

## **SEX-BIASED PARENT-OFFSPRING CONFLICT**

by

**TOMAS REDONDO<sup>1</sup>), MONTSERRAT GOMENDIO<sup>2</sup>)  
and ROSARIO MEDINA<sup>3,4</sup>)**

(<sup>1</sup> Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK and Estación Biológica de Doñana (C.S.I.C.), Pabellón del Perú, Apdo. 1056, E-41080 Sevilla, Spain, <sup>2</sup> Sub-Department of Animal Behaviour (Department of Zoology), University of Cambridge, Madingley, Cambridge CB3 8AA, UK and Museo Nacional de Ciencias Naturales (C.S.I.C.), Jose Gutierrez Abascal 2, 28006 Madrid, Spain, and <sup>3</sup> Departamento de Biología Animal (Etología), Facultad de Ciencias, Universidad de Córdoba, 14071 Córdoba, Spain)

(With 5 Figures)  
(Acc. 17-XII-1992)

### **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.

---

<sup>4</sup>) We are grateful to T. CLUTTON-BROCK, R. DUNBAR, J. LAZARUS, G. PARKER and an anonymous referee for many helpful comments on an earlier draft, and to K. TEATHER for kindly providing his unpublished material. R. HINDE, B. KEVERNE and M. SIMPSON allowed MG access to the facilities available at the Sub-Department of Animal Behaviour and gave her permission to study the Madingley colony which is funded by the MRC. While doing the study, MG was a Research Fellow at Trinity Hall, Cambridge. F. PHENIX allowed RM to study sheep while she enjoyed a MEC (PFPI) grant as a postgraduate at the Departamento de Medicina y Sanidad Animal Facultad de Veterinaria, Cáceres. TR was supported by a MEC postdoctoral grant (Perfeccionamiento de Doctores en España) and a Fleming MEC/British Council Fellowship.

## 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

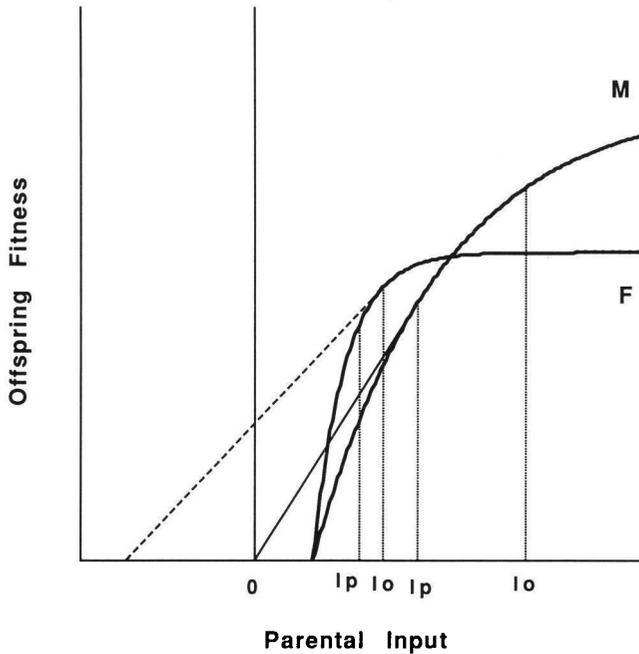


Fig. 1. The graphical illustration of the PARKER-MACNAIR model of parent-offspring conflict when offspring fitness (solid curves) varies in relation to parental input PI according to offspring sex in sexually dimorphic species. It is assumed that marginal fitness returns are greater for male offspring. 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).

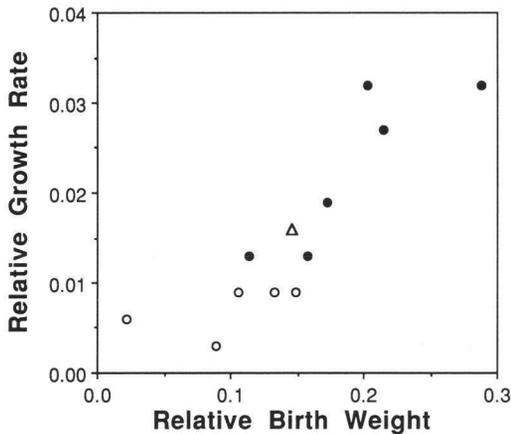


Fig. 2. Plot of the two indexes of relative maternal investment for 12 species of ungulates: the growth rate  $^{0.75}$ /maternal weight  $^{0.75}$  ratio (ordinate) and the birth weight  $^{0.75}$ /maternal weight  $^{0.75}$  ratio (abscissa). Those species showing low scores in both variables are less 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 <sup>1)</sup>		
	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

