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Who wants to live forever? Roe deer survival in a favourable environment

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Abstract The survival rates and body masses of roe deer (*Capreolus capreolus*) were studied on the island of Storfosna in central Norway in relation to sex, age, season and year. There were no predators on the island, and hunting was halted during the study period, resulting in a population increase from 10 to 40 individuals per km² during the period 1991–1994. A total of 352 individual roe deer were radio-monitored on a monthly basis. Survival rates were analyzed using the MARK software. An age effect in survival was found separating fawns from yearlings and adults, and for yearlings and adults we furthermore found a year effect. There was evidence for density dependence in body masses of fawns and yearlings, but no density effect in survival rates. We found no sex effect in winter body mass, but a significant sex effect in survival rates. We conclude that (1) increased population density can have an effect on body masses without causing a change in survival rates (2) roe deer can maintain very high survival rates under favourable environmental conditions even at very high population densities (3) male adults can reach equally high survival rates as females under favourable circumstances.

Keywords Roe deer · *Capreolus capreolus* · Mortality · Survival analysis · Density dependence · Program MARK

Introduction

The population dynamics of European roe deer (*Capreolus capreolus*) are, as for most herbivores, influenced by a range of factors. For example, various studies have documented a wide range of factors that are

limiting roe deer population growth through mortality. These tend to be dominated by human harvest, predation, vehicle collisions, accidents (drowning, falling), winter starvation and agricultural activities (e.g. Borg 1991; Jarnemo 2002). The extent to which these mortality causes are modulated by population density and climatic factors varies throughout the range of roe deer (Focardi et al. 2002; Gaillard et al. 1993, 1997, 1998). In fact, studying the degree of density dependence in roe deer dynamics has been one of the defining issues in the study of this species during the late Twentieth century (Andersen and Linnell 2000; Bobek 1977; Strandgaard 1972; Gaillard et al. 1998). Various studies have described density dependence in a range of life history traits, including home range size, litter size, fawn body masses and fawn survival [Gaillard et al. (1998) on litter size, and fawn body masses and survival, Kjellander et al. (2004) on home range size, Kjellander et al. 2006 on fawn body masses, Pettorelli et al. (2005) on fawn survival]. However, it is clear that different environmental context among populations may lead to different density-dependent responses. Yet, one of the most pressing issues for roe deer ecology in the 21st century concerns assessing the impact of predation (human and non-human). This need is stimulated by the increasing populations of large carnivores like Eurasian lynx (*Lynx lynx*) and wolves (*Canis lupus*) in many parts of Europe (Mattioli et al. 2004; Molinari-Jobin et al. 2002), by the increasing awareness of the role of red foxes (*Vulpes vulpes*) as predators of fawns (Aanes and Andersen 1996; Jarnemo et al. 2004), and the concern about the impacts of hunter harvest (Cederlund et al. 1998). Central to any understanding of the impact of predation is the issue of whether predation is compensatory or additive (Pöysä et al. 2004). In the ideal world studies about the compensatory nature of mortality would be designed as experiments. However, because of the logistical constraints of conducting such experiments on large ungulates and their large carnivore predators, we are often left with making cautious inferences from comparisons of vital rates collected from different populations.

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In this study we report data on the survival rates of roe deer from a study conducted in the period 1990–1994 on the island of Storfosna in central Norway. The island provides favourable habitats, lacks predators and climatic extremes, and human harvest was halted during the study period. As a result the population increased from 10 to 40 animals per km² between 1990 and 1994 (Andersen et al. 1995). This material allows us to supplement early analyses on the effects of density on neonatal growth rates, neonatal survival and reproductive rates (Andersen and Linnell 1997, 1998, 2000) with one of mortality and body masses of all age classes, except of senescent animals. In addition, it allows us to obtain reference values for survival rates in the absence of predation and climatic extremes. Based on the literature on roe deer (Gaillard et al. 1998), we expected (P1) that females would experience higher survival rates than males, especially at higher densities, (P2) that mortality rates would be higher for younger animals, (P3) that mortality of fawns would be highest in the period following birth, (P4) that overall mortality rates in this study would be very low compared to populations with higher predation pressure or climate extremes, (P5) that any density effects would be most apparent on younger age classes, and (P6) that body masses would decline with density, especially among younger age classes.

