



0 Long-lived and heavier females give birth earlier in roe deer 53

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15 In seasonal environments, parturition of most vertebrates generally occurs within a short time-window each year. This
synchrony is generally interpreted as being adaptive, as early born young survive better over the critical season than late
born young. Among large herbivores, the factors involved in driving among- and within-individual variation in parturition
date are poorly understood. We explored this question by analyzing the relative importance of attributes linked to female
quality (longevity, median adult body mass and cohort), time-dependent attributes linked to female condition (reproduc-
tive success the previous year, relative annual body mass and offspring cohort (year)), and age in shaping observed variation
in parturition date of roe deer. A measure of quality combining the effects of female longevity and median adult body
mass accounted for 11% of the observed among-individual variation in parturition date. Females of 2 yr old give birth 5 d
later than older females. Our study demonstrates that high quality (heavy and long-lived) females give birth earlier than
low quality females. Temporally variable attributes linked to female condition, such as reproductive success in the previous
year and relative annual body mass, had no detectable influence on parturition date. We conclude that parturition date, a
crucial determinant of reproductive success, is shaped by attributes linked to female quality rather than by time-dependent
attributes linked to female condition in income breeders (individuals that rely on current resource intake rather than on
accumulated body reserves to offset the increased energy requirements due to reproduction) such as roe deer. 70
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30 Most large herbivores in temperate areas are characterized
by highly seasonal and synchronous birth periods (Bronson
1989). Two main evolutionary hypotheses have been proposed
to explain the adaptive value of synchronous births. First, a
high density of newborns at a given time might lead to rapid
satiation of predators (swamping) while decreasing the prob-
ability of a given newborn being preyed-upon (Ims 1990).
35 Second, seasonal variation in forage availability and/or quality
prevents females from meeting the energetic costs of late ges-
tation and early lactation (Clutton-Brock et al. 1989) outside
of a short time window when the vegetation flush occurs. To
be optimal, parturition timing should thus match this vegeta-
tion flush (Rutberg 1987). Early born neonates should benefit
40 from a longer period of growth prior to the onset of the harsh
season compared to late born neonates (Feder et al. 2008) but,
very early newborns should suffer from a higher risk of mortal-
ity caused by harsh early spring conditions and/or mismatch-
ing with the vegetation flush (Wilson et al. 2005). Therefore
strong selective pressure against late births should occur in
seasonal environments. 90
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0 adult mass and longevity). In contrast, the term condition
(sensu McNamara and Houston 1996) corresponds to attributes
that can vary markedly over time. This includes annual
body mass and annual reproductive status. Previous work has
5 mainly focused on the link between birth date and female
condition (Table 1), providing clear evidence for strong
effects of annual body condition, previous annual reproductive
success and age on parturition date. In general, heavier
and/or older females give birth earlier than lighter and/or
10 younger females (Feder et al. 2008). Environmental conditions
also influence parturition date (Forchhammer et al. 2001)
through female-specific responses. Indeed, poor environmental
conditions may negatively impact female condition, thereby
delaying the reproductive cycle and leading to a decrease in
15 reproductive success. Nonetheless, parturition date has been
reported to be partly heritable in some species (in the red
squirrel *Tamiasciurus hudsonicus*, Réale et al. (2003) and in
the bighorn sheep *Ovis canadensis*, Feder et al. (2008))
and is highly repeatable in roe deer *Capreolus capreolus*
(Plard et al. 2013), so that the parturition dates of a given
roe deer female are quite similar from year to year. However,
to date, there is little information available on the influence
of female quality on parturition dates in vertebrates (but see
Nussey et al. 2006, Stopher et al. 2008).

The relative influence of female condition and of female
25 quality on parturition date should differ among species in
relation to their tactic of resource allocation to reproduction.
These tactics vary along a continuum from capital breeders,
which rely on accumulated body reserves to offset the increased
energy requirements of reproduction, to income breeders, which
30 depend on current resource intake (Drent and Daan 1980, Jönsson
1997). Hence, support for the general rule that parturition date
should vary among years according to the physiological state of
a female (McNamara and Houston 1996) likely varies among
species in relation to resource allocation tactics. In a capital
35 breeder, female body condition at a given reproductive attempt
depends on both environmental conditions (i.e. climate and population
density) and on her previous reproductive status. For example,
female body mass in the autumn before parturition partly
determines parturition date in bighorn sheep (Feder et al.
40 2008). Therefore, capital breeding females could be expected
to adjust their reproductive cycle in relation to their condition
in the previous autumn. In an income breeder, body condition
should depend on currently available resources only. As energy
45 acquisition is crucial for giving birth early, in a species like
roe deer in which females display highly sedentary habits
(Strandgaard 1972) and spend their entire life within small
and spatially stable home ranges (< 30 ha in the studied area,
Saïd et al. (2009)), only females with abundant high quality
50 food in their home range or with high assimilation capabilities
(Nilsen et al. 2004) are expected to give birth early. Parturition
dates of individual females should thus be consistent over years
and depend on female quality rather than on female condition
in income breeders.

