
Keywords: 8FR/body condition/body mass/Capreolus capreolus/climate/demography/density dependence/Malme/roe deer/sexual selection

Abstract: Because first-year survival and age at sexual maturity of northern ungulates of northern ungulates often depend on body mass of fawns during winter, knowledge of factors affecting body mass of fawns is necessary to understand population dynamics and management of ungulates in temperate regions. Therefore, we compared body mass of roe deer (Caprioles) fawns during winter in two enclosed populations with contrasting climatic and demographic characteristic: Chile (CH) in western France (mild winters, less abundant food and lower birthrates), and Trios Fountains (TF) in eastern France (cold winters, abundant food and high birthrates). We weighed 2,077 fawns (1,212 in TF and 865 in CH) of both sexes captured with drive-nets in January and February from 1976 to 1993. Mass of male fawns was greater than of female in both populations (P< 0.01). Body mass varied among years for both sexes in each population (P < 0.01 in CH; P < 0.01 in TF). Neither climatic conditions between April and December nor population density accounted for yearly variation in body mass of fawns in TF. Rather, body mass fluctuated randomly about a mean, with no long-term effects on population dynamics. By contrast, body mass of fawns in CH was correlated with mean daily temperature in June-July (P = 0.01 for males; P = 0.04 for females) and population density P = 0.02 for males; P = 0.03 for females). Body mass of fawns was greater in years following cool summers and in years of low population density (r² = 0.75, P < 0.01 for males; r² = 0.50, P = 0.02 for females). Mass of male fawns but not female fawns was greater in January-February when total rainfall in the previous April-May was low (P = 0.01). In CH, yearly variation in fawn body mass supports the range quality hypothesis which states that fawns entering winter are small owing to poor nutritional conditions the previous summer or high population density. As a consequence, yearly variations in body mass probably have long-lasting effects on population dynamics in CH.
BODY MASS OF ROE DEER FAWNS DURING WINTER IN 2 CONTRASTING POPULATIONS

JEAN-MICHELE GAILLARD, URA CNRS 243, UCB Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cédex, France
DANIEL DELORME, Office National de la Chasse, CNRRA Cerdes-Sangliers, 820 Avenue de Wagrain, 75017 Paris, France
JEAN-MARIE BOUTIN, Office National de la Chasse, CNRRA Cerdes-Sangliers, 820 Avenue de Wagrain, 75017 Paris, France
GuY VAN LABRÉ, Office National de la Chasse, CNRRA Cerdes-Sangliers, 820 Avenue de Wagrain, 75017 Paris, France
BERNARD BOSCAUERET, Office National de la Chasse, CNRRA Cerdes-Sangliers, 820 Avenue de Wagrain, 75017 Paris, France
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Abstract: Because first-year survival and age at sexual maturity of northern ungulates often depend on body mass of fawns during winter, knowledge of factors affecting body mass of fawns is necessary to understand population dynamics and management of ungulates in temperate regions. Therefore, we compared body mass of roe deer (Capreolus capreolus) fawns during winter in two enclosed populations with contrasting climatic and demographic characteristics: Chal (CH) in western France (mild winters, less abundant food and lower births), and Trot Fontaines (TF) in eastern France (cold winters, abundant food and high births). We weighed 2,077 fawns (1,212 in TF and 865 in CH) of both sexes captured with drive-nets in January and February from 1976 to 1993. Mean of male fawns was greater than of females in both populations (P < 0.01). Body mass varied among years for both sexes in each population (P < 0.01 in CH; P < 0.01 in TF). Neither climatic conditions between April and December nor population density accounted for yearly variation in body mass of fawns in TF. Rather, body mass fluctuated randomly about a mean, with no long-term effects on population dynamics. By contrast, body mass of fawns in CH was correlated with mean daily temperature in June-July (P < 0.01 for males; P < 0.04 for females) and population density (P < 0.02 for males; P = 0.05 for females). Body mass of fawns was greater in years following cool summers and in years of low population density (r² = 0.75, P < 0.03 for males; r² = 0.50, P = 0.02 for females). Male of mean fawns but not female fawns was greater in January-February when total rainfall in the previous April-May was low (P = 0.01). In CH, yearly variation in fawn body mass supports the range quality hypothesis which states that fawns entering winter are small owing to poor nutritional conditions the previous summer or high population density. As a consequence, yearly variations in body mass probably have long-lasting effects on population dynamics in CH.

