

SEX-BIASED PARENT-OFFSPRING CONFLICT

by

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(With 5 Figures)
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Summary

In species showing sexual dimorphism, parents may obtain different fitness returns per unit of parental expenditure from sons and daughters. Under these circumstances, parents are expected to invest extra resources in offspring of the most profitable sex. However, it is unclear whether sex-biased expenditure is the result of selection acting on parents, their offspring, or both. Current parent-offspring conflict theory is used to investigate whether sex biases in parental expenditure should be accompanied by sex biases in parent-offspring conflict. It is suggested that, in general, greater conflict should be expected between parents and offspring of the favoured sex. Specifically, greater conflict is predicted among mother-son dyads than among mother-daughter dyads in most polygynous birds and mammals. Data on domestic sheep, as well as empirical evidence available for other species (mainly ungulates), lends support to the prediction. The prediction is further extended to cercopithecine primates, a group which lacks clear sex-biases in parental investment. In this case, differences in fitness returns per unit of parental expenditure between the daughters of dominant and subordinate mothers are positively related to differences in the extent of mother-daughter conflict. The results from this study highlight the important role that selective pressures acting on the offspring phenotype may have played in the evolution of sex-biased patterns of parental investment.

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Introduction

FISHER (1930) argued that, among natural populations, natural selection would favour equal parental expenditure in male and female offspring. More recent models have addressed the issue of whether, within populations, individual females would be expected to bias their investment towards males or females. These models have shown that, when brood size is small and a given amount of parental expenditure affects the reproductive success of male and female offspring differently, deviations from the 1:1 ratio should be expected (CHARNOV, 1982; FRANK, 1987, 1990). Implicit in these considerations is the assumption that parental resources expended in current offspring ('parental input' PI (EVANS, 1990) or 'parental expenditure' in CLUTTON-BROCK's (1991) terminology) are limited, so that expenditure on a given offspring reduces the parent's residual reproductive value to an extent referred to as parental investment (TRIVERS, 1972; CLUTTON-BROCK, 1991).

One way in which parents can bias their investment is by allocating more resources to individual offspring of one sex during the pre-weaning period. Two models have examined the conditions under which differential investment should be expected, and have predicted in which direction it should be biased, leading virtually to the same prediction (FRANK, 1987). TRIVERS & WILLARD (1973) suggested that, when PI affects offspring reproductive success, mothers who can afford to invest heavily (*i.e.* mothers in good physical condition) should invest more in the sex with greater variance in reproductive success, or in the sex whose reproductive success will be influenced by that investment to a greater extent (see CLUTTON-BROCK & ALBON, 1982). On the other hand, MAYNARD SMITH (1980) concluded, from a game-theory approach, that in populations with a 1:1 sex ratio where parents can recognize offspring sex and offspring benefit differently from PI according to their sex, it is an ESS to allocate greater PI in offspring of the sex suffering a higher mortality rate and/or which benefits more from higher amounts of investment under frequency-dependent selection. In most polygynous mammals, these models predict that mothers should invest more heavily in males, since males have a greater variance in reproductive success than females (CLUTTON-BROCK, 1988) and maternal investment has a considerable influence upon male reproductive success (CLUTTON-BROCK *et al.*, 1986, 1988). In addition, differential investment towards offspring of the non-dispersing sex is predicted under conditions of local resource competition even for non-polygynous animals, provided that offspring receiving extra investment

are likely to gain an advantage in future competitive interactions with members of the same sex (CLARK, 1978; FRANK, 1990).

A growing body of evidence shows that in polygynous mammals mothers do invest more heavily in sons (REITER *et al.*, 1978; CLUTTON-BROCK *et al.*, 1981, 1982; COSTA & GENTRY, 1986; LEE & MOSS, 1986; ANDERSON & FEDAK, 1987; WOLFF, 1988; BOYD & McCANN, 1989; LE BOEUF *et al.*, 1989); as a consequence mothers incur greater survival and reproductive costs when they raise males. These trends are, however, not common to all polygynous mammals. In some cercopithecine primates, maternal attributes, such as dominance rank, influence offspring reproductive success to a great extent. The evidence regarding differential pre-weaning investment in these species is rather contradictory, but recent studies suggest that complex interactions between maternal rank and infant sex may be involved (GOMENDIO, 1990). In this case, male body size is not an important determinant of reproductive success (PACKER, 1977; FEDIGAN, 1983; reviews in SILK, 1987 and WALTERS & SEYFARTH, 1987). Among birds, some studies in polygynous icterids have also reported greater investment towards male nestlings (FIALA & CONGDON, 1983; TEATHER & WEATHERHEAD, 1988; YASUKAWA *et al.*, 1990).

Theoretical models have suggested that, in sexually reproducing species, parents and offspring should be expected to disagree over the amount of PI (TRIVERS, 1974; MACNAIR & PARKER, 1978, 1979; PARKER & MACNAIR, 1978, 1979; STAMPS *et al.*, 1978; STAMPS & METCALF, 1980; PARKER, 1985; LAZARUS & INGLIS, 1986). This conflict would be the result of a genetic conflict of interests between parents and offspring. Parental benefits gained from a given amount of PI should be, on average, half those gained by the offspring while costs incurred by the offspring are equal or less than those incurred by parents (LAZARUS & INGLIS, 1986). As a consequence, PI optima for the offspring will exceed parental optima and offspring will be selected to demand more PI and for longer than parents have been selected to provide. Parent-offspring conflict at the genetic level is likely to become expressed as behavioural conflict at the phenotypic level (TRIVERS, 1974, 1985) characterized by conspicuous soliciting and sneaking behaviour by offspring and rejecting behaviour by parents. A likely solution for this conflict is that parents will give more PI than their optimum (but less than the offspring's optimum) in response to solicitation ('*pro rata*' compromise, PARKER & MACNAIR, 1979). Empirical evidence for the existence of an overt conflict between parents and their offspring has been recently summarized by CLUTTON-BROCK (1991).

