Acta Theriologica 41 (2): 187–198, 1996.
PL ISSN 0001–7051

Variation in the fecundity of roe deer in Britain: effects of age and body weight

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Hewison A. J. M. 1996. Variation in the fecundity of roe deer in Britain: effects of age and body weight. Acta Theriologica 41: 187–198.

This paper investigates variation in female fecundity in relation to effects of age and body weight within and between 15 populations of roe deer *Capreolus capreolus* (Linnaeus, 1758) in Britain. Analyses were based on carcass material and fecundity was assessed from the presence/absence and number of fertilised ovulations (*corpora lutea*) and implanted foetuses. A significant proportion (> 10%) of does ovulated in their first year in some populations, but such precocious reproductive activity rarely resulted in successful implantation of a foetus. Generally, the majority of yearling does (in their second year) conceived successfully, but average potential litter size was lower than among older animals. There was no consistent age-related variation in fecundity among does older than 2 years. Differences in fecundity between age and body weight classes suggest weight thresholds may exist for the onset of puberty and for successful conception as an adult. Fecundity of adults and yearlings was highly variable between populations and in some populations was considerably lower than previously reported for this species. Although differences between populations were correlated with differences in body weight, this relationship was insufficient to explain the wide variation in fecundity across Britain, suggesting fecundity body weight thresholds will be defined independently in separate populations.

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Key words: *Capreolus capreolus*, age, body weight, fecundity

Introduction

If there is variation in reproductive potential between animals of different ages within a species, the age structure of a population may itself have a significant impact on the dynamics of the population (Clutton-Brock *et al.* 1982, Sadleir 1987). Fisher (1930) was the first to suggest that, in species where reproductive value declines with age, the reproductive effort expended by an individual should increase towards the end of its life span. However, in mammals, field data suggest that, following an initial period of relatively low productivity prior to adulthood, the number of offspring produced per female subsequently remains fairly constant, though in some cases there may be a slight decline during later life (Sadleir 1987,

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Mitchell and Brown 1974, Sinclair 1977, Guinness *et al.* 1978). For roe deer *Capreolus capreolus* (Linnaeus, 1758) some authors have also suggested that female productivity declines during the later stages of life (Borg 1971, Kałuziński 1982), although Gaillard *et al.* (1992) found a uniformly high level of fecundity once does were more than two years of age. Few studies have been able to demonstrate whether age-related changes in productivity are adaptive, or merely the result of puberty and senescence, although Clutton-Brock (1984) suggests that there is evidence that red deer *Cervus elaphus* hinds, as they grow older, invest more heavily in their calves at lactation, ensuring increased rates of juvenile survival at the stage of terminal investment.

In mammals, the critical factor by which sexual maturity is advanced or delayed is often variation in maternal body weight, with puberty dependent on some critical threshold body mass (cattle – Joubert 1954, rats – Widdowson *et al.* 1964, humans – Frisch 1984). Furthermore, post-pubertal weight is often a highly influential factor determining subsequent pregnancy success, as has been shown in a variety of cervid species (red deer – Mitchell 1973, Hamilton and Blaxter 1980, Clutton-Brock *et al.* 1983, Albon *et al.* 1986, reindeer *Rangifer tarandus* – Reimers 1983, roe deer – Gaillard *et al.* 1992).

The reproductive performance, and hence the potential for expansion of a given population is defined by the age-related species-specific intrinsic growth rate of the population, modified by environmental factors, whether density-dependent or density-independent. This paper investigates variation in a component of female reproductive performance, fecundity, in 15 populations of roe deer in Britain and considers to what extent this is related to age and maternal body weight. Such relationships have not been examined in detail previously for roe deer, and rarely across such a number of different populations, each with a very extensive data set, for any deer species.

Methods

Study areas

The data for this study were derived from 15 sites, nine Forestry Authority commercial forests and six Ministry of Defence training areas (Fig. 1), selected to represent the full geographical range of this species in Britain, and covering a range of different environments and habitat types. All nine Forestry Authority sites were principally coniferous woodland, with Scot's pine *Pinus sylvestris*, Sitka spruce *Picea sitchensis* and Corsican pine *Pinus maritima* predominant, but Japanese larch *Larix raempferi*, Douglas fir *Pseudotsuga* sp. and Norway spruce *Picea abies* were often also present. Each site was a mosaic of single species compartments, comprising of mature stands, closed canopy thickets, open canopy thickets and restock sites in the establishment phase, with occasional small areas of broad-leaved woodland. The Ministry of Defence sites were more diverse, each generally containing a considerable area of open ground, (grassland, scrub or agricultural land), but also including some small pockets of woodland, usually oak and birch together with some conifers, as well as areas of scrub. In some sites, red deer and/or sika deer *Cervus nippon* were also present.