<sup>1)</sup> 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-

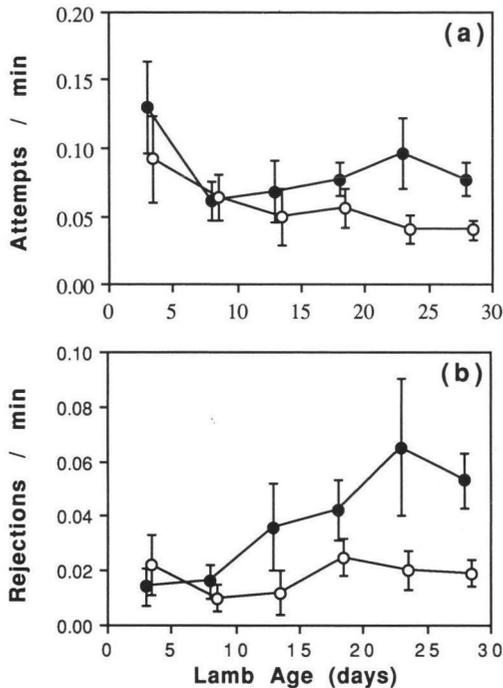


Fig. 3. Mother-offspring conflict in merino sheep in relation to lamb sex. (a) Solicitation (suckling attempt) rates (mean  $\pm$  SE) by female (open dots) and male (black dots) lambs during their first month of life (two-way ANOVA, Age  $F = 1.95$ ,  $df = 1,5$ , ns; Sex  $F = 5.67$ ,  $df = 1,1$ ,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

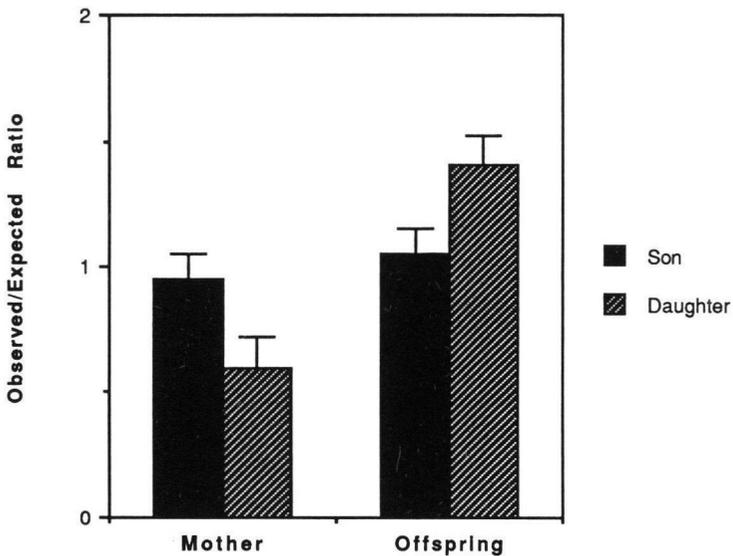


Fig. 4. Sexual differences in the frequency of withdrawals (movements resulting in an increase in spatial distance between mother and lamb) initiated by the mother or initiated by the lamb according to lamb sex. Shown are means ( $\pm$  SE) of the ratio between observed and expected frequencies of withdrawals 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;

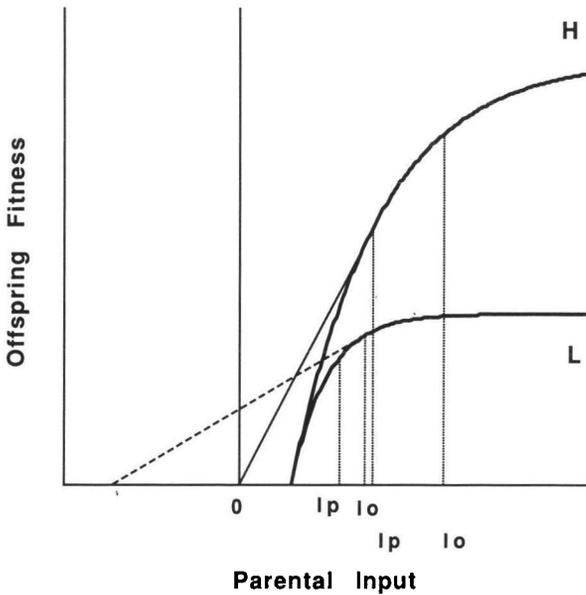


Fig. 5. Fitness curves for two mother-daughter rhesus macaque dyads according to mother's dominance rank, as a function of maternal input (milk transfer). High ranking (H) mothers incur lower costs per unit of parental input than low ranking (L) mothers. As a consequence, marginal fitness returns are 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.