Given that parents and offspring disagree over the benefits of PI

(LAZARUS & INGLIS, 1986), it is worth asking whether sex should affect the intensity of the conflict between parents and their offspring in species where variations in PI affect the reproductive value of sons and daughters differently. To formalize how parents and offspring should interact in species showing sex-biased PI is not a trivial matter. MAYNARD SMITH (1980) already realized that, from an operational perspective, the main problem of a theory of differential sexual investment is to distinguish between the hypothesis it proposes and the hypothesis that offspring are differentially competing for resources with their parents or each other. Many others have wondered whether an observed pattern of differential PI should be explained in terms of parents promoting it or offspring of the favoured sex being more successful at garnering parental resources (PRATT & ANDERSON, 1979; KOVACS & LAVIGNE, 1986; LEE & MOSS, 1986; OFTEDAL *et. al.*, 1987; CLUTTON-BROCK, 1991). In many parasitic Hymenoptera, there is good evidence that parents vary the resources available to sons and daughters (KING, 1987). However, in species where parents and offspring interact during the period of parental care (as in most altricial birds and mammals), the situation is far less clear (CLUTTON-BROCK, 1991).

In theory, the ability of any party to shift the level of PI transferred towards its own optimum should depend on the relative pressures derived from fitness changes associated with deviations of PI from each optimum (LAZARUS & INGLIS, 1986; CLUTTON-BROCK, 1991). Parent-offspring conflict theory thus provides a suitable theoretical framework for testing the possibility that observed patterns of sex-biased PI are, at least in part, the result of stronger selection for conflicting behaviour in offspring of the favoured sex.

In this paper we suggest that parent-offspring conflict is expected to vary according to offspring sex when fitness returns per unit of investment are different for male and female offspring. Although, for simplicity, the following considerations are deliberately restricted to polygynous dimorphic species in which males have an additional frequency-dependent component of fitness related to intrasexual competition for females, they also apply to situations of local resource competition in monomorphic species. Rather than developing a formal theoretical model of parent-offspring conflict in species with sex-biased PI, we rely on predictions made by previous models (PARKER & MACNAIR, 1978; LAZARUS & INGLIS, 1986). To avoid making this paper too extensive and redundant, the original models will not be commented here in detail. We encourage readers to refer to them and, in particular, to the summarized versions

given in PARKER (1984, 1985), CLUTTON-BROCK (1991) and GODFRAY & PARKER (1991). Finally, we also review evidence of sex-biased parent-offspring conflict in species of birds and mammals showing differential investment by sex.

Parent-offspring conflict in species with sexual dimorphism

Models of parent-offspring conflict are aimed at identifying the conditions under which conflicting traits can spread, and the resulting evolutionary equilibrium, by analyzing changes in parental and offspring inclusive fitness resulting from behavioural adjustments by the other party. As a first step, the optimum strategies for both the parent and young are calculated and compared, and the intensity of conflict is assumed to depend on the magnitude of the discrepancy between offspring and parental optima (TRIVERS, 1974; LAZARUS & INGLIS, 1986). Since, when dealing with parent-offspring conflict, competition between family members is involved, and the optimum strategies for parents and their offspring depend on the strategy adopted by the other party, a second step is to analyze the evolutionary stability of optima by an ESS analysis (PARKER & MACNAIR, 1978; PARKER, 1985; HARPER, 1986; GODFRAY & PARKER, 1991). In ESS models, more conflict is also expected when the discrepancy between optima is greater (GODFRAY & PARKER, 1991). In this section we will be concerned with how sexual differences in fitness resulting from different amounts of PI are likely to affect the intensity of parent-offspring conflict. Our aim is to identify which sex is under stronger selection to extract resources beyond the parent's optimum, *i.e.* the more conflicting sex.

Consider an iteroparous, single-brooded polygynous species in which male-male competition for mates has selected for higher growth rates and energetic requirements in males during the period of PI. Also assume that the potential reproductive success of offspring (including both viability and mating success) depends upon the amount of PI obtained during development. Under such conditions, benefit curves for male and female offspring differ because PI influences differently the reproductive success of sons and daughters (Fig. 1). Compared with a male, a female can reach her asymptotic reproductive success at low values of PI. The maximum potential reproductive success of a male may exceed that of an average female in the population but it requires additional amounts of PI. Below a certain minimum level of PI, male reproductive success may be lower than that of an average female but fitness returns per unit of PI are larger

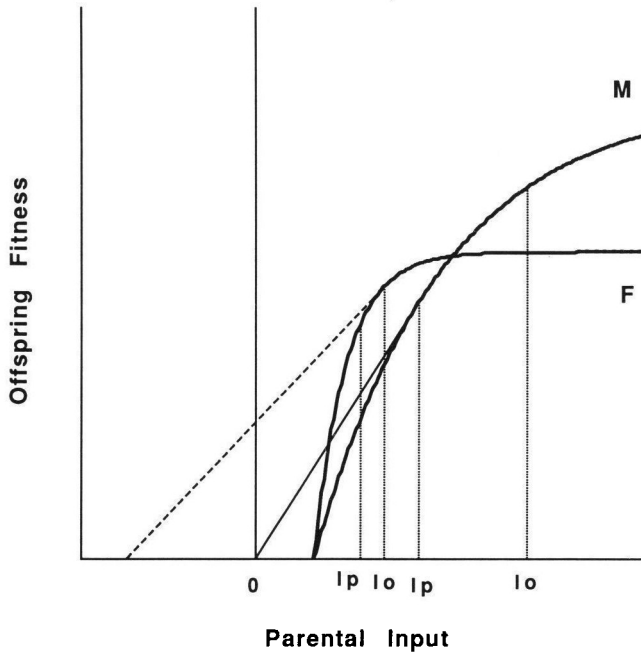


Fig. 1. The graphical illustration of the PARKER-MACNAIR model of parent-offspring conflict when offspring fitness (solid curves) varies in relation to parental input PI according to offspring sex in sexually dimorphic species. It is assumed that marginal fitness returns are greater for male offspring. The parental optimum I_p is calculated as the point where a tangent rooted at the origin (here shown for a male offspring, solid line) touches the curve. When all offspring are full siblings, the optimum for the offspring I_o is calculated as the point where a tangent rooted at a distance to the left from the origin equal to I_o (here shown for a female offspring, dashed line) touches the curve. As the genetic relatedness between the parent providing care and its offspring decreases, the difference between the roots of the I_p and the I_o tangents increases. The amount of PI which is an ESS lies at some point between the parental and offspring optima. The evolutionary potential for conflict increases as the discrepancy between I_o and I_p increases.

for males at moderate to high PI values. This last condition is crucial for the analysis (GODFRAY & PARKER, 1991) and is justified on the grounds that male reproductive success is more sensitive to variations in levels of PI. This statement is based on the following observations:

- a) Male viability and growth during the period of PI is more sensitive to variations in food supply than those of females (CLUTTON-BROCK, 1991).
- b) Males in polygynous species have been shown to be more likely to die than females after parental care is terminated (CLUTTON-BROCK & IASON, 1986). Since sex differences in juvenile mortality are most pronounced

when food is scarce (CLUTTON-BROCK, 1991), this means that males face disproportionately higher mortality costs if supplied with insufficient amounts of PI.

c) Male body mass at weaning is related to adult body mass and fighting ability, so that larger males enjoy an advantage in intrasexual competition for females during the breeding season (TRIVERS & WILLARD, 1973; CLUTTON-BROCK, 1991).

