

Factors affecting maternal care in an income breeder, the European roe deer

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Summary

1. Maternal care is a major component of demographic tactics in mammals. In ungulates most work has been done on capital breeders (e.g. bighorn sheep), which rely heavily on body reserves to raise their young. Roe deer, in contrast, are close to the income breeder end of the capital–income breeder continuum, and show high levels of maternal care.

2. The aim of this study was to explore the factors determining the level of maternal care in roe deer, in particular the effects of maternal body weight, mother's parity, litter size and year of birth on the amount of prenatal care (i.e. the average mass of an offspring multiplied by the number of offspring) and postnatal care (i.e. the average growth rate of the offspring multiplied by their number). The study was carried out on a captive population of roe deer fed *ad libitum*, and in a wild population.

3. In both populations prenatal care increased with increasing maternal body weight. In the population fed *ad libitum* this effect was found in light females only (< 22 kg); in the wild population the positive relationship between maternal body weight and prenatal care was entirely accounted for by variation in litter size (i.e. heaviest females produced larger litters) and density (i.e. females were lightest in years with high population density). Parity did not affect prenatal care.

4. In 14 females fed *ad libitum* there was no relationship between postnatal care and maternal body weight. Multiparous females had higher levels of postnatal care. In contrast, 20 wild females showed a positive relationship between postnatal care and maternal body weight, and only litter size affected the level of postnatal care.

5. Even after accounting for the confounding effects of maternal body weight, parity, litter size and population density, we found no trade-off between pre- and postnatal care in any of the two populations. The conditions under which the pattern of maternal care could impose trade-offs that affect the individual offspring are discussed.

Key-words: allometry, birth weight, *Capreolus capreolus*, growth, income–capital breeder continuum.

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Introduction

Life-history theory predicts that animals should show optimal levels of parental investment (*sensu* Evans 1990) where the energy expenditure for current offspring is balanced against the effects on the parents' chances of survival and future reproduction

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(Roff 1992; Stearns 1992). Parents should therefore make decisions at every stage in the reproductive cycle in order to maximize their reproductive value (*sensu* Leimar 1996), by investing energy in their current offspring to increase the offspring's chances of survival and future reproduction, while not unduly jeopardizing their own survival and future reproduction (Williams 1966; Sargent & Gross 1985). In ungulates, males contribute no parental care, consequently the number, size and growth of offspring are determined solely by the energy allocated by the mother, i.e. the level of maternal care (*sensu* Evans 1990). Maternal care is a major component of demographic tactics in mammals. Comparative analyses have identified a covariation between the amount of maternal care and the semelparity–iteroparity continuum among mammalian species, with most iteroparous species such as ungulates having much higher maternal care than most semelparous species such as rodents (Pontier, Gaillard & Allainé 1993). Maternal care can be defined as the amount of resources invested in an offspring multiplied by the number of offspring. Prenatal care is used to produce, and postnatal care to raise, offspring. According to resource allocation theory (Williams 1966), the level of pre- and postnatal maternal care may vary according to maternal attributes like body weight or parity, litter size, offspring sex, and may also be affected by environmental factors like weather and population density (reviewed by Clutton-Brock 1991).

As a group, ungulates have high levels of energy allocation in each breeding attempt (Pélabon *et al.* 1995). However, both the amount and the source of energy allocated to reproduction differ among ungulate species. Bighorn sheep *Ovis canadensis* (Shaw), red deer *Cervus elaphus* L., fallow deer *Dama dama* L. and reindeer *Rangifer tarandus* L. only produce a single offspring per breeding attempt, while saiga *Saiga tatarica* L., white-tailed deer *Odocoileus virginianus* (Zimmermann), pronghorn *Antilocapra americana* (Ord) and roe deer *Capreolus capreolus* L. most often have twins. Because relative size at birth and early growth of individual offspring do not differ between monotocous and polytocous species, the latter show much greater levels of maternal care than the former (Portier 1997). Earlier studies (Gaillard, Delorme & Jullien 1993; Andersen & Linnell 1997) have reported high birth weight and high postnatal growth rates in roe deer. Tactics of use of energy also vary among ungulates. As in other taxonomic groups, there is a continuum from capital breeders that use stored energy for reproduction, to income breeders that use energy acquired during the reproductive period (Stearns 1992; Jönsson 1997). Ungulates, as large animals, are generally viewed as capital breeders (Stearns 1992). Bighorn sheep ewes illustrate this tactic by relying heavily on body reserves for raising their offspring (Festa-Bianchet,

Gaillard & Jorgensen 1998). As expected for a capital breeder (Jönsson 1997), the body weight of bighorn ewes fluctuates strongly, both seasonally (Festa-Bianchet *et al.* 1996) and annually (Festa-Bianchet *et al.* 1998). Body weight and reproductive success affect each other reciprocally (Festa-Bianchet *et al.* 1998). However, small ungulates like roe deer seem to be closer to the income breeder end of the continuum (Andersen *et al.* 1998). As expected in an income breeder, body weights of roe deer does only vary weakly with season (Appendix 1; Hewison *et al.* 1996) and year (Appendix 1), are not affected by previous reproductive success, and do not affect reproductive success (Appendix 1). Roe deer therefore show high levels of both prenatal and postnatal care, belong to the group of high expenditure species, and are closer to the income breeder tactic of energy utilization.

