Cap. 5: Fecundidad ♀.

The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*)

C. San José, F. Braza, and S. Aragón

Abstract: In this paper we tested whether prenatal expenditure of resources in fallow deer (*Dama dama*) is affected by the age and reproductive experience of mothers. The study was carried out on the wild fallow deer population in Doñana National Park in southwestern Spain. Between 1985 and 1996 a total of 60 different females were monitored by direct observation during the fawning season. The exact age of 22 of these females was known, and 59 fawns born of these females were captured. The mother's age had more influence on the fawn's birth mass than the mother's experience did. Fallow deer fawns born of adult multiparous mothers (5–8 years old) were heavier than fawns born of young multiparous mothers (3–4 years old), whereas birth masses of fawns born of primiparous mothers (2–3 years) and young multiparous mothers showed no significant difference. Fawns were born earlier in the breeding season as the mother's age increased. The trade-off required between resources allocated to reproduction and resources available for growth and maintenance may limit reproduction and the possibility of increasing prenatal expenditure by both young primiparous and young multiparous female fallow deer. Sexual dimorphism in birth mass was detected, males being heavier than females, independently of the age and parity of the mothers. This confirms the finding that fallow deer mothers are selected to expend more resources on their male offspring.

Résumé : Dans cet article, nous nous demandons si la dépense prénatal du daim (*Dama dama*) est influencé par l'âge et l'expérience reproductive des mères. Le travail a été fait sur une population de daims en liberté du Parc National de Doñana. Entre 1985 et 1996 nous avons observé directement un total de 60 femelles différentes pendant la période des naissances. Nous connaissions l'âge exact de 22 femelles et 59 faons de ces femelles connues furent capturés. L'âge de la mère s'est révélé plus déterminant que sont expérience reproductive sur le poids de naissance des faons. Les petits nés de mères adultes multipares (5–8 ans) furent plus lourds que les petits nés de jeunes mères multipares (3–4 ans); mais les mères primipares (2–3 ans) et les jeunes multipares n'ont pas montré de différence significative dans le poids de leurs petits. Plus les mères étaient agées plus leurs faons sont nés en avance dans la période des naissances. L'équilibre entre les ressources offertes à la reproduction et à la croissance peut limiter la reproduction même et la possibilité d'augmenter la dépense prénatal chez les jeunes mères (aussi bien les primipares que les multipares). Les faons mâles pesérent davantage à la naissance que les femelles indépendamment de l'âge et de l'expérience reproductive de leurs mères. Ce résultat confirme que les mères des daims sont sélectionnées pour dépenser davantage sur leurs petits mâles.

[Traduit par la Rédaction]

Introduction

The fallow deer (*Dama dama*) is a polygynous species (Langbein and Thirgood 1989) in which females provide all the parental care. Since, in polygynous species, male reproductive success varies more with adult body size than does female reproductive success (Clutton-Brock et al. 1988; Komers et al. 1997) and early growth affects adult body size (Case 1978; Shine 1990), variation in the level of maternal investment during gestation and early postnatal growth of the offspring is likely to cause more variation in fitness of individual male offspring than of female offspring, and in theory, mothers would be expected to invest heavily in their male offspring (Trivers and Willard 1973; Maynard-Smith 1980).

Some evidence of male-biased prenatal expenditure has been found in fallow deer (male fawns were heavier at birth than female fawns; Braza et al. 1988; Birgersson and Ekvall 1997) as well as in other polygynous ungulate species (red deer, *Cervus elaphus*, Clutton-Brock et al. 1982; bighorn sheep, *Ovis canadensis*, Hogg et al. 1992; reindeer, *Rangifer tarandus*, Kojola 1993; American bison, *Bison bison*, Wolff 1988; African elephant, *Loxodonta africana*, Lee and Moss 1986).

Based on the ratio of birth mass to maternal mass, the fallow deer was classified as a species close to its maximum reproductive effort, so there are limits to extra investment in

Received January 8, 1999. Accepted July 5, 1999.