Based on a dataset of roe deer females with known life-
55 histories in the Trois Fontaines population, we quantified
the relative influence of female attributes linked to female
quality, including a synthetic variable combining the effects
of longevity and median adult body mass (Clutton-Brock
60 1988, Gaillard et al. 2000) and year of birth (cohort, Albon

et al. 1987), versus attributes linked to female condition, 61
including previous reproductive success, residual annual
body mass and year on parturition date. We also tested the
effect of age (a variable known to influence parturition date
in caribou (Adams and Dale 1998) and red deer (Nussey 65
et al. 2006)) for explaining the observed individual variation
in parturition date. Roe deer females are income breeders
(Andersen et al. 2000) and have been recently shown to give
birth at approximately the same time throughout their life-
70 time (Plard et al. 2013). We thus expected female quality to
influence parturition date more than female condition, with
earlier parturition in high quality females, characterized by a
long life and a high median body mass.

75 Material and methods

Study population

Data used were sampled by the Office National de la Chasse
80 et de la Faune Sauvage from a roe deer population located
at Trois Fontaines (48°3'N, 2°61'W), an enclosed 1360 ha
forest in north-eastern France. The climate is continental,
with relatively cold winters (minimum daily average temperature
in January of 2°C) and warm summers (maximum daily average
85 temperature in July of 18.5°C). The forest is dominated by oak
Quercus sp. and beech *Fagus sylvatica*. Hornbeam
Carpinus betulus comprises 70% of the cop-pice. Ivy
Hedera helix and bramble *Rubus* sp. dominate the under-
90 story. This roe deer population has been intensively
monitored since 1976 using a capture–mark–recapture
(CMR) protocol. Captured animals are individually marked
using collars (either numbered, VHF or GPS) and ear tags.
The population of Trois Fontaines is highly productive,
mostly because of the rich habitats and soils which promote
95 high forest productivity (Pettorelli et al. 2006).

Roe deer mating takes place in July and August. After
100 copulation, embryos stop their development and embryonic
implantation is delayed by a five month diapause. Embryonic
development then restarts in late December–early January.
Births are highly seasonal, synchronous (Fig. 1) and occur
from mid-April to mid-June (Gaillard et al. 1993). Females
are monoestrous and give birth to one to three fawns, once
per year from 2 yr of age onwards.

105 Data collection

From the beginning of the birth season (late April), a sys-
110 tematic search for fawns was conducted every year from
1985 to 2010 by the Office National de la Chasse et de la
Faune Sauvage. Between 21 and 63 fawns were found each
year through either intensive searches performed by a line of
people or by directed searches targeted towards the fawns of
radio-collared females. Fawns were handled by experienced
115 people, ear-tagged and weighed. The sex was recorded for
most fawns (98.9%). Fawn age was estimated using umbilic-
ular characteristics and behavior at marking (Jullien et al.
1992). Error when estimating capture age has been shown
to be < 2 d (Gaillard et al. 1993). Birth date was therefore
back-calculated based on the fawn's estimated age at the date
120 it was found. The identity of the mother for a given fawn was

Table 1. Summary of variables influencing parturition date in different species of large herbivores from published individual-based studies. Estimates and statistical tests are reported as given in the original papers. Y (yes) in the column W. P. (wild population) indicates a free-ranging population.