In this study we used a multifactorial approach to analyse the factors affecting the level of pre- and postnatal maternal care in roe deer. In a wild Norwegian population we examined the effects of maternal body weight, litter size, parity and year of birth. In contrast, we only examined the effects of parity and maternal body weight in a captive French population, where litter size was constant and food was provided *ad libitum*. Based on earlier findings showing a lack of sexual dimorphism in birth weights and growth rates (Gaillard *et al.* 1993; Andersen & Linnell 1997), sex was not included in the analyses. Generally, based on the assumption that roe deer display the income breeder tactic in energy utilization, with low levels of fat accumulation (Holand 1990) and low seasonal variation in body weight (Holand 1992; Hewison *et al.* 1996), we predicted that the same pattern in pre- and postnatal care should be found in a captive population fed *ad libitum* and a wild free-ranging population. More specifically, we tested the following series of predictions. (i) The amount of both pre- and postnatal care should increase with increasing maternal body weight: this was expected because marked allometric relationships have been reported between components of maternal care and body weight from interspecific comparisons (Oftedal 1984; Pontier *et al.* 1993). Large size is commonly correlated with phenotypic quality, and large mothers may allocate more energy to offspring than smaller ones for a given cost in a given population (Reznick 1985; Van Noordwijk & De Jong 1986). (ii) Pluriparous does should show higher pre- and postnatal care than primiparous does: this was expected from the common observation that pluriparous does are more successful in raising offspring than primiparous does (Ozoga & Verme 1986 for white-tailed deer). (iii) Does giving birth to the largest litter size should show the highest amount of pre- and postnatal maternal care and vice versa: this was expected because, for a given body mass, polytocous species

have higher levels of maternal care than monotonous species in ungulates (Portier 1997) at the inter-specific level, and due to mechanical constraints when giving birth, offspring from a litter size of one cannot be expected to be three times as large as offspring from a litter of three. (iv) The amount of maternal care should decrease during poor years (harsh climatic conditions and/or high population density): at high population densities vertebrates commonly invest less in maternal care (Clutton-Brock 1991). (v) In an income breeder there should be no trade-off between pre- and postnatal care. However, as differences in phenotypic quality among mothers can mask trade-offs (Reznick 1985), we looked for a trade-off between pre- and postnatal care in individual roe deer after controlling for the confounding effects of maternal body weight, parity, litter size and year quality. If a trade-off occurs it should be especially visible in the wild population.

Materials and methods

CHIZÉ POPULATION

At the Centre d'Études Biologiques de Chizé (CEBC), in western France (46°05N, 0°25 W) a total of 21 reproductive events occurred (nine primiparous and 12 pluriparous) among 14 individual roe deer does held in captivity between 1987 and 1995. All does produced twins, and exact birth weights were obtained for all the 42 fawns. The fawns were raised in groups of an adult male and between two and five adult does in 0.5-ha enclosures, part wooded and part grassland. Natural foods were supplemented *ad libitum* with a mixture of commercial pellets for milking goats (CHEVRETTE®, Alicoop Proxima, F-79 800 Pamproux, France), wheat winnowings; and twice a week with branches of preferred trees, oak *Quercus* sp. L. and hornbeam (*Carpinus betula* L.). Female body weight ranged from 18.7 to 27.1 kg. Levels of postnatal care (fawn growth rates) were estimated for 15 litters (four primiparous and 11 pluriparous). The fawns were weighed on electronic balances (± 1 g up to 5 kg, ± 10 g thereafter) at least weekly for their first month, during which growth can be assumed to be linear (Gaillard *et al.* 1993; Andersen & Linnell 1997). Weighing took place at times that were unrelated to feeding.

STORFOSNA POPULATION

The island of Storfosna (10.5 km²) is situated 2 km from the tip of Fosen peninsula in central Norway (63°40N). The intensive study area (8 km²) is made up of a mosaic of fields (35%, mainly grass for silage), moorland (33%), rough meadows (18%) and woodland (12%). More than 400 plant species occur on the island; despite the high latitude, the cli-

mate is characterized by mild winters and with a growing season of 160–180 days year⁻¹. From 1991 to 1994 the roe deer population increased from 10 deer m⁻² to 40.6 deer km⁻² (Andersen & Linnell 1997), due to a halt in the harvest and reduced level of poaching.