Hence, we assume that changes in marginal fitness returns are determined by how sensitive offspring fitness is to variations in PI at moderate-to-high PI levels. For example, sons may be more sensitive than daughters to variations in the amount of milk consumed near the end of the period of lactation. The above assumptions are generally acknowledged as a realistic representation of the different consequences that variations in PI may have on the fitness of male and female offspring in polygynous species (FRANK, 1987, 1990).

SMITH & FRETWELL (1974) and LLOYD (1987) developed a model of the selective consequences of different PI allocations among offspring. This model is appropriate for our analysis because further studies have extended it to derive the prediction that when offspring differ in the expected fitness returns for the same amount of PI, parents should invest more in the offspring with greater returns (HAIG, 1990). In addition, the SMITH-FRETWELL model was extended by PARKER & MACNAIR (1978) to develop a general theoretical framework for parent-offspring conflict.

The model assumes that there is some minimum PI below which an offspring has zero fitness and that fitness is an increasing, decelerating function of PI. PARKER & MACNAIR (1978) provided a method for computing optimal PI values for parents and their offspring which is illustrated in Fig. 1. This figure shows that the location of optima is determined by the degree of saturation of the fitness curve, so that a curve which becomes saturated at low PI values deserves lower PI optima (PARKER & MACNAIR, 1978; PARKER, 1985; GODFRAY & PARKER, 1991). In the original models, the degree of saturation of the curve is determined by the cost per unit PI: the larger the cost, the lower the PI level at which it is saturated (PARKER & MACNAIR, 1978). Now, the condition for conflict intensity (*i.e.* the difference between optimum minus parental optimum) to vary with offspring sex is entirely dependent upon the rate at which offspring fitness increases beyond the parental optimum, so that more conflict is expected when marginal returns (*i.e.* the slope values of the fitness function) are greater (GODFRAY & PARKER, 1991). Again, as the curve becomes saturated at lower PI values, the discrepancy between optima decreases (Fig.

1). It should be mentioned here that a lower conflict intensity with increasing cost per unit PI is also predicted by non-ESS optimality models of parent-offspring conflict (LAZARUS & INGLIS, 1986). Under the above assumption concerning male and female differences in marginal fitness returns per unit PI, it is predicted that mothers who are selected to invest more in males also should experience a more intense conflict with sons than with daughters.

Consequently, there are grounds to suspect that, in species with male-biased PI, sons may be under stronger selection than daughters for garnering PI beyond the mother optimum, even if mothers are selected to invest more in sons. This prediction may provide a test of the idea that observed patterns of sex-biased PI are, at least in part, the result of sexual selection acting on offspring phenotypes. We must first assume the existence of overt behavioural conflict between parents and their offspring. Second, we assume that parents are capable of exerting some sort of adaptive control over the amount of PI which is to be transferred (*e.g.* by rejecting a soliciting offspring), so that greater selection for conflict in sons is partly compensated for by more efficient behavioural retaliation by its mother (PARKER & MACNAIR, 1979). If such conditions are met, the prediction could be tested by looking at whether mothers engage in more intense behavioural conflict with sons than with daughters.

Testing the prediction

1. Measurements of parent-offspring conflict.

Despite widespread interest in parent-offspring conflict theory, there are few empirical data on this subject (STAMPS *et al.*, 1985). This may be partly due to the lack of operational definitions for variables which reflect conflict at the behavioural or physiological level. It may be worth pointing out that conflict necessarily involves an interaction between two partners and, therefore, that the behaviour of just one individual is unlikely to be meaningful in this context. The following categories are generally assumed to be good measures of parent-offspring conflict:

a) parent rejects a soliciting offspring. This may range from simply preventing the offspring from obtaining resources by ignoring it, to physical punishment. Some instances of maternal aggression which do not affect PI (*e.g.* CROWELL-DAVIS, 1985; NAKAMICHI *et al.*, 1990) are not included here. We will consider that offspring of one sex experience more intense conflict whenever they (i) both solicit from, and are rejected by

their mother at a higher rate, and/or (ii) have a higher proportion of their solicitation attempts rejected.

b) Parent avoids contact with offspring and offspring seeks contact with parent. PI transfer from parent to offspring requires that both are in close contact. Parental avoidance of a contact-seeking offspring may accurately reflect conflict (*e.g.* WHITE & HINDE, 1975; HAUSER & FAIRBANKS, 1988).

c) Offspring solicitation. Loud begging by nestlings birds and pestering of the mother by a young mammal attempting to suckle probably entails costs in terms of time, energy and risk (TRIVERS, 1985; HARPER, 1986; REDONDO & CASTRO, 1992a, b). The existence of costly begging signals is commonly interpreted as proof that they have evolved in the context of parent-offspring conflict (HARPER, 1986; GODFRAY, 1991). Theory predicts that more intense conflict (*i.e.* a greater discrepancy between optima) should promote the evolution of more intense solicitation behaviour (PARKER, 1985; HARPER, 1986). Conflict could then be measured by the extent of solicitation being inflicted upon a parent in the absence of parental response (PARKER, 1985), or by an increase in the ratio of solicitation behaviour to parental input (LAZARUS & INGLIS, 1986). In practice, however, solicitation may be a poor estimator of conflict intensity. This is so because solicitation (*e.g.* begging) is likely to vary for reasons unrelated to the extent of conflict, like nutritional need (GODFRAY, 1991; REDONDO & CASTRO, 1992b), body condition (GRAFEN, 1990), or social factors (see below), so there is no full guarantee that it provides a measure of the intensity of conflict (CLUTTON-BROCK, 1991).

d) Offspring distress. Although many of the observed instances of vigorous 'crying' and 'temper tantrum' behaviour (TRIVERS, 1985) may be specialized forms of solicitation behaviour, they may function as nuisance behaviour directed at the mother (STAMPS & METCALF, 1980) and they could be considered in a separate category.

The following sections are aimed at testing the prediction in two sets of unpublished data and to review published information on this subject.