Methods

Study background

The survival rates and body masses of roe deer were studied on Storfosna Island, a 10 km², predator-free island 2 km off the west-central coast of Norway. There was no legal harvest of roe deer during the 1991–1994 study period and poaching was reduced to a minimum through cooperation among local hunters, local wildlife managers, and project personnel (Andersen and Linnell 1998). As a result, the population density increased from 1991 to 1994, with density estimates in spring of 10.0, 19.2, 30.4, 40.6 animals per km² for the respective years (Andersen et al. 1995). A total of 372 animals were captured, weighed and radio-collared in this period, between January 1991 and August 1994. Animals were checked at regular intervals, never less than once a month. For a complete overview of the characteristics of the study area, the study population and the methods of trapping and collaring animals, see Andersen and Linnell (1997, 1998, 2000).

Body mass

We analysed body masses for each age class (fawns, yearlings and adults) to see if there was a decreasing trend with increasing animal density, and for a difference between sexes. For this we only used masses taken in the

winter period, January till the first half of April. Since the four density estimates were obtained in late winter/spring of 1991–1994 (Andersen et al. 1995) and roe deer are primarily born in May, we assumed the biological year runs from May to April, and that density affects animal condition in the following year. Thus, winter masses of 1992 are affected by the density of spring 1991, and so on. Since the roe deer densities are estimated from spring 1991, we only took into account the masses taken in the winters of the years 1992, 1993 and 1994, and omitted the few masses taken in 1991.

Our data contains three age classes. Fawns are newborns up till 1 year of age, yearlings are animals from 1 to 2, and adults all animals 2 years and older. First we made a global general linear model (GLM-Univariate, SPSS Inc., 2004) including factors sex and age, and covariates day of the year on which the body mass was taken and year, and all possible 2-way, 3-way and 4-way interactions. After this we splitted the data set into the three age classes (see Table 1 for sample sizes). To be able to apply linear regression we first tested within each age class, whether the data were normally distributed, using the Chi Square Test, CHITEST, provided by Excel (Microsoft Office Excel 2003). Thereafter, we used linear regression with enter method (Regression Linear, SPSS Inc., 2004) to test for a significant trend in the measured masses for the subsequent years for each age class, while controlling for day of the year. Next to this, we checked for a sex effect. After this we checked again for any significant interactions of day, year and sex within each age class by using a general linear model (GLM-Univariate, SPSS Inc., 2004) including main effects as well as all possible 2-way and 3-way interactions of these.

Body masses could not be included into the survival analysis because animals were weighed too infrequently (on average once or twice a lifetime) to be comparable to the fine scaled monthly survival analysis.

Survival

From the survival analysis we omitted four male and two female fawns, whose deaths were directly or indirectly caused by the study. Next to these, two more animals of unrecorded sex and age were not included in the analysis. We defined May 1991 as the time of origin of the study to obtain sufficient precision in the survival estimates. At this point a total of 48 animals were radio-collared (Pollock et al. 1989). As a result, the

Table 1 Sample sizes for body mass calculations

	1992	1993	1994	Males	Females
Fawns	14	16	24	28	26
Yearlings	2	7	9	9	9
Adults	13	15	8	15	21

Table 2 Cumulative survival based on monthly survival rates estimated with the saturated model, and the estimated SEs

	1991		1992		1993		1994 ^a	
	S	SE	S	SE	S	SE	S	SE
Fawn male	0.65	0.175	0.73	0.076	0.62	0.074	0.56	0.076
Fawn female	0.55	0.154	0.70	0.087	0.61	0.104	0.59	0.070
Yearling male	1.00	1.1E-6	0.89	0.093	0.72	0.126	0.91	0.059
Yearling female	1.00	4.1E-7	0.90	0.085	0.64	0.164	1.00	0
Adult male	1.00	1.7E-7	0.93	0.064	0.71	0.135	0.96	0.038
Adult female	1.00	1.0E-7	0.91	0.056	0.94	0.045	0.97	0.025