C. San José, F. Braza,[1] and S. Aragón. Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Avenida Maria Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain.

[1]Author to whom all correspondence should be addressed (e-mail: braza@ebd.csic.es).

offspring of one sex (Byers and Moodie 1990). In contrast, recent results have revealed that a certain margin does exist, allowing variation in prenatal investment in fallow deer, depending on variations in environmental factors (Braza et al. 1999).

One consequence of investing heavily in offspring of either sex is the cost imposed in terms of the mother's own energy reserves for growth and maintenance. In this respect, several authors have shown that age (red deer, Guinness et al. 1978*a*; roe deer, *Capreolus capreolus*, Gaillard et al. 1992; mountain goats, *Oreamnos americanus*, Bailey 1991; bighorn sheep, Festa-Bianchet et al. 1995), reproductive experience (red deer, Mitchell et al. 1976; fallow deer, Birgersson and Ekvall 1997), and physical condition (chamois, *Rupricapra rupricapra*, Bauer 1987; red deer, Hamilton and Blaxter 1980; moose, *Alces alces*, Sæther and Haagenrud 1983; reindeer, Cameron et al. 1993; fallow deer, Birgersson and Ekvall 1997) affect the reproductive success of female ungulates. In species like the fallow deer that show male-biased parental care, variation in prenatal resource expenditure according to the age and parity of the mother can be expected.

Little information is available concerning variation in prenatal resource expenditure in wild fallow deer populations. A long-term study of the wild, unmanaged fallow deer population in Doñana National Park has provided data on the reproductive experience (parity) of several females of known age, as well as the sex, birth date, and birth mass of their fawns.

Considering that (*i*) selection may have acted on mothers in polygynous species to invest heavily in their male offspring, and (*ii*) the fallow deer is a polygynous species with high reproductive effort, it would be particularly interesting to analyse how factors related to the maturity of females (such as age and parity) affect their ability to reproduce and invest in their offspring.

The aim of this study was to analyse how prenatal resource expenditure in fallow deer is affected by the age and reproductive experience of mothers. Our hypothesis was that adult multiparous mothers (females that have completed their own growth and development) produce fawns with higher birth mass. Furthermore, we tested whether sex-related differences in birth date and birth mass vary according to the age and parity of mothers.

Materials and methods

Study area

The study was carried out in Doñana National Park in southwestern Spain (37°N, 6°30′W). This park covers 70 000 ha and includes a central Biological Reserve with an area of 7500 ha. Three main biotopes can be distinguished: sand dunes, Mediterranean shrubland, and marshes (Allier et al. 1974). Fallow deer congregate (about 80% of the population) in an ecotone area between marshes and shrub consisting of different kinds of meadow and patches of rushes (*Juncus* sp.) (Braza 1975; Ojeda et al. 1983; Braza and Alvarez 1987). The climate in Doñana National Park is Mediterranean. The average annual temperature is 17°C; August is the hottest month (mean 24°C) and January the coldest (mean 11°C). Mean annual rainfall is 500 mm.

The ecotone area of the Biological Reserve (6.5 km^2, 1 km long) was chosen as the study area. The number of female fallow deer in that area fluctuated between 127 and 180 from 1985 to 1996 (Braza et al. 1990; San José and Braza 1992, 1997).

The rutting season takes place during the first 2 weeks in October (Braza et al. 1986). Female fallow deer give birth to a single fawn in late May – early June (Braza et al. 1988; San José and Braza 1992) after a gestation period of 236 days (San José 1988). Fawns usually remain in the home range of their mother until she is about to give birth in the next fawning season. Daughters remain within the mother's home range in relatively stable matrilineal groups (Cases 1987; San José and Braza 1993). Female fallow deer reach puberty at about 16 months of age (Chapman and Chapman 1975). We estimate that female fallow deer in Doñana National Park reach a maximum age of 10 years (F. Braza and C. San José, unpublished data).

Study subjects and procedure

Sample sizes in this study were affected by the unmanaged conditions in the study area and by some methodological problems: females sometimes left the area, some females lost their ear tags, or their fawns avoided capture.

