Early body development of roe deer *Capreolus capreolus* in a sub-Mediterranean ecosystem

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Patterns of roe deer *Capreolus capreolus* body development are particularly interesting in view of the wide distribution range and different habitat conditions faced by the species throughout Europe. In order to investigate patterns of roe deer fawn body development in a sub-Mediterranean ecosystem, we caught 78 fawns during the four fawning seasons of 1997-2000. We investigated the effect of gender and date and year of birth on body mass of fawns in their first month of life. In agreement with earlier studies, there was a period of linear growth during which we found no differences in body mass between the sexes. Body mass varied significantly between years. The mean birth weight of 1,500 g did not show overall yearly variations, but fawns were heavier in 2000 than in 1998. Daily weight gain was more variable between years with fawns born in 2000 growing faster than fawns born in 1999 and 1997. Lastly, when fawns were split into two categories according to birth weight, light-born fawns had a significantly faster body development than heavy-born fawns. Therefore, we suggest that roe deer fawns may compensate for a low weight at birth. Such a compensatory process allows light-born fawns to catch up with heavy-born fawns by the end of their first month of life.

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The role of body development in ungulate population dynamics has been recognised in several species. It is believed to influence the level of juvenile survival and age at first reproduction (Albon, Clutton-Brock & Guinness 1987, Clutton-Brock, Albon & Guinness 1987). Therefore, early growth and development have long-term effects on demography and population dynamics.

The study of body development patterns is particularly relevant for roe deer *Capreolus capreolus*, because they range broadly across Europe and face contrasting habitats and climatic conditions. This makes roe deer an ideal species for intraspecific comparison. Maternal investment in roe deer is well known for captive (Mauget, Mauget & Sempéré 1999, Portier, Duncan, Gaillard, Guillon & Sempéré 2000) and wild French and Norwegian populations (Gaillard, Delorme & Jullien 1993a, Andersen & Linnell 1997), but data from the southernmost part of the species' range are still lacking.

The aim of our work was to assess the pattern of juvenile development over a four-year study period in an Italian roe deer population located in the southern area of the species' distribution range. Based on previous find-

ings on roe deer fawn body development, we hypothesised the following:

- A cohort effect on body size exists (*sensu* Albon et al. 1987), mainly due to variation in birth weight. Weather-dependent variations in birth weight from year to year have been found in roe deer (Gaillard et al. 1993a, Andersen & Linnell 1997), and environmental conditions during the year of birth are known to affect body growth and size in roe deer (Hewison, Vincent, Bideau, Angibault & Putman 1996) and other ungulates (Loison, Langvatn & Solberg 1999).
- Time of birth does not affect fawn birth weight and growth rate. The timing of birth in some ungulates seems to follow a seasonal gradient (Rutberg 1987), so that parturition occurs when lactating females have the greatest seasonal food availability and quality. The birth period is likely to pose an important constraint at northern latitudes where the climate is more extreme than further south. Indeed, the birth period affects the growth rates of roe deer fawn in Storfosna in Norway (Andersen & Linnell 1997), whereas it does not influence fawn body weight in France (Gaillard et al. 1993a). Accordingly, in the southernmost parts of the roe deer's range in Europe, where climate conditions in late winter and early spring are milder and more stable, the birth period is not expected to affect the body development of fawns.
- Sex of fawns does not affect birth weight and daily gain. Although the essential condition for a sex-biased investment under current sexual selection theory is that early maternal investment has a greater effect on male than on female lifetime reproductive success, this has been illustrated in a limited number of studies (Clutton-Brock, Albon & Guinness 1988). Even though in many dimorphic and polygynous species male offspring show greater birth weights and growth rates than females (for review see Pélabon, Gaillard, Loison & Portier 1995), roe deer show only a slight sexual dimorphism in size and a weak polygyny with small-sized breeding groups (Liberg, Johansson, Andersen & Linnell 1998). Accordingly, gender is not expected to play a significant role on fawn body development in the species (Gaillard et al. 1993a, Andersen & Linnell 1997).
- During the first months of life, compensatory growth allows light-born fawns to gain more weight than heavy-born fawns. In roe deer, Gaillard, Delorme & Jullien (1993b) found no relationship between fawn body mass at the onset of winter and birth weight, but no studies have yet tested for a difference in growth rate between light and heavy-born fawns.