A total of 26 litters from 24 different wild radio-collared does (17 pluriparous and nine primiparous) was included in these analyses. Parity was known, as all pluriparous does included in this study produced fawns the previous year, while all primiparous does had originally been captured as yearlings (which never reproduced in this population). All does were weighed during the mid-gestation period (February and March), and intensively tracked prior to the time of giving birth (Linnell & Andersen 1998). As pregnant does carry a small fetal mass in February and early March [for 15 does shot between 12 February and 7 March embryonic weight ($n = 27$) varied between 2.96 g and 76.86 g, with a mean of 20.96 g; Strandgaard 1972] the effect of litter size would be negligible if comparing winter weights of adult does.

The does produced a total of 54 fawns (five produced singletons, 14 produced twins and seven produced triplets). Exact birth weights were known for 10 fawns, for other fawns birth weights were estimated from linear regressions using their specific growth rate and known birth date. As most fawns were found shortly (0–3 days) after birth, this estimation will not impose much error. Fawns were radio-collared, which allowed re-weighing at 2–5 day intervals for at least the first 2–4 weeks of life (details in Andersen & Linnell 1997). For four fawns with unknown birth weights and growth rates, the average values for siblings in the same litters were used. One adult doe died after giving birth to triplets, four does lost their fawns shortly (0–4 days) after giving birth, and growth rate was not obtained for one of the fawns in one twin group due to transmitter failure. Therefore, only 20 does were used in analyses of postnatal care. Female body weight ranged from 24 to 33 kg.

MEASURES OF MATERNAL CARE

In both populations prenatal care was estimated as the litter weight, i.e. the sum of individual birth weights in the litter, and postnatal care was estimated as the sum of the average daily growth rate of individual fawns in the strict lactation period (Pontier *et al.* 1989), which corresponds to at least the first 4 weeks following birth when growth is linear (Gaillard *et al.* 1993; Andersen & Linnell 1997).

STATISTICAL PROCEDURES

We first checked for linearity in the allometric relationships between maternal care (prenatal and post-

natal) and maternal body weight using linear regression models after log-transformation of both variables. When linearity was acceptable (i.e. no evidence for a quadratic relationship), we applied generalized linear modelling procedures. In order to control for the cumulative effects of parity, year and litter size, as well as their interactions, we calculated both the slope and the level (intercept) of these relationships between maternal care and maternal weight. The variables were included as factors in a one-way (parity only) ANCOVA for the Chizé population and a three-way (parity, litter size and year) ANCOVA for the Storfosna population, the maternal body weight being consistently used as a covariate. All calculations were performed using GLIM software (Francis, Green & Payne 1993). To account for the unbalanced sampling design (different sample size per category), we used a backward procedure (Searle 1971): the most general model was fitted first, then we tested for possible effects of higher order interactions, then lower order interactions, and finally main effects of factors. Due to the small sample size, we paid special attention to all non-significant effects of factors by assessing the strength and biological meaning of the tests we performed. Because retrospective (a posteriori) power analysis is meaningless, we used information provided by confidence intervals as recommended by Steidl, Hayes & Schauber (1997). Thus, for each non-significant main effect, we calculated the proportional change induced by using the upper limit of the 95% confidence interval. We arbitrarily chose a 5% change as the threshold for a biologically significant effect. When the observed proportional change was less than 5%, we concluded that the null hypothesis could be accepted despite the low sample size (Steidl *et al.* 1997).

To account for pseudo-replication problems arising from an analysis of 21 reproductive events involving only 14 females at Chizé, we used mean individual values for body weight, prenatal care and

postnatal measures. Because replicates were available for only four females, usual procedures involving repeated measures were not retained. On Storfosna, 24 females made 26 reproductive attempts. Because the two females for which we had two replicates showed different litter sizes between the two years of sampling (twins then triplets for doe 70 and triplets then twins for doe 66) and showed therefore very different prenatal and postnatal care, we assumed that pseudo-replication did not occur for this data set.

Results

PRENATAL CARE IN THE CHIZÉ POPULATION

The overall relationship between prenatal care and maternal body weight was quadratic after log-transformation (second-order term, $P < 0.001$) and accounted for 90% of the variation observed in prenatal care. Thus, the level of prenatal care reached an asymptotic level, i.e. there was no further increase in litter weight despite increasing maternal body weight at 22 kg (Fig. 1). We then separated the data using 22 kg as a threshold for analysing the variation in prenatal care. In both data sets, parity did not affect the allometric relationship between prenatal care and maternal body weight (light does: $F = 1.81$, d.f. = 1,4, $P = 0.250$; heavy does: $F = 0.23$, d.f. = 1,5, $P = 0.65$). For light does (22 kg or less), prenatal care increased markedly with body weight [slope of 2.502 (SE = 0.383), $P < 0.001$] and parity had no detectable effect on this relationship [difference between primiparous and multiparous does in intercept of 0.01208 (SE = 0.04334), $P = 0.79$]. Using the upper limit of the 95% confidence interval of this difference, the increase in prenatal care from primiparous to multiparous does was only 1.32%. Prenatal care in heavy does (> 22 kg) was not affected by body weight [slope of 0.052 (SE = 0.282), $P = 0.86$]. Using the upper limit of the 95% confi-