For the years 1991–1993 annual survival is given. For the year 1994 this is the cumulative survival for the months May–August

^a $n = 4$ months only

Table 3 Cumulative survival based on monthly survival rates estimated with the saturated model, and the estimated SEs

	1991		1992		1993		1994	
	S	SE	S	SE	S	SE	S	SE
Fawn male	0.79	0.135	0.73	0.076	0.62	0.074	0.56	0.076
Fawn female	0.62	0.123	0.70	0.070	0.69	0.077	0.59	0.070
Yearling male	1.00	3.0E-7	0.89	0.093	0.90	0.060	0.91	0.059
Yearling female	1.00	3.0E-7	0.90	0.085	0.89	0.066	1.00	0
Adult male	1.00	1.4E-7	1.00	0	0.90	0.058	0.96	0.038
Adult female	1.00	0	0.91	0.056	0.97	0.029	0.97	0.025

For all years the cumulative survival for the months May–August is given

total period analysed consists of 40 months, from May 1991 to August 1994, providing 40 monthly survival estimates. We estimated survival rates with the known fate model of program MARK (White and Burnham 1999). We provided the input in Kaplan-Meier format, obtained using the staggered entry design (Pollock et al. 1989; Burnham et al. 2006), a modification of the Kaplan-Meier procedure (Kaplan and Meier 1958). The number of animals at risk in month i (r_i) includes animals added to the study in month i and excludes animals censored in this month. Monthly survival estimates are based on r_i and the number of animals that died in month i (d_i). Based on its sex and age at capture, an animal was placed into one of six classification groups, based on 2 sex classes and 3 age classes. The roe deer were registered as fawns for a maximum of 1 year, then 1 year as yearlings, and remained in the adult age class until they died or were censored (e.g. due to collar failure or dispersal). In practice an animal was censored out of its age class each year and added to the next age class. If an animal's birth month was unknown, it was assumed to have been born in May, shifting age classes in May of each year (Linnell and Andersen 1998). Fawns that were found dead due to stillbirth or that died within the first month after birth, have been included in the analysis, entering and leaving the population in the same month. This was done because the majority of deaths occur in the first weeks after birth (Andersen and Linnell 1998), and failure to include these individuals would drastically underestimate mortality. Since the study period ended with August

1994, resulting in incomplete data for this—biological-year, the data for the year 1994 only consists of four months.

Fitting the fully saturated model $S(\sim \text{age} + \text{sex} + \text{time} + (\text{age} \times \text{sex} \times \text{time}))$ in program MARK (Cooch and White 2007), we obtained the survival estimates in each study month for each classification group. Next to this, we fitted a set of models to the dataset, a priori based on the following predictions, taking into account the biology and current knowledge of roe deer (e.g. Gaillard et al. 1998):

1. Females have a higher survival rate than males
2. Survival rate is affected by the age of the animal, but
3. There is no significant difference between survival rates of yearlings and adults
4. Fawn survival rates are lower in May and June compared to the rest of the year, and
5. Survival rates do not decrease with increasing animal density

We designed 9 models to describe all relevant combinations and full interactions of two different age effects, respectively, consisting of three age classes and of two age classes, with yearlings and adults considered as one class in the latter, and no age effect, and two different year effects that, respectively, divided the years 1991/1992 from 1993/1994, and 1991 from 1992/1994 and 1993, and no year effect. The year effects were based on the survival estimates of the fully saturated model (see Fig. 2). In the second part of the

Table 4 The tested main factors, corrected Aikake weight, model likelihood and deviance from the data