Species	W.P.	n	Variable acting on parturition date	Estimate	Test	Other non significant variables tested	Ref
<i>Rangifer tarandus</i>	Y	55	maternal body mass (autumn)		R ² = 0.082	maternal body mass (winter)	Adams and Dale (1998)
		302	maternal age		chi ² = 28.21	summer and winter conditions	
		295	previous lactation status		chi ² = 4.69		
<i>Rangifer tarandus</i>		12	snowfall (late winter)		r = 0.699	snowfall (gestation)	Holand et al. (2004)
	N	180	maternal body mass (September) maternal social rank	0.15	t = 2.05	year	
<i>Cervus elaphus</i>	N	63	treatment (age/sex structure) young sex	3.11	F = 3.63		Cook et al. (2004)
			maternal body fat (autumn)	-0.93	t = 2.68		
<i>Cervus elaphus</i>		16	previous parturition date		R ² = 0.14		Nussey et al. (2006)
	Y	2120	breeding date	0.606	R ² = 0.21	age at last reproduction	
			maternal age	-3.468	F = 20.00		
			maternal age ²	0.208	F = 26.92		
<i>Cervus elaphus</i>			reproductive status		F = 23.86		Stopher et al. (2008)
	Y	674	age at first reproduction	2.469	F = 12.50	dominance density	
			maternal age				
<i>Odocoileus virginianus</i> , <i>Odocoileus hemionus</i>			previous reproductive status				Haskell et al. (2008)
			maternal quality				
			year, rainfall (autumn), offspring birth mass				
	Y	138	maternal body mass (April)	-0.009	chi ² = 5.53	rainfall(gestation), young sex	
			maternal age	-0.028	chi ² = 11.91		
<i>Oreamnos americanus</i>			rainfall (autumn)	-0.006	chi ² = 10.76		Côté and Festa-Bianchet (2001)
			species	0.698	chi ² = 289.05		
			location	-0.124	chi ² = 13.71	maternal age, previous breeding experience	
	Y					maternal social rank, density	
<i>Ovis canadensis</i>	Y	185	maternal body mass (autumn)	-2.103	IC -4.461, 0.335	maternal age, rainfall (rut), temperature (rut)	Feder et al. (2008)
			previous reproductive status	0.359	IC -0.045, 0.747	fecal crude protein (summer), young sex	
<i>Ovis canadensis</i>	Y	91	population size	0.006	p = 0.013	maternal body mass (September)	Rioux-Paquette et al. (2011)
			young sex (female)	0.210	p = 0.055	maternal age, previous reproductive status	
			inbreeding	0.171	p = 0.124	snowfall (winter), temperature (winter)	
<i>Ovis aries</i>			lamb sex (female) × inbreeding	-0.292	p = 0.039	faecal crude protein (summer)	Forchhammer et al. (2001)
	Y	543	maternal birth body mass	0.782	p = 0.070	maternal age	
			NAO _{t-1}	-0.347	p = 0.002	litter size	
			N _{t-1}	-0.007	p = 0.010		

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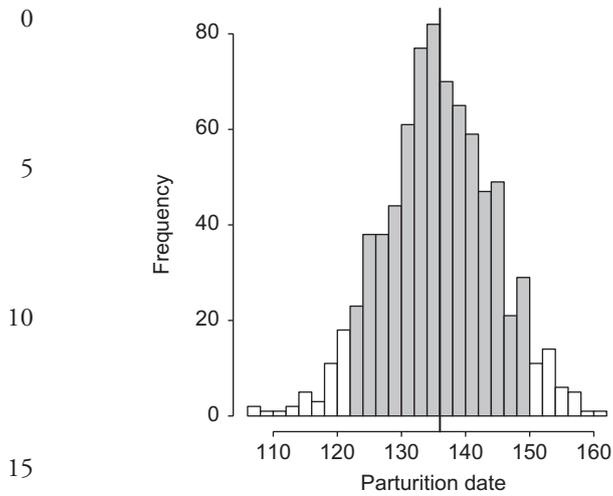


Figure 1. Frequency distribution of the 784 parturition dates (Julian dates) in the roe deer population of Trois Fontaines, France, from 1985 to 2010. The median parturition date (16 May) is represented by a black vertical line and the interval including 80% of births is shaded in grey. The parturition dates are normally distributed from day 107 (17 April) to day 161 (10 June).

established through direct observation of lactation behavior or by identification of escaping females in the vicinity of the fawn. Roe deer fawns display a 'hider' tactic, only coming into close contact with the mother for feeding. However, the mother stays in close proximity to her fawns, while isolating themselves spatially from other females.

Winter captures of roe deer older than 8 months of age took place each year between January and March. At each recapture, animals were weighed. Adult body mass is described by the median of all available measures for a given female from 4 to 10 yr of age, corresponding to the age at which a female had attained its maximum body mass (Hewison et al. 2011). For 11 females, the only measurements of body mass were recorded at one, two or three years of age. In these cases, we estimated adult body mass from the observed relationship between age and body mass (female adult body mass = body mass at 1 y.o. + 4.947; body mass at 2 y.o. + 0.884; body mass at 3 y.o. + 0.701, all $R^2 > 0.12$, Nussey et al. (2011)). The age of all reproducing females analyzed here was known exactly because they were first captured either as newborns or at 8 months of age during winter captures (identified using the tooth eruption sequence, Flerov (1952)). The intensive field observations (with an annual detection probability of 0.84, Gaillard et al. (2000)) and the recovery of substantial numbers of dead roe deer allowed us to estimate individual longevity accurately (9.7 ± 2.7 yr on average, with a maximum longevity of 18 yr at Trois Fontaines, Loison et al. (1999)). Reproductive success was estimated by direct observation of females between September and December to determine the number of weaned fawns.