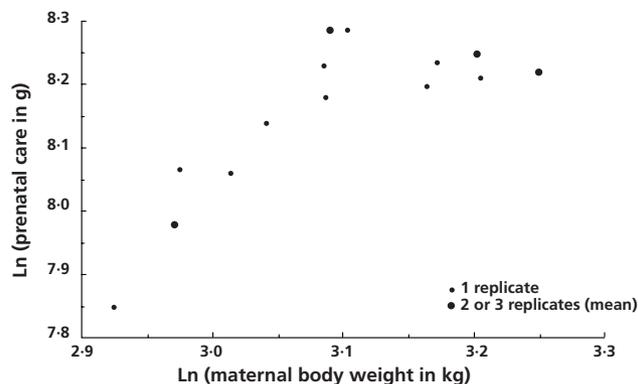


Fig. 1. The allometric relationship between prenatal care and maternal body weight in a roe deer population fed *ad libitum*.

dence interval of the slope indicated an increase in prenatal care of only 1.25% with an increase in maternal body weight from 22 kg to 27 kg. Likewise, parity did not affect prenatal care by heavy females [difference in intercept between primiparous and multiparous does of -0.0006 ($SE = 0.032$), $P = 0.99$]. Using the upper limit of the 95% confidence interval of this difference indicated an increase in prenatal care of only 0.75% from primiparous to multiparous does.

PRENATAL CARE IN THE STORFOSNA POPULATION

The overall relationship between prenatal care and maternal body weight was linear ($R = 0.612$, $P < 0.001$). Parity, litter size and year did not affect the slope of this allometric relationship ($F = 0.09$, d.f. = 1,8, $P = 0.77$; $F = 2.00$, d.f. = 2,9, $P = 0.19$; $F = 0.20$, d.f. = 2,9, $P = 0.83$, respectively). Neither parity [difference between primiparous and multiparous does in intercept of -0.006 ($SE = 0.037$), $P = 0.41$] nor maternal body weight [slope of 0.342 ($SE = 0.259$), $P = 0.11$] affected the level of prenatal care (i.e. the intercept). Using the upper limit of the 95% confidence interval to assess the strength of this relationship, we found that prenatal care of multiparous could only be 0.1% higher than the mean prenatal care of primiparous 25-kg does, and that the steepest slope led to an increase in prenatal care of only 3.03% when maternal weight increased from 24 to 33 kg. The variation in prenatal care was only due to the additive effects of litter size ($F = 9.56$, d.f. = 2,20, $P = 0.001$) and year ($F = 3.24$, d.f. = 3,21, $P = 0.043$). Consequently, the positive relationship between prenatal care and maternal body weight was entirely accounted for by body weight differences related to litter size and year. By increasing litter size from 1 to 2, does increased their prenatal care by 1490 g (95% CI: 1254–1745 g), and when

comparing does with single fawns and does with triplets prenatal care increased by 2690 g (95% CI: 1371–4540 g). The year effect could be due to the increasing population density that occurred in the study area. For any litter size, does decreased their prenatal care by 170 g (95% CI: 77–258 g) from low/medium (1991–93) to high (1994) population density (Fig. 2).

POSTNATAL CARE IN THE CHIZÉ POPULATION

There was no allometric relationship between postnatal care and maternal body weight [slope of -0.471 ($SE = 0.698$), $P = 0.52$] even when parity was taken into account. The slope was unexpectedly negative, and using the upper limit of the 95% confidence interval of this slope led to an increase in postnatal care of only 3.3% from 19 to 27 kg. On the other hand, parity affected the level (intercept) of postnatal care ($F = 5.24$, d.f. = 1,7, $P = 0.05$), with an increase of 77 g day⁻¹ (95% CI: 26–139 g day⁻¹) from primiparous to pluriparous does.

POSTNATAL CARE IN THE STORFOSNA POPULATION

In contrast to the pattern shown by does in the captive population, does in the wild population showed a positive allometric relationship between maternal body weight and postnatal care [slope of 1.155 ($SE = 0.364$), $P = 0.03$]. However, in accordance with the results obtained for prenatal care, parity ($F = 0.54$, d.f. = 1,8, $P = 0.48$), litter size ($F = 0.30$, d.f. = 2,9, $P = 0.75$) and year ($F = 0.73$, d.f. = 1,8, $P = 0.42$) did not affect the slope of the allometric relationship between postnatal care and maternal body weight. Parity of the does did not affect the level of postnatal care ($F = 0.15$, d.f. = 1,14, $P = 0.71$). Primiparous does even tended to have higher postnatal care than multiparous does, with a difference in intercept between these categories of -0.021 ($SE = 0.056$). Using the upper limit of the 95% confidence interval to assess the strength of this result, we found that postnatal care of multiparous was only 1.8% higher than that of primiparous 25-kg does. Postnatal care tended to be higher at high density (in 1994) than at low density (in 1991–93) but the difference in intercept (0.086, $SE = 0.051$) was not significant ($F = 2.53$, d.f. = 1,14, $P = 0.13$). The upper limit of the 95% confidence interval on intercept could only lead to a decrease of 0.3% postnatal care from low to high density. As expected postnatal care increased from singletons to triplets [difference of 0.992 ($SE = 0.071$), $P = 0.005$]. Consequently, the final model includes only the additive effects of litter size and maternal body weight to account for most variation in the level of postnatal care. There was therefore an overall allometric relationship between postnatal