Model description	AICc	Model likelihood	Deviance
S{~age2 + sex + season + year2 + (age × sex × season × year)}	821.67	1.000	96.75
S{~age2 + season + year2 + (age × season × year)}	832.18	0.005	119.35
S{~age2 + season + year1 + (age × season × year)}	835.13	0.001	126.32
S{~age2 + sex + season + year1 + (age × sex × season × year)}	835.80	0.001	110.89
S{~age2 + sex + season + (age × sex × season)}	839.22	0.000	130.41
S{~age1 + season + year2 + (age × season × year)}	844.05	0.000	115.10
S{~age1 + sex + season + year2 + (age × sex × season × year)}	857.55	0.000	92.08
S{~sex + season + year2 + (sex × season × year)}	940.12	0.000	223.26
S{~age2 + sex + year2 + (age × sex × year)}	1034.50	0.000	317.64
S{.}	1104.51	0.000	409.74
S{~age1 + sex + time + (age × sex × time)}	1204.86	0.000	0.00

Explanation of the tested effects: age effects: 1, fawns vs yearlings vs adults (3 classes); 2, fawns vs yearlings and adults (2 classes); sex effect: male vs female; season effect: May and June vs July through April (2 classes); year effects: 1, 1991 and 1992 vs 1993 and 1994 (2 classes); 2, 1991 vs 1992 and 1994 vs 1993 (3 classes)

Table 5 The tested interactions of main factors of the best model found in Table 4, corrected Aikake weight, model likelihood and deviance from the data

Model description	AICc	Model likelihood	Deviance
S{~age2 + sex + season + year2 + (age × sex × season × year)}	821.67	1.000	96.75
S{~age2 + sex + season + year2 + (age × season × year) + (sex × season × year)}	827.75	0.048	102.84
S{~age2 + sex + season + year2 + (age × season × year) + (age × sex × season)}	830.84	0.010	109.96
S{~age2 + sex + season + year2 + (age × sex × season) + (sex × season × year)}	845.49	0.000	126.62
S{~age2 + sex + season + year2 + (age × sex × year) + (sex × season × year)}	850.89	0.000	125.97
S{~age2 + sex + season + year2 + (age × sex × year) + (age × sex × season)}	855.89	0.000	132.99
S{~age2 + sex + season + year2 + (age × season × year) + (age × sex × year)}	859.28	0.000	136.38
S{~age2 + sex + season + year2}	884.92	0.000	180.13
S{.}	1104.51	0.000	409.74
S{~age1 + sex + time + (age × sex × time)}	1204.86	0.000	0.00

The overall order of the models in the two Tables 4 and 5 can be constructed using AICc. Explanation of the tested effects: age effects: 1, fawns vs yearlings vs adults (3 classes); 2, fawns vs yearlings and adults (2 classes); sex effect: male vs female; season effect: May and June vs July through April (2 classes); year effects: 1, 1991 and 1992 vs 1993 and 1994 (2 classes); 2, 1991 vs 1992 and 1994 vs 1993 (3 classes)

study the survival decreased overall (see Tables 2 and 3). In the years 1991 and 1992 the population density was fairly common, up to 20 animals per square kilometer, while in 1993 and 1994 the density increased up to very high values of 30 and 40 animals per square kilometer. Separating 1991/1992 from 1993/1994 thus seems logical when you combine the density and survival information. The other year effect, separating 1991 from the combined period 1992/1994 and from 1993, follows survival estimates more strictly and assumes that 1993 was a relatively bad year. All of these tested models include a sex effect and the expected season effect for fawns, with differing survival rates for the months May and June versus the rest of the year. Thereafter the most likely model was tested against the same model, subsequently excluding the season effect, excluding the age effect and excluding the sex effect. For this last model, without sex effect, we again varied the year effect. These model structures are in Table 4. Then we tested the significance of all one-way interactions in the model and we built one model without any interactions. These tested factor interactions are in Table 5. Model ranking and likelihoods are based on Akaike's information criterion

corrected for small sample sizes, AICc (Burnham and Anderson 1998).

Results

Body mass

See Fig. 1. Fitting our global model we found a significant main effect of AGE ($P = 0.025$) and significant effects of all interactions including a SEX × AGE interaction (SEX × AGE $P = 0.002$; SEX × AGE × DAY $P = 0.017$; SEX × AGE × YEAR $P = 0.007$; SEX × AGE × DAY × YEAR $P = 0.017$). We were expecting a significant AGE × YEAR effect (see Fig. 1a). This interaction had a P -value of 0.058. To further investigate we decided to split the data into the three different age categories and make separate analyses for them.