Between 1985 and 1996 a total of 60 different females were monitored (over different years) by direct observation during the fawning season. The exact age of 22 of these females was known, since they were captured and marked with plastic ear tags at birth. It was possible to capture, sex, and weigh 59 fawns born of these 22 females.

The capture of fawns was carried out during the fawning season. This was done on foot (sometimes with the aid of a vehicle or a guard on horseback) and by observing pregnant females from a 30 m high tower, using a binocular telescope (20/40 × 80/500).

The following information concerning fawns and females was recorded for analysis: fawn's sex: all captured fawns were sexed by visual inspection; fawn's birth date: this was estimated according to different criteria, e.g., the presence of remains of the placenta, the moist fur of the fawn, the degree of healing of the umbilical cord, and the hardening of the hooves and the presence of cartilage on their points (Braza et al. 1988; San José and Braza 1992; Pélabon 1995); fawn's birth mass: the captured fawns were weighed using a spring balance (100 g accuracy); only masses of "newborn fawns" (less than 24 h old according to the birth-date criteria) were used in this study; proportion of breeding females: the proportion of females that gave birth to fawns; mother's age in years; mother's reproductive experience: females were classified as primiparous when they produced a fawn for the first time. Females that had bred for the second time or more were identified as multiparous.

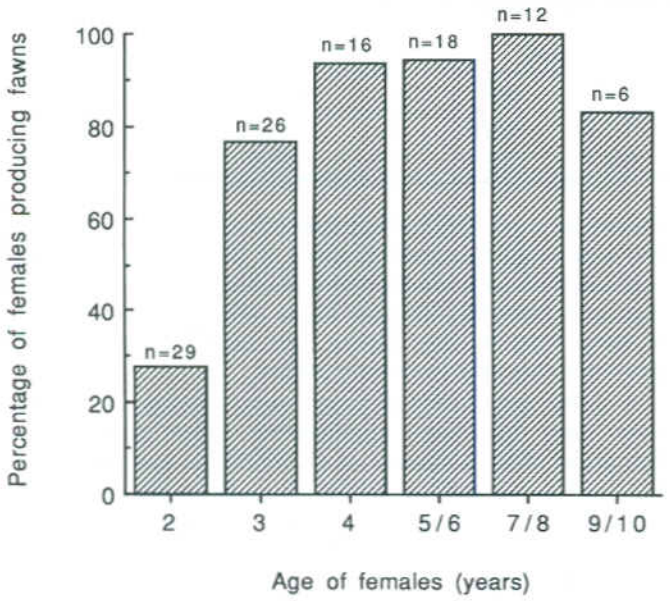
Data on actual reproductive cost to the mothers were not available. Nevertheless, based on other studies (for a review see Pélabon et al. 1995) we considered birth mass to be a suitable measure of maternal resource expenditure and prenatal investment.

Statistical analysis

The fact that females were monitored over several years creates a potential dependency problem for statistical testing in the analysis with all fawns pooled. To estimate the degree of dependence on data from fawns born of the same mother, we applied a one-way ANOVA for both variables, fawn's birth mass and fawn's birth date, with individual mothers who contributed data from more than three fawns as a factor. Only three females contributed more than three fawns to the sample, and no significant effect of individual female on fawn's birth mass ($F_{[2,14]} = 0.30$, $P = 0.75$) or fawn's birth date ($F_{[2,15]} = 3.25$, $P = 0.07$) was detected.

We also carried out a one-way ANOVA to test differences between years during the study period. There was no significant effect of year on fawn's birth mass ($F_{[11,39]} = 1.50$, $P = 0.17$) or

Fig. 1. Proportions of breeding females at different ages.



birth date ($F_{[11,42]}$ = 1.67, P = 0.11) over the study, therefore data from all years were pooled for analysis.