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Key words: body mass, Capreolus capreolus, climatic effects, density-dependence, fawn, roe deer, sexual selection.

Variation in body mass plays a fundamental role in population biology. For example, both variability in life history traits and reproductive performance of individuals are related to inter-specific and intra-specific variability in body mass, respectively (e.g., Peters 1983, Clutton-Brock 1986). Among ungulates, individuals with high body mass generally occupy a high social rank (Clutton-Brock et al. 1982), breed early (Sadleir 1969), survive well (Thorner et al. 1976, Bart- mann et al. 1992) and invest relatively less energy in reproduction (Clutton-Brock 1991). The first winter is a critical stage for ungulates living in temperate regions. Unless body mass exceeds a certain threshold before the onset of the winter, chances of survival to sexual maturity are reduced (White et al. 1987, Clutton-Brock and Albon 1986). Further, the probability of breeding precocially is related to body mass (Sadleir, 1987). Thus, harsh environmental conditions during the first months of life can determine survival and reproductive rates of cohorts. This cohort effect was first described in red deer (Al- bon et al. 1987) and later in other species (Albon et al. 1992). Knowledge of factors affecting body mass, therefore, would improve our understanding of population dynamics and management of temperate ungulates.

Three main hypotheses have been proposed to explain the variability in mass of ungulates (see further and Hein 1993 for a recent study): (1) range quality hypothesis—body mass is di- rectly related to food supply, (2) timing of births hypothesis—body mass is due to individual dif- ferences in birth dates, and (3) maternal effects hypothesis—body mass is due to differences in
the mothers’ ability to raise their offspring. Al-
though these hypotheses are not mutually ex-
sclusive (Saether and Hein 1990), our objective
was to evaluate whether the range quality hy-
thesis accounted for variation in body mass of
roe deer fawns measured at the outset of the
winter in two populations differing in demo-
graphic and climatic conditions. We tried to
answer the following two questions: (1) Is body
mass related to factors that influence habitat
quality such as population density and weather
patterns during the previous summer and winter
(periods when food supply is expected to be
limited)? and (2) Are these relations more pro-
nounced in a less productive environment where
population density was allowed to increase than in
a more productive environment where popu-
lation size was limited by clipping? Further,
because previous studies have reported growth
of males is more rapid than females and more
susceptible toextrinsic influences(Clutton-Brock
et al. 1982, Leberg and Smith 1993) we sought
answers to two additional questions: (3) Are male
fawns heavier than female fawns during their
first winter? and (4) Are male fawns more sus-
cceptible to harsh environmental conditions than
female fawns?

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vided by the staff of Office National de la Chasse
and numerous volunteers. We are grateful to L.
Ellisen, B. Gill, M. Hewison, A. Loison, C. Pél-
labon, D. Pontier, H. Strandgaard and two ref-
ers for constructive comments on earlier drafts
of this work.

STUDY AREAS

The study was conducted on two areas that
differed in climate and demographic charac-
teristics of the deer populations. Trois Fontaines
(TF) is a 1,360-ha reserve situated in north-
eastern France (49°43’ N, 2°26’ E). The climate
was continental, characterized by cold winters
and hot summers. Forest overstories were dom-
inated by oak, Quercus sp. (65.5% of timber
trees) and beech, Fagus sylvatica (19.5% of tim-
ber trees), whereas coppice was composed pri-
marily of hornbeam, Carpinus betulus (70%).
Upland forests were dominated by ivy (Hedera
helix) and brambles (Rubus sp.), which were
highly selected by roe deer. Soil at TF was fertile
and highly productive (long-term average of
5.92 m² of wood produced/ha/yr, Inventaire Na-
tional Forestier) and based on our current
knowledge of food habits of roe deer in France
(Maublanc et al. 1991). TF was considered to
be suitable habitat. The roe deer population in
TF was maintained from 1977 to 1990 at 200–
250 individual s >1-year-old in March by inten-
sive culling (Galillard 1988). That population
was highly productive with all 2-year-old females
breeding (Galillard 1989), recruitment rate in
fall averaging 1.8 fawns per reproductive fe-
nale (Boutin et al. 1987), and annual survival
rates averaging 0.82 and 0.95 for >8-month-old
males and females (Galillard et al. 1995a). The
annual finite rate of increase (λ) averaged 1.57
(Galillard et al. 1995a) which is close to the in-
trinsic rate of increase for roe deer (i.e. r-max
sensu Caughley 1977).