## References

- ALTMANN, J. (1980). Baboon mothers and infants. — Harvard University Press, Cambridge, Massachusetts.
- & ALBERTS, S. (1987). Body mass and growth rates in a wild primate population. — *Oecologia* 72, p. 15-20.
- ANDERSON, S. S. & FEDAK, M. A. (1987). Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. — *J. Zool. Lond.* 211, p. 667-679.
- ARNOLD, G. W., WALLACE, S. R. & MALLER, R. A. (1979). Some factors involved in natural weaning processes in sheep. — *Appl. Anim. Ethol.* 5, p. 43-50.
- BANCROFT, G. T. (1984). Growth and sexual dimorphism of the boat-tailed grackle. — *Condor* 86, p. 423-432.
- BELDA, A. S. & TRUJILLANO, M. C. S. (1986). Razas Ovinas Españolas. — Publicaciones del Ministerio de Agricultura, Pesca y Alimentación, Madrid.
- BERMAN, C. M. (1982). The ontogeny of social relationships with group companions among

- free-ranging infant rhesus monkeys. I. Social networks and differentiation. — *Anim. Behav.* 30, p. 149-162.
- (1984). Variation in mother-infant relationships: traditional and non-traditional factors. — In: *Female primates: Studies by women primatologists* (M. F. SMALL, ed.). Alan R. Liss, New York, p. 245-281.
- (1988). Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. — *Am. Nat.* 131, p. 307-328.
- BOURKE, M. E. (1967). A study of mating behaviour of merino rams. — *Aust. J. Exp. Agric. Anim. Husband.* 7, p. 203-205.
- BOYD, I. L. (1985). Investment in growth by pregnant wild rabbits in relation to litter size and sex of the offspring. — *J. Anim. Ecol.* 54, p. 137-147.
- & McCANN, T. S. (1989). Pre-natal investment in reproduction by female Antarctic fur seals. — *Behav. Ecol. Sociobiol.* 24, p. 377-385.
- BURFENING, P. J. (1972). Prenatal and postnatal competition among twin lambs. — *Anim. Prod.* 15, p. 61-66.
- BURLEY, N. (1986). Sex-ratio manipulation in color-banded populations of zebra finches. — *Evolution* 40, p. 1191-1206.
- BURRIS, M. J. & BAUGUS, C. A. (1955). Milk consumption and growth of suckling lambs. — *J. Anim. Sci.* 14, p. 186-191.
- BYERS, J. A. & MOODIE, J. D. (1990). Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. — *Behav. Ecol. Sociobiol.* 26, p. 157-164.
- CHARNOV, E. L. (1982). *The theory of sex allocation*. — Princeton University Press, Princeton.
- CHENEY, D. L., SEYFARTH, R. M., ANDELMAN, S. J. & LEE, P. C. (1988). Reproductive success in vervet monkeys. — In: *Reproductive success* (T. H. CLUTTON-BROCK, ed.). University of Chicago Press, Chicago, p. 384-402.
- CLARK, A. B. (1978). Sex ratio and local resource competition in a prosimian primate. — *Science* 201, p. 163-165.
- CLARK, M. M., BONE, S. & GALEF, B. G. Jr. (1990). Evidence of sex-biased postnatal maternal investment by Mongolian gerbils. — *Anim. Behav.* 39, p. 735-744.
- CLUTTON-BROCK, T. H. (1988). Reproductive success. — In: *Reproductive success* (T. H. CLUTTON-BROCK, ed.). University of Chicago Press, Chicago, p. 472-486.
- (1991). *The evolution of parental care*. — Princeton University Press, Princeton.
- & ALBON, S. D. (1982). Parental investment in male and female offspring in mammals. — In: *Current problems in sociobiology* (King's College Sociobiology Group, ed.). Cambridge University Press, Cambridge, p. 223-247.
- , — & GUINNESS, F. E. (1981). Parental investment in male and female offspring in polygynous mammals. *Nature* 289, p. 487-489.
- , —, & — (1982). Red deer: Behaviour and ecology of two sexes. — University of Chicago Press, Chicago.
- , —, & — (1986). Great expectations: maternal dominance sex ratios and offspring reproductive success in red deer. — *Anim. Behav.* 34, p. 460-471.
- , —, & — (1988). Reproductive success in red deer. — In: *Reproductive success* (T. H. CLUTTON-BROCK, ed.). University of Chicago Press, Chicago, p. 325-343.
- & IASON, G. R. (1986). Sex ratio variation in mammals. — *Q. Rev. Biol.* 61, p. 339-374.
- COLLINGE, N. E. (1987). Weaning variability in semi-free-ranging Japanese macaques (*Macaca fuscata*). — *Fol. Primatol.* 48, p. 137-150.
- COSTA, D. P. & GENTRY, R. L. (1986). Free ranging and reproductive energetics of the northern fur seal. — In: *Fur seals: Maternal strategies on land and sea* (R. L. GENTRY & G. L. KOOYMAN, eds). Princeton University Press, Princeton.
- CROWELL-DAVIS, S. L. (1985). Nursing behaviour and maternal aggression among Welsh ponies (*Equus caballus*). — *Appl. Anim. Behav. Sci.* 14, p. 11-25.

