Variation of male-biased maternal investment in fallow deer (*Dama dama*)

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Abstract

In this study 529 fallow deer fawns were captured and weighed at Doñana National Park, Spain. An annual index of male-biased maternal investment (MBMI) was calculated, and this index was found to vary in relation to environmental factors. Thus, the level of MBMI was sensitive to fluctuations of autumn rainfall and the male-biased maternal investment carried out by mothers in the previous year (MBMI_P). Our results reveal that those factors related to the female's body condition at the beginning of gestation have a high contribution to the variation of differential pre-natal maternal investment. It has been hypothesized by other authors that male-biased maternal investment is limited by the level of total maternal expenditure and these authors classified the fallow deer as a species near to its maximum reproductive effort, in which no sex-biased maternal investment exists. Our study reveals that male-biased maternal investment in fallow deer does exist and supports the hypothesis that sensitivity of maternal investment to environmental conditions could be expected to occur in species with high reproductive effort and sex-biased maternal investment.

Key words: *Dama dama*, fallow deer, male-biased maternal investment

INTRODUCTION

In polygynous mammals, where variance in reproductive success is greater in males than in females and is influenced by the amount of parental investment they receive, the investment theory predicts that parental investment will be sex-biased towards males (Trivers & Willard, 1973; Maynard Smith, 1980).

Among polygynous ungulates, differential parental investment occurs in certain species (i.e. Clutton-Brock, Guinness & Albon, 1982; Lee & Moss, 1986; Hogg, Hass & Jemi, 1992; Kojola, 1993). Two studies have discussed the hypothesis that sex-biased maternal investment could be limited by total maternal expenditure in polygynous ungulates: while Byers & Moodie (1990) concluded that the differential investment across species was negatively related to the level of total maternal expenditure, Pélabon et al. (1995) did not find any relationship between sex-biased care and total maternal expenditure across different species.

The main problem in studies on parental investment is how to measure maternal expenditure. Byers & Moodie (1990) based their hypothesis on the fact that a greater

part of the total cost of reproduction in ungulates occurs during lactation (see also Oftedal, 1984; Gittleman & Thompson, 1988). Pélabon et al. (1995) showed a list of studies (see Fletcher, 1971; Anderson & Fedak, 1987; Festa-Bianchet, 1988; Lee, Majluf & Gordon, 1991; Birgersson & Ekvall, 1997), which allowed them to consider birth weight as a more suitable variable than either post-natal growth or suckling performance to represent maternal expenditure. Birgersson & Ekvall (1997) suggested that the greater weight and size of male fallow deer *Dama dama* at birth and their faster growth compared with female offspring could determine their greater efficiency in suckling despite an equal frequency and duration of suckling. In fact, in the Doñana fallow deer population some indications suggest that the physical condition of male fawns influences the mothers' behaviour, inducing a higher investment in heavier fawns (Braza & San José, 1988). Thus, it seems that pre-natal investment in birth weight could determine the demand of post-natal investment.

Taking into account the positive correlation between birth weight and adult weight and reproductive success (Clutton-Brock, Albon & Guinness, 1988; Clutton-Brock, 1991), we consider birth weight an appropriate variable for measuring sex-biased maternal care in fallow deer.

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Previous studies on pre-natal investment in fallow deer revealed a bias towards males at birth: male fawns are born heavier and larger than females, and pre-natal growth is faster for males (Braza, San José & Blom, 1988; Birgersson & Ekvall, 1997).

Another aspect of parental investment is the variation in the level of maternal investment as a result of environmental fluctuations. At Donana, a Mediterranean area in south-western Spain, environmental conditions are unpredictable. The main mortality factors are predation and sporadic events, such as drought. In this area, environmental stress seems to play a more important role in the variation of fallow deer mating strategies than social stress (San José & Braza, 1997). Furthermore, some results concerning the fallow deer fawning season at Donana revealed that population density and environmental conditions during the last month of gestation had repercussions on the reproductive performance of females (Braza, San José, Blom, Cases et al., 1990).

A hypothesis of energy constraint on sex-biased maternal expenditure related to environmental variations was recently proposed by Byers & Hogg (1995): species far from the maximum reproductive effort should show a reproductive performance less sensitive to environmental variations than species near to the maximum possible level of maternal investment. According to this hypothesis (see also Byers & Moodie, 1990), species near to the maximum reproductive effort should not have a bias in favour of male offspring.

Our aim was to test whether the yearly variation of the male-biased maternal investment is influenced by environmental variations and/or by the mother's previous maternal investment. Extra investment in male fawns after favourable weather conditions and low previous maternal investment could be expected.

METHODS

Donana National Park (south-western Spain) includes 3 main biotopes: sand dunes, Mediterranean shrubland, and marshes (Allier, González-Bernáldez & Ramírez, 1974). The mean temperature ranges from 8–11 °C in winter to 23–28 °C in summer; rainfall fluctuates over the years and mainly occurs in autumn–winter ($\bar{x}$ = 415 mm, sD = 202) (data from 1980–96).