Methods

Study area and roe deer population

We carried out the study in the northern Apennines, Italy, in the 800 ha open hunting estate 'C.I.T.' at Tredozio in the province of Forlì-Cesena (11°44'30"E, 44°04'37"N). The study area ranges altitudinally within 350-980 m a.s.l. It has many streams and is characterised by the alternate presence of woods and clearings, agricultural land and fallow fields. The woods are dominated by oak *Quercus cerris* and *Q. pubescens*, hop-hornbeam *Ostrya carpinifolia* and chestnut trees *Castanea sativa*. Artificial stands of conifers *Pinus nigra* are scattered throughout the natural forest. Ivy *Hedera helix*, brambles *Rubus* sp. and broom *Cystus scoparius* dominate the understorey. The climate is sub-Mediterranean with a total annual precipitation of 810 mm which mostly falls in autumn, and a mean annual temperature of 12.3°C, the warmest periods being July and August (24°C) and the coldest January (3.9°C). Usually little snow occurs and it mainly falls during December and January.

Wolves *Canis lupus*, red foxes *Vulpes vulpes* and free ranging dogs *Canis lupus familiaris* are the main predators on roe deer in the study area.

Our study forms part of a long-term project on roe deer ecology which includes radio monitoring of almost 30 adults each year. The roe deer population has been monitored in annual counts since 1995, and the density has been estimated using mark-resight methods (Focardi, Raganella Pelliccioni, Petrucco & Toso 2002). From 1997 to 2000, the roe deer density declined from 57.8 deer/km² (95% CI = 46.6-79.5) to 38.4 deer/km² (95% CI = 35.5-44.2) in March. A variable fawn survival averaging 0.38 ± 0.07 and a female productivity of 1.44 ± 0.10 embryos per female (Focardi et al. 2002) characterise the population. Hunting of roe deer by selective stalking has only been allowed in the study area since 1995, and males are hunted during August-September, females during February-March.

Data collection and analysis

Fawns were captured based on active searching, observation of lactating females and close monitoring of radio-collared does. Simulation of fawn cries helped in many cases to locate hidden young by eliciting maternal vigilance of adult does. Each year, efforts to capture fawns began as soon as the first fawn was observed in the study area and went on for as long as we were able to catch the fawns.

Fawn age was determined by direct observation of birth or according to Jullien, Delorme & Gaillard (1992), i.e. through detailed scrutiny of the umbilical cord and be-

haviour at capture and handling. Their age was assessed to the nearest day. Fawns were sexed, weighed, individually marked with ear tags and fitted with expandable radio collars (Televilt TXE, weight 60 g). Fawns were relocated daily by 'homing in' (White & Garrott 1990) and were recaptured and reweighed at 5-day intervals up to a maximum of three times. Maximum age at last recapture was 28 days.

SPSS 8.0 (1998) was used in all statistical analyses. Any departure from the expected proportion of 0.5 in the sex ratio of captured fawns was tested using the binomial test (Zar 1996), for each year separately and overall.

Overall and yearly relationships between body mass and age were calculated for all fawns using Linear Regression (Zar 1996). The effects of year, sex and date of birth on body mass were assessed using an Analysis of Variance (ANOVA) on standardised residuals from the regression of age and weight at first capture. As the mean birth date and the distribution of birth dates did not vary during the study period (S. Toso, unpubl. data), data were pooled to investigate the effect of birth date. Fawns were divided into three groups: fawns born early (before 28 May; N = 27), fawns born during the birth peak (during 28 May-9 June; N = 27) and finally those born late (after 10 June; N = 24). The groups were chosen to obtain a balanced sample size in each category (Gaillard et al. 1993a). When an effect was found to be significant, an Analysis of Covariance (ANCOVA; Zar 1996) in a General Linear Model (GLM) was performed using weights at first capture and all the re-weighings, to compare estimated birth weights (intercepts) and growth rates (slopes).