Fig. 1. The location of the study sites (filled circles are Forestry Commission plantations, open circles are Ministry of Defence training areas).

Data

Data were extracted from record cards completed by stalkers for each animal shot during routine culling operations. Data were available for a minimum of 6 years (maximum 21 years), constituting a total of over 5000 individual animals. Each shot female was identified by a code number and the clean body weight (total weight less viscera, but head and feet on) recorded. Age and reproductive condition for each animal were assessed as below.

The age of each female was estimated initially by the stalker, immediately after death, as kid of the year, yearling or adult, by examination of the dentition for tooth eruption and wear. For all females shot on Forestry Authority land, the lower mandible was retained and, for these animals, age was subsequently assessed more precisely from the tooth eruption pattern and by tooth sectioning. In roe deer, eruption of all permanent teeth is complete by 10 to 15 months, therefore kids were readily identifiable, as the jaw still held a tricuspid third premolar but lacked a third molar (Ratcliffe and Mayle 1992). The age of older animals was determined by counting cementum annuli in a section of the tooth root (Aitken 1975, Ratcliffe and Mayle 1992). This more precise ageing was not possible for animals shot in the Ministry of Defence sites, as jaws were not available.

The reproductive condition of each animal was assessed, where possible, by two methods. Firstly, the number of embryos in the uterus of each culled female was ascertained at the time of death. The uterine horns were cut longitudinally and the embryos counted (Strandgaard 1972a). However, roe deer exhibit embryonic diapause of the fertilised blastocysts (Aitken 1974), and, thus, for the first half of the doe cull season (which extends from October to March) it was not possible to determine pregnancy in this way. Therefore, in the analyses relating to the presence of foetuses, only animals shot after the first of January were included. In the second method, the ovaries were collected from animals shot on Forestry Authority land, and stored in dilute (5%) formalin solution. Subsequently, the ovaries were dissected to count the number of *corpora lutea* (Strandgaard 1972a) representing the potential litter size of the female for that breeding season. *Corpora lutea* are apparent immediately following ovulation and can therefore be counted throughout the duration of the cull. No females were shot after 31st March.

From these data, four parameters were calculated for each specified age class within each population to describe variation in fecundity: (1) percentage of does ovulating (*corpora lutea* present), (2) average number of fertilised ova (*corpora lutea*) per ovulating doe, (3) percentage of does pregnant (embryos present), (4) average number of embryos per pregnant doe.

Data analysis

In order to estimate to what extent variation in fecundity is a response to differences in doe body weight, the following analyses were performed. For each population, the total number of individuals in a given age class was divided, according to increasing body weight, into four groups of equal size. The effects of the factors 'population' and 'body weight group' on the four fecundity parameters was then analysed as follows. For the parameters which were expressed as percentages (1 and 3 above), logistic linear models were used, while for the parameters measuring potential litter size (2 and 4 above), weighted analysis of variance (ANOVA) was performed. Both the above analytical approaches take account of variation in sample sizes between populations. Where significant variation was identified, this could be examined further using Scheffe's multiple range tests to determine the significance of differences between pairs of populations. Analysis was performed separately for kids (< 12 months), yearlings (12–24 months) and adults (> 24 months). A series of regressions of body weight of a particular animal against the date it was shot within each site identified a trend of slight weight loss over the winter for both adults and yearlings but this trend constituted only a minor weight differential and was not significant. Therefore, I assumed the effect of the date that the deer was shot was negligible and weights used were clean weights recorded at death. I also assumed that there was no inter-annual variation.

Results

Variation in fecundity with respect to age

Table 1 presents the percentage ovulation and percentage pregnancy for kids, yearlings and adults, in each of the fifteen study sites (data pooled for all years). In order to determine if there was any variation in fecundity with age among adult does, potential litter size (average number of *corpora lutea* and average number of foetuses per doe) was calculated for each single year age class from 2 years old upwards within each site. Only at one site, Spadeadam, was the variation between different age classes of animals found to be significant (one-way ANOVA: $p < 0.05$), and this exception was due to a lower fecundity rate among the 2 and 3 year old does at this site. Therefore, the simpler age classification into kids, yearlings and adults was retained in subsequent analysis.