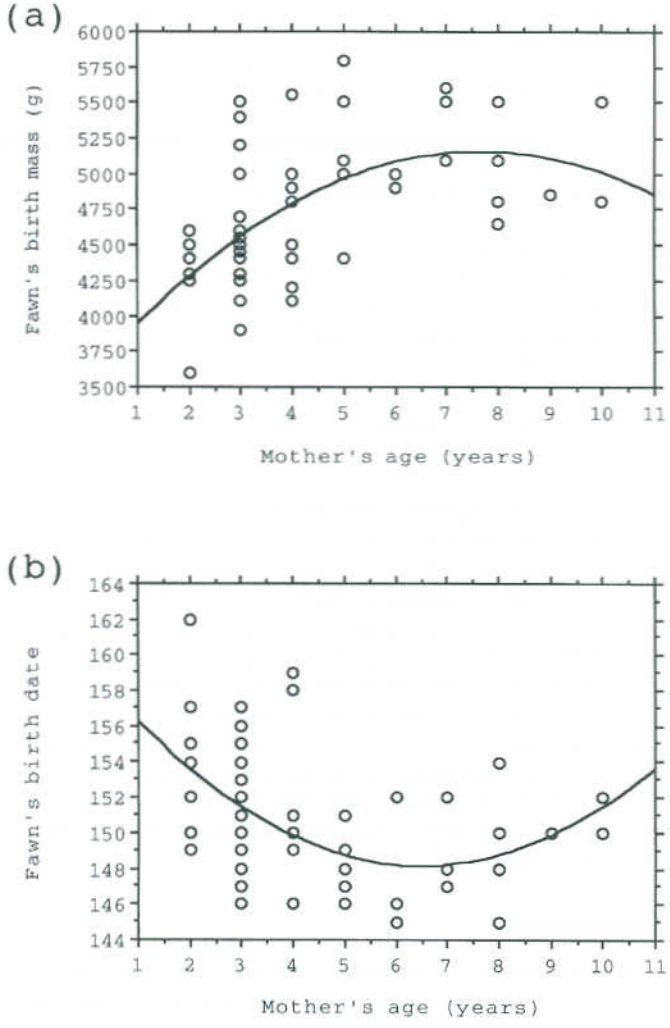
To test whether the proportion of breeding females varied according to age, χ^2 tests were performed. A polynomial regression model of order 2 was used to test the effect of mother's age on fawn's birth mass and birth date. One-way ANOVAs were applied to analyse differences in fawn's birth mass and birth date between different age and parity categories of females. Data on body mass of females were not available, but the age and parity categories considered are in accordance with the maturity phases of female fallow deer. A two-way ANOVA was carried out to test the influence of fawn's sex and age and parity of mothers on fawn's birth mass and birth date (Zar 1984).

Results

Two-year-olds constituted the lowest proportion of breeding females (27.6%) (Fig. 1). The proportion of breeding females increased to almost 80% of 3-year-olds, then remained near 100% for 4- to 8-year-olds and declined slightly among old females (9–10 years). Differences in the proportion of breeding females were detected between 2-year-old and older females (χ^2 = 38.28, df = 1, P = 0.0001). Differences in the proportion of breeding females among age categories above 3 years were not significant (χ^2 = 6.52, df = 4, P = 0.16). All 2-year-old mothers were primiparous. Of the 3-year-olds, 75% were primiparous and 25% had given birth the previous year. Only 13.3% of 4-year-old mothers were primiparous, while 100% of mothers aged 5 years or more were multiparous.

Mother's age had a significant effect on fawn's birth mass and birth date (Fig. 2). With increase in the mother's age up to 5 years, fawns were born heavier and earlier in the breeding season (Fig. 2; second-order polynomial regression, R^2 = 0.33, $F_{[2,48]}$ = 11.95, P = 0.0001 for birth mass; R^2 = 0.19, $F_{[2,51]}$ = 5.87, P = 0.005 for birth date). Mothers aged 5–8 years had the heaviest and earliest born fawns. Mothers over 8 years seemed to breed later and bear lighter fawns (Fig. 2); these females were excluded from further analysis.

Fig. 2. Second-order polynomial regression of fawn's birth mass (*a*) and fawn's birth date (*b*) on mother's age.