- DAWKINS, R. & KREBS, J. R. (1979). Arms races between and within species. — *Proc. R. Soc. London B* 205, p. 489-511.
- DONEY, J. M., PEART, J. N. & SMITH, W. F. (1981). The effect of interaction of ewe and lamb genotype on milk production of ewes and on growth of lambs to weaning. — *Anim. Prod.* 33, p. 137-142.
- DROGE, D. L., GOWATY, P. A. & WEATHERS, W. W. (1991). Sex-biased provisioning: a test for differences in field metabolic rates of nestling eastern bluebirds. — *Condor* 93, p. 793-798.
- DUNBAR, R. I. M. (1988). *Primate social systems*. — Croom Helm, London.
- DUNCAN, P., HARVEY, P. H. & WELLS, S. M. (1984). On lactation and associated behaviour in a natural herd of horses. — *Anim. Behav.* 32, p. 255-263.
- ESTEP, D. Q., PRICE, E. O., WALLACH, S. J. R. & DALLY, M. R. (1989). Social preferences of domestic ewes for rams (*Ovis aries*). — *Appl. Anim. Behav. Sci.* 24, p. 287-300.
- EVANS, R. M. (1990). The relationship between parental input and investment. — *Anim. Behav.* 39, p. 797-798.
- EWBANK, R. (1967) Nursing and suckling behaviour amongst Clun Forest ewes and lambs. — *Anim. Behav.* 15, p. 251-258.
- FAIRBANKS, L. A. (1988). Mother-infant behavior in vervet monkeys. Response to failure of last pregnancy. — *Behav. Ecol. Sociobiol.* 23, p. 157-165.
- & MCGUIRE, M. T. (1985). Relationships of vervet monkeys with sons and daughters from one through three years of age. — *Anim. Behav.* 33, p. 40-50.
- FEDIGAN, L. M. (1983). Dominance and reproductive success in primates. — *Yearbook Phys. Anthropol.* 26, p. 9-129.
- FESTA-BIANCHET, M. (1988). Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. — *Anim. Behav.* 36, p. 1445-1454.
- (1989). Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). — *J. Anim. Ecol.* 58, p. 785-795.
- FIALA, K. L. (1981). Reproductive cost and the sex ratio in red-winged blackbirds. — In: *Natural selection and social behaviour* (R. D. ALEXANDER & D. W. TINKLE, eds). Chiron, New York, p. 198-214.
- & CONGDON, J. D. (1983). Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. — *Ecology* 64, p. 642-647.
- FISHER, R. A. (1930). *The genetical theory of natural selection*. — Oxford University Press, Oxford.
- FLETCHER, I. C. (1971). Relationships between frequency of suckling, lamb growth and *post-partum* oestrous behaviour in ewes. — *Anim. Behav.* 19, p. 108-111.
- FOGDEN, S.C.L. (1971). Mother-young behaviour of grey seal breeding beaches. — *J. Zool. Lond.* 164, p. 61-92.
- FOURIE, P. D., KIRTON, A. H. & JURY, K. E. (1970). Growth and development of sheep. II. Effect of breed and sex on the growth and carcass composition of the Southdown and Romney and their cross. — *N.Z.J. Agric. Res.* 13, p. 753-770.
- FRANK, S. A. (1987). Individual and population sex allocation patterns. — *Theor. Popul. Biol.* 31, p. 1-28.
- (1990). Sex allocation theory for birds and mammals. — *Ann. Rev. Ecol. Syst.* 21, p. 13-55.
- GARDNER, R. W., HOGUE, D. E. & BENSADOUN, A. (1964). Body composition and efficiency of growth of suckling lambs as affected by level of food intake. — *J. Anim. Sci.* 23, p. 943-952.
- GAUTHIER D. & BARRETTE, C. (1985). Suckling and weaning in captive white-tailed and fallow deer. — *Behaviour* 94, p. 128-149.
- GITTLEMAN, J. L. & THOMPSON, S. D. (1988). Energy allocation in mammalian reproduction. — *Amer. Zool.* 28, p. 863-875.
- GODFRAY, H. C. J. (1991). Signalling of need by offspring to their parents. — *Nature* 352, p. 328-330.