Clearly, ovulation among kids is not common, generally below 10%, except at one site, Pickering, North Yorkshire, where almost half of all kids sampled had ovulated. Furthermore, only at this particular site did a significant proportion of these animals (8%) go on successfully to implant a foetus. In contrast, ovulation among yearlings was generally high, but at Queens there was a notable proportion of yearling does that did not ovulate successfully. Values for yearlings were not

Table 1. The proportion of roe deer ovulating/pregnant among kids (< 12 months), yearlings (12 to 24 months) and adults (> 24 months).

Study site	Ovulation						Pregnancy					
	Kids		Yearlings		Adults		Kids		Yearlings		Adults	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
Alice Holt	11	47	100	51	99	186	0	24	96	27	91	117
Thetford	5	110	98	181	99	344	1	96	81	118	90	216
Ringwood	4	51	100	12	99	171	0	35	71	7	84	110
Spadeadam	1	81	92	25	99	188	0	51	56	16	75	115
Kershope	9	103	95	38	99	206	0	49	35	23	67	116
Pickering	48	232	99	67	99	368	8	167	74	39	79	239
Craigellachie	0	75	97	107	100	219	0	24	62	34	70	81
Queens	0	9	74	19	99	76	0	4	55	11	68	37
South Strome	17	12	100	11	98	92	0	1	100	1	81	37
Salisbury Plain							0	43	36	14	83	67
Lulworth							0	7	75	12	78	60
Aldershot							0	7	75	4	82	28
Bramley							0	23	83	6	84	39
Stanford							0	25	44	9	94	33
Kirkcudbright							0	16	45	11	86	28

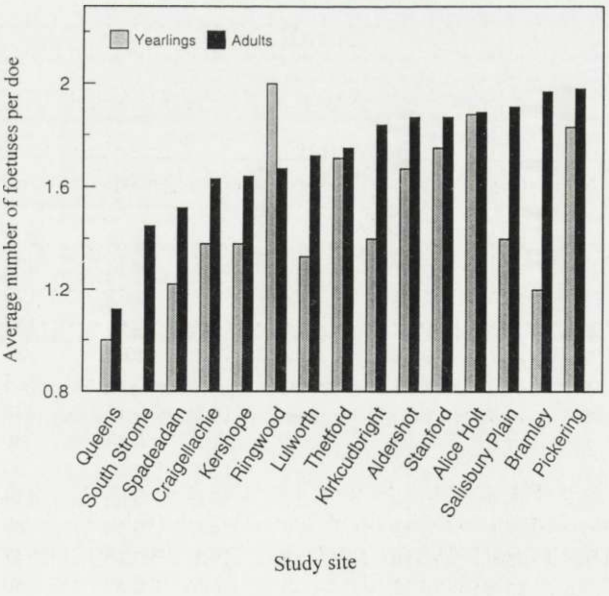

Fig. 2. Bar graph of the average potential litter size (number of foetuses) per doe among yearlings and adults in each population. Sample sizes are as given for percentage pregnancy in Table 1.

greatly different from those among adults at the same study site, which approached 100% in almost all cases. Rates of actual pregnancy among yearlings approximated to those of the adult age class in about half the study, however, overall, a clear difference was apparent between yearling and adult pregnancy rates within sites. There were also very large differences in potential litter size between age classes within a site, assessed both in terms of average number of *corpora lutea* and average number of embryos per doe, due to the smaller potential litter sizes among yearlings (Fig. 2).

Variation in fecundity in relation to body weight and population

Body weight varied widely between populations for all age classes (Table 2), thus, the relationship between body weight and fecundity was investigated. Among all 3 age classes, some or all measures of fecundity increased with increasing body weight. Thus, heavier kids were more likely to ovulate successfully (log-linear model: $\chi^2 = 39.41$, df = 3, $p < 0.001$) and become pregnant ($\chi^2 = 15.98$, df = 3, $p = 0.001$), but body weight had no effect on potential litter size of this age class (weighted ANOVA: $F = 0.38$, df = 3,11, $p = 0.766$ for *corpora lutea*; $F = 0.17$, df = 3,1, $p = 0.983$ for foetuses). Heavier yearlings were more likely to ovulate (log-linear model: $\chi^2 = 28.83$, df = 3, $p < 0.001$), become pregnant ($\chi^2 = 12.77$, df = 3, $p = 0.005$), and on average carried more *corpora lutea* ($F = 13.52$, df = 3,24, $p < 0.001$) and more embryos ($F = 4.29$, df = 3,35, $p = 0.011$). Similarly, among adults body weight was positively correlated with the proportion of does ovulating ($\chi^2 = 11.34$, df = 3, $p = 0.01$) and the average number of *corpora lutea* ($F = 10.55$,

