was recently supported by

Kölliker et al. (2000). Only great tit mothers significantly responded to nestling begging calls in playback experiments, and in the maternal line only a (positive) origin-related covariation of nestling begging call intensity and maternal response was found, with no significant relationship in the paternal line. One explanation of this result is a genetic covariation between nestling begging call intensity and parental response that is expressed in the maternal line only. This interpretation would suggest that different (sets of) genes are expressed in great tit mothers and fathers, and that the maternally expressed loci are linked to the loci expressed in the offspring (see Kölliker et al. 2000).

LIMITATIONS OF EMPIRICAL STUDIES

Cross-fostering young animals shortly after birth is a powerful tool to reduce or eliminate the effect of the common rearing environment on offspring solicitation behaviour and to control for a nonrandom distribution of genotypes in the habitat (Roff 1997). However, the common environment before birth (e.g. in the egg or uterus), or during the first few hours after birth, often cannot be controlled experimentally (but see Dwyer et al. 1998). Parental effects before the cross-fostering may therefore inflate the estimated genetic component of variation. A further experimental restriction in cross-fostering designs, but with conservative effects on the estimation of genetic components of variation, results from the necessity of exchanging young animals between broods or litters of approximately the same age. This procedure excludes the measurement of the potential genetic variation related to birth date.

Behavioural differences between breeds or strains suggest that genetic differences between breeds are responsible for differences in offspring or parental behaviour. However, such differences may be due to the artificial breeding history, and extrapolations to natural conditions may be difficult to make. Many breeds or strains (especially in mice) are derived from small founder populations, often single breeding pairs, and have been maintained through intense inbreeding such as brother-sister matings. Any random mutation present in the small founder population, or occurring during the course of breeding, which would be deleterious under natural conditions, might have been maintained in the strain only through the intense artificial inbreeding. The problem of accumulated deleterious mutations in the gene pool of artificial strains is indicated by the high incidence of developmental problems, such as tumours, in some mouse strains.

Targeted mutations can disrupt the expression of a specific gene, leading to nonfunctional gene products. The lack of functional gene products, however, is probably very different in biological meaning from natural variation in functional gene products. The complete disruption of a gene's expression might result in major developmental disorders in the animal, for example if its product is required for the regulation of other genes' expression. It may then not be surprising that such a mutant individual is unable to reproduce successfully.

Studies investigating the divergent coevolution of offspring solicitation and parental response between the maternal and paternal lines are confronted with the problem of nonindependence of maternal and paternal responses to begging when both parents feed their young. Such effects may blur a sex difference in the parental response to offspring solicitation, if parents respond not only to begging, but also to each other's feeding efforts. Ideally, studies should control experimentally for such effects, or specifically address the question of how females and males adjust their own responses to both their offspring's begging and their mate's response to begging.

FUTURE DIRECTIONS

Both verbal arguments and empirical evidence suggest that a runaway process, the signalling of genetic quality and the divergent coevolution of offspring solicitation and parental response between the parental lines are at least possible. These evolutionary processes have not explicitly been included in the theory of parent-offspring conflict and the coevolution of offspring solicitation and parental response. Thus, it is not yet fully understood how the consideration of these processes will change our current view on conflict resolution. Formal models are now required to investigate the evolutionary causes of these processes and the extent to which they can influence conflict resolution and the coevolution of the behaviours involved.

The existing empirical evidence for genetic variability in offspring solicitation and parental response confirms the fundamental assumption of the theory of parent-offspring conflict that behaviours involved in the evolutionary resolution of the conflict are genetically variable. However, we also emphasize that much of the currently available empirical evidence is indirect and cannot fully exclude alternative interpretations. Thus, further empirical research on the genetic bases of offspring solicitation and parental response are needed. Given that these behaviours are highly sensitive to environmental factors, well-designed experiments will be required to disentangle genetic variation and environmental and/or parental effects.

CONCLUSIONS

Empirical research on the evolutionary aspects of parent-offspring interaction has until recently focused on phenotypic predictions of theoretical models. We hope to stimulate with this review an approach to the study of parent-offspring conflict that incorporates both the phenotypic and the genotypic level. The potential benefits that may be derived from such an integrated approach is demonstrated in the research on sexual conflict and the evolution of elaborate male ornaments and female choice. Knowledge of the nature of behavioural/phenotypic interactions between females and males during mate choice and the genetic bases of male ornaments and female preferences have both been of central

importance to the understanding of the evolution of male ornaments and female preference (e.g. Andersson 1994; Bakker & Pomiankowski 1995).

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