

## Growth of European roe deer: patterns and rates

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Portier C., Duncan P., Gaillard J.-M., Guillon N. and Sempéré A. J. 2000. Growth of European roe deer: patterns and rates. *Acta Theriologica* 45: 87-94.

The aim of this study was to describe the pattern and rates of growth of roe deer fawns up to the age of weaning. Eighteen fawns of *Capreolus capreolus* (Linnaeus, 1758) raised by their mothers in enclosures grew at decelerating rates after birth, with a monomolecular rather than sigmoid pattern. Bottle rearing modified profoundly the natural pattern of growth, but these fawns caught up with mother-reared fawns by weaning (about six months). There was no evidence for differential investment by the mothers in male and female offspring. Most mother-reared fawns showed an initial, near-linear phase in their first month (10/12 individuals). During this period milk provides all, or nearly all the nutrients; the rates of growth were high (145 g/day), and close to the value observed in a highly productive wild population. The decelerating rate of growth may be a consequence of allocation of resources to movement as these "hider" young become more active; and the monomolecular pattern may be commoner among ungulates than is currently realised.

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*Key words:* *Capreolus capreolus*, growth, curve fitting, resource allocation

### Introduction

Growth occupies a central place in the life history strategies of animals and resource allocation theory shows that the quantities of nutrients available for growth are constrained by the nutrients allocated to maintenance and movements (Williams 1966). The resulting patterns and rates of growth reflect the pressures of selection acting on animals, within the limits of the species' physiological and developmental constraints (Sibly *et al.* 1985). Within these limits there are covariations between life history parameters (Stearns 1992). In mammals where

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juvenile mortality is often high compared with adult mortality, post-natal growth rates tend to be high (Case 1978). Roe deer *Capreolus capreolus* (Linnaeus, 1758) are known to have high growth rates in the immediate postnatal period (Gaillard *et al.* 1993), a time when growth is almost entirely dependent on the mother's investment in the form of milk (Lavigneur and Barrette 1992), and which has been termed the strict lactation period (Pontier *et al.* 1989). The data available show that there are no differences between males and females in the rates of growth during the first few days of life (Gaillard *et al.* 1993), but there are no published longitudinal data on the patterns of growth beyond one month of age, and differences could exist at later stages.

It is often assumed that postnatal growth in mammals follows a sigmoid pattern (eg Zullinger *et al.* 1984), and Gompertz and Von Bertalanffy models are often used to fit data on growth across a range of species (Zullinger *et al.* 1984, Georgiadis 1985). In this study we provide longitudinal data on growth in roe deer fawns and test the hypothesis that the pattern of growth is sigmoid.

Mammalian growth is often studied using bottle-reared animals. Here we were able to obtain data on both mother- and bottle-reared fawns: before pooling the data we tested the hypotheses that there was no effect of bottle-rearing or gender on the patterns and rates of growth.

## Material and methods

### Study conditions

This analysis is based on a set of longitudinal data on 29 fawns raised at the Centre d'Etudes Biologiques de Chizé (CEBC), in the central part of the Atlantic coast of France (46°05'N, 0°25'W). The females weighed 23.0 kg  $\pm$  1.53 (SD,  $n = 13$ ) in autumn, litter size was 1.95 ( $n = 20$ ), and the fawns we studied weighed 1.795 kg  $\pm$  0.214 (SD,  $n = 29$ ) at birth; with no differences between primiparous and other mothers in body mass, litter size or in the birth weight of the fawns.

There were two methods of raising the fawns, both aimed at providing nutrients *ad libitum*. Eighteen mother-reared fawns were raised in groups of a male and 2–5 females in enclosures 0.5 ha, part wooded, and part grassed. The natural food was complemented *ad libitum* with a mixture of commercial pellets for milking goats and wheat winnowings; and twice a week with branches of preferred trees, oak *Quercus* sp. and hornbeam *Carpinus betula*. Eleven bottle-reared fawns were brought in from the wild (ages were estimated as in Jullien *et al.* 1992) or taken from their captive mothers at one day, and were raised indoors on powdered goat milk *ad libitum* (CAPRIVAL, 24% crude protein, 23% fat). They were offered a bottle containing 150 ml six times a day (three times after one month), and initially took c. 250 g/day, increasing to 700 g/day at one month. They also had access to earth and to fresh flowers and leaves of a variety of plants, especially clover *Trifolium repens*. At about ten days of age they spent their days in a grassed pen. None of the mother-reared fawns showed any signs of suffering from health problems; of the bottle-reared ones four had diarrhoea for a few days.