Chizé (CH) is a 2,614-ha reserve located in
southwestern France (49°05’ N, 9°25’ W). The
climate was oceanic, with mild winters and hot,
dry summers. Soils of CH were shallow, stony,
and less fertile than those of TF. Two broad
vegetation associations were found on CH: (1)
a lime tree-beech forest (1,010 ha) in which
coppice was almost absent and understory cover
was composed mainly of woodland-brome (Brom-
chloa angustifolia sp.) and butcher’s broom (Ruscus
aculeatus), neither of which are favored forages
of roe deer, ivy (ivy abundance decreased fol-
lowing the peak population size in 1983-84),
wild madder (Rubus peregrinus) and wood mel-
lock (Melica arenaria), and (2) an oak forest (990
ha) in which coppice with hornbeam, wilder-
sevoir (Viburnum tomentosum) and Montpellier maple
(Acer monspessulanum) were abundant. Pro-
ductivity of the CH forest was low, due partly
to summer drought (long-term average of 3.77
m² of wood produced/ha/yr, Inventaire Na-
tional Forestier). In contrast to TF, the CH roe
der population fluctuated during the study pe-
riod, increasing from 350 >1-year-old deer in
1979 to 520 >1-year-old deer in 1985 and decr-
asing to <200 in 1989 (Galillard et al. 1995a).
The population increased because few
roe deer were removed annually whereas the de-
crease occurred due to both high annual cull-
ing and density-dependent responses of popu-
lation. Recruitment decreased from 1.7 to 1.3
fawns per reproductive doe following the pop-
ulation peak in 1985 (Boutin et al. 1987). Most
does first breed as 2-year olds but does born
during the peak first breed only as 3 or 4 year olds
(Galillard et al. 1992b).

METHODS

In both study areas, populations of roe deer
were fenced and managed by the Office Na-
tiential de la Chasse. Numbers of deer in both populations have been monitored for >15 years. In each population, we marked >70% of individuals using numbered leather collars (Strandgaard 1967) and ear-tags, which allowed us to estimate population size using capture-recapture models similar to that of Cormack-Jolly-Seber (Gaillard et al. 1989, Gaillard et al. 1986, Pollock et al. 1990). Deer were marked at each study area during dollars that were conducted annually to limit growth of these enclosed popu-
ulations. Each year in both study areas, the deer were conducted every Tuesday and every third or fourth Thursday of January and February (Jossaubert and Bontin 1988). This procedure led to about 10 days of capture per year and allowed us to keep the probability of capture of deer constant over years (Gaillard et al. 1996a).

These operations required 150–200 people per day to drive deer into >3 km-long nets that were set each morning and afternoon. Deer managers caught 150–300 animals every year on each site, of which 80–200 were removed each year depending on management objective. The remains were marked and re-
turned to the populations. Managers weighed (≥500 g) each caught and classified each as fawn or >1-year-old animal. Fawns were easily identified on the basis of milk incisors and distinctive third premolars (Flerov 1952). The mortality rate induced by capture was low (<3%, Van Laree and Bontin 1990). We used a 2-way analysis of variance (ANOVA) to examine effects of sex, age and winter body mass of roe deer fawns, and to study in-
teractions between these factors. We considered effects significant when P < 0.05. To account for the unbalanced sampling design (i.e., dif-
f erent sample sizes among the 2×16 (CH) or 2×18 (TF) cases of the ANOVA table), we used GLIM software (Baker 1972) for the calcula-
tions. Following Searle (1971), we used the most general model, including all the interactions, as a starting point for analyses. We tested various effects by successively withdrawing first the 2-way interaction and then 1 of each of the 2 factors. Because of pronounced differences in body weights between sites, we did not compare body mass of roe deer fawns between CH and TF, but rather conducted separate analyses for each study area.