From 1985 to 2010, we recorded the birth dates of 1062 fawns (784 litters). The mothers of 173 of these litters were identified. This corresponds to 93 mothers with an average of 1.86 (range from 1 to 7) parturitions per female during its lifetime. Longevity was known for all females, but the female's previous reproductive status was only available for

118 of these litters (72 females), while female annual body mass was available for 76 litters (47 females).

Statistical analysis

To test our prediction that female quality should override female condition in determining parturition date, we investigated the relative influence of females attributes linked to female quality (longevity, median adult body mass, and maternal cohort) and of female condition (previous annual reproductive status, residual annual body mass, and current year) on parturition date. The current year describes the current environmental conditions that potentially influence annual body condition and so annual parturition date. We also included possible effects of female age because increasing age, especially in relation to accumulated experience, has been shown to have marked effects on female parturition date in large mammals (Adams and Dale 1998, Haskell et al. 2008). Body mass can be considered as a time-dependent female attribute linked to current female condition. Its median value during adulthood can, however, be considered as a time-invariant attribute linked to female quality in an income breeder such as roe deer (Hamel et al. 2009) because within-individual variation in adult mass over time is much smaller than among-individual variation (24 and 76% of body mass variance, respectively). Consequently, we used two different metrics of body mass to describe its link with female quality and with female condition. First, the difference between body mass in a given year and its median value between 4 and 10 yr of age was used to measure female condition in that year. Second, female quality was measured by a synthetic variable combining the effects of both longevity and adult body mass. We performed a principal component analysis (PCA, equivalent to an orthogonal regression) on longevity and adult body mass (Hamel et al. 2009). We used the individual's score on the first principal component axis to describe female quality. Current year and the female's year of birth (maternal cohort) were included in our models as discrete factors. Previous annual reproductive status was entered as a 2-level factor taking 1 for successful (i.e. at least one fawn alive at the onset of winter the previous year) and 0 for unsuccessful (i.e. no fawn alive at the onset of winter the previous year) weaning. The influence of age on parturition date was analyzed using different age structures: a full-age-dependent model, a three-level factor for primiparous females (2 yr old), prime-aged females (3–8 yr old) and senescent females (> 8 yr old), and a two-level factor separating primiparous (2 yr old) from multiparous (> 2 yr old) females. Age at first reproduction is generally two years for female roe deer (Hewison and Gaillard 2001) and the proportion of breeding females at this age is high and does not differ from the proportion of breeding females at older ages at Trois Fontaines (Gaillard et al. 1998).

Model selection was performed on the data set containing 173 parturition dates using all the explanatory variables, with the exception of previous annual reproductive status and residual annual body mass, using the Akaike information criterion (AIC) (Burnham and Anderson 2002). AIC weights (w_i) were calculated to measure the likelihood of a candidate model being the best among the set of fitted

0 models. As the distribution of parturition dates was normally distributed (Kolmogorov–Smirnov test $D = 0.035$, $p = 0.283$), we fitted linear mixed models. We performed model selection based on the maximum likelihood fit, but presented parameter estimates from the selected model using the restricted maximum likelihood estimates, as recommended by Bolker et al. (2009) and calculated R^2 for fixed effects (Edwards et al. 2008) as a measure of effect size. The influence of previous annual reproductive status and of residual annual body mass on parturition date were analyzed separately by adding each of these variables to the best selected model using restricted data sets ($n = 118$ for previous reproductive status and $n = 76$ for residual annual body mass) and performing likelihood ratio tests.

15 The factor year was not retained in the model selection (see below). However, as it was a 26 level factor, it could have been excluded from the best model due to the high number of parameters. Consequently, we estimated the relative variance explained by among-female variation (time-invariant variation) and among-year variation (time-dependent variation) by fitting a linear mixed model linking parturition date to a constant fixed intercept with two random effects on the intercept: female identity and year of parturition. The proportion of variance explained by female identity can include three sources of variation: variations induced by identified factors (cohort, longevity, ...), by unidentified factors and random variations. Female attributes linked to female quality will thus explain only a part of this variance explained by female identity.

30 Results

35 Mean and median Julian dates of parturition were similar (136.25 ± 8.62 and 136 respectively), corresponding to the 16 May (Fig. 1). Ninety-two percent of all parturitions occurred in May and eighty percent between 5 and 27 May. The average birth date did not differ between male and female fawns (t -test = -1.06 , $p = 0.29$). We therefore pooled birth dates for male and female fawns in the subsequent analyses.

40 The first axis of the PCA between longevity and median adult body mass captured 60% of the total inertia. As expected, this first axis (PC1) sorted females along a continuum of phenotypic quality, opposing heavy and long-lived females to light and short-lived ones (Fig. 2).