The bottle-reared fawns were weighed on electronic balances ( $\pm 1$  g up to 5 kg,  $\pm 10$  g thereafter), generally before feeding, at least every two days during the first month. Fawns with their mothers in the parks were weighed less frequently, when possible once a week, at times which were unrelated to feeding. After the first month, weighings were less frequent, and were done monthly by the time of natural weaning. By milking the mothers we found that this occurred progressively, and was complete at about 5 months (see also Sempéré *et al.* 1988).

### Data analysis

The sets of data were adjusted to the general Chapman-Richards model, which is flexible and can be adjusted to a range of patterns from the monomolecular to the logistic (Debouche 1979, Gaillard *et al.* 1997). It has four parameters:

$$W_t = \frac{A}{\left(1 + [n-1] e^{(K)(t_0-t)}\right)^{\frac{1}{n-1}}}$$

where  $W_t$  – weight at time “ $t$ ”,  $A$  – adult weight,  $K$  – rate,  $n$  – shape parameter which situates the position of the inflexion point, and for particular values of  $n$ , this model reduces to one of the three parameter models: when  $n = 0$ , it is the monomolecular model, when  $n = 1$ , the Gompertz, and when  $n = 2$ , the logistic.

Goodness-of-fit was based on two criteria: convergence and biological relevance of estimates. Convergence was not attained for six fawns, these were discarded from the subsequent analyses. For the remaining individuals, the biological relevance of estimates was checked, and when curve fitting led to obvious errors in adult and birth weights, the model was rejected. Adult body weight estimates were accepted between 19 and 35 kg and birth weights between 0.8 and 2.5 kg (the ranges occurring in our data set, and R. A. Andersen's, pers. comm.). We compared the performance of growth models for individuals that satisfied these criteria.

The effects of the type of rearing, and the gender of the fawns, were first tested on the shape parameter ( $n$ ). The mean values for the fawns of each rearing type and of each sex were obtained by averaging the calculated weights of all fawns for each day. The values of the average parameters were then obtained by modelling the average weights in the same way as for the individual weights. Differences between the parameters were tested using the Wald's test (Rao 1973). Because of the high autocorrelation between estimates of adult and birth weights, we also compared growth rates during the strict lactation period to test for the effects of type of rearing and sex of fawns. Although growth is a non-linear process in mammals, the early stage of growth is often satisfactorily fitted by simple linear regressions (see Gaillard *et al.* 1992, 1993 for examples in ungulates). We determined for each individual the period during which growth was linear, using polynomial regressions to assess the deviations from the linear model statistically. Early growth rates were then estimated as the individual slopes of these regressions. The effects of type of rearing and sex of fawns on these growth rates were tested using a two-way ANOVA in the GLIM software (Francis *et al.* 1993) as the design was unbalanced.

### Results

The Chapman-Richards model fitted the data from 12 of the 18 mother-reared fawns; for the other six the goodness-of-fit criterion of convergence was not reached mainly because too few weighings were available within the 20 first days of life (only four points for four individuals, five points for one, and seven points for the other). For the remaining individuals, the parameters of the fitted models were all within the recorded ranges of birth weights (0.8–2.5 kg), and adult weights (19–35 kg). These growth curves all fitted the monomolecular model. The Gompertz and the Logistic models were not accepted for 10/12 and 11/12 mother-reared individuals respectively (Table 1). Growth curves could be fitted to 10 of the 11 bottle-reared fawns. The Gompertz fitted five individuals, the monomolecular three, and the logistic only one; and four were intermediate (Table 1). The inflexion point was significantly later for the bottle-reared fawns than for the mother-reared fawns (average  $n = 0.16$  vs 0.58, Wald test,  $\varepsilon = 3.09$ ,  $p = 0.002$ , Fig. 1). A linear phase of

Table 1. Summary of the models of growth curves which it was possible to fit to the data on individual roe deer. M/F - males/females, B/M - Bottle/Mother-reared, G/M/L - Gompertz/Monomolecular/Logistic. <sup>(1)</sup> Intermediate between Monomolecular and Gompertz models