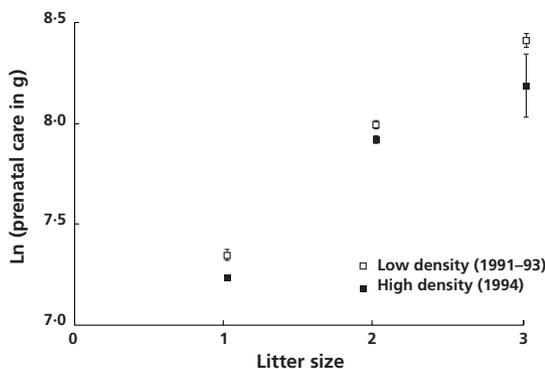


Fig. 2. The relationship between prenatal care and litter size in a wild population of roe deer at high and low density.

care and maternal body weight [slope of 0.933 (SE = 0.327) for a given litter] and the level (intercepts) of this relationship was affected by litter size; at a body weight of 25 kg, postnatal care increased from 132 g d⁻¹ (95% CI: 16–1096 g d⁻¹) to 289 g d⁻¹ (95% CI: 259–323 g d⁻¹) and 366 g d⁻¹ (95% CI: 318–421 g d⁻¹) for single, twin and triplet litters, respectively.

IS THERE A TRADE-OFF BETWEEN PRE- AND POSTNATAL CARE?

In the captive population, there was no overall relationship between prenatal and postnatal care ($R = -0.197$, $P = 0.611$). After accounting for the effect of maternal body weight on prenatal care [i.e. obtaining a measure of prenatal care at a given female weight by using $\text{Ln}(\text{prenatal care}) + 64.89 - 46.24 \text{Ln}(\text{maternal body weight}) + 7.31 \text{Ln}(\text{maternal body weight}) \times \text{Ln}(\text{maternal body weight})$] and for the effect of parity on postnatal care [i.e. obtaining a measure of postnatal care at a given parity (primiparous) by applying $\text{Ln}(\text{postnatal care}) - 0.323$ to the multiparous does], the same result was found ($r = -0.331$, $P = 0.384$), i.e. there was no trade-off between prenatal and postnatal maternal care in captive roe deer.

In the wild population, there was a highly significant positive relationship between prenatal care and postnatal care ($R = 0.942$, $P < 0.001$), with a slope close to 1 (1.067, 95% CI: 0.879–1.255). Given the significant effects on prenatal and postnatal care of the variables studied, we first corrected prenatal care for the density effect, i.e. obtaining a measure of prenatal care at a given density by applying $\text{Ln}(\text{prenatal care}) + 0.122$ to high density measures. Then we corrected postnatal care for the effect of maternal body weight, i.e. obtaining a measure of postnatal care at a given doe mass by using $\text{Ln}(\text{postnatal care}) - 0.933 \text{Ln}(\text{maternal body weight})$. There was still a marked positive relationship between prenatal care and postnatal care ($R = 0.945$, $P < 0.001$). Such a positive relationship may be accounted for entirely by variation in litter size observed in the wild population. We tested this possibility by performing a one-way ANCOVA with litter size as a factor. Litter size did not affect the slope of the relationship between pre- and postnatal care ($F = 1.42$, d.f. = 2, 16, $P = 0.27$). However, as expected, litter size influenced the intercepts of the relationships between prenatal and postnatal care ($F = 4.64$, d.f. = 2, 18, $P = 0.02$): for a given prenatal care (e.g. 2000 g), postnatal care increased from 130 g d⁻¹ with a litter size of one to 260 g d⁻¹ with a litter size of three. When taking litter size into account, the relationship between postnatal care and prenatal care disappeared ($F = 0.75$, d.f. = 1, 17, $P = 0.40$). Because the estimated slope was consistently positive in all three models, no trade-off could be detected between post-

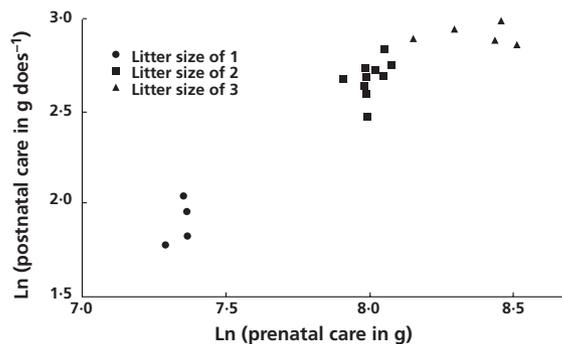


Fig. 3. The relationship between pre- and postnatal care in 20 wild roe deer does.

natal and prenatal care in wild roe deer (Fig. 3). Considering the relationship between postnatal care and prenatal care within each litter size category (i.e. under the model with interaction), a positive, but non-significant, trend still occurred in all the three categories.