One-way ANOVA revealed no significant differences in fawn's birth mass between primiparous 2-year-old mothers (n = 6) and primiparous 3-year-old mothers (n = 14) ($F_{[1,18]}$ = 1.64, P = 0.22), but primiparous 2-year-old mothers (n = 7) bred later than primiparous 3-year-old mothers (n = 15) ($F_{[1,20]}$ = 6.05, P = 0.02).

In the cases of 5 captured fawns out of 37, the multiparous mothers had failed to breed the previous year. These five fawns were excluded from the analysis. No significant differences in fawn's birth mass ($F_{[1,8]}$ = 1.22, P = 0.30) or birth date ($F_{[1,9]}$ = 0.70, P = 0.42) were detected between multiparous 3-year-old mothers (n = 4) and multiparous 4-year-old mothers (n = 6). Multiparous 5- to 6-year-old mothers (n = 9) gave birth significantly earlier in the breeding season than multiparous 3- to 4-year-old mothers (n = 11) ($F_{[1,18]}$ = 6.67, P = 0.02) and had significantly heavier fawns ($F_{1,17}$ = 7.23, P = 0.01; n = 9 and 10, respectively). No significant differences in fawn's birth mass or birth date were detected between multiparous 5- to 6-year-old mothers (n = 9) and multiparous 7- to 8-year-old mothers (n = 7) ($F_{[1,14]}$ = 0.33, P = 0.57 for birth mass; $F_{[1,14]}$ = 1.10, P = 0.31 for birth date).

Table 1. Birth masses (in grams) of fallow deer fawns born of mothers in different age and parity categories.

	Young (2–3 years old) primiparous mothers			Young (3–4 years old) multiparous mothers			Adult (5–8 years old) multiparous mothers		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Male fawns	9	4561.1	544.2	4	4775.0	450.0	7	5328.6	359.2
Female fawns	11	4368.2	278.6	6	4466.7	301.1	9	4950.0	310.2

To analyse sex-related differences in birth date, a two-way ANOVA was performed on four categories of females: primiparous 2-year-old mothers (n = 7; 4 male and 3 female fawns), primiparous 3-year-old mothers (n = 15; 6 male and 9 female fawns), multiparous 3- to 4-year-old mothers (n = 11; 5 male and 6 female fawns), and multiparous 5- to 8-year-old mothers (n = 16; 7 male and 9 female fawns). Significant differences in parturition date among these categories of females were detected ($F_{[3,41]} = 4.77$, $P = 0.006$), but no sex-related differences were found ($F_{[1,41]} = 0.25$, $P = 0.62$).

To analyse sex-related differences in fawn's birth mass we used three categories of females: young (2–3 years old) primiparous mothers (n = 20; 9 male and 11 female fawns), young (3–4 years old) multiparous mothers (n = 10; 4 male and 6 female fawns), and adult (5–8 years old) multiparous mothers (n = 16; 7 male and 9 female fawns). A two-way ANOVA revealed that adult multiparous mothers produced significantly heavier fawns than mothers in either of the other categories ($F_{[2,40]} = 14.42$, $P = 0.0001$), and that there were sex-related differences in fawn's birth mass ($F_{[1,40]} = 6.17$, $P = 0.01$). The interaction between fawn's sex and age and parity of the mother was not significant ($F_{[2,40]} = 0.27$, $P = 0.76$) (Table 1).

Discussion

The proportion of breeding females increased progressively up to 4 years of age (when there was still a small percentage of females that bred for the first time). In several deer species (including the fallow deer), unless a female reaches a particular threshold mass she will not ovulate (Mitchell and Brown 1974; Staines 1978; Teer 1984; Ratcliffe and Rowe 1985; Putman 1988). According to this evidence, the fact that the percentage of reproducing females in the fallow deer population in Doñana National Park increases until they reach 4 years of age suggests that females continue to grow until they reach this age.