To look for compensatory growth, individual birth weight and growth rate were estimated for fawns with at least three weighings (N = 23). These fawns were then divided into two groups depending on the estimated individual birth weight: light, if their birth weights were lower than the mean yearly birth weight, and heavy, if they were heavier. Individual estimated growth rate of the two groups were compared using a t-test. The regression lines of light and heavy fawns were finally plotted to estimate the age at which the two groups reached the same body mass.

In the fawning seasons of 1997, 1998, 1999 and 2000, we caught a total of 78 fawns (21, 16, 17 and 24, respectively). Of the 78 fawns, 45 were males (1997: 15, 1998: 10, 1999: 11, 2000: 9) and 33 were females (1997: 6, 1998: 6, 1999: 6, 2000: 15). No significant departure from parity was found in the sex ratio of captured fawns, neiher yearly nor overall (Binomial test: P > 0.05). Moreover, the sex ratio of captured fawns did not differ from the sex ratio *in utero* (Focardi et al. 2002). A strong linear relationship was detected between age and body weight during the 28 days following birth (r = 0.85, P < 0.001), with age explaining nearly three quarters of the observed variability (r^2 = 0.73). Mean birth weight was 1,500 g (95% CI = 1,357-1,653), and the postnatal growth rate was 124 g/day (95% CI = 112-136). Pooling data of all years, the birth weights of fawns captured at the age of one day ranged within 1,230-2,000 g.

The three-way ANOVA on mean standardised residuals (MSR) showed variations between years (F = 2.99, P = 0.038), with fawns born in 2000 being heavier at a given age than fawns born in the previous years (MSR: 0.60 vs -0.16, -0.44 and -0.24 for 1997, 1998 and 1999, respectively). Although females were slightly heavier than males (MSR: 0.04 vs -0.03), the effect of gender was not significant (F = 0.80, P = 0.37), and there was no significant sex by year interaction (F = 1.47, P = 0.23); i.e. male and female fawns had similar body mass in all the years considered. Likewise, the birth period did
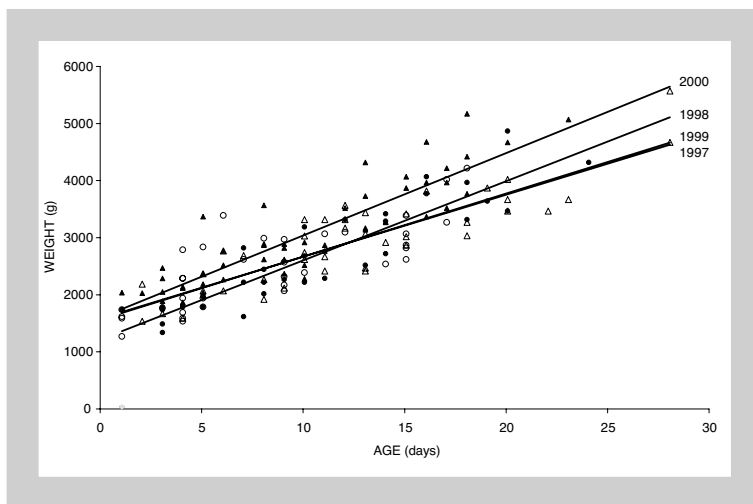

Figure 1. Regression between body weight (in g) and age (in days) of roe deer fawns in central Italy during 1997 (○; Y = 108.6x + 1550.6; r^2 = 0.62), 1998 (●; Y = 138.7x + 1185.5; r^2 = 0.83), 1999 (▲; Y = 110.5x + 1532.8; r^2 = 0.77) and 2000 (△; Y = 144.3x + 1566.0; r^2 = 0.79).
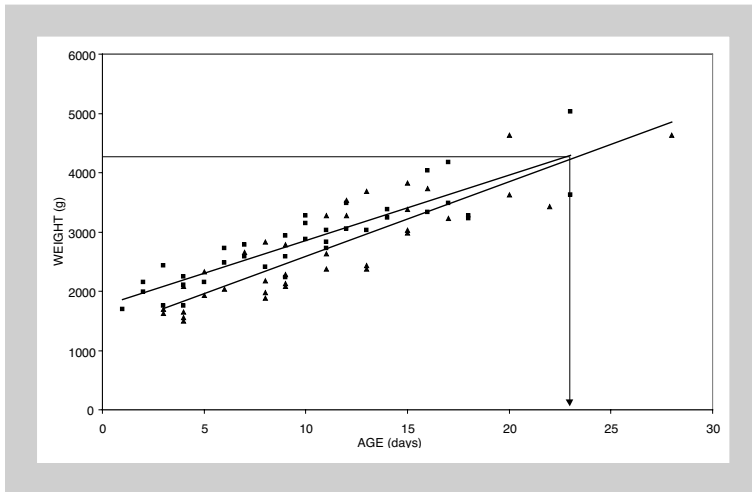
Figure 2. Regression between body weight (in g) and age (in days) for the two groups of fawns: light (□, N = 11) and heavy (■, N = 12). The two groups were divided according to the yearly estimated birth weight.