Discussion

Five main results emerge from this study (Fig. 4): (i) contrary to our first prediction, maternal body weight did not have a pervasive effect on components of maternal care; (ii) contrary to our second prediction, multiparous does did not show consistently higher levels of maternal care; (iii) in support of our third prediction, litter size accounted for a large part of variation in both pre- and postnatal care; (iv) as expected from our fourth prediction, prenatal care decreased with increasing density in the wild population, however, postnatal care was not affected by population density; (v) finally, as expected, we did not find any evidence for a trade-off between pre- and postnatal care. However, also contrary to our general prediction, the captive and wild population differed in several of the effects considered.

DIFFERENCES BETWEEN THE CAPTIVE AND THE WILD POPULATION

The most striking difference between the captive and the wild population was that maternal weight affected the level of postnatal care only in the wild population, whereas parity affected the level of postnatal care in the captive population. In concordance with earlier studies (Ozoga & Verme 1986) it is not surprising that parity affected the level of postnatal care in the captive population. The lack of such a relationship in the wild population is hard to explain. One potential explanation could be that our sample from the wild population is truncated by the possibility of very light does not giving birth at all

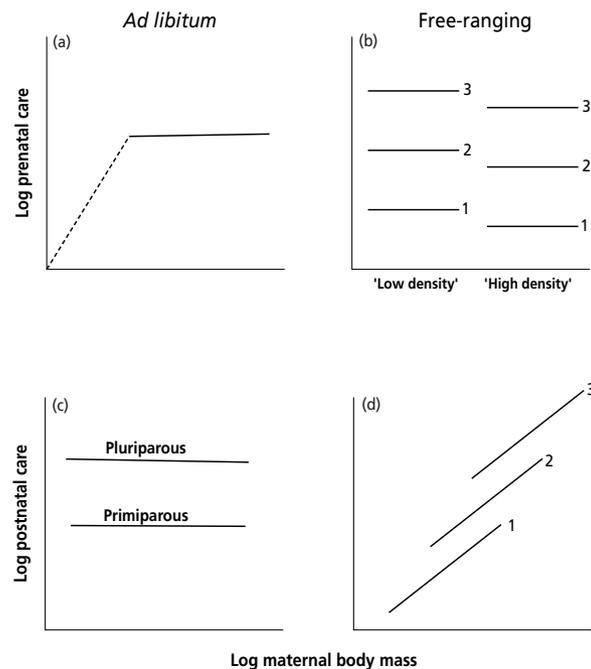


Fig. 4. A schematic presentation of the relationships between pre- and postnatal care and maternal body mass, parity, litter size and density in two roe deer populations. (a) An allometric relationship between prenatal care and maternal body mass only for captive does with low body mass (< 22 kg); (b) for wild does the variation in prenatal care was explained only by the additive effects of litter size and year (i.e. population density); (c) the reproductive status (i.e. primiparous or pluriparous) of the does affected postnatal care in animals fed *ad libitum*; (d) litter size and maternal body mass explained the variation in postnatal care in wild does.

(and therefore not being included in the analysis for either prenatal or postnatal care), whereas the *ad libitum*-fed captive does were all able to give birth, regardless of their quality. Although earlier studies have shown consistently high ovulation rates for roe deer (Andersen *et al.* 1998), there is substantial evidence that threshold weights exist, but that these may be specific to individual populations (Hewison 1996). Another potential explanation could lie in a possible difference in life-history strategy between Norwegian and French roe deer (Andersen *et al.* 1998). Teasing apart these explanations would require data from wild roe deer from the Chizé area, and *ad libitum* feeding of a captive population of roe deer from Storfosna.

The main conclusion that emerges based on the contrasting results from the captive and the wild population is that maternal care is not always correlated with maternal body weight (*per se*). Therefore caution must be taken when using captive animals to study the functional relationship between different traits.