With regard to fawn's birth date, the mother's age seems to be a relevant factor: fawns were born earlier in the breeding season as the mother's age increased. Furthermore, differences were found within primiparous mothers (between 2- and 3-year-old females) and within multiparous mothers (between 3- to 4-year-old and 5- to 8-year-old females). Age and parity are related and a larger sample size is necessary to test independent effects of these factors on fawn's birth date.

Being born earlier in the breeding season confers a certain advantage on a fawn, since its prewinter body mass depends on the length of time available for growth before weaning (Birgersson and Ekvall 1997), and late-born offspring are more likely to suffer mortality due to predation and undernutrition than those born earlier in the breeding season (Guinness et al. 1978*b*; Clutton-Brock et al. 1982). The fact that none of the late-born offspring of fallow deer in Doñana National Park survived the summer confirms this hypothesis (San José 1988; San José and Braza 1992). The survival rate of fawns born to older fallow deer mothers may have increased if they had been born earlier.

A direct relationship between early calving and female body mass has been reported for other deer species (Skogland 1983; Cameron et al. 1993). In our opinion, a threshold mass, limited by the energetic costs of growth, could explain the delay in calving time (and probably in conception date) observed among young females in our study population.

The data on fawn's birth mass reveal that the mother's age has a greater influence than the mother's experience. Fawns born to adult (5–8 years old) multiparous mothers were heavier than those of young (3–4 years old) multiparous mothers, whereas fawns born of young (2–3 years old) primiparous mothers and young multiparous mothers showed no significant differences in birth mass.

From these results we conclude that the age of female fallow deer affects their reproduction (both fawn's birth mass and birth date) and that it is a more relevant factor than experience, at least for fawn's birth mass.

A recent study on farmed fallow deer has shown that the mother's body mass (which is correlated with her age) was correlated with fawn's birth mass, birth date, and growth rate (Birgersson and Ekvall 1997). Our results suggest that the trade-off between resources allocated to prenatal investment and resources available for growth and maintenance may limit the reproduction of young (both multiparous and primiparous) female fallow deer. Theoretical approaches have assumed that diversion of energy from growth to offspring production is a cost of reproduction (Charnov 1991), and evidence from many deer species reveals that females continues to grow until they are more than 3 years old (Putman 1988).

No sex-related differences in fawn's birth date were found, therefore the observed variation in birth date with mother's age occurs for male as well as female fawns. In contrast, sexual dimorphism in birth mass was detected, males being heavier than females, independently of the age and parity of the mother. The strong synchronization of births detected among fallow deer in Doñana National Park (Braza et al. 1988; San José and Braza 1992) might limit variation in birth date.

To sum up, fallow deer fawns are heavier and are born earlier in the breeding season as the mother's age increases, with optimum reproduction occurring between 5 and 8 years of age. Although there does not seem to be any variation in birth date according to the fawn's sex, a margin of variation in the mother's expenditure in the fawns birth mass exists,

and all mothers (regardless of their age and parity) seem to be selected to invest more in their male offspring.

Our results confirm that sex-biased prenatal expenditure occurs in fallow deer, and contrast with Byers and Moodie's (1990) hypothesis by providing evidence that species close to their maximum reproductive effort, such as the fallow deer, have extra resources available to put into offspring of one sex. This possibility had already been suggested by the results of an earlier study (Braza et al. 1999) that analysed the influence of different ecological factors on variation in the extra resource expenditure on male fawns observed in the fallow deer population in Doñana National Park.

Further studies on the mechanisms governing maternal investment in fallow deer would be of great interest.

Acknowledgements

This study was supported by the Dirección General de Investigación Científica y Técnica (projects PR84-0243-C07-01 and PB87-0316), CSIC, and the Junta de Andalucía. The study period was so long that a great number of people (impossible to list) were required, and have been of great help, especially the guards at Doñana National Park and the different managers and staff at the Biological Reserve in Doñana. Furthermore we thank Allard Blom, Annie and Rita Braza, Tica Cases, Juan E. García Yuste, Alicia Prieto, and Iván Varela for their consistent and continuous assistance. Enrique Collado has always given us the benefit of his knowledge on the management and analysis of data. Dr. Fernando Alvarez not only participated in the fieldwork but also critically revised the manuscript. We also thank Dr. Pedro Jordano for his assistance in analysing the results. The appropriate comments of Dr. Festa-Bianchet and an anonymous reviewer improved our manuscript.