45 The model that best described the observed among-individual variation in parturition date included the additive effects of the synthetic variable combining the effect of longevity and adult body mass (PC1) and age, and the random effect of female identity (Table 2). Of all candidate models, this model had the strongest statistical support ($w_i = 0.596$) and accounted for 18.5% of the observed variation in parturition date. Including previous annual reproductive success or residual annual body mass in the best model, but on restricted data sets, did not improve the fit ($LRT = 0.277$, $p = 0.598$ for previous annual reproductive success and $LRT = 0.638$, $p = 0.424$ for residual annual body mass, see Table 3).

50 Female quality, described by a synthetic variable combining body mass and longevity accounted for 11.5% of

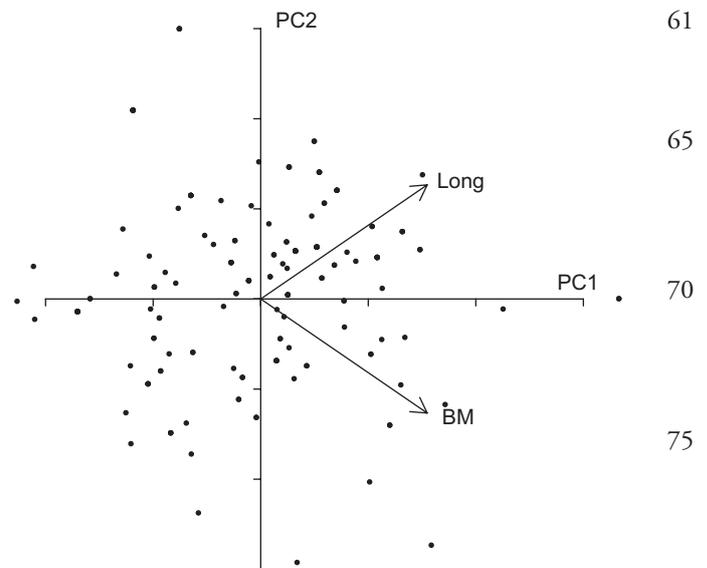


Figure 2. Principal component analysis of female longevity and body mass in the roe deer population of Trois Fontaines, France. The figure provides the projection of both the variables (longevity and body mass, arrows) and of the individuals (points) on the axes of the first two principal components.

the observed variation in parturition date (Table 3, model (A)). In support of our prediction, heavier females that lived longer gave birth earlier than lighter and short-lived females. Thus, females that lived for 14 yr and weighed 28 kg gave birth, on average, 12 d earlier than females that died at 4.5 yr and weighed 21 kg (Fig. 3). Of the

Table 2. Effects of a measure of female quality based on a combination of longevity and median adult body mass (individual's score on the first principal component axis, PC1), year of birth (Cohort), age (primiparous, i.e. 2 y.o. vs adult, > 2 y.o. females) (Age), and current year (Year) on parturition date (PD) of roe deer females in the population of Trois Fontaines, France. For each model, female identity was included as a random effect on the intercept. k indicates the number of estimated parameters, LL is the maximum log-Likelihood, ΔAIC indicates the difference in the Akaike information criterion between two competing models, and w_i indicates Akaike weights.

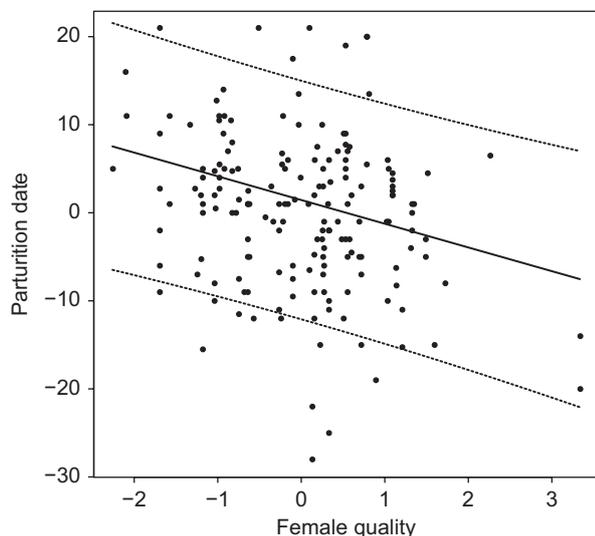
Model	k	LL	ΔAIC	w_i
1 PD~PC1 + Age	5	-614.063	0.000	0.596
2 PD~PC1 * Age	6	-613.729	1.333	0.306
3 PD~PC1	4	-617.009	3.893	0.085
4 PD~Age	4	-619.431	8.737	0.008
5 PD~PC1 + Age + Year	30	-594.090	10.055	0.004
6 PD~PC1 + Year	29	-596.656	13.187	0.001
7 PD~Constant	3	-622.710	13.295	0.001
8 PD~PC1 + Age + Cohort	27	-600.272	16.419	<0.001
9 PD~Age + Year	29	-599.359	18.592	<0.001
10 PD~Age + Cohort	26	-603.842	21.558	<0.001
11 PD~PC1 + Cohort	26	-604.438	22.751	<0.001
12 PD~Year	28	-602.735	23.345	<0.001
13 PD~Cohort	25	-608.132	28.138	<0.001
14 PD~PC1 + Age + Year + Cohort	52	-582.591	31.057	<0.001
15 PD~PC1 + Year + Cohort	51	-586.475	36.825	<0.001
16 PD~Age + Year + Cohort	51	-587.491	38.856	<0.001
17 PD~Year + Cohort	50	-591.040	43.954	<0.001