2. Case study 1: domestic sheep.

Domestic sheep are among the most suitable subjects for testing the prediction. First, there is a good deal of data which are difficult to obtain in wild species. Second, it fulfils most of the basic assumptions on which the model is based. Under seminatural conditions, sheep mate polygynously (BOURKE, 1967) and larger rams obtain more copulations (ESTEP *et al.*, 1989). The physical condition of lambs at weaning is sensitive to

variations in maternal condition (TRIVERS & WILLARD, 1973; CLUTTON-BROCK & ALBON, 1982; PEÑA BLANCO, 1985a) and differences in body condition at weaning become exacerbated in the adult stage (TRIVERS & WILLARD, 1973; MAVROGENIS & CONSTANTINOU, 1990).

Do ewes invest more in sons or daughters? Males are born heavier than females (FOURIE *et al.*, 1970), they gain mass at a faster rate during lactation (FOURIE *et al.*, 1970; FLETCHER, 1971; LOPEZ DE TORRE *et al.*, 1984; PEÑA BLANCO, 1985a) and outweigh females after several weeks of lactation (FOURIE *et al.*, 1970; STAPLETON *et al.*, 1980; WOHL *et al.*, 1981; PEÑA BLANCO, 1985a). Males probably spend more time engaged in energetically costly activities (play, SACHS & HARRIS, 1978) than females do. In addition, males have higher rates of heat loss (SLEE, in CLUTTON-BROCK, 1991). Thus, sexual differences in size cannot be attributed to lower energetic expenditure by males. This evidence suggests that males may be receiving more milk from their mothers. Lamb mass at weaning has proved to be a good index of the amount of milk consumed, irrespective of sex (BURRIS & BAUGUS, 1955; RICORDEAU & BOCCARD, 1961; GARDNER *et al.*, 1964; DONEY *et al.*, 1981; PEÑA BLANCO, 1985a). PEÑA BLANCO (1985a) found that Spanish merino ewes nursing male lambs produced more milk than ewes nursing female lambs. The difference was consistent over 8 weeks *post-partum* over a three year study (signs test, $p < 0.001$). In addition, tissues of lactating male lambs contain a larger proportion of bone and muscle (FOURIE *et al.*, 1970; LOPEZ DE TORRE *et al.*, 1984; MASEDA *et al.*, 1984a), which indicates a greater provisioning of calcium and protein. In absolute terms, males should be energetically more costly to raise than females because larger lambs consume more milk (RICORDEAU *et al.*, 1960; MASEDA *et al.*, 1984b; PEÑA BLANCO, 1985b). It is widely acknowledged that lactation entails an important energetic cost (MILLAR, 1977, 1978; GITTLEMAN & THOMPSON, 1988), and this may explain why smaller ewes produce less milk (BURRIS & BAUGUS, 1955; PEÑA BLANCO, 1985b) and why ewes fed on a protein-enriched diet produced more milk and allowed lambs to suckle for longer (ARNOLD *et al.*, 1979). However, while FESTA-BIANCHET (1989) found that female bighorn sheep *Ovis canadensis* incurred greater reproductive costs after weaning a son, FLETCHER (1971) did not find significant effects of lamb sex upon the duration of *post-partum* anoestrous interval in domestic sheep. It is not known whether mothers in good physical condition were more likely to conceive sons.

Recently, BYERS & MOODIE (1990) have argued that the ability of a mother to invest extra resources in a son may be constrained by the rate of

parental investment (investment per unit of maternal weight), especially for species with high relative maternal investment, such as ungulates. In support of their idea, they found that species for which evidence of male-biased investment exists, had lower average values of two measurements which are likely to reflect relative investment: birth weight $^{0.75}$ /maternal weight $^{0.75}$ / ratio and growth rate $^{0.75}$ /maternal weight $^{0.75}$ ratio. Fig. 2 shows that the situation for sheep is intermediate between species with evident male-biased investment and species with equal investment in both sexes, which may imply that the ability for sheep to invest more in sons is not severely constrained. All together, the more logical conclusion which can be drawn from these results is that sheep show a moderate degree of differential investment towards sons (KENT, 1992).

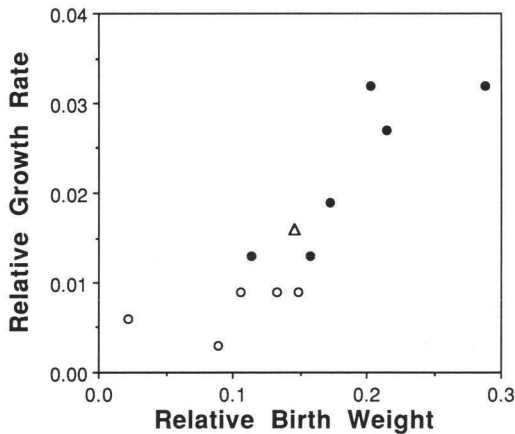


Fig. 2. Plot of the two indexes of relative maternal investment for 12 species of ungulates: the growth rate $^{0.75}$ /maternal weight $^{0.75}$ ratio (ordinate) and the birth weight $^{0.75}$ /maternal weight $^{0.75}$ ratio (abscissa). Those species showing low scores in both variables are less constrained to provide extra resources to offspring of a given sex. Open dots are species for which there is good evidence of sex-biased maternal expenditure in sons. The Spanish merino sheep is represented by a triangle. Data for sheep from BELDA & TRUJILLANO (1986), and for the remaining species from BYERS & MOODIE (1990).

If not artificially terminated, weaning takes place between four and six months (HERSHER *et al.*, 1963; ARNOLD *et al.*, 1979) but, as in other ungulates (GAUTHIER & BARRETTE, 1985), manifestations of parent-offspring conflict may begin much earlier. Specifically, the period around the fourth week of lamb age seems to be especially critical. It is characterised by a drop in milk production (PEÑA BLANCO, 1985b), a drop in

TABLE 1. Comparison between average suckling rates (in bouts/min), suckling bout duration (in s) and time spent suckling (in s per h of observation time, logarithmic transformation) for male and female lambs

	Male		Female		Effects ¹⁾		
	Mean	SE	Mean	SE	Sex	Age	Age × sex
Suckling rate	0.044	0.006	0.036	0.005	1.14	6.51***	0.97
Bout duration	118.0	11.97	100.6	9.25	1.93	10.08***	0.59
Time suckling	0.593	0.057	0.534	0.063	0.71	9.52***	1.95

¹⁾ Two-way ANOVA, F values with 1,1 (sex); 1,5 (age); and 1,5 (age × sex) degrees of freedom.