ALLOMETRIC EFFECTS, LITTER SIZE AND PHENOTYPIC QUALITY: INCOME VERSUS CAPITAL BREEDERS

Although variation in reproductive traits is often constrained by body mass at the interspecific level

(Oftedal 1984), maternal body mass *per se* did not affect prenatal care in wild roe deer. The positive relationship between prenatal care and maternal body mass was indeed totally accounted for by litter size and population density, i.e. does of high phenotypic quality were able to produce more offspring and these were less likely to be affected by potential reductions in food availability when density increased. In contrast to prenatal care, an allometric effect was found in postnatal care in wild roe deer. After accounting for litter size and parity, heavier does still had higher postnatal care than lighter ones. Allometric relationships between maternal body weight and prenatal care have been reported in capital breeders like reindeer (Kojola 1993) and fallow deer (Birgersson & Ekvall 1997). In such monotocous species having low energy expenditures per breeding attempt, large body weights of high quality mothers at conception time can be used as a predictor of good rearing conditions, and vice versa. Thus, high quality mothers in capital breeder species are expected to allocate more energy to their single offspring than poor quality mothers, leading to marked allometric relationships for both pre- and postnatal care. On the other hand, in polytocous species like roe deer high quality does should produce larger litters than poor quality does in response to the high variability of rearing success. However, high quality does are not expected to produce larger

offspring, even for a given litter size. Because offspring survival is unpredictable in income breeders (Gaillard, Festa-Bianchet & Yoccoz 1998b), including roe deer (Gaillard *et al.* 1997, 1998a; Andersen & Linnell 1998), successful raising of offspring will depend mostly on resource availability during lactation, for which females have no information during gestation. Roe deer mothers should thus be selected to maximize the number of offspring to produce according to their body weight.

Because the absolute costs of lactation are so much higher than those of gestation (Oftedal 1984) even extreme capital breeders are likely to be more dependent on forage availability than on body reserves during lactation. Therefore, fewer differences are expected to occur between income and capital breeders for postnatal than prenatal care. Indeed, for a given litter size and for a given set of environmental conditions during lactation, roe deer mothers should allocate energy to their offspring according to their body weight, just as capital breeders are expected to do. Because reproductive costs are allometric (Oftedal 1984), lighter does have to invest more energy than heavier ones to support an equal growth of offspring. This will cause a disproportional decrease in body reserves in light capital breeder females. As shown by Crête & Huot (1993), lactating caribou are not able to meet their energy demands just by increasing their food intake after giving birth. The heaviest females are able to utilize their own body reserves in addition to energy extracted from daily foraging, and achieve a higher level of postnatal care. For income breeders like roe deer, the same allometric rules allow large females to be more efficient in converting food resources into offspring growth than small females.

POPULATION DENSITY AND MATERNAL CARE IN INCOME BREEDERS

The increasing density in the wild population affected prenatal care only, and this was due to a reduction in weights of individual fawns at birth (Fig. 4b; Andersen & Linnell 1997). This is in line with other studies of polytocous species such as white-tailed deer. In both penned (Verme 1963) and wild (Verme 1977) populations access to adequate nutrition in the last part of gestation was of vital importance for foetal development. Although increasing density led to less prenatal care, density surprisingly had no significant effect on postnatal care, and most does were able to achieve high postnatal growth rates for their individual fawns (Andersen & Linnell 1997). One explanation could be that does with low prenatal care at high population density are able to achieve a higher level of postnatal care. As we report no evidence for a trade-off, it seems more likely that does with low levels of prenatal care at high density are not able to raise their

fawns at all. Indeed, from our limited sample, three does fitted this: one female gave birth to two still-born fawns, another to one still-born, and one female lost one fawn by drowning. Another explanation could lie with the fact that the birth season coincides closely with the period of spring flush in the vegetation on the Storfosna study site (Linnell & Andersen 1998). There is therefore a great abundance of good quality forage available to support the costs of lactation.

TRADE-OFFS AND PHENOTYPIC QUALITY

Not surprisingly does fed *ad libitum* did not show any trade-off between pre- and postnatal care. However, the lack of such a trade-off in the Storfosna population, even after correcting for population density and maternal body mass, shows that even in the wild, roe deer are able to maintain high levels of both pre- and postnatal care. In fact a clear positive relationship is observed between these components as does giving birth to triplets have much higher pre- and postnatal care than does having twins. The same relationship exists between does with twins compared with does with singletons. Several interspecific studies have shown the same pattern (Lazarus & Inglis 1986; Winkler 1987); however, few studies have corrected for the phenotypic quality of the animals (reviewed by Roff 1992; Stearns 1992). When we accounted for this phenotypic effect (i.e. maternal body weight and litter size), the relationship between pre- and postnatal care disappeared. Based on the present analyses we can conclude that there is clearly no trade-off between pre- and postnatal care in roe deer does.

Although the present study clearly demonstrates the lack of any trade-off between pre- and postnatal maternal care, it is important to realize that the pattern of maternal care could impose trade-offs that affect the individual offspring. In several mammalian species, life-history trade-offs have been found between offspring quantity and quality, as mothers incur higher personal costs for larger than average litters (Mock & Parker 1997). In laboratory rodents (Mendl 1988) offspring from large litters tend to be lighter at birth, have a slower growth rate and have a higher postnatal mortality. Earlier studies of the wild Storfosna population and a wild population in Chizé (Andersen & Linnell 1997, 1998; Gaillard *et al.* 1997) confirm that several of these traits are found in roe deer as well.