0 Table 3. Parameter estimates and associated standard error (SE) from
 three models explaining observed variation in parturition date of roe
 deer females in the population of Trois Fontaines, France. (A) The
 best model selected in Table 2 included a measure of female quality
 based on a combination of longevity and median adult body mass
 (PC1) and age (as a two-level factor: primiparous vs multiparous)
 5 (Age) (173 parturition dates of 93 females). (B) The best model
 selected in (A) was then applied to a restricted data-set (118 parturi-
 tion dates of 72 females) with reproductive success the previous
 year (PRS) included as an additional explanatory variable. (C) The
 model selected in (A) was then applied to another restricted data-set
 10 (76 parturition dates of 47 females) with female residual annual
 body mass (ABM) included as an additional explanatory variable.
 Estimates and standard errors are presented for each variable that
 was first (both centred (relative to its mean) and standardized
 (divided by its standard deviation)). A p-value indicates the statisti-
 cal significance of the difference of each value from 0 and an R²
 value indicates the proportion of the total variance that is explained
 by each selected variable.

	Variable	Estimate	SE	p-value	R ²
0	(A) Intercept	135.784	0.800	<0.001	
	PC1	-2.574	0.776	0.001	0.115
	Age	-1.478	0.599	0.016	0.071
5	(B) Intercept	136.424	0.944	<0.001	
	PC1	-3.243	0.941	0.001	0.152
	Age	-1.861	0.976	0.063	0.083
	PRS	0.514	0.996	0.608	0.006
10	(C) Intercept	135.448	1.144	<0.001	
	PC1	-3.494	1.134	0.004	0.185
	Age	-1.481	1.310	0.268	0.025
	ABM	-1.004	1.300	0.447	0.022

15 attributes linked to female quality we considered, only the
 20 mother's cohort was not related to parturition date.

In agreement with our predictions for an income breed-
 ing species, none of the attributes linked to female condi-
 tion that we considered were retained in the best model



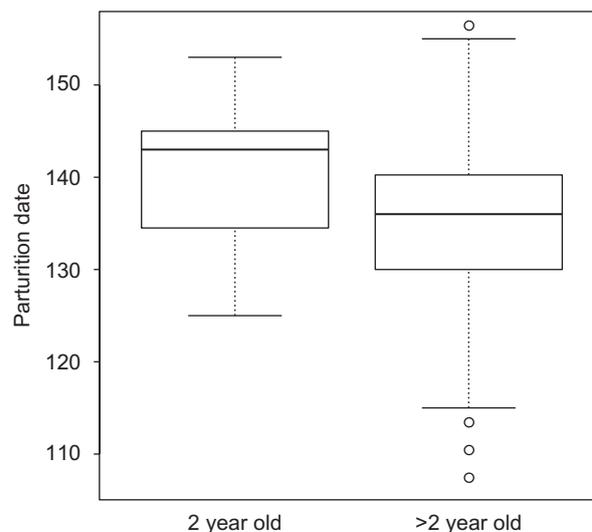
25 Figure 3. Partial effects of our measure of female quality (expressed
 as the individual scores on the first principal components axis of the
 orthogonal regression between median adult body mass and longev-
 ity for a given female) on parturition date (corrected for age) in
 the roe deer population of Trois Fontaines, France. The predicted
 relationships (black lines) were estimated from the selected model
 (see Table 3 for estimates).

(restricted data sets). In these restricted data sets, previous
 annual reproductive success explained 0.6% of the observed
 variation in parturition date vs 15.2% for the measure of
 quality (Table 3, model (B)). Similar results were obtained
 for residual annual body mass which explained 2.2% of the
 65 observed variation in parturition date vs 18.5% for the mea-
 sure of quality (Table 3, model (C)). Year included as a ran-
 dom effect accounted for 5%, whereas female identity for
 44% of the total variation in parturition date.