In Donana, 80% of the fallow population concentrates in an ecotone area between marshes and shrub (Braza, 1975; Ojeda et al., 1983; Braza & Alvarez, 1987). This ecotone area of the Biological Reserve (1 × 6.5 km, included in the National Park) was selected as the study area. The fallow deer population living in that area ranged from 103 to 373 individuals between 1981 and 1996 (summer census data; see Braza, San José, Blom, Cases et al., 1990 for method).

In Donana, the rutting season occurs during the first half of October (Braza, García & Alvarez, 1986). Females give birth to a single fawn at the end of May to the beginning of June (Braza, San José & Blom, 1988;

Fig. 1. Mean male weight at birth regressed on mean female weight at birth (means from 15 years: 1981–83 and 1985–96); $y = 2447.044 + 0.548x$; $R^2 = 0.319$.

San José & Braza, 1992). They mostly select the cover of rushes *Juncus* in the ecotone area for parturition (San José & Braza, 1992).

Study sample and method

For 16 years (1981–96) the ecotone area of the Biological Reserve was searched daily during the fawning season to find newborn fawns. This was done on foot and sometimes with the assistance of a guard on horseback. A total of 529 fawns were marked with ear-tags and weighed, and their sex and age were recorded.

When birth was not seen the fawn's age was estimated according to the following criteria: the presence of remains of placenta, the still moist fur, the degree of healing of the umbilical cord, the hardening of the hooves and the presence of cartilage on their points (Braza, San José & Blom, 1988; San José & Braza, 1992; Pélabon, 1995).

Only data from 'newborn' fawns (< 24 h) were used for the analysis; 1984 was excluded from this study because of the small sample size.

Variables considered and statistical analysis

Dependent variable

Male-biased maternal investment (MBMI)

We regressed the mean birth weight of male fawns on the mean birth weight of female fawns for each year, and used the residuals from this regression as an index of the extra-investment by mothers in male fawns (Fig. 1; $R^2 = 0.319$, $F = 6.100$, $P = 0.0281$). This index was used as a dependent variable in a stepwise regression (F to remove = 4; StatView 4.5, Abacus Concepts, Inc. 1992–95) to analyse the factors contributing to the yearly variation in sex-biased maternal investment.

Table 1. Principal component loadings from autumn-winter climatic variables in the study area over the period 1980-1996 (T = mean temperature, R = accumulated rainfall, TR = mean emperature and accumulated rainfall)

	Principal components	
	I (TR Winter)	II (Earliness R Autumn)
T October—November	0.749	—0.302
T December—January	0.931	—0.033
T February—March	0.184	0.043
R October	—0.0003	0.777
R November	—0.002	—0.769
R December	0.841	0.349
R January	0.800	—0.023
R February	—0.168	—0.0002
R March	0.312	—0.014
Eigen values	3.10	1.71
Proportion of variance	34.50	19.00

Independent variables

Male-biased maternal investment in the previous year (MBMI_P)

Calculated as MBMI on fawns born in the previous spring.

Climate in autumn—winter

Since data concerning forage productivity were not available, we used the climatic variables as an indirect measure of availability of resources in this season: monthly mean temperature and monthly accumulated rainfall for October—March for 1980—96. These variables were compacted by a principal components analysis (VARIMAX rotation; StatView 4.5, Abacus Concepts Inc. 1992—95). As Table 1 shows, the climatic principal components resulting from that analysis were temperature in autumn—winter, rainfall in winter (TR Winter) and rainfall in autumn (Earliness R Autumn). These factors were included as independent variables in the stepwise regression.

Forage productivity

Measured in spring—summer as dry biomass per area (kg/m²) (R. Soriguer, pers. comm.). Data of productivity

were available for 1983—90 and 1992—96 (range = 10—39 kg/m²).

Female density

Number of females per 100 ha in the study area; 7—32 female/100 ha (summer census data; see Braza, San José, Blom, Cases et al., 1990 for method).

Statistical analyses were performed according to Zar (1984). All tests were 2-tailed.

RESULTS

The mean fawn weight at birth was positively correlated with MBMI (Pearson's correlation, $r = 0.530$, $P = 0.040$; $n = 15$). No significant correlations were detected between sex-ratio at birth and mean fawn's birth weight ($r = -0.253$, $P = 0.3711$) or MBMI (Pearson's correlations: $r = 0.140$, $P = 0.6258$).

We tested the effect of the MBMI_P, climatic factors in autumn—winter, forage productivity, and female density (independent variables) on the MBMI (dependent variable) in a stepwise regression. Table 2 reveals a negative contribution of both MBMI_P and Earliness R Autumn to the MBMI. A lower MBMI_P, as well as a later autumn rainfall determined an increase in MBMI the following year. The independent variables were not significantly correlated (Pearson's correlations).

DISCUSSION

Our results revealed that male-biased maternal investment (MBMI) in fallow deer at Donana is affected by the earliness of autumn rainfall and the level of extra-male investment made by mothers in the previous breeding season (MBMI_P).