We chose CHITEST intervals in such a manner that each interval had a minimum frequency of 5. P -values were $P = 0.749$, $P = 0.916$ and $P = 0.835$ for the respective age classes of fawns, yearlings and adults. Thus we concluded that the body masses within each age class were normally distributed.

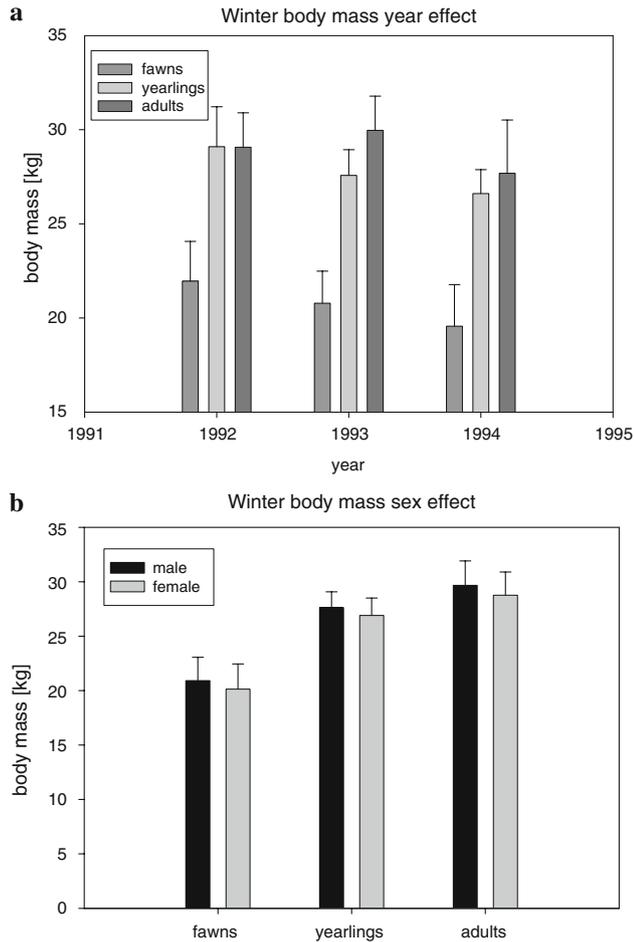


Fig. 1 Density and sex effect in winter body mass for roe deer age classes fawn, yearling and adult

For fawns, linear regression implied that the body masses were dependent of both DAY (slope = -0.033 with SE = 0.014 ; $P = 0.024$) and YEAR (slope = 1.047 with SE = 0.330 ; $P = 0.003$). SEX as an explanatory factor had a P -value of 0.231 . For yearlings, the body masses were dependent on YEAR only (slope = -1.151 with SE = 0.467 ; $P = 0.025$). The P -value for DAY as an explaining factor was 0.931 , P -value for SEX was 0.186 . For adults, the body masses were dependent of DAY only (slope = -0.043 with SE = 0.015 ; $P = 0.007$). The P -value for YEAR as an explaining factor is 0.389 , for SEX is 0.245 .

The GLMs built to further investigate the possible interactions of sex, day and year within each age class showed no significant interactions for fawns and yearlings. For adults all interactions were significant (SEX \times DAY \times YEAR, $P = 0.012$; SEX \times DAY, $P = 0.012$; SEX \times YEAR, $P = 0.006$; DAY \times YEAR, $P = 0.007$).