***p<0.001.

suckling rate (EWBANK, 1967; FLETCHER, 1971), a peak in nursing solicitation by lambs (HINCH, 1989) and a peak in maternal rejections (MANDIKI *et al.*, 1989). After this period, the mother no longer initiates suckling bouts (HINCH *et al.*, 1987).

Data on ewe-lamb interactions between 1 and 30 days of lamb age were collected during the spring of 1988. Continuous, 30-min focal animal samples were obtained for 8 male and 8 female Spanish merino lambs and their mothers under semi-free ranging conditions. Observation time yielded 193 h of continuous recording. Suckling attempts were considered successful if the lamb managed to maintain nipple contact for 5 s or longer (HINCH, 1989). Shorter suckling bouts interrupted by the mother were considered as rejections. Lamb body mass was measured at 3 days intervals. Individual behavioural rates for each 5-days age were included as separate data points in two-way ANOVAs accounting for the effects of both sex and age of lambs.

Lamb sex had no significant effect upon three suckling measures (Table 1). This is not surprising since, in both domestic (FLETCHER, 1971) and wild sheep (FESTA-BIANCHET, 1988), behavioural measurements of suckling are poor indicators of milk transfer. Failure to detect sex differences in suckling variables in species which are likely to show differential investment towards males suggests that males may suckle harder and acquire milk at a more rapid rate (ANDERSON & FEDAK, 1987; FESTA-BIANCHET, 1988). Male lambs tended to grow faster than female lambs but again differences were not statistically significant (Linear growth; Mass (kg) = 0.26 Age (days) + 4.29 for males; Mass = 0.21 Age + 4.62 for females; Analysis of Covariance, F (slopes) = 1.25, df = 1, 148, ns; F (elevations) = 0.75, df = 1, 149, ns). As in most previous studies (STA-

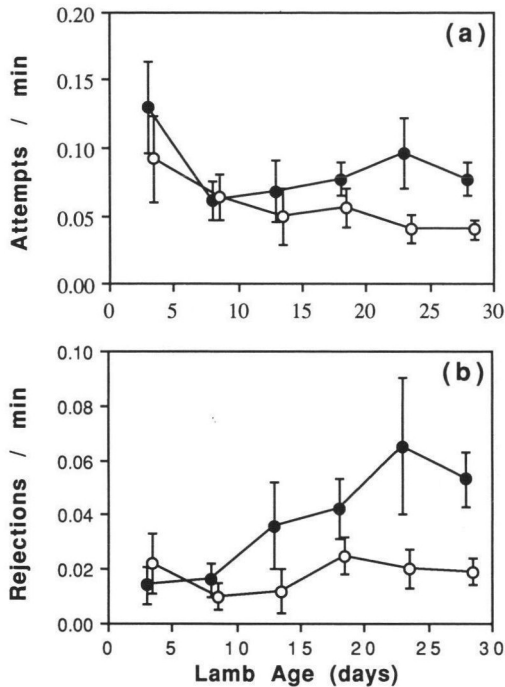


Fig. 3. Mother-offspring conflict in merino sheep in relation to lamb sex. (a) Solicitation (suckling attempt) rates (mean \pm SE) by female (open dots) and male (black dots) lambs during their first month of life (two-way ANOVA, Age $F = 1.95$, $df = 1,5$, ns; Sex $F = 5.67$, $df = 1,1$, $p = 0.019$; Age \times Sex $F = 0.51$, $df = 1,5$, ns). (b) Maternal rejection rates (mean \pm SE) of lamb suckling attempts (two-way ANOVA, Age $F = 2.0$, $df = 1,5$, ns; Sex $F = 9.12$, $df = 1,1$, $p = 0.003$; Age \times Sex $F = 1.48$, $df = 1,5$, ns).

PLETON *et al.*, 1980; FOURIE *et al.*, 1970; WOHL *et al.*, 1981; PEÑA BLANCO, 1985a) no significant sex differences in size were found prior to the first month of age. However, the higher protein content of males during lactation (mainly due to a larger proportion of skeletal muscle and digestive tissues, FOURIE *et al.*, 1970; LOPEZ DE TORRE *et al.*, 1984; MASEDA *et al.*, 1984a) indicates that they are supplied with comparatively more energy than females, as far as nutritional requirements per unit body mass are probably higher for males (CLUTTON-BROCK, 1991).

In agreement with the prediction, lamb sex had a significant effect upon two measurements of conflict. Males solicited nursing more frequently and were more frequently rejected by their mothers (Fig. 3), particularly at older ages. Changes in spatial proximity between mothers and their lambs also revealed sex differences. Mothers of male lambs were

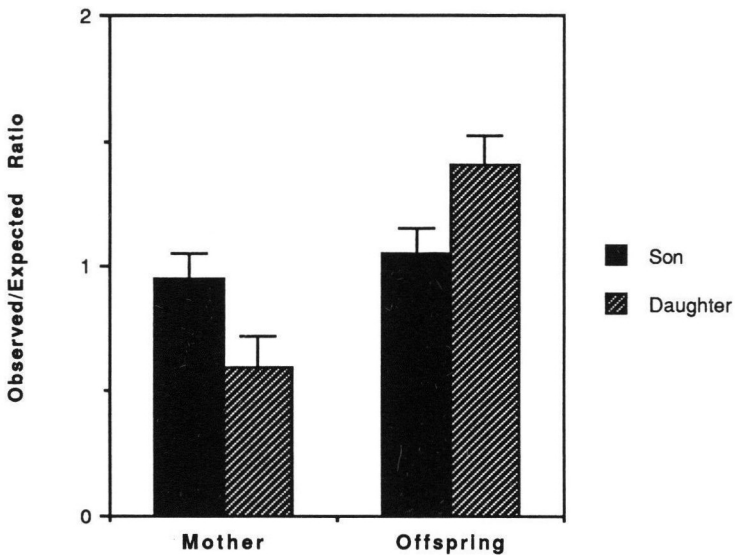


Fig. 4. Sexual differences in the frequency of withdrawals (movements resulting in an increase in spatial distance between mother and lamb) initiated by the mother or initiated by the lamb according to lamb sex. Shown are means (\pm SE) of the ratio between observed and expected frequencies of withdrawals initiated by each party. Expected frequencies were calculated assuming an equal probability of either mother or lamb initiating a withdrawal for each mother-lamb dyad. Differences between sexes are significant in both categories (Mann-Whitney test, $Z = 1.9$, $p < 0.05$, $N = 8$ dyads in each sex group).

more willing to initiate movements resulting in an increase in distance between both partners. The percentage of withdrawals initiated by the mother was higher for males (47.7%) than for females (30.2%) (One-way ANOVA, $F = 5.2$, $df = 1,14$, $p = 0.038$). In addition, males withdrew from their mothers less than females (Fig. 4). No such differences were observed in relation to approaching behaviour.