The yearly variation detected in MBMI establishes additional evidence that male-biased maternal investment in fallow deer is possible. Previous results related to adoptive behaviour in the same fallow deer population already suggested that a margin in the amount of parental investment allocated by a mother to her fawn probably exists, depending on different factors such as the sex of the fawn or its own physical condition (San José & Braza, 1993).

Table 2. Male-biased maternal investment (MBMI) stepwise regression on climatic factors, forage productivity (Kg/m²), female density, and MBMI_P. Parameters after the second and last step

Multiple R	0.74	Adjusted R ²	0.44	Mean square	F	P
Multiple R ²	0.54					
Residuals	185.65	d.f.				
Analysis of variance	Sum of squares					
Regression	365887.98	2		182943.99	5.308	0.03
Residual	310193.70	9		34465.97		
Variables	Coefficient	sE	Standard coefficient	F-to-remove		
Intercept	—22.82	54.26	—22.82	0.18		
Earliness R Autumn	—143.58	50.76	—0.65	7.99		
MBMI _P	—0.48	—0.24	—0.47	4.15		

Furthermore, the fact that the level of MBMI was sensitive to environmental conditions and the $MBMI_P$, suggests that fallow deer can be considered as a high-reproductive-effort species. This agrees with Byers & Hogg's (1995) hypothesis that predicts for ungulates a higher sensitivity of the reproductive performance to environmental conditions in high-reproductive-expenditure species than in lower ones. However, we disagree with Byers & Hogg's hypothesis (1995; see also Byers & Moodie, 1990) when contending that females of high-reproductive-expenditure species do not show differential expenditure by offspring sex.

Our results show that sensitivity of maternal investment to environmental conditions could be expected to occur in species with high reproductive effort and sex-biased maternal investment, mainly in populations living under environmental stochasticity as in the fallow deer in Donana. Yearly fluctuations in the fawns' birth weight had already been detected in this population (Braza, San José & Blom, 1988). The sensitivity of maternal investment to environmental conditions may be particularly evident in the extra-investment that mothers can afford to make in male offspring each year. In some species dimorphism in neonatal weight decreases (by lower male birth weights) when conditions become harsh (Skogland, 1990; Robertson et al., 1992), and variations in male-biased early growth affected by the mother's condition has been described for fallow deer (Birgersson & Ekvall, 1997).

Concerning the detected influence of the females' previous reproductive effort ($MBMI_P$) on the MBMI in the following breeding season, our results agree with the information proceeding from other studies on several species, which reveal a reduction in the subsequent reproductive performance of females after rearing male vs female offspring (Clutton-Brock, Guinness & Albon, 1982; Lee & Moss, 1986; Wolff, 1988; Clutton-Brock, Albon & Guinness, 1989; Clutton-Brock, 1991; Bêrubé, Festa-Bianchet & Jorgenson, 1996; Clutton-Brock, Stevenson et al., 1996).

A negative influence of the earliness of autumn rainfall on the MBMI was also detected in the Donana fallow deer population, which could be related to two factors:

(1) Autumn forage productivity in Mediterranean habitats (Lazo, 1992) which could positively influence the mother's physical condition in winter. Although data on autumn forage productivity at Donana are not available, the most plausible hypothesis is that this variable affects the physical condition of mother and offspring in the early phase of gestation. A recent study on fallow deer (Birgersson & Ekvall, 1997) has revealed that the fawn's birth mass and early growth rate were significantly correlated to the mother's body mass; furthermore, pre- and post-natal growth rates were higher for male fawns. Since sex-differences in growth rate seems to start at the beginning of gestation, the mother's physical condition at that moment could be influencing the initial growth rate of the offspring and

the level of sex-differences in weight (through an extra-male maternal investment) that will be maintained throughout the gestation.

According to several authors (see review in Gittleman & Thompson, 1988) ungulates buffer the costs of gestation by laying down fat reserves before conception. In red deer the energy costs of gestation and lactation have a marked effect on the maternal condition during the summer and on subsequent fecundity (Clutton-Brock, Guinness & Albon, 1982, 1983). Our study suggests that the physical condition of females at the moment of conception and early gestation also determines the level of extra-investment they can afford to make in male offspring.

(2) We would expect the most vigorous mothers to conceive and give birth earlier to larger offspring, as has been observed in other deer species (Clutton-Brock, Albon & Guinness, 1984, 1986; Birgersson & Ekvall, 1997). Our results reveal that the earliness of autumn rainfall seems to contribute negatively to the MBMI the following year. This could be a result of a delay in the rutting season caused by early autumn rainfall. This delay could decrease the number of bigger male offspring and the male fawn's birth weight the following year.

In summary, our study on fallow deer shows an effect of environmental factors and the mother's previous reproductive effort on the yearly variation of male-biased maternal investment, emphasizing the importance of the moment of conception and the early phase of gestation. Fallow deer can be considered as a species close to the maximum reproductive effort, but with a margin to vary the amount of maternal investment allocated to male fawns.

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