Table 2. Mean female body weight (eviscerated, head and feet on, in kg) for kids, yearlings and adults (2+ yrs) in each study site, with standard errors and sample sizes.

Study site	Kids			Yearlings			Adults		
	n	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
Alice Holt	94	12.9	0.16	59	18.1	0.19	207	18.4	0.12
Thetford	130	9.1	0.21	197	13.6	0.13	378	14.1	0.11
Ringwood	53	10.5	0.23	12	16.1	0.33	170	16.4	0.14
Spadeadam	73	9.8	0.24	24	14.8	0.50	182	15.0	0.15
Kershope	107	11.4	0.16	42	15.4	0.39	233	16.0	0.15
Pickering	247	12.8	0.12	66	16.5	0.26	368	17.2	0.11
Craigellachie	86	9.7	0.21	114	14.3	0.17	232	14.7	0.13
Queens	9	7.6	0.37	20	11.2	0.44	86	12.1	0.18
South Strome	12	10.7	0.43	11	14.1	0.57	90	14.8	0.19
Salisbury	90	13.9	0.20	27	16.0	0.50	114	18.7	0.15
Lulworth	35	10.8	0.29	22	14.8	0.43	87	16.3	0.18
Aldershot	11	13.8	0.39	12	17.1	0.38	42	18.7	0.32
Bramley	30	11.8	0.33	8	15.5	0.32	50	17.8	0.23
Stanford	42	10.8	0.35	23	14.7	0.47	64	16.4	0.18
Kirkcudbright	37	11.7	0.22	17	14.5	0.64	58	17.1	0.23

df = 3,24, $p < 0.001$) and embryos ($F = 8.36$, df = 3,42, $p < 0.001$) present, but weight did not influence the proportion of adult does becoming pregnant (log-linear model: $\chi^2 = 3.09$, df = 3, $p = 0.378$).

Except for percentage ovulation among adults (log-linear model: $\chi^2 = 7.19$, df = 8, $p = 0.516$), which approached 100% in all cases, and the average number of foetuses per doe among kids (weighted ANOVA: $F = 0.15$, df = 2,1, $p = 0.877$), which was 0 in almost all cases, variation between study sites in each of the measures of fecundity was highly significant for all age classes. The reproductive activity among kids at Pickering in particular meant that significant inter-population variation was detected in the proportion of kids ovulating ($\chi^2 = 207.33$, df = 8, $p < 0.001$) and pregnant ($\chi^2 = 26.95$, df = 14, $p = 0.020$), as well as the average number of *corpora lutea* per doe kid ($F = 3.35$, df = 6,11, $p < 0.040$). While the proportion of yearlings ovulating varied significantly between populations primarily due to the low value for Queens ($\chi^2 = 25.51$, df = 8, $p = 0.001$), the proportion of yearlings pregnant ($\chi^2 = 51.50$, df = 14, $p < 0.001$), and the average number of *corpora lutea* ($F = 8.12$, df = 8,24, $p < 0.001$) and foetuses ($F = 3.37$, df = 14,35, $p < 0.002$) per yearling doe varied more widely (Table 1, Fig. 2). Among adults, the variation between populations in the proportion of does pregnant ($\chi^2 = 94.32$, df = 14, $p < 0.001$), and the average number of *corpora lutea* ($F = 24.30$, df = 8,24, $p < 0.001$) and foetuses ($F = 6.65$, df = 14,42, $p < 0.001$) per doe was very highly significant. Indeed, in multiple range tests a number of significant differences between particular pairs of populations were detected, particularly when considering the number of *corpora lutea* per adult doe (Table 3). Specifically, at each of Alice Holt, Thetford and Pickering (classified as high fecundity populations), does, on average, produced significantly more *corpora lutea* than at each of Queens, Craigellachie and Spadeadam (low fecundity populations), (Scheffe's test, $p < 0.05$). Thus, assessed on the basis of these parameters, the study sites fall into well defined groupings of high (Alice Holt, Thetford, Pickering, and all Ministry of Defence sites), medium (Ringwood, Kershope, South Strome) and low

Table 3. Multiple range tests on the average number of *corpora lutea* per ovulating doe for adults (over 2 years old). Significance of differences: * – $p < 0.05$, ns – not significant.