not affect fawn body mass at a given age (F = 0.68, P = 0.51), nor did it interact with year of birth (F = 1.43, P = 0.21) or gender (F = 0.85, P = 0.434). The three-way interaction between year of birth, birth period and sex was not significant (F = 1.14, P = 0.346).

The birth weights (intercept comparison with the ANCOVA) did not show overall annual variation (F = 1.67, P = 0.17), even though fawns born in 2000 were heavier at birth than fawns born in 1998 (t = -2.01, P = 0.045). Likewise, fawns born in 2000 gained more weight than fawns born in 1999 (t = -2.32, P = 0.022) and 1997 (t = -2.09, P = 0.038), with an overall significant effect (F = 2.74, P = 0.045). Fawns born in 2000 therefore had the highest birth weights (1,566 g) and highest daily gain (144 g/day; Fig. 1).

Heavy-born fawns had a lower growth rate than light-born fawns (114.12 g/day ± 7.99 and 143.76 g/day ± 10.42, respectively; t = 2.28, P = 0.033, N = 23); i.e. lighter fawns gain more in the 28 days following birth than heavier fawns. The regression line of light and heavy-born fawns shows that the compensatory process is likely to be complete at the end of the first month of life (Fig. 2).

Discussion

The linear growth and the absence of differences in body mass between the sexes that we observed in our study are in agreement with previous findings on wild and captive roe deer populations, and this suggests that they can be considered constant traits of maternal investment in roe deer. Birth period did not account for any variation in fawn body weight in our study, so that early born, mid-period born and late born fawns have the same body mass for a given age which contrasts the findings of Andersen & Linnell (1997). Influence of birth date on body mass is expected when the vegetative season is short, so that fawns born earlier or later can not match the optimal period for both climatic and feeding reasons (Andersen & Linnell 1997). In our study area, the fawning season is quite stable from year to year with a peak in late May, whereas the vegetative season spreads over a longer period than in Norway or France and has higher daily temperatures in April, averaging 12°C.

The lack of differences in body mass between the sexes is expected on the basis of the theory of sexual selection, and is also reported for other population parameters of this species, such as fawn summer survival (Gaillard, Boutin, Delorme, Van Laere, Duncan & Lebreton 1997). Two main factors could explain this finding. First, in roe deer the male lifetime reproductive success does not seem to be more variable than female success, as roe deer are slightly polygynous with < 5 females per territorial male (Liberg et al. 1998). Second, body mass in this species does not seem to be a conservative feature: differences in estimated individual growth rates suggest that there could be a compensatory mechanism that causes the surviving young with lower birth weight, resulting from restricted growth *in utero*, to gain more weight during the summer following birth. Compensatory growth is defined as better growth shown by individuals previously subjected to undernutrition than in their counterparts who were not exposed to such a restriction (Verme 1963). The occurrence of compensatory growth could support the lack of relationship between birth weight and weight at the onset of winter observed in populations not limited by resources, such as captive individuals fed *ad libitum* (Verme 1963), and highly productive forest roe deer populations (Gaillard et al. 1993b, Gaillard, Andersen, Delorme & Linnell 1998). Conversely, in poor conditions due to high population density, weight at birth can be considered a good predictor of weight at the onset of winter in different ungulate species (e.g. Soay sheep *Ovis aries* on Saint Kilda (Clutton-Brock, Price, Albon & Jewell 1992) and red deer *Cervus elaphus* on Rum (Clutton-Brock, Guinness & Albon 1982)). Evolutionary constraints that prevent compensatory growth are expect-