Survival

In Fig. 2 we present the monthly survival rates for each of the sex-age classes for the full study, based on the

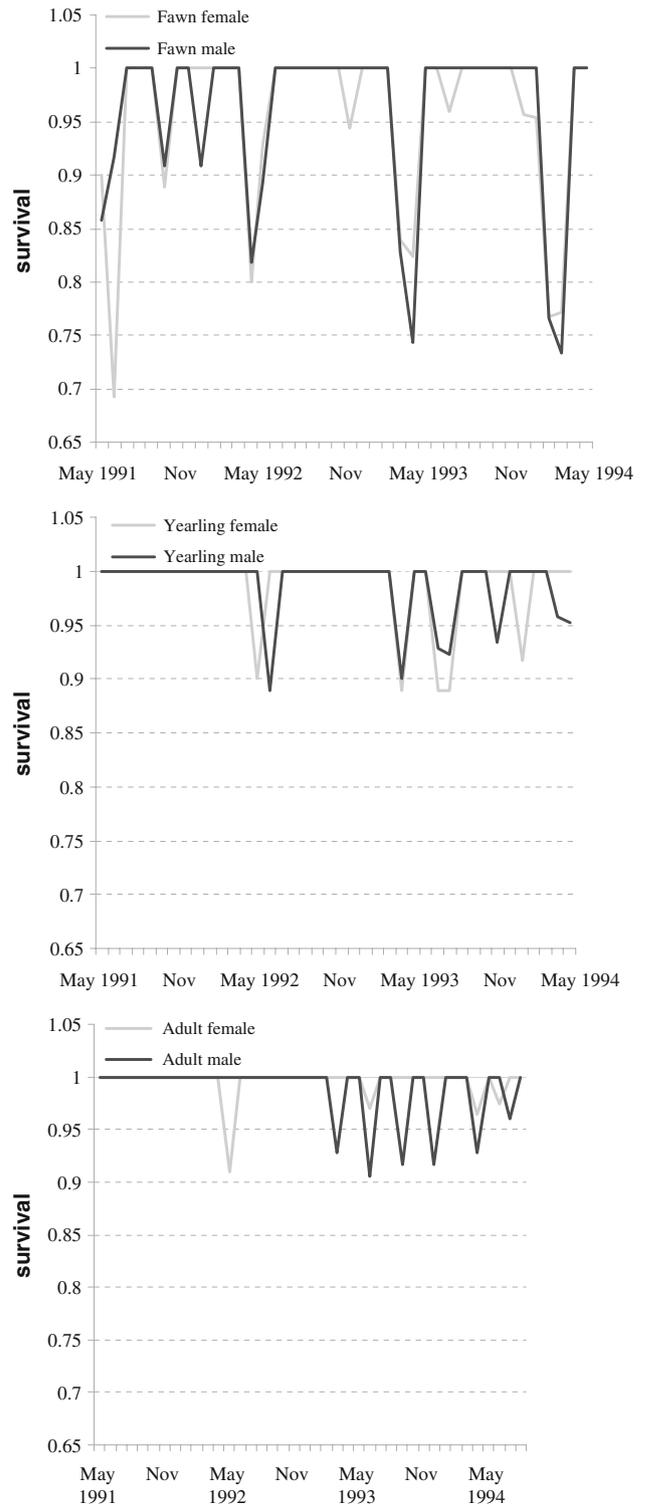


Fig. 2 Monthly survival estimates from the saturated model for the study period for each of six sex \times age classes

fully saturated model. Annual survival and seasonal survival (May–August) per year based on these estimates are shown in Tables 2 and 3. This last table (Table 3) was included to compare survival among years

Table 6 Survival estimates from the best model

Season in year	Male			Female		
	Estimate	SE	95% confidence interval	Estimate	SE	95% confidence interval
Fawns						
May/June 1991	0.895	0.070	0.663–0.974	0.783	0.086	0.572–0.907
July–April 1991	0.982	0.125	0.931–0.996	0.989	0.011	0.925–0.998
May/June 92/94	0.797	0.0342	0.722–0.856	0.805	0.032	0.735–0.860
July–April 92/94	1.000	0.000	1.000–1.000	0.996	0.004	0.973–0.999
May/June 1993	0.784	0.048	0.676–0.863	0.831	0.047	0.720–0.904
July–April 1993	1.000	0.000	1.000–1.000	0.987	0.007	0.962–0.996
Yearlings and Adults						
May/June 1991	1.000	0.000	1.000–1.000	1.000	0.000	1.000–1.000
July–April 1991	1.000	0.000	1.000–1.000	1.000	0.000	1.000–1.000
May/June 92/94	1.000	0.000	1.000–1.000	0.976	0.012	0.938–0.991
July–April 92/94	0.982	0.008	0.957–0.992	1.000	0.000	1.000–1.000
May/June 1993	0.951	0.024	0.876–0.981	0.971	0.017	0.914–0.991
July–April 1993	0.989	0.009	0.953–0.990	0.989	0.005	0.971–0.996