- & PARKER, G. A. (1991). Clutch size, fecundity and parent-offspring conflict. — *Phil. Trans. R. Soc. Lond. B* 332, p. 67-79.
- GOMENDIO, M. (1989a). Suckling behaviour and fertility in rhesus macaques. — *J. Zool. Lond.* 217, p. 449-467.
- (1989b). Differences in fertility and suckling patterns between primiparous and multiparous rhesus mothers (*Macaca mulatta*). — *J. Rep. Fert.* 87, p. 529-542.
- (1990). The influence of maternal rank and infant sex on maternal investment trends in rhesus macaques: birth sex ratios, inter-birth intervals and suckling patterns. — *Behav. Ecol. Sociobiol.* 27, p. 365-375.
- (1991). Parent-offspring conflict and maternal investment in rhesus macaques. — *Anim. Behav.* 42, p. 993-1005.
- , CLUTTON-BROCK, T. H., ALBON, S. D., GUINNESS, F. E. & SIMPSON, M. J. A. (1990). Mammalian sex ratios and variation in the costs of rearing sons and daughters. — *Nature* 343, p. 261-263.
- GOSLING, L. M., BAKER, S. J. & WRIGHT, K. M. H. (1984). Differential investment by female coypus (*Myocastor coypus*) during lactation. — *Symp. zool. Soc. Lond.* 51, p. 273-300.
- GRAFEN, A. (1990). Biological signals as handicaps. — *J. theor. Biol.* 144, p. 517-546.
- GREEN, W. C. H. & BERGER, J. (1990). Maternal investment in sons and daughters, problems of methodology. — *Behav. Ecol. Sociobiol.* 27, p. 99-102.
- HAIG, D. (1990). Brood reduction and optimal parental investment when offspring differ in quality. — *Am. Nat.* 136, p. 550-566.
- HARPER, A. B. (1986). The evolution of begging: sibling competition and parent-offspring conflict. — *Am. Nat.* 128, p. 99-114.
- HAUSER, M. D. & FAIRBANKS, L. A. (1988). Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. — *Anim. Behav.* 36, p. 802-813.
- HERSHER, L., RICHMOND, J. B. & MOORE, A. U. (1963). Maternal behaviour in sheep and goats. — In: *Maternal behaviour in mammals* (H. L. REINHOLD, ed.). John Wiley, London, p. 203-232.
- HINCH, G. N. (1989). The suckling behaviour of triplet, twin and single lambs at pasture. — *Appl. Anim. Behav. Sci.* 22, p. 39-48.
- , LECRIVAIN, E., LYNCH, J. J. & ELWIN, R. L. (1987). Changes in maternal-young associations with increasing age of lambs. — *Appl. Anim. Behav. Sci.* 17, p. 305-318.
- HORROCKS, J. (1986). Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaues*) in Barbados, West Indies. — *Int. J. Primatol.* 7, p. 31-47.
- HOWE, H. F. (1976). Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. — *Ecology* 57, p. 1195-1207.
- HRDY, S. B. (1987). Sex-biased parental investment among primates and other mammals: a critical evaluation of the TRIVERS-WILLARD hypothesis. — In: *Child abuse and neglect: Biosocial dimensions* (R. GELLES & J. LANCASTER, eds). Aldine, Hawthorne, New York, p. 97-147.
- JENSEN, G. D., BOBBITT, R. A. & GORDON, B. N. (1968). Sex differences in the development of independence in infant monkeys. — *Behaviour* 30, p. 1-14.
- JOHNSON, R. L. & SOUTHWICK, C. H. (1984). Structural diversity and mother-infant relations among rhesus monkeys in India and Nepal. — *Fol. Primatol.* 43, p. 198-215.
- KAPLAN, J. (1972). Differences in the mother-infant relations of squirrel monkeys housed in social and restricted environments. — *Dev. Psychobiol.* 5, p. 43-52.
- KENT, J. P. (1992). Birth sex ratios in sheep over six lambing seasons. — *Behav. Ecol. Sociobiol.* 30, p. 151-155.
- KING, B. H. (1987). Offspring sex ratios in parasitoid wasps. — *Q. Rev. Biol.* 62, p. 367-396.
- KOVACS, K. M. (1987a). Maternal behaviour and early behavioural ontogeny of grey seals (*Halichoerus grypus*) on the Isle of May, UK. — *J. Zool. Lond.* 213, p. 697-715.
- (1987b). Maternal behaviour and early behavioural ontogeny of harp seals, *Phoca groenlandica*. — *Anim. Behav.* 35, p. 844-855.