We examined association among population density, climate and winter body mass of fawns using correlation coefficients and simple and multiple regressions. Using correlation coeffi-
cients we first checked whether independent variables were statistically independent. We did so to avoid redundancy and confusion between variables in multiple regression. To examine the influence of density on body size we computed density from population estimate of March from the previous year divided by the total area of the study site. To examine the influence of weather in size of fawns, we computed 2 weather variables for each of 4 seasons, including mean daily temperature (T) and total precipitation (P) during (1) April and May, the fetal growth pe-
riod, (2) June and July, the postnatal growth period before the rut, (3) September and Oc-
tober, the postnatal growth period between the rut and weaning, and (4) November and De-
ember, the pre-winter period. We obtained monthly mean estimates of T and P from weather stations located ≤5 km from the study areas (Saint-Dizier for TF and Beaufort-sur-Niort for CH) and monitored by Météo France. We ex-
namined linearity in the relations using correla-
tion coefficients and simple regressions. We se-
lected the best multiple regression model that explained variation in winter body mass using Mallows’ Cp (Mallows 1973, Draper and Smith 1981). Because Mallows’ Cp is only a criterion (Bursbam and Anderson 1992), we selected the model exhibiting the lowest Cp-value when the difference in Cp-values was >1. When differ-
ces in Cp-values between two or more models was <1, we selected the best model based on biological considerations (Bursbam and Ande-
son 1992).

RESULTS

Vital Status of Roe Deer Fawns

Château Population... We sampled and weighed 865 fawns in CH between 1975 and 1983. In CH, the interaction between sex and year of capture was marginal (2-way interaction: P = 0.16), 15, 833 df, P = 0.05). Body mass of roe deer fawns differed between the sexes (F = 21.21, 3, 848 df, P < 0.01), and among years (F = 12.85, 15, 848 df, P < 0.01). Mean body mass of roe deer fawns varied up to 5.8 and 2.6 kg between years for males and females (Table 1). Males were heavier than females in 12 of 16 years (Table 1).

Tres Fontaines Population... We sampled and weighed 1,212 fawns in TF between 1575 and 1965. In TF, sex and year of capture influ-
enced body mass of fawns independently (2-
way interaction: P = 0.66, 17, 1,176 df, P = 0.94). Body mass of fawns differed between the sexes
Table 1. Mean body mass (g) of female and male roe deer females during winter in Chisel, 1978-79.

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(F = 58.65, 1, 1193 df, P < 0.01) and among years (F = 11.32, 17, 1193 df, P < 0.01). Mean body mass of roe deer females varied up to 5.9 and 5.1 kg between years for males and females respectively (Table 2). Males were consistently heavier than females (Table 2).

Variation in Body Mass in Relation to Environmental Variables

Chisel Population.—Only one relation (population density-T during April-May) between independent variables was significant (F = 8.14; 1, 12 df, P = 0.015; Table 3). Because body mass differed between the sexes, we examined the relations between body mass and environment separately for each sex. For both sexes of females, climatic conditions prevailing during September-December, T during April-May and P during June-July did not affect winter mass (Table 4). Precipitation during April-May, T during June-July, and population density the previous March however, all negatively affected mean mass of female fawns (Table 4). Linear regressions described these relations satisfactorily (Fig. 1). Using the Mallows’ Cp, we selected a multiple regression model containing all 3 significant variables, which accounted for 75% of variability in body mass (Body mass = Body mass = 33.41 + 0.12 Demin + 0.35 T during June-July + 0.006 P during April-May, P < 0.01). As in male fawns, T during June-July and the population density the previous March were inversely correlated with winter mass of female fawns, but winter mass of females was independent of P during April-May (Table 3). Linear regressions satisfactorily described both relations (Fig. 1).

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Table 3. Coefficients of correlation between the independent variables: population density (D), mean daily temperature (T) and total precipitation (P) during April-May (4-5), June-July (6-7), September-October (9-10) and November-December (11-12) in Chisel (above the main diagonal of 1) and Trois Fontaines (below the main diagonal of 1). Coefficients of correlation significantly different from 0 appear in italics.

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the Mallows’ Cp, we selected a multiple regression model containing these two variables, which accounted for 50% of variability in body mass of female fawns (Body Mass = 21.54 - 0.11 * Density - 0.33 * T during Jun-Jul; P = 0.03). On the basis of the best models selected in both sexes for describing the yearly variation of fawn mass, the average mass of male fawns was about 2 kg heavier than of females. Sensitivity of mass fawn to density and T during June-July however, did not differ between sexes (same slopes in both sexes for density, F = 0.18; 1, 24 df; P = 0.68 and for T during Jun-Jul, F = 0.50; 1, 26 df; P = 0.44).