Study site	Queens	Spadeadam	Craigellachie	South Strome	Ringwood	Kershope	Thetford	Alice Holt	Pickering
Queens	–								
Spadeadam	ns	–							
Craigellachie	*	ns	–						
South Strome	*	ns	ns	–					
Ringwood	*	ns	ns	ns	–				
Kershope	*	ns	ns	ns	ns	–			
Thetford	*	*	*	ns	ns	ns	–		
Alice Holt	*	*	*	*	*	*	ns	–	
Pickering	*	*	*	*	*	*	*	ns	–

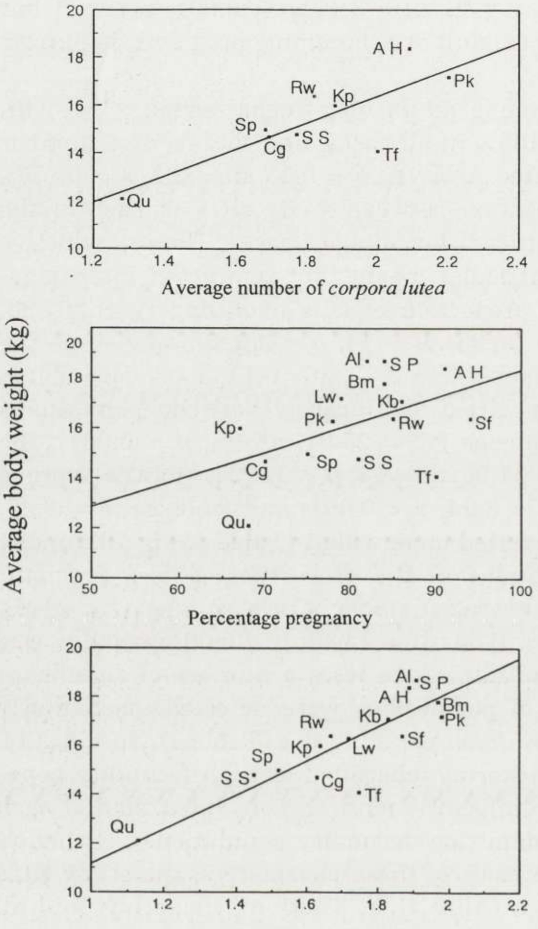

Fig. 3. The relationship between adult fecundity (three measures) and average maternal body weight across fifteen populations (all correlations, $p < 0.001$). Al – Aldershot, AH – Alice Holt, Bm – Bramley, Cg – Craigellachie, Kp – Kershope, Kb – Kirkcudbright, Lw – Lulworth, Pk – Pickering, Qu – Queens, Rw – Ringwood, SP – Salisbury Plain, SS – South Strome, Sp – Spadeadam, Sf – Stanford, Tf – Thetford.

(Spadeadam, Craigellachie, Queens) fecundity populations. Variation in body weight, despite being strongly related to variation in percentage pregnancy and both measures of potential litter size (Fig. 3), may be unable to fully explain the large differences between sites in these three fecundity parameters.

Discussion

In many mammalian species, reproductive performance reaches a peak at a certain age, and thereafter declines (eg for red deer – Clutton-Brock and Albon 1989). Such a response has been suggested for roe deer in a few studies (Borg 1971, Kałuziński 1982). However, from the data presented here, there is little indication of any consistent relationship of fecundity with age among roe deer of 2 years or older. Comparisons of fecundity between single year adult age categories revealed very few differences. Only at Spadeadam was there a discernible pattern with a significant shortfall in fecundity among 2 and 3 year olds, indicating that puberty is substantially delayed at this low performance site.