Sex	Rearing Conditions	Duration of the monitoring (in days)	Position of the inflexion point	Upper and lower 95% confidence limits of the inflexion point	Possible models	R <sup>2</sup>
F	B	81	1	0.05 - 1.94	G	0.993
F	B	44	1.07	0.85 - 1.29	G	0.984
F	B	44	1.09	0.73 - 1.46	G	0.989
F	B	44	0.59	-0.64 - 1.82	G - M	0.981
F	B	16	0.28	-1.56 - 2.13	G - M - L	0.980
F	B	107	0.85	0.74 - 0.97	- <sup>(1)</sup>	0.995
F	B	192	0.41	0.19 - 0.63	- <sup>(1)</sup>	0.972
F	B	50	0.46	-0.20 - 0.72	M	0.967
F	B	192	0.37	0.23 - 0.51	- <sup>(1)</sup>	0.981
M	B	44	0.62	0.34 - 0.90	- <sup>(1)</sup>	0.991
F	M	39	0.0042	-0.13 - 0.13	M	0.996
F	M	36	0.057	-0.43 - 0.55	M	0.991
F	M	13	0.45	-0.43 - 0.55	G - M	0.995
F	M	39	0.07	-0.48 - 1.36	M	0.997
F	M	164	0.034	-0.15 - 0.29	M	0.928
M	M	336	0.19	-0.0013 - 0.069	M	0.835
M	M	14	0.46	-0.045 - 0.42	M - G - L	0.974
M	M	298	0.30	-1.1864 - 2.11	M	0.883
M	M	31	0.42	-0.01 - 0.84	M	0.997
M	M	14	0.21	-0.34 - 0.77	M	0.998
M	M	290	0.024	-0.48 - 0.53	M	0.805
M	M	177	0.047	-0.13 - 0.23	M	0.886

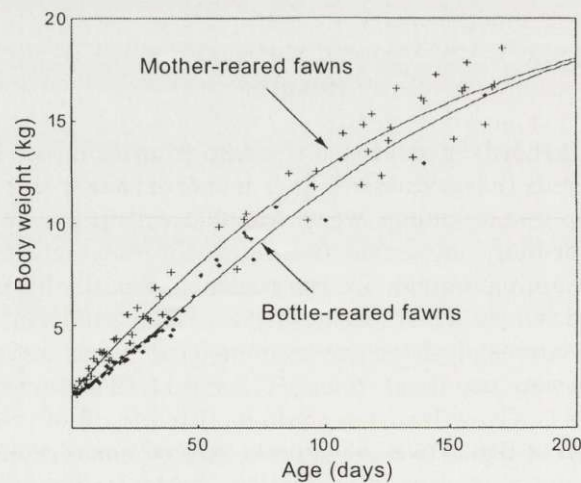


Fig. 1. The pattern of growth of mother- and bottle-reared roe deer fawns: the fitted models are Chapman-Richards (see text).

growth prior to 30 days of age occurred in 7/10 bottle-reared fawns and in 10/12 mother-reared fawns. The mother-reared fawns grew faster in early life than the bottle-reared fawns (146 g/day *vs* 79 g/day,  $F = 31.63$ ,  $df = 1, 14$ ,  $p < 0.0001$ ). The latter commonly showed weight losses for 2 or 3 days after removal from their mothers. When their rates of growth were recalculated after removal of days with weight losses, their average rate was still much lower than that of the mother-reared fawns (99 g/day).

The shape of the growth curve did not differ between sexes (average  $n = 0.62$  *vs* 0.68 for bottle-reared, Wald test,  $\varepsilon = 0.18$ ,  $p = 0.858$ ; average  $n = 0.21$  *vs* 0.14 for mother-reared, Wald test,  $\varepsilon = 0.21$ ,  $p = 0.834$  for males and females respectively). No interaction between the effects of rearing type and sex of fawn was detected ( $F = 2.01$ ,  $df = 1, 13$ ,  $p = 0.180$ ). The gender of fawns did not affect the early growth rate of mother-reared fawns (142 g/day *vs* 154 g/day for mother-reared males and females respectively,  $F = 0.011$ ,  $df = 1, 14$ ,  $p > 0.5$ ).

### Discussion

The Gompertz and Von Bertalanffy models are assumed to represent satisfactorily the patterns of growth in mammals (Zullinger *et al.* 1984, Derrickson 1992), and in ungulates in particular (Georgiadis 1985), but this is not the case for roe deer. Instead of growing at the highest rate when about 30% of growth has occurred, roe deer show their maximal growth rate at birth and then grow at a decelerating rate to adulthood. This difference between our results and those of most previous studies on wild mammals could be methodological: many of the other studies were based on transverse data (across individuals) with low precision, while this analysis is based on longitudinal data. Moreover, contrary to this study where the fit by different models was compared statistically, in previous studies the procedure for selecting a model was based on goodness-of-fit criteria (the percentage of variance accounted for by the model). Goodness-of-fit is not necessarily the best criterion because the pooled residuals may not be randomly distributed (Zach *et al.* 1984). Since the logistic and Gompertz models generally accounted for more than 90% of the variation in the roe deer data, we would have accepted these models. This study therefore suggests that it is premature to conclude that mammalian growth is generally sigmoid.