BURFENING (1972) and CLUTTON-BROCK (1991) also showed that male lambs in mixed sex twin pairs grew faster and survived better than did those raised with male twins, while the opposite trend was found for female lambs. BURFENING concluded that males enjoyed some kind of competitive advantage over females during lactation.

3. Case study 2: Rhesus monkeys.

The data presented in this section come from a study of the Madingley colony of rhesus macaques carried out by MG. Details of the study

subjects and the methodology used have been published elsewhere (GOMENDIO, 1989a, b, 1990, 1991).

Among primates, as well as other mammals, the frequency of nipple stimulation has an important influence upon maternal reproduction and is thus a good measure of maternal investment (LOUDON *et al.*, 1983; SHORT, 1984; LEE, 1987; GOMENDIO, 1989a). A high frequency of nipple stimulation inhibits maternal reproduction in non-seasonally as well as seasonally breeding primates. Mothers who suckle their infants frequently tend to be in poor physical condition and produce milk at slow rates (LOUDON *et al.*, 1983; LUNN, 1988; GOMENDIO, 1989b; MENDEL & PAUL, 1989). Infants respond to slow or insufficient milk yields by increasing suckling frequency in order to obtain adequate nourishment. In addition social factors can also modify suckling patterns (see below).

The results from this study did not reveal any overall effect of infant sex upon suckling frequency (GOMENDIO, 1990). As a consequence, mothers did not experience differential reproductive costs after raising male or female infants. There was, however, an important interaction between infant sex and maternal rank (GOMENDIO, 1990; GOMENDIO *et al.*, 1990). High ranking mothers did not suffer reproductive costs, irrespective of the sex of their infants. Low ranking mothers, on the other hand, did not experience reproductive costs after raising sons, but failed to reproduce the year after raising daughters. The reproductive delays suffered by low ranking mothers with daughters can be explained by the high suckling frequency experienced by these mothers. Low ranking mothers with daughters receive high levels of aggression (SILK *et al.*, 1981b; SILK, 1983; SIMPSON & SIMPSON, 1985; VAN SCHAİK & DE VISSER, 1990) which may prompt a protective response of the part of these mothers, resulting in a high frequency of nipple stimulation. It is also possible that the high levels of stress experienced by these mothers curtail milk production, thus forcing infants to suckle frequently in order to obtain enough milk.

In conclusion, low ranking mothers invested more in female offspring than in male offspring, and more than high ranking mothers invested in either sex. In order to make predictions concerning parent-offspring conflict following the ideas developed in this paper, information on the reproductive success of offspring is required. Regrettably, data on the reproductive success of males born to high and low ranking females is still lacking, making it impossible to include males in the following comparisons. We will therefore restrict the predictions to female offspring born to high and low ranking mothers.

Rhesus macaques are matrilocal and daughters inherit their mother's

rank (see reviews in MELNICK & PEARL, 1987; DUNBAR, 1988). Thus, the daughters of high ranking mothers become dominant themselves and attain higher reproductive success than the daughters of low ranking mothers. The latter suffer high mortality rates and, if they survive, they do not produce many offspring (SILK, 1988). Low ranking mothers incur higher costs per unit of PI (milk) because they experience higher rates of nipple stimulation. According to the PARKER-MACNAIR model, conflict should be more intense in high ranking mother-daughter dyads. This is so because fitness returns are higher for high ranking daughters, since the cost per unit of PI is lower (PARKER & MACNAIR, 1978). In addition, there is no ground to suspect that low ranking daughters should benefit more from extra PI given beyond their mother optimum than high ranking daughters, because the low reproductive success of low ranking daughters is primarily determined by external social factors, and there is little variance in their reproductive success (SILK, 1988). The situation for both kinds of females is shown in Fig. 5.

This prediction seems to be supported by empirical evidence. The daughters of low ranking mothers tried to get on the nipple more frequently than the daughters of high ranking females (ANOVA, $F = 4.78$, $df = 1,160$, $p = 0.03$). On the other hand, low ranking mothers were less rejecting than high ranking mothers ($F = 3.90$, $df = 1,160$, $p = 0.05$). Since the daughters of low ranking mothers were more demanding and had less rejecting mothers than the daughters of high ranking mothers, low ranking daughters had a much lower proportion of their attempts rejected than did daughters of high ranking mothers ($F = 26.44$, $df = 1,160$, $p = 0.0004$). Thus, the daughters of low ranking mothers experienced less intense behavioural conflict with their mothers than the daughters of high ranking females.

As in the male-female model, a positive association is found between the intensity of parent-offspring conflict and the fitness returns per unit of maternal investment (*e.g.* sons in polygynous species with male-biased PI and daughters born to high ranking female macaques).

4. Evidence from other studies.

During the last two decades there has been growing interest in the study of sex-biases in parental investment. It is unfortunate that most of these studies lack information on variables relevant to parent-offspring conflict (*e.g.* rabbits: BOYD, 1985; rodents: GOSLING *et al.*, 1984; LABOV *et al.*, 1986; WRIGHT *et al.*, 1988; KRACKOW & HOECK, 1989; CLARK *et al.*, 1990;

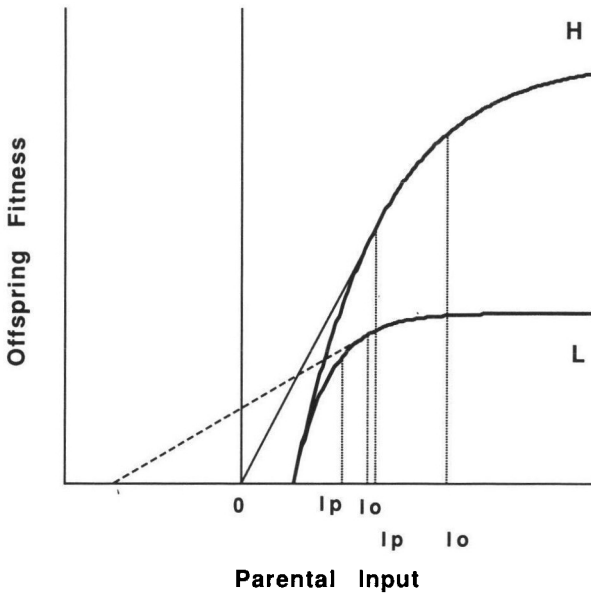


Fig. 5. Fitness curves for two mother-daughter rhesus macaque dyads according to mother's dominance rank, as a function of maternal input (milk transfer). High ranking (H) mothers incur lower costs per unit of parental input than low ranking (L) mothers. As a consequence, marginal fitness returns are lower for L daughters, and the discrepancy between offspring and parental optima is small compared to H daughters. Other explanations as in Fig. 1.