ed to be stronger in highly polygynous species than in weakly polygynous species (Pélabon 1997). In polygynous species, the conservative feature of early maternal investment is very important because extra investment in male sons is believed to increase their fitness (Clutton-Brock 1991, Maynard-Smith 1980). In weakly polygynous species, it is to be expected that the occurrence of compensatory growth is more dependent on nutritional condition. Birth weight is likely to affect juvenile survival in roe deer (Andersen and Linnell 1998), red deer (Guinness, Clutton-Brock & Albon 1978) and mule deer *Odocoileus hemionus* (Unsworth, Pac, White & Bartmann 1999), but compensatory growth could decrease the probability of death during the first summer of life, dependent on the quality and availability of resources. So there may be a threshold body mass, below which the chance of survival is negligible, and the ability to compensate for the initial disadvantage in the form of a low birth weight is only possible during more favorable years. Compensatory growth is likely to be a very complex mechanism affected by environmental and individual factors. Due to the low sample size per year, we failed to detect a link between cohort and ability to compensate, and a better assessment of this hypothesis is needed.

Beyond these general patterns of linear growth and a lack of sex differences in body size, a variability in growth parameter values was found compared to other European roe deer populations. These differences could reflect individual maternal weight variability as well as the effect of different environmental and climatic constraints affecting maintenance requirements in diverse habitats.

The mean birth weights found in our study lie within the range known for the species and are comparable to the values reported by Andersen & Linnell (1997; 1,360-1,561 g) from Storfosna in Norway and by Gaillard et al. (1993a; 1,300-1,700 g) from Trois Fontaines in France. Daily gain is more variable and ranges between 108 g/day and 143 g/day. Gaillard et al. (1993a) found higher and more stable values of growth rate (140 g/day), as did Andersen & Linnell (1997) who reported a maximum value of 155 g/day sustained by the high body weight of female roe deer in Storfosna. Patterns of body development in captive animals show similar values of 145 g/day (Portier et al. 2000) and 135 g/day (Mauget et al. 1999).

In our study the cohort effect is mainly due to variation in daily gain, as mean birth weight is less variable which contrasts the findings of Gaillard et al. (1993a) and Andersen & Linnell (1997) who found a marked cohort effect in birth weights with only litter size sig-

nificantly affecting the growth rates of fawns (Andersen & Linnell 1997). As an income breeder, the roe deer relies more on resource availability to rear its young than on stored fat reserves which are very modest in the species (Holand 1992). The lactation capabilities of the mother are strictly dependent on food supply (Mauget, Mauget & Sémperé 1997), in terms of quality and availability. Moreover, in smaller ungulate species, milk production tends to decline much faster than in larger species (Robbins, Podbielancik, Wilson & Mould 1981), and it is strongly affected by vegetative phenology (Robbins et al. 1981). In this regard, fawn growth rate following birth may be considered directly dependent upon the food resources available to the does. Due to the high level of sedentarity shown by the females, their nutrition is affected by variation in food quality/availability inside their home ranges. Range quality has been found to affect fawn winter body mass in a way that is interactive with density and forage conditions (Gaillard, Delorme, Boutin, Van Laere & Boisaubert 1996). In red deer, females are distributed in an ideally free manner with respect to use of high quality forage (Conradt, Clutton-Brock & Guinness 1999), but the hind density in better habitats offsets any advantage offered by increased access to preferred forage (Conradt et al. 1999), thereby affecting lifetime reproductive success. In our study area, agricultural field management may cause a different habitat selection and range use in pregnant and lactating females along with a different energy input in terms of quality/availability. This point requires further analysis to clarify the underlying mechanism of nutritional limitations.

Body mass is a life history trait which is partly hereditary, but also seems to be influenced to a great extent by environmental variation (Alatalo, Gustafsson & Lundberg 1990). The differences found in fawn body development could reflect the adaptation of this life history trait in different roe deer populations.

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