correcting for the incomplete study year of 1994. The model results of the survival analysis are presented in Tables 4 and 5, with the best model, equal for both, on top. In all years fawns experienced relatively low survival in the two months directly after birth, and very high survival in the other months (as high as yearlings and adults, see Table 6). In yearlings and adults survival rates were consistently high in all months, although with on average lower survival in 1993 (Table 6). Survival estimates from the best model are presented in Table 6.

Discussion

Survival rates

We found that roe deer on Storfosna experience very high survival rates. With the exception of the first two months after birth, in which the estimated survival was on average 81%, our best model indicates that roe deer of both sexes and all age classes have an estimated monthly survival probability of over 99% (see Table 6). To our knowledge, no study has shown such high survival probabilities for roe deer, or indeed any other small ungulate, before (Toïgo and Gaillard 2003). It should be noted however that a lengthier study would likely provide a more thorough investigation of roe deer survival variation, as our study period was fairly short compared to roe deer longevity.

Gaillard et al. (1993) reported an annual survival of adult roe deer of both sexes in the range of 0.82–0.97, and for female adults of 0.92–0.97, whereas we find an annual survival rate for adults of 0.71–1.00, and for females of 0.91–1.00. For “juveniles” (8–20 months of age) Gaillard et al. (1993) found a cumulative annual survival probability of 0.74–0.88. Taking into account age and calculating the comparable annual survival probability for “juveniles”, we find survival probabilities in the range of 0.85–0.94 in our data set. For fawns, the overall cumulative summer survival range from 0.19–

1.00 (see Raganella-Pelliccioni et al. 2006 and references therein). Raganella-Pelliccioni et al. (2006) found an average annual survival rate of 0.23 for fawns, whereas in our population the annual rate of survival of fawns ranged between 0.55 and 0.73 over years (see Table 2). If we define our summer survival as the cumulative survival over the months May to 15 August, we find an average of 0.64 based on our best model (see Table 6). Raganella-Pelliccioni et al. (2006) stated that the cumulative probability of survival over summer for fawns in their study was 0.33. Other studies referred to by Raganella-Pelliccioni et al. (2006) found values ranging from 0.38 in bad years to 0.82 in good years, with the absolute lowest value being 0.19 for bad years in bad habitats (Gaillard et al. 1997; Pettorelli et al. 2005). Kjellander (2000) found values ranging from 0.58 to 1.00 with a high overall mean survival of 0.78.

Sex effects

Strandgaard (1972), Rowe (1982), Pielowski and Brezinski (1982), Fiser (1987) and Gaillard et al. (1993) among others, stated that prime-aged roe deer females survive better than prime-age males and that life-expectancy is higher in females. In our results we find a sex effect, but we also find that this sex effect is significantly dependent on age, year and season (see Table 5). From the survival estimates in Table 6 it is clear that females in our study do not have a consistently higher survival than males. During the whole study period, conditions were very favourable for roe deer, although yearlings and adults in 1991, 1992 and 1994 show better survival than in 1993. Toïgo and Gaillard (2003) concluded that male survival in adult ungulates decreases more than female survival under harsher conditions, without direct influence of sexual size dimorphism. When we have a look at the survival estimates of the model that includes 3 age classes (see Table 7), splitting yearlings from adults compared to the model found to

Table 7 Survival estimates from the model with 3 age classes, splitting yearlings and adults compared to the best model

	May/June 1993		July–April 1993	
	Estimate	SE	Estimate	SE
Yearling males	0.95	0.034	0.98	0.012
Yearling females	0.95	0.036	0.97	0.017
Adult males	0.95	0.034	0.98	0.012
Adult females	0.98	0.015	0.99	0.004

be best (see Table 4), we see that yearlings of both sexes and adult males have a similar survival in the bad year 1993 which is lower than female adult survival. This effect was not strong enough to be significant, but the model does explain most variation in the data (see Table 4).