Age-specific differences in parturition date explained
 7% of the total variance in parturition date and were best
 described by a two-level age effect (i.e. primiparous vs mul-
 tiparous, Table 3, model (A)). The best model remained
 unchanged when using any of the age-dependent model
 structures (Supplementary material Appendix 1). As
 75 expected from previous studies on large herbivores, prim-
 iparous females (i.e. 2 yr-olds) gave birth on average 5 (± 2)
 d later than prime-aged (i.e. older than 2 yr of age) females
 (Fig. 4, Table 3).

Discussion

Our study demonstrates that parturition date in roe deer
 is highly dependent on attributes that are linked to female
 quality with high quality females giving birth earlier than
 low quality females. Indeed, we found that 62% of the vari-
 85 ance in parturition date explained by the best model was
 accounted for by our measure of female quality, generated
 from a linear combination of longevity and median adult
 body mass. To our knowledge, no study has yet reported
 an association between longevity and parturition date for
 any mammal, although Nussey et al. (2006) found indirect
 evidence for a similar pattern using age at last reproduction
 in red deer. We also demonstrated that age influences par-
 95 turition date in roe deer, with 2 yr old females giving birth
 on average 5 d later than older females (see also Adams and
 Dale (1998) on caribou *Rangifer tarandus*). In contrast, we
 showed that parturition date of roe deer females was rather



100 Figure 4. Influence of female age on parturition date in the roe deer
 population of Trois Fontaines, France.

0 insensitive to the current condition of the female, as expected
 for an income breeder (Jönsson 1997). Accordingly, repro-
 ductive success the previous year and residual annual body
 mass did not influence parturition date of roe deer females.

5 In species closer to the capital breeder end of the income
 breeder-capital breeder continuum, five of the six studies
 that have analyzed the influence of female body mass in a
 given year on parturition date (Table 1) found that female
 body mass in a given year strongly affects parturition date
 in the following spring, with heavy females in a given year
 10 giving birth earlier in that same year than lighter females
 (Table 1). Moreover, previous reproductive investment is
 known to influence subsequent reproductive success in spe-
 cies of large herbivore which are close to the capital breeding
 end of the continuum (Festa-Bianchet et al. 1998), and simi-
 15 larly influences the date of subsequent parturition in those
 species (Table 1, Adams and Dale (1998), Stopher et al.
 (2008)). These empirical observations support the state-
 dependent model proposed by McNamara and Houston
 (1996), which is expected to work well in capital breeders.

20 In capital breeding species, female condition varies substan-
 tially among years in relation to the energy balance between
 accumulation (body reserves) and expenditure (reproduction
 and thermoregulation). We therefore expect this temporal
 variation in condition to influence parturition date in spe-
 25 cies that rely on accumulated body reserves to fill the cost of
 the reproduction, while, in income breeders, like roe deer,
 adult female body mass is rather constant over time for a
 given individual (Andersen et al. 2000) and depends pre-
 dominantly on early life conditions (Pettorelli et al. 2002).

30 Female attributes describing variation in condition explained
 less than 3% of the observed variation in parturition date in
 our roe deer population, while maternal body mass explained
 8% (caribou, Adams and Dale (1998)) and 14% (red deer,
 Cook et al. (2004)) of the observed variation in parturi-
 35 tion date in two species that are closer to the capital breeder
 end of the continuum compared to roe deer (Table 1). In
 income breeding species, the adult body mass can be reliably
 interpreted as a measure of female quality. Consequently, we
 suggest that parturition date is shaped by attributes linked
 40 to female quality in income breeders, whereas condition-
 dependent factors should be more influential in capital
 breeders (although female quality is also likely to shape par-
 turition date to some degree in capital breeders, see Stopher
 et al. (2008), Table 1, and female condition could influence
 45 parturition date to some degree, even in species close to the
 income breeder end of the income-capital continuum, when
 resource availability is very low). We encourage further stud-
 ies to test this prediction.

50 While recent reviews have highlighted that there is no
 universal definition of individual quality (Wilson and Nussey
 2010), it is generally viewed as the co-variation among life-
 history traits that best explains among-individual variance
 in fitness (Hamel et al. 2009). Under this definition, time-
 invariant attributes appear to be better surrogates of fit-
 55 ness than time-dependent traits, as the latter have a higher
 within-individual variance than among-individual variance.
 Even though certain components of female quality are likely
 to vary over an individual's lifetime, the relative quality of
 different females should remain constant throughout their
 60 lifetime. For instance, high quality individuals should resist
 better against sickness or harsh environmental conditions
 than poor quality individuals. As a consequence, time-
 invariant individual attributes such as longevity should be
 preferred over time-dependent attributes when attempting
 to assess individual quality, whereas time-dependent indi-
 65 vidual attributes rather describe individual condition or state
 (McNamara and Houston 1996).