- & LAVIGNE, D. M. (1986). Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. — *Can. J. Zool.* 64, p. 1937-1943.
- KRACKOW, S. & HOECK, H. N. (1989). Sex ratio manipulation, maternal investment and behaviour during concurrent pregnancy and lactation in house mice. — *Anim. Behav.* 37, p. 177-186.
- LABOV, J. B., HUCK, U. W., VASWANI, P. & LISK, R. D. (1986). Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (*Mesocricetus auratus*). — *Behav. Ecol. Sociobiol.* 18, p. 241-249.
- LAZARUS, J. & INGLIS, I. R. (1986). Shared and unshared parental investment, parent-offspring conflict and brood size. — *Anim. Behav.* 34, p. 1791-1804.
- LE BOEUF, B. J., CONDIT, R. & REITER, J. (1989). Parental investment and the secondary sex ratio in northern elephant seals. — *Behav. Ecol. Sociobiol.* 25, p. 109-117.
- LEE, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. — *Primates* 25, p. 36-47.
- (1987). Nutrition, fertility and maternal investment in primates. — *J. Zool. Lond.* 213, p. 409-422.
- & MOSS, C. J. (1986). Early maternal investment in male and female African elephant calves. — *Behav. Ecol. Sociobiol.* 18, p. 353-361.
- LLOYD, D. G. (1983). Evolutionarily stable sex ratios and sex allocations. — *J. theor. Biol.* 105, p. 525-539.
- (1987). Selection of offspring size at independence and other size-versus-number strategies. — *Am. Nat.* 129, p. 800-817.
- LOPEZ DE TORRE, G., MEMBRILLO, J. & ALVAREZ, E. (1984). Comparación del crecimiento y características de las canales de corderos merinos puros con corderos hijos de padre merino y madre F1 (Romanov x Merino). — *An. INIA Ser. Ganadera* 19, p. 141-149.
- LOUDON, A. S. I., MCNEILLY, A. S. & MILNE, J. A. (1983). Nutrition and lactational control of fertility in red deer. — *Nature* 302, p. 145-147.
- LUNN, P. G. (1988). Malnutrition and fertility. — In: *Natural human fertility* (P. DIGGORY, M. POTTS & S. TEPER, eds). MacMillan, London, p. 135-152.
- MACNAIR, M. R. & PARKER, G. A. (1978). Models of parent-offspring conflict. II. Promiscuity. — *Anim. Behav.* 26, p. 111-122.
- & — (1979). Models of parent-offspring conflict. III. Intra-brood conflict. — *Anim. Behav.* 27, p. 1202-1209.
- MANDIKI, S. N. M., FOSSION, M. & PAQUAY, R. (1989). Daily variations in suckling behaviour and relationship between suckling intensity and lactation anestrus in Texel ewes. — *Appl. Anim. Behav. Sci.* 23, p. 247-255.
- MASEDA, F., CAÑEQUE, V. & GALVEZ, J. F. (1984a). Lactancia artificial y engorde de corderos de raza 'manchega'. III. Influencia del sexo y de la cantidad de leche ingerida en la calidad de la canal. — *An. INIA Ser. Ganadera* 19, p. 99-119.
- , — & — (1984b). Lactancia artificial y engorde de corderos de raza 'manchega'. II. Influencia del sexo y del peso al nacimiento sobre el crecimiento y el consumo de alimento. — *An. INIA Ser. Ganadera* 19, p. 89-97.
- MAVROGENIS, A. P. & CONSTANTINOU, A. (1990). Relationships between pre-weaning growth, post-weaning growth and mature body size in Chios sheep. — *Anim. prod.* 50, p. 271-275.
- MAYNARD SMITH, J. (1980). A new theory of sexual investment. — *Behav. Ecol. Sociobiol.* 7, p. 247-251.
- MCCANN, T. S., FEDAK, M. A. & HARWOOD, J. (1989). Parental investment in southern elephant seals, *Mirounga leonina*. — *Behav. Ecol. Sociobiol.* 25, p. 81-87.
- MELNICK, D. J. & PEARL, M. C. (1987). Cercopithecines in multimale groups: genetic diversity and population structure. — In: *Primate societies* (B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM & T. T. STRUSHAKER, eds). University of Chicago Press, Chicago, p. 121-134.

- MENDL, M. & PAUL, E. S. (1989). Observation of nursing and suckling behaviour as an indicator of milk transfer and parental investment. — *Anim. Behav.* 37, p. 513-515.
- MILLAR, J. S. (1977). Adaptive features of mammalian reproduction. — *Evolution* 31, p. 370-386.
- (1978). Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. — *Ecology* 59, p. 1055-1061.
- MITCHELL, G. D. (1968). Attachment differences in male and female infant monkeys. — *Child Dev.* 39, p. 612-620.
- NAKAMICHI, M., CHO, F. & MINAMI, T. (1990). Mother-infant interactions of wild-born, individually-caged Cynomolgus monkeys (*Macaca fascicularis*) during the first 14 weeks of infant life. — *Primates* 31, p. 213-224.
- NASH, L. T. (1978). The development of the mother-infant relationship in wild baboons (*Papio anubis*). — *Anim. Behav.* 26, p. 746-759.
- NICOLSON, N. A. (1982). Weaning and the development of independence in olive baboons. — Ph. D. thesis, Harvard University.
- (1987). Infants, mothers, and other females. — In: *Primate societies* (B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM & T. T. STRUSHAKER, eds). University of Chicago Press, Chicago, p. 330-342.
- OFTEDAL, O. T., IVERSON, S. J. & BONESS, D. J. (1987). Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. — *Physiol. Zool.* 60, p. 560-575.
- OHSAKO, Y. (1989). Sex allocation in parental care and sex-biased feeding in the Japanese wagtail *Motacilla grandis*. *Jap. J. Ornithol.* 37, p. 198.
- ORTIZ, C. L., LE BOEUF, B. J. & COSTA, D. P. (1984). Milk intake of elephant seal pups: an index of parental investment. — *Am. Nat.* 124, p. 416-422.
- PACKER, C. (1977). Reciprocal altruism in olive baboons. — *Nature* 265, p. 441-443.
- PARKER, G. A. (1984). Evolutionarily stable strategies. — In: *Behavioural ecology. An evolutionary approach*, 2nd ed. (J. R. KREBS & N. B. DAVIES, eds). Blackwell, Oxford, p. 30-61.
- 1985. Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. — *Anim. Behav.* 33, p. 519-533.
- & MACNAIR, M. R. (1978). Models of parents-offspring conflict. I. Monogamy. — *Anim. Behav.* 26, p. 97-110.
- & — (1979). Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. — *Anim. Behav.* 27, p. 1210-1235.
- PEÑA BLANCO, F. (1985a). Producción lactea en ovejas de raza merina durante la fase de amamantamiento. — *Arch. Zootecnia* 34, p. 235-247.
- (1985b). Crecimiento en corderos de raza merina española: periodo de lactación. — *Arch. Zootecnia* 34, p. 95-103.
- PRATT, D. M. & ANDERSON, V. H. (1979). Giraffe cow-calf relationships and social development of the calf in the Serengeti. — *Z. Tierpsychol.* 51, p. 233-251.
- REDONDO, T. & CASTRO, F. (1992a). The increase in risk of predation with begging activity in broods of magpies *Pica pica*. — *Ibis* 134, p. 180-187.
- & — (1992b). Signalling of nutritional need by magpie nestlings. — *Ethology*, 92, p. 193-204.
- REITER, J., STINSON, N. L. & LE BOEUF, B. J. (1978). Northern elephant seal development: the transition from weaning to nutritional independence. — *Behav. Ecol. Sociobiol.* 3, p. 337-367.
- RICORDEAU, G. & BOCCARD, R. (1961). Relations entre la quantité de lait consommé par les agneaux et leur croissance. — *Ann. Zootech.* 10, p. 113-125.
- & — & DENAMUR, R. (1960). Mesure de la production laitière des brebis pendant le période d'allaitement. — *Ann. Zootech.* 9, p. 97-120.
- RICHTER, W. (1983). Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. — *Am. Nat.* 121, p. 158-171.