Irrespective of these methodological issues, roe deer show both decelerating growth from birth (this study) and high growth rates (Gaillard *et al.* 1993, this study). If (as did Peters 1983) we consider growth from conception to death as sigmoid, the inflexion point in roe deer must occur during gestation whereas in other mammals it occurs after birth (Zullinger *et al.* 1984). This means that the exponential phase of growth stops earlier than in other mammals. In response to past and present selective pressures such as environmental stochasticity and predation, roe deer mothers invest heavily in their individual offspring. Moreover high maternal investment in the current litter has been recently shown to

disadvantage subsequent litters (Bérubé *et al.* 1996 for bighorn sheep) and high birth weight could increase parturition difficulties (Grubb 1974). We therefore expect that strong selection pressure against high maternal investment close to birth to occur in roe deer. This could lead to the unusual monomolecular growth pattern observed in our study. Roe deer, typical hider strategists (Espmark 1969, Lent 1974), spend most of their first weeks after birth inactive in a bedding site hidden in vegetation (Gaillard and Delorme 1989). Consequently, little energy is expended in activity and fawns can allocate more to growth (Carl and Robbins 1988). The deceleration in their rate of growth from birth to adulthood could result from a gradual increase in activity. We hypothesize that hider ungulates show both monomolecular patterns of growth and high early growth rates as a consequence of low costs of locomotion.

The pattern of growth of bottle-reared fawns differs from that of the mother-reared ones. Initially slower, the growth rate of the bottle-reared fawns later increased so that the fawns of the two groups had very similar liveweights at about 7 months. This kind of compensatory growth, resulting from early environmental stress, has been described in domestic, as well as in wild ungulates (eg Reimers *et al.* 1983). Bottle-rearing induced a sigmoid pattern of growth: 1–3 days seem to be required for fawns to accept the bottle, which delayed the growth peak (see also Krzywiński *et al.* 1984); however, when this transitional period was eliminated, the initial growth rate of bottle-reared fawns was still lower than that of mother-reared fawns. Studies based on bottle-reared animals are therefore likely to provide biased pictures of growth patterns and rates in roe deer.

There were no significant differences between mother-reared males and females, which had growth rates of 142 and 154 g/day respectively, a result closely similar to that obtained by Gaillard *et al.* (1993) in a wild population. Likewise, the shape and the parameters of the growth curve did not differ between sexes. This absence of differences between the sexes is related to the weak sexual selection in roe deer compared to other cervids living in temperate regions. Roe deer are slightly dimorphic (adult males only weigh about 10% more than adult females, Niethammer and Krapp 1986) and show a low level of polygyny (Liberg *et al.* 1998). Other holarctic cervids are markedly dimorphic and exhibit high levels of polygyny (Clutton-Brock *et al.* 1982). In such species, male fawns are born heavier, grow faster in the strict lactation period and grow for longer than female fawns: *Rangifer tarandus* (Kojola 1993), *Cervus elaphus* (Clutton-Brock *et al.* 1982), *Dama dama* (Asher and Adam 1985). Roe deer seem to be much closer to small tropical deer species like pudu *Pudu pudu* (Czernay 1977) than to larger sympatric deer species in their growth patterns.

The fact that these captive deer had growth rates similar to those observed in a highly productive wild population suggests that the processes described in this herd, with an *ad libitum* food supply, were not affected by captivity. This analysis of longitudinal data allows us to draw three major conclusions: (1) growth in roe deer raised by their mothers does not fit the classical sigmoid curve, rather fawns grow

at decelerating rates, with a monomolecular pattern from birth to weaning and beyond, (2) the type of rearing affected the growth shape, initial growth being much slower in bottle-reared fawns than in mother-reared ones, but no difference could be detected between rearing types in body weight at 7 months of age. This was because bottle-reared fawns grew sigmoidally, rather than in a monomolecular fashion like mother-reared fawns, and (3) no differences between the sexes were found up to the age of 7 months, either in the pattern or the rate of growth.

Acknowledgements: We thank Nadine Guillon for the care she takes with the captive roe deer.

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Received 5 May 1998, accepted 23 June 1999.