pinnipeds: ORTIZ *et al.*, 1984; TRILLMICH, 1986; KOVACS & LAVIGNE, 1986; ANDERSON & FEDAK, 1987; KOVACS, 1987a, b; OFTEDAL *et al.*, 1987; LE BOEUF *et al.*, 1989; ungulates: DUNCAN *et al.*, 1984; CROWEL-DAVIS, 1985; FESTA-BIANCHET, 1988; WOLFF, 1988; *cf.* GREEN & BERGER, 1990; birds: HOWE, 1976; RICHTER, 1983; BANCROFT, 1984; RØSKAFT & SLAGSVOLD, 1985; SLAGSVOLD *et al.*, 1986; OHSAKO, 1989; DROGE *et al.*, 1991). The best evidence now available comes from studies on ungulates.

Among African elephants (*Loxodonta africana*), male calves suckle more frequently than female calves. Males also solicit from, and are rejected by their mothers at higher rates, specially at older ages. The percentage of suckling interruptions promoted by the mother is also greater for older males. If rejected by their mothers, males were more likely to show distress and "appeared somewhat more likely to conflict with the mother over the duration of suckling bouts, specially at the older, less successful, ages" (LEE & MOSS, 1986). Red deer (*Cervus elaphus*) hinds nurse their male calves for longer than their female calves and sons have higher rejection rates than daughters (CLUTTON-BROCK *et al.*, 1982). Male calves also

solicited at higher rates but still their probability of being rejected by the mother per suckling attempt was higher than in female calves (CLUTTON-BROCK, 1991). In addition, males in male-female twin pairs are born heavier, grow at higher rates and survive better than male-male twins (CLUTTON-BROCK & ALBON, 1982), which may indicate that males are better at extracting resources than females. In the American antelope *Antilocapra americana*, there is a weak trend for daughters to be nursed more than sons at earlier ages and daughters are rejected at higher rates at the end of the suckling period (BYERS & MOODIE, 1990).

Among primates there is little evidence of sex biases in maternal investment. Some studies have reported sex differences in maternal and offspring behaviour but the findings from different studies tend to be rather contradictory (see reviews in BERMAN, 1984; HRDY, 1987; NICOLSON, 1987). In addition, it is not clear whether the kind of behavioural differences reported are related to differences in maternal investment, *i.e.* suckling. The few studies in which data on suckling have been collected have found no differences between male and female infants (NICOLSON, 1982; GOMENDIO, 1990). ROWELL & CHISM (1986) found sex differences only towards the end of the first year of life. An alternative way in which differences in investment can be looked at is by measuring the costs involved in raising male and female infants, which are reflected in the duration of the inter-birth intervals. Again, most studies have found no differences between male and female offspring (SILK *et al.*, 1981a; SMALL & SMITH, 1984; CHENEY *et al.*, 1988; SILK, 1988; but see BERMAN, 1988 for longer anoestrous intervals after raising males, and SIMPSON *et al.*, 1981 for a similar finding for female infants). The lack of sex-biases in maternal investment is related to the fact that in cercopithecine primates there are no major differences in growth rates before weaning (VAN WAGENEN & CATCHPOLE, 1956; SNOW, 1967; SMALL & SMITH, 1984; HORROCKS, 1986; SHARMA & LAL, 1986; ALTMANN & ALBERTS, 1987). In these primates, adult body size dimorphism seems to be achieved through pubertal growth spurt, which occurs years after offspring become nutritionally independent (for a more detailed discussion see GOMENDIO, 1990). It may be worth mentioning here that adult body size is not an important determinant of reproductive success among these primates (PACKER, 1977; FEDIGAN, 1983). Thus, in cercopithecine primates social factors may play a greater role in determining differential investment than differences in body size between male and female offspring. As suggested for rhesus macaques, the aggression received by the daughters of low ranking mothers may explain why they are more costly to raise.

The lack of clear sex differences in maternal investment among primates predicts no bias in the intensity of parent-offspring conflict in relation to infant sex. It should be mentioned, however, that some studies have reported higher rejection rates for males (JENSEN *et al.*, 1968; MITCHELL, 1968; WHITE & HINDE, 1975; STEVENSON-HINDE & SIMPSON, 1981; BERMAN, 1982, 1984; THOMMEN, 1982; SIMPSON, 1983; JOHNSON & SOUTHWICK, 1984; FAIRBANKS & MCGUIRE, 1985; ROWELL & CHISM, 1986) while others have found no sex differences (KAPLAN, 1972; YOUNG & BRAMBLETT, 1977; NASH, 1978; ALTMANN, 1980; NICOLSON, 1982; LEE, 1984; COLLINGE, 1987; FAIRBANKS, 1988). So far, no satisfactory explanation has been offered which integrates all these results, but the consideration of maternal rank and infant sex simultaneously may prove helpful.

In the southern elephant seal (*Mirounga leonina*), sons are born larger than daughters and pup size correlates with mother size. The correlation is significant for female but not for male pups because some large male pups are born from small females. Since pup size is both the result of the mother's ability to provide resources and the resource garnering ability of the offspring, this finding could imply that sons proportionately demand more from small mothers than daughters (McCANN *et al.*, 1989). See also TRITES (1991) for a putatively similar example in southern fur seals *Callorhinus ursinus*.

Studies on sex-biased PI in birds are even more scarce and pose some particular problems (STAMPS, 1990). Conflict is expected to become expressed in the form of conspicuous solicitation behaviour or some other adaptation improving resource acquisition by the offspring. The models considered here assume that the intensity of solicitation by an offspring is independent from that of past or future sibs, as it happens when sibs are reared sequentially (but see MACNAIR & PARKER, 1979). However, if offspring are reared in mixed-sex broods, as in many birds, the models need to account for the likely event that more intense solicitation by males may lead to selection in females for soliciting vigorously too, in order to ameliorate their competitive disadvantage (STAMPS, 1990).