- RØSKAFT, E. & SLAGSVOLD, T. (1985). Differential mortality of male and female offspring in experimentally manipulated broods of the rook. — *J. Anim. Ecol.* 54, p. 261-266.
- ROWELL, T. E. & CHISM, J. (1986). The ontogeny of sex differences in the behavior of patas monkeys. — *Int. J. Primatol.* 7, p. 83-106.
- SACHS, B. D. & HARRIS, V. S. (1978). Sex differences and developmental changes in selected juvenile activities (play) of domestic lambs. — *Anim. Behav.* 26, p. 678-684.
- VAN SCHAIK C. P. & DE VISSER, J. A. G. M. (1990). Fragile sons of harassed daughters? — *Fol. Primatol.* 55, p. 10-23.
- SHARMA, D. N. & LAL, K. C. (1986). Age-related growth patterns of colony-born rhesus monkeys. — In: *Primate ontogeny, cognition and social behaviour* (J. G. ELSE & P. C. LEE, eds). Cambridge University Press, Cambridge, p. 141-146.
- SHORT, R. V. (1984). Breast feeding. — *Sci. Amer.* 250, p. 35-41.
- SILK, J. B. (1983). Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. — *Am. Nat.* 121, p. 56-66.
- (1987). Social behaviour in evolutionary perspective. In: *Primate societies* (B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM & T. T. STRUSHAKER, eds). University of Chicago Press, Chicago, p. 319-329.
- (1988). Maternal investment in captive bonnet macaques (*Macaca radiata*). — *Am. Nat.* 132, p. 1-19.
- , CLARK-WHEATLEY, C. B., RODMAN, P. S. & SAMUELS, A. (1981a). Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques. — *Anim. Behav.* 29, p. 1106-1120.
- , SAMUELS, A. & RODMAN, P. S. (1981b). The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). — *Behaviour* 78, p. 111-137.
- SIMPSON, A. E. & SIMPSON, M. J. A. (1985). Short-term consequences of different breeding histories for captive rhesus macaque mothers and young. — *Behav. Ecol. Sociobiol.* 18, p. 83-89.
- SIMPSON, M. J. A. (1983). Effect of the sex of an infant on the mother-infant relationship and the mother's subsequent reproduction. — In: *Primate social relationships* (R. A. HINDE, ed.). Blackwell, Oxford, p. 53-57.
- , SIMPSON, A. E., HOOLEY, J. & ZUNZ, M. (1981). Infant-related influences on birth intervals in rhesus monkeys — *Nature* 290, p. 49-51.
- SLAGSVOLD, T., RØSKAFT, E. & ENGEN, S. (1986). Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care. FISHER'S theory applied to birds. — *Ornis Scand.* 17, p. 117-125.
- SMALL, M. F. & SMITH, D. G. (1984). Sex differences in maternal investment by *Macaca mulatta*. — *Behav. Ecol. Sociobiol.* 14, p. 313-314.
- SMITH, C. C. & FRETWELL, S. D. (1974). The optimal balance between size and number of offspring. — *Am. Nat.* 108, p. 499-506.
- SNOW, C. C. (1967). The physical growth and development of the open-land baboon *Papio doguera*. — Ph. D. thesis, University of Arizona.
- STAMPS, J. A. (1990). When should avian parents differentially provision sons and daughters? — *Am. Nat.* 135, p. 671-685.
- , CLARK, A., KUS, B. & ARROWOOD, P. (1985). Parent-offspring conflict in budgerigars. — *Behaviour* 94, p. 1-40.
- , —, — & — (1987). The effects of parent and offspring gender on food allocation in budgerigars. — *Behaviour* 101, p. 177-199.
- , —, —, & — (1989). Begging behavior in budgerigars. — *Ethology* 81, p. 177-192.
- & METCALF, R. A. (1980). Parent-offspring conflict. — In: *Sociobiology: Beyond nature-nurture?* (G. W. BARLOW & J. SILVERBERG, eds). Westview Press, Boulder, Colorado, p. 589-618.