While body mass is often seen as reflecting the condi-
 tion of a female, it has previously been considered as a
 reliable indicator of individual quality in large herbivores
 70 (Hamel et al. 2009). For instance, the positive correlation
 we observed in the Trois Fontaines population between lon-
 gevity and adult body mass when including very heavy and
 long-lived females (Gaillard et al. 2000) suggests that heavy,
 long-lived females are the highest quality individuals. Indeed,
 75 we found that roe deer females that were both long-lived and
 heavy gave birth much earlier than light, short-lived females,
 suggesting that females of high quality increase their prob-
 ability of successfully weaning a fawn by giving birth early
 and so increasing the fawn's probability of survival. To give
 80 birth earlier than poor quality females, high quality females
 can either mate earlier, end their diapause earlier, or shorten
 the length of their effective gestation period. The third pos-
 sibility is unlikely because in the closely related red deer and
 reindeer, females that give birth early in the birthing period
 85 actually have a longer rather than a shorter gestation length
 (Mysterud et al. 2009). Rather, females give birth earlier
 by mating earlier (Scott et al. 2008, Mysterud et al. 2009,
 Rowell and Shipka 2009) so that conception date is more
 influential than gestation length in determining parturi-
 90 tion date (Clements et al. 2011). Low quality females may
 delay the onset of their subsequent reproductive cycle due to
 the high expenditure incurred prior to weaning their previ-
 ous offspring (Hogg et al. 1992, Langvatn et al. 2004). We
 suggest that in a species such as roe deer, with high alloca-
 95 tion to reproduction relative to its small body size (Mauget
 et al. 1999), high quality females also exhibit earlier oestrus.
 Indeed, as a consequence of the unusual feature of a 5 month
 embryonic diapause, the process of weaning the young of
 the year and the following oestrous are almost simultaneous
 100 events in roe deer which presumably imposes severe physi-
 ological constraints on females. The alternative possibility
 is that high quality females end their diapause earlier than
 low quality females. Since the knowledge on the roe deer's
 reproductive cycle remains somewhat superficial, we are cur-
 105 rently unable to discriminate between these two possibilities.
 Nonetheless, this latter alternative appears less likely as the
 duration of diapause appears to be regulated by an endoge-
 nous mechanism controlled by the embryo itself rather than
 its mother (Lambert 2005). Consequently, we hypothesize
 110 that fawns of high quality mothers that are born earlier were
 also conceived earlier.

Among bird species, hatching and laying dates are often
 used explicitly as a proxy of female quality (Cobley et al.
 1998, Blackmer 2005). While evidence of a link between
 115 birth timing and fitness is uncommon (but see Saino et al.
 2012), it has been much less studied than the link between
 birth timing and juvenile survival or annual reproduc-
 tive success (Sydeman and Eddy 1995, Lewis et al. 2006).
 Sheldon et al. (2003) have shown that laying date is nega-
 120 tively related to relative lifetime reproductive success in the

- 0 collared flycatcher (see also Saino et al. 2012). However, despite its crucial influence on juvenile survival (Côté and Festa-Bianchet 2001, Feder et al. 2008), parturition date in mammals has rarely been used as a surrogate of female quality. Nonetheless, Coulson et al. (2003) revealed that fitness is indirectly affected by parturition date via different pathways. Although further analysis directly linking fitness and parturition date are still lacking (but see Réale et al. 2003), our results suggest that the timing of birth is an individual trait such that high quality females give birth earlier and so increase their reproductive success. This trait is thus a component of the multi-dimensionality of individual quality. Moreover this pattern seems shared by many vertebrates, despite their very different physiological birth mechanisms (oviparity, viviparity, ...). Nonetheless, while females that give birth earliest in the birthing period may be considered as of the highest quality in our population, in other, harsher, contexts, very early born young may suffer from low survival due to predation or to a mismatch between resource availability and birth (Wilson et al. 2005).
- 15 In conclusion, we have shown that this high among female variation in parturition date was mostly shaped by female quality. In the context of climate change, the start of the spring vegetation flush is occurring increasingly earlier (Sherry et al. 2007) and studies have shown the importance of matching birth with spring phenology (Visser et al. 2004, Moyes et al. 2011). Furthermore, a recent study has highlighted the fact that the demographic performance of roe deer is poorer when spring occurs earlier in the year (Gaillard et al. 2013). As a result, we might predict that, by giving birth early in the season, high quality female should therefore perform even better relative to low quality females in recent years with early springs.
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45 Supplementary material (Appendix ECOG-00414 at <www.oikosoffice.lu.se/appendix>). Appendix 1. 105

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