There is evidence of female-biased PI in the Australian budgerigar *Melopsittacus undulatus*. Female nestlings are fed more by both parents, show higher begging rates and begin to emit begging calls at earlier ages than males (STAMPS *et al.*, 1987, 1989). Whether nestlings of both sexes differ in the acoustic properties of their begging calls is unknown but such a difference has been reported in the zebra finch *Taeniopygia guttata* (BURLEY, 1986). Parents do not actually discriminate between sons and daughters within a brood but they (especially fathers) fed more female-biased

broods. As a consequence, female nestlings obtained more food and fledged earlier. Fledging dates affected female, but not male reproductive success at their first breeding season (STAMPS *et al.*, 1987, 1989). Among polygynous icterids, circumstantial evidence suggesting more intense begging behaviour in male nestlings is now available for two species. Male red-winged blackbirds (*Agelaius phoeniceus*) nestlings grow heavier, consume more food and are more costly to raise than female nestlings (FIALA & CONGDON, 1983). Parents seem to adjust their feeding rates to clues related to nestling demands and broods with a sex ratio biased towards males are fed at higher rates (YASUKAWA *et al.*, 1990). In great-tailed grackles *Quiscalus mexicanus*, sons are also heavier, consume more food and are more costly to raise (TEATHER & WEATHERHEAD, 1988). TEATHER (1987) estimated food consumption by laboratory-reared nestlings by 'ad libitum' feeding them until they stopped gaping and found that males solicited higher amounts of food (for a similar result in redwings see FIALA, 1981). In addition, TEATHER & WEATHERHEAD (1989) found that broods with a higher sex ratio were more vulnerable to predation, perhaps as a result of their more intense vocal activity. These cases, however, should not be considered as supporting evidence for the prediction unless it could be demonstrated that: (i) begging provides a measure of the intensity of conflict, and (ii) if so, the ratio of begging to parental input is greater for the sex receiving extra PI. In this sense, STAMPS *et al.*, (1989) failed to detect differences in the average beg/feed ratio of female- *vs.* male-biased families. Similar negative results have been obtained by TEATHER (1992) with red-winged blackbirds.

Conclusions

In this paper we suggest that when parents invest differentially according to offspring sex, greater levels of parent-offspring conflict should be expected between parents and offspring of the favoured sex. Thus, in dimorphic polygynous species in which parents invest more in males, greater conflict should be expected between parents and sons than between parents and daughters. A review of the current literature reveals that the available data lend support to this prediction. However, our conclusions are necessarily speculative given the scarcity of relevant information. While this prediction has a rather wide applicability, it should be kept in mind that when the conditions of the model change the prediction may vary. Furthermore, these considerations may also be applied to offspring showing different benefit/cost curves, irrespective of

their sex. In particular, when offspring which are costly to raise, *i.e.* receive extra investment, also show low fitness returns, low levels of conflict should be expected. This case may be of relevance to some primate groups.

It has been acknowledged for some time that TRIVERS' (1974) original parent-offspring conflict theory has originated few testable predictions (STAMPS *et al.*, 1985; CLUTTON-BROCK, 1991; GOMENDIO, 1991). This is partly due to the difficulties involved in measuring lifetime reproductive benefits and costs with the accuracy that the original model requires. Thus, these problems are unlikely to be overcome in the future. One of the conclusions to be drawn from this paper is that a more profitable approach may be to derive second order predictions from the original model, as an indirect way of testing its validity.

The positive relationship found between differential PI and conflict intensity leaves open the question of whether parents invest more in offspring of one sex in order to make them more competitive or because they are more efficient in garnering resources (MAYNARD SMITH, 1980; LEE & MOSS, 1986; CLUTTON-BROCK, 1991). We lack theoretical genetic models aimed at showing whether a sex-linked conflictor allele could spread within a population (*i.e.* offspring are able to induce sex-biased PI). But if, as current theory suggests, most instances of observable conflict are better explained as '*pro rata*' strategies (PARKER & MACNAIR, 1979), the most prudent conclusion which can be drawn is that the amount of PI actually transferred towards the favoured sex is the evolutionary outcome of selection acting on both the parent and the offspring for sex-biased PI.

From an operational perspective, in order to tease apart parental and offspring effects upon the level of PI transferred one would have to compare the observed levels of PI in sons and daughters with optima for parents *vs.* offspring, but, in practice, this is seldom possible (CLUTTON-BROCK, 1991). However, the PARKER-MACNAIR model sets up a theoretical framework in which sex-biased PI and conflict are likely to coevolve in a sort of feed-forward runaway process ending in a '*pro rata*' compromise concerning the amount of PI transferred. From this viewpoint, the possibility must be considered that many (perhaps most) observed patterns of sex-biased parental investment are a by-product of sexual selection acting on offspring phenotypes. A clear example is provided by phocid seals, in which total milk production depends on fat reserves previously stored by the mother (ANDERSON & FEDAK, 1987). Grey seal pups apparently obtain milk on demand (FOGDEN, 1971) and sons are reported to solicit at higher rates (KOVACS, 1987a). In these species, greater investment toward sons is

likely to have evolved by selection pressures acting entirely on offspring phenotypes, because it seems unlikely that mothers would restrain their foraging ability during gestation after conceiving daughters. This could explain why in elephant seals *Mirounga angustirostris*, where sons obtain more milk than daughters, a long-term study failed to detect any effect of weaning sex upon subsequent reproductive performance of the females (LE BOEUF *et al.*, 1989). In fact, current evidence concerning parent-offspring relationships in birds and mammals showing differential investment by sex strongly suggest that offspring are largely (if not entirely) responsible for the observed bias in parental expenditure (CLUTTON-BROCK, 1991).

Theoretical models aimed at predicting patterns of investment allocation according to offspring sex have largely emphasized the role of parental phenotypes as the major target for selection (WILLSON & PIANKA, 1963; MAYNARD SMITH, 1980; CHARNOV, 1982; LLOYD, 1983; FRANK, 1987; STAMPS, 1990), while they have paid little or no attention to the offspring as an active evolutionary force with which parents must necessarily coevolve (DAWKINS & KREBS, 1979). On theoretical grounds, it is widely accepted that offspring are capable of inducing deviations from optimal parental levels of PI as a result of genetic parent-offspring conflict (STAMPS *et al.*, 1978; STAMPS & METCALF, 1980; PARKER, 1985). This study has shown that, at least under certain conditions, offspring may have played a major role in the evolution of patterns of investment which are commonly interpreted as parental strategies. We would like to suggest, as some have did before (TRIVERS, 1974; CLUTTON-BROCK, 1991; GODFRAY & PARKER, 1991), that there is an urgent need to incorporate offspring roles in many theoretical treatments of parental behaviour.

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