References

Allier, C., González Bernáldez, F., and Ramírez, L. 1974. Doñana: mapa ecológico. Estación Biológica de Doñana, CSIC, Seville, Spain.

Bailey, J.A. 1991. Reproductive success in female mountain goats. Can. J. Zool. **69**: 2956–2961.

Bauer, J.J. 1987. Factors determining the onset of sexual maturity in New Zealand chamois (*Rupricapra rupricapra* L.). Z. Sauegetierkd. **52**: 116–125.

Birgersson, B., and Ekvall, K. 1997. Early growth in male and female fallow deer fawns. Behav. Ecol. **8**: 493–499.

Braza, F. 1975. Censo del gamo (*Dama dama*) en Doñana. Nat. Hisp. **3**: 1–27.

Braza, F., and Alvarez, F. 1987. Habitat use by red deer and fallow deer in Doñana National Park. Misc. Zool. **11**: 363–367.

Braza, F., García, J.E., and Alvarez, F. 1986. Rutting behaviour of fallow deer. Acta Theriol. **31**: 467–478.

Braza, F., San José, C., and Blom, A. 1988. Birth measurements, parturition dates and progeny sex ratio of *Dama dama* in Doñana, Spain. J. Mammal. **69**: 607–610.

Braza, F., San José, C., Blom, A., Cases, V., and García, J.E. 1990. Population parameters of fallow deer at Doñana National Park (SW Spain). Acta Theriol. **35**: 277–288.

Braza, F., San José, C., and Aragón, S. 1999. Variation of male-biased maternal investment in fallow deer (*Dama dama*). J. Zool. (Lond.), **249**. In press.

Byers, J.A., and Moodie, J.A. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit as differential provisioning in ungulates. Behav. Ecol. Sociobiol. **26**: 157–164.

Cameron, R.D., Smith, W.T., Fancy, S.G., Gerhart, K.L., and White, R.G. 1993. Calving success of female caribou in relation to body weight. Can. J. Zool. **71**: 480–486.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. **53**: 243–282.

Cases, V. 1987. Afinidades gregarias del gamo (*Dama dama*) en Doñana durante el periodo juvenil. Tesina de licenciatura, Universidad de Valencia, Valencia, Spain.

Chapman, D., and Chapman, N. 1975. Fallow deer (*Dama dama*). Terence Dalton Ltd., Levenham, Suffolk, England.

Charnov, E.L. 1991. Evolution of life history variation among female mammals. Proc. Natl. Acad. Sci. U.S.A. **88**: 1134–1137.

Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1982. Red deer: behavior and ecology of two sexes, Edinburgh University Press, Edinburgh.

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1988. Reproductive success in male and female red deer. *In* Reproductive success. *Edited by* T.H. Clutton-Brock. The Chicago University Press, Chicago. pp. 325–343.

Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M., and Wishart, W.D. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. Ecology, **76**: 871–881.

Gaillard, J.M., Sempéré, A.J., Boutin, J.M., Van Laere, G., and Boisaubert, B. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Can. J. Zool. **70**: 1541–1545.

Guinness, F.E., Albon, S.D., and Clutton-Brock, T.H. 1978*a*. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds of Rhum. J. Reprod. Fertil. **54**: 325–334.

Guinness, F.E., Clutton-Brock, T.H., and Albon, S.D. 1978*b*. Factors affecting calf mortality in red deer. J. Anim. Ecol. **31**: 243–251.

Hamilton, W.J., and Blaxter, K.L. 1980. Reproduction in farmed red deer. 1. Hind and stag fertility. J. Agri. Sci. (Camb.), **95**: 261–273.

Hogg, J.T., Hass, C.C., and Jenni, D.A. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. Behav. Ecol. Sociobiol. **31**: 243–251.