Consistent with this, our body mass analysis does not show any sex effects for fawns and yearlings, yet gives a significant sex \times day \times year interaction for adults, implying that adult males and females show different body masses among and between years.

Age effects

Four stages can be defined for survival in roe deer (for an overview see Gaillard et al. 1998): fawns, yearlings, prime aged adults and adults affected by senescence. For fawns survival can be divided into two components (e.g. Guinness et al. 1978): summer (postnatal) and winter survival. Yearlings have high survival, usually close to the maximum survival of prime-age roe deer (Gaillard et al. 1998), which is commonly more than 90% of the females surviving from one year to the next (Gaillard et al. 1993). Animals older than 7 years of age show signs of senescence (see Gaillard et al. 2000 for a review). We could not investigate this last group separately because we lacked precise age estimates for the animals in the adult age class. This is also a problem for the analysis of the body masses, since there is clear evidence that body mass of roe deer decreases after 10 years of age (Pettorelli et al. 2002). However, of the 372 animals captured for our study, only 42 were captured as adults. These are the only animals for which there is any chance that they were older than 7 years of age at a certain moment in the study period. All other individuals were captured as fawns or yearlings, and as a result of the short study period, we know that for all of these our analyses have not been affected by senescence. We find a marked season effect, separating survival in May and June from the rest of the year, which is significantly dependent on age, year and sex. Andersen and Linnell (1998) find for the same dataset that the newborns are actually particularly vulnerable in the first 35 days after birth, and that a lot of mortality is concentrated into the first 5 days. We found no overall difference between yearling and adult survival. Gaillard et al. (1993) found

that the survival of “juvenile” roe deer was more sensitive to external influences compared to adult survival. We do find this difference in the model with the lowest deviance from the data, but this effect was not significant. Overall our predictions of higher mortality rates for younger animals and highest mortality rates for fawns directly after birth are supported by our data.

As can be expected we found a very significant age effect on body mass. Within each age class body masses could be explained by different other factors.

Density effects

Previously documented density effects among cervids include a decrease in sexual dimorphism in size, a decrease in body mass, survival, and litter size and increased age at first reproduction (e.g. Cheatum and Severinghaus 1950; Taber and Dasmann 1957; Staines 1978; Case and McCullough 1987; Leberg and Smith 1993; Gaillard et al. 1997; Sæther 1997). We found no evidence for a density effect on roe deer survival in our data. However, we did find a significant density effect on body mass for fawns and yearlings. For fawns in the same dataset Andersen and Linnell (1998) found a significant density effect in the proportion of still-births only. Therefore, our results do not support the hypothesis that roe deer survival is affected by density. In contrast, our prediction of decreasing body masses with increasing density is partly supported by significant negative year effect on body mass for both fawns and yearlings, although other effects that can change systematically over time (e.g. climate) can not be completely ruled out. Adult body masses show a sex effect in their response to increased density, as implied by the significant sex \times year effect we found in the body mass analysis.

Conclusions

We studied the effect of population density increase on body mass and survival rates of roe deer. The results indicated a density effect on body mass for fawns and yearlings, but we found no evidence for a density effect in survival rates in any age class. This supports our prediction that body masses decline with increasing density and that this effect is more noticeable in younger age classes, but fail to support the prediction that survival rates are density dependent. We thus conclude that investigation of body mass cannot be a replacement for direct measurements of survival rates. This conclusion however may depend on the short duration of our study, limiting the strengths of our test to explore the relationship between body mass and survival rates. Ultimately, we would expect that survival rates would have been affected by decreasing body mass when the body mass drops below a certain threshold. In this study we showed for the first time that roe deer can maintain very

high demographic performance in benign environments, even under very high absolute animal densities, supporting earlier conclusions that survival rates of adult roe deer are in general high and not sensitive to external factors (at least in the absence of hunting and large carnivores). Another novel aspect in roe deer survival is that adult males can reach equally high survival rates as females under such favourable circumstances.

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