- , — & KRISHNAN, V. V. (1978). A genetic analysis of parent-offspring conflict. — *Behav. Ecol. Sociobiol.* 3, p. 369-392.
- STAPLETON, D. L., HINCH, G. N., THWAITES, C. J. & EDEY, T. N. (1980). Effect of sex and litter size on the suckling behaviour of the lamb. — *Proc. Aust. Soc. Anim. Prod.* 13, p. 333-336.
- STEVENSON-HINDE, J. & SIMPSON, M. J. A. (1981). Mothers' characteristics, interactions, and infants' characteristics. — *Child Dev.* 52, p. 1246-1254.
- TEATHER, K. L. (1987). Intersexual differences in food consumption by hand-reared great-tailed grackle (*Quiscalus mexicanus*) nestlings. — *Auk* 104, p. 635-639.
- (1992). An experimental study of competition for food between male and female nestlings of the red-winged blackbird. — *Behav. Ecol. Sociobiol.* 31, p. 81-87.
- & WEATHERHEAD, P. J. (1988). Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. — *J. Anim. Ecol.* 57, p. 659-668.
- & — (1989). Sex-specific mortality in nestling great-tailed grackles. — *Ecology* 70, p. 1485-1493.
- THOMMEN, D. R. (1982). Zur Sozialentwicklung der Javaneraffen (*Macaca fascicularis*) während der ersten drei Lebensmonate. — Ph. D. thesis, Basel University.
- TRILLMICH, F. (1986). Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. — *Behav. Ecol. Sociobiol.* 19, p. 157-164.
- TRITES, A. W. (1991). Fetal growth of northern fur seals: life history strategy and sources of variation. — *Can. J. Zool.* 69, p. 2608-2617.
- TRIVERS, R. L. (1972). Parental investment and sexual selection. — In: *Sexual selection and the descent of Man* (B. CAMPBELL, ed.). Aldine, Chicago, p. 136-179.
- (1974). Parent-offspring conflict. — *Amer. Zool.* 14, p. 249-264.
- (1985). *Social evolution*. — The Benjamin/Cummings Publishing Company, Menlo Park, California.
- & WILLARD, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. — *Science* 179, p. 90-91.
- VAN WAGENEN & CATCHPOLE, H. R. (1956). Physical growth of the rhesus monkey (*Macaca mulatta*). — *Am. J. Phys. Anthropol.* 14, p. 245-273.
- WALTERS, J. R. (1987). Conflict and cooperation. In: *Primate societies* (B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM & T. T. STRUSHAKER, eds). University of Chicago Press, Chicago, p. 306-317.
- WHITE, L. E. & HINDE, R. A. (1975). Some factors affecting mother-infant relations in rhesus monkeys. — *Anim. Behav.* 23, p. 527-542.
- WILLSON, M. F. & PIANKA, E. F. (1963). Sexual selection, sex ratio and mating system. — *Am. Nat.* 97, p. 405-407.
- WOHL, J. E., KLEIN, D. H., VANDERNOOT, G. W., SELFRIDGE, D. J. & NOVOTNEY, C. A. (1981). Effect of stage of lactation, age of ewe, sibling status, and sex of lamb on gross and minor constituents of Dorset ewe milk. — *J. Dairy Sci.* 64, p. 2175-2184.
- WOLFF, J. O. (1988). Maternal investment and sex ratio adjustment in American bison calves. — *Behav. Ecol. Sociobiol.* 23, p. 127-133.
- WRIGHT, S. L., CRAWFORD, C. B. & ANDERSON, J. L. (1988). Allocation of reproductive effort in *Mus domesticus*: responses of offspring sex ratio and quality to social density and food availability. — *Behav. Ecol. Sociobiol.* 23, p. 357-365.
- YASUKAWA, K., MCCLOURE, J. L., BOLEY, R. A. & ZANOCCHIO, J. (1990). Provisioning of nestlings by male and female red-winged blackbirds, *Agelaius phoeniceus*. — *Anim. Behav.* 40, p. 153-166.
- YOUNG, G. H. & BRAMBLETT, C. A. (1977). Gender and environment as determinants of behavior in infant common baboons (*Papio cynocephalus*). — *Arch. Sexual Behav.* 6, p. 365-385.