Kojola, I. 1993. Early maternal investment and growth in reindeer. Can. J. Zool. **71**: 2509–2517.

Komers, P, Pélabon, C., and Stenström, D. 1997. Age at first reproduction in male fallow deer: age versus dominance-specific behaviours. Behav. Ecol. **8**: 456–462.

Langbein, J., and Thirgood, S.J. 1989. Variation in mating systems in fallow deer (*Dama dama*) in relation to ecology. Ethology, **83**: 195–214.

Lee, P.C., and Moss, C.J. 1986. Early maternal investment in male and female African elephant calves. Behav. Ecol. Sociobiol. **18**: 353–361.

Maynard-Smith, J. 1980. A new theory of sexual investment. Behav. Ecol. Sociobiol. **7**: 247–251.

Mitchell, B., and Brown D. 1974. The effects of age and body size on fertility in female red deer (*Cervus elaphus* L.). *In* Proceedings of XI International Congress of Game Biologists, Stockholm, Sweden, 3–7 September 1973. *Edited by* I. Kjerner and P. Bjurholm. Swedish National Environment Protection Board, Stockholm. pp. 89–98.

Mitchell, B., McCowan, D., and Nicholson, I.A. 1976. Annual cycles of body weight and condition in Scottish red deer. J. Zool. (1965–1984), **180**: 107–127.

Ojeda, G., Braza, F., Alvarez, F., and Azcárate, T. 1983. La población de gamos del Parque Nacional de Doñana en 1979. Doñana Acta Vertebr. **10**: 221–224.

Pélabon, C. 1995. Variabilité des critères d'estimation de l'âge des faons de daim (*Dama dama*) au cours des premiers jours suivant la naissance. Mammalia, **59**: 141–146.

Pélabon, C., Gaillard, J.M., Loison, A., and Portier, C. 1995). Is sex-biased maternal care limited by total maternal expenditure in polygynous ungulates? Behav. Ecol. Sociobiol. **37**: 311–319.

Putman, R. 1988. The natural history of deer. Christopher Helm, London.

Ratcliffe, P.R., and Rowe, J.J. 1985. A biological basis for managing red and roe deer in British forests. *In* Proceedings of XVII Congress of Game Biologists, Brussels, Belguim, 17–21 September 1985. Vol. 1. *Edited by* Simon A. de Crombruggle. Ministère de l'Agriculture, Brussels. pp. 917–925.

Saether, B.E., and Haagenrud, H. 1983. Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. J. Mammal. **64**: 226–232.

San José, C. 1988. Estrategias reproductivas de las hembras de gamo (*Dama dama*). Tesis doctoral, Universidad Complutense de Madrid, Madrid. pp. 318.

San José, C., and Braza, F. 1992. Antipredator aspects of fallow deer behaviour during calving season at Doñana National Park (Spain). Ethol. Ecol. Evol. **4**: 139–149.

San José, C., and Braza, F. 1993. Diferencias sexuales en el gregarismo y uso del espacio en el gamo (*Dama dama*). Bol. Soc. Zool. Uruguay, **8**: 328–335.

San José, C., and Braza, F. 1997. Ecological and behavioural variables affecting the fallow deer mating system in Doñana. Ethol. Ecol. Evol. **2**: 133–148.

Shine, R. 1990. Proximate determinants of sexual differences in adult body size. Am. Nat. **135**: 278–283.

Skogland, T. 1983. The effect of density-dependent resource limitation on size of wild reindeer. Oecologia, **60**: 156–168.

Staines, B.W. 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). J. Zool. (1965–1984), **184**: 403–419.

Teer, J.G. 1984. White-tailed deer population management: lessons from the Lano Basin, Texas. *In* White-tailed deer: ecology and management. *Edited by* L.K. Halls. Stackpole Books, Harrisburg, Pa. pp. 261–292.

Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science (Washington, D.C.), **179**: 90–92.

Wolff, J.O. 1988. Maternal investment and sex ratio adjustment in American bison calves. Behav. Ecol. Sociobiol. **23**: 127–133.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.