EFFECTS OF VARIATION IN MATERNAL CARE ON POPULATION DYNAMICS

Ungulate parents are better able to survive adverse conditions than their offspring (Gaillard *et al.* 1998b). Ungulate mothers should therefore decrease their levels of parental care when the resource avail-

ability is low (for a case study on bighorn sheep see Festa-Bianchet & Jorgenson 1998). As they have a high level of iteroparity (8–16 breeding attempts; Gaillard *et al.* 1998a), roe deer does should fit this pattern and not jeopardize their own future reproductive capability. Even in rodents that have a lower level of iteroparity, there are strong indications that litter size is adjusted either prenatally (Mendl 1988) or postnatally (Day & Galef 1977) to fit either the current ecological situation or parental capacity (Bronson 1989). In roe deer, Gaillard *et al.* (1998a) have demonstrated the existence of family effects, i.e. non-independence among siblings, in several components of fawn fitness. A marked difference between twins and triplets was found, and more variation in body weights and growth rates was found in groups of triplets. However, variation in population density affected the family effects: in years of high population density the birth weights of fawns was low, and a high proportion of fawns died soon after birth. In the same study area Andersen & Linnell (1998) showed a strong relationship between density and the proportion of still-born fawns. We suggest that income breeders like roe deer, which rely heavily on the availability of resources during the reproductive period, need to have mechanisms to adjust the level of maternal care: the selective absorption of a foetus could be such a mechanism. However, because optimal levels of expenditure cannot be identified, it is usually difficult to distinguish adaptive changes in parental expenditure from direct non-adaptive consequences of reduced food availability. Furthermore, although the measurement of trade-off conducted in this study could be put in the category of phenotypic correlations and experimental manipulations (*sensu* Reznick 1985), and consequently is not able to demonstrate that the trade-off is under genetic control, it still provides insight into the functional relationship between traits (Roff 1992).

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Appendix 1. Empirical evidence for ranking roe deer as an income breeder strategist

Jönsson (1997) identified four criteria to rank species along the capital–income breeder continuum (Table 1). Analysis of data from wild and captive roe deer females demonstrated that all four weight criteria supported the hypothesis that roe deer is close to the income breeder end of the continuum; roe showed low levels of seasonal weight variation, a high repeatability of weight over their lifetime, no effect of previous reproductive success on doe weight, and weak individual weight difference between reproductive successful and unsuccessful years.

Table 1. Contrasting four different female weight characteristics relevant for ranking species along the capital–income breeder continuum, according to Jönsson (1997). Data from captive (Chizé) and wild (Trois Fontaines) roe deer does are contrasted with data from a typical capital breeder, bighorn sheep ewes

Female weight characteristics	Data analysed	Roe deer	Comparative results for Bighorn sheep
Seasonal variation	August and April weights contrasted for 14 captive does from Chizé	Mean relative change: 0.107 (SD = 0.101) (Holand 1992; 0.144 for roe deer in Norway)	Mean relative change (6-year-old females): 0.360 (SD = 0.120) (Festa-Bianchet <i>et al.</i> 1996)
Inter-annual variation	A minimum of five weights on 19 wild does in Trois Fontaines	Correlations between successive measurements: $r = 0.80$ for 3–8-year-old does	Correlations between successive measurements: mean value $r = 0.38$ (Festa-Bianchet <i>et al.</i> 1996)
Effect of previous reproductive success	Weight change between January (implantation of foetus) and September (end of lactation) for 10 breeding and eight non-breeding females	The magnitude of weight change did not differ according to the breeding status. Breeding does lost 6.4% of their weight, whereas non-breeding lost 9.5% ($P = 0.371$)	Females that weaned a lamb weighed 10% less than barren females the next year (Festa-Bianchet <i>et al.</i> 1998)
Effect on reproductive success	Contrasting winter body weights of 23 females in Trois Fontaines between years when they raised twins with years when they lost both twins	Mean weight difference 0.30 kg (SD = 1.73) in favour of years when does were successful ($P = 0.415$).	Ewes successfully weaning a lamb were significantly heavier than ewes losing their lamb before weaning (Festa-Bianchet 1998).

Additional evidence placing roe deer at the income end of the continuum comes from studies of fat deposition. Compared to other temperate and northern cervids, roe deer deposit very limited fat stores, reaching a maximum of only 10% of ingesta-free body weight in Norwegian roe deer (Holand 1990, 1992). Therefore, roe deer have a very limited potential to accumulate 'capital'. Consequently the tests of Jönsson's four predictions and the data on seasonal patterns in body fat composition provide a highly consistent pattern, making it possible to rank roe deer at the income end of the capital–income breeder continuum with confidence.