However, fecundity between the younger classes was much more variable and indicated, as Hanks (1981) suggested, that decline in reproductive vigour in relation to extrinsic pressures is initially most apparent among juveniles. In some populations of roe deer in Britain, kids may exceptionally become sexually mature (see Ratcliffe and Mayle 1992). However, while there was significant ovulation and fertilisation among kids at two sites (Pickering 48%, South Strome 17%), in reality very few, if any, of these animals actually implant a foetus and carry it through to full term (pregnancy rates recorded were 8% and 0% respectively). In general, roe are more usually considered to breed for the first time in their second year (Strandgaard 1972b, Pole 1973, Kałuziński 1982) and indeed yearling ovulation rates approached 100% in each site in this study. Furthermore, a significant proportion of these animals went on to successfully implant a foetus, although this proportion differed between study sites. A significantly lower pregnancy rate among yearling roe deer has been noted previously (Borg 1971, Gaillard *et al.* 1992), but in some 'high performance' populations in this study yearling pregnancy was approximately equivalent to that of older animals. This indicates potential for a substantial contribution of this age class to population recruitment at these sites, depending on population age structure, and suggests that these populations may be approaching their maximal reproductive capacity in terms of proportion of pregnant animals. At most sites, yearling pregnancy was rather lower than that among adults. However, at the 'low fecundity' Queens, both yearling and adult pregnancy were equally low, suggesting fecundity had been suppressed among both classes, a more advanced stage in the sequence of decreasing demographic vigour proposed by Hanks (1981).

Differences between age classes in the proportion of animals ovulating and becoming pregnant may be largely explicable in terms of variation in maternal body weight, suggesting a weight threshold for successful reproduction. Loudon (1987) defined such a threshold weight of 18 kg (eviscerated weight at death) across several populations above which there was a 90% chance of a roe doe producing two or more *corpora lutea*. However, the wide inter-population variation in maternal body weight presented here indicates that if any thresholds exist, they are specific to individual populations, as has been shown for red deer (Clutton-Brock and Albon 1989). For example, in certain sites where the animals were particularly heavy (eg Alice Holt and Pickering), the average weight of kids exceeded the average for both yearlings and adults at Queens. But, despite this, the proportion of kids that successfully reproduced at these sites was very low.

The vast majority of variation in fecundity identified in this study was attributable to differences between populations. Except the proportion of adults ovulating and the average number of foetuses per kid, each measure of fecundity varied significantly between study sites for all age classes. Bobek (1977) suggested that roe deer exhibited a relatively uniform level of fecundity across their European range, defining a measure of variation in fecundity as the ratio of the minimum and maximum reported values for average number of *corpora lutea* produced per female. His calculation of 1.3 was substantially lower than equivalent figures for mule deer *Odocoileus hemionus* (Nellis 1968) and white-tailed deer *Odocoileus virginianus* (Chaetum and Severinghaus 1950) of 1.9 and 3.1, respectively. The equivalent figure for roe deer based on this study alone was 1.7 and this rises to 2.0 when data from other roe deer studies (Borg 1971) are included. This study included some exceptionally low fecundity rates in the poor performance populations. Adult pregnancy is generally estimated as 90% or more (eg Chaplin *et al.* 1966, Prusaite *et al.* 1977, Kałuziński 1982). Values up to 30% lower were found in some populations (particularly Queens) in this study. Likewise, estimates for average potential litter size at several study sites fell below the lowest values previously recorded (Chapman and Chapman 1971, Ellenberg 1978).

Body weight clearly influences fecundity of roe deer. Heavier does of all age classes were more likely to ovulate and/or produced larger potential litter sizes than lighter does, and this effect was consistent across the 15 populations studied. However, it is notable that no relationship was observed between the proportion of adult does pregnant and body weight (cf Gaillard *et al.* 1992), suggesting that other factors may influence the implantation of the fertilised blastocyst. Furthermore, although a strong relationship of female fecundity with maternal body weight was observed across populations (Fig. 3), these relationships seem insufficient to explain the high level of variation in fecundity between populations. This suggests other factors (eg density, food availability, climate) may also have a significant influence on fecundity of roe deer in Britain.

Acknowledgements: I wish to thank the many people from the Forestry Commission and the Ministry of Defence who have helped compile the data over the years. In particular, I would like to acknowledge R. Putman and P. Ratcliffe who initiated this work and have continued to contribute throughout, and J. Langbein for his help and comments. J.-M. Gaillard was of great assistance for the statistics. This work was funded by the S.E.R.C and the Forestry Commission.

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Received 18 August 1994, revised 6 February 1996, accepted 8 February 1996.