Trots Fontaines Population. — Two pairs of independent variables (population density-T during Apr-May and T-P during Jun-Jul) were significantly correlated (Table 3). We examined relations between average mass and environmental variables for each sex, but body mass was unrelated to weather and population density for both sexes (Table 4).

DISCUSSION
Our findings are consistent with the hypothesis that yearly variation of winter mass in roe deer fawns is related to range quality. Both predictions of that hypothesis were observed: body mass was related to population density and sum-

Fig. 1. Regression between mean winter body mass of roe deer fawns according to sex and (a) precipitations in April-May, (b) mean temperature in June-July, and (c) population density during 15 consecutive years in the Crezis Reserve (1978-92, only 1980-89 for population density).
Table 4. Coefficients of correlation (r) between mean mass of roe deer fawns during January-February and population density, temperature (°T) and precipitation (P) during April-December the preceding year in the Chiol Reserve, 1978-83 (1980-83 for population density), and Tras Fontanesi Reserves, 1978-83 (1978-83 for population density). Significant relationships (P < 0.05) appear in italics.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Chiol Male</th>
<th>Chiol Female</th>
<th>Tras Fontanesi Male</th>
<th>Tras Fontanesi Female</th>
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<tr>
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<td>r</td>
<td>P-value</td>
<td>r</td>
<td>P-value</td>
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<td>Population density</td>
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<td>-0.58</td>
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<td>Jun-Jul P</td>
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<td>0.48</td>
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<td>Nov-Dec P</td>
<td>-0.19</td>
<td>0.48</td>
<td>-0.24</td>
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During the summer will be required to better understand the effects of weather and population density on fawn body mass.

The marked between-population difference in favor of TF (average of 18.5 kg vs. 14.7 kg for males, 17.3 vs. 14 for females) despite a higher mean density indicates that effects of population density and forage conditions (quality and quantity) are interactive. Population density is only important when forage is limited. This points out the interrelatedness of concepts of density dependence and independence (e.g., McCullough 1980).

Climate conditions prevailing during September-October have shown to be an important period when poorly developed fawns may compensate for delayed early growth (Gaillard et al. 1985d). Our findings suggest that climatic conditions during early winter never affected availability of food, contrary to other populations of temperate ungulates (e.g., Cedrolini et al. 1991) and although winter severity affected the annual survival in this roe deer population (Gaillard et al. 1985a). In TF, January is the coldest month. Because the effect of climate on body mass can be delayed, the end of severe winters rather than the beginning is more likely to correspond to the critical stage for roe deer. However, the high habitat productivity during summer may buffer the effects of severe winters on body mass (Gaillard et al., unpublished data).

Although males were consistently heavier than female fawns during winter (as in other ungulates...
lates: red deer, Cervus elaphus; Clutton-Brock and Albon 1986; moose, Alces alces; Seather 1985; sika deer, Cervus nippon: Feldhamer et al. (1985), we found no evidence that growth of males and females was influenced significantly by environmental limitations. In contrast, previous studies revealed that males of highly di- morphic and polygynous cervids, as red deer (Clutton-Brock et al. 1982) or white-tailed deer (Odocoileus virginianus) (Leberg and Smith 1993), were more sensitive to harsh environ- mental conditions. We speculate that differ- ences among species may be related to inter- specific differences in mating systems and sexual selection. Indeed, roe deer are only slightly po- lygynous and sexual selection is less important in this species than in other ungulates previously studied: timing and synchrony of births (Gail- lard et al. 1993b), mass at birth, and postnatal growth rate until 30 days of age (Gaillard et al. 1993c) do not differ between sexes in roe deer.

MANAGEMENT IMPLICATIONS

Mass attained by fawns at the onset of winter is important for temperate ungulate popula- tions. This study points out the existence of two ends of a continuum in characteristics of roe deer populations that differ in management po- tential: (1) populations in productive habitats (e.g. TF) where abundance of food in summer allows even small fawns to compensate for their slow early body development. A marked yearly variation still occurs in fawn winter mass but has no long-term consequences for population dynamics and (2) populations in less productive habitats (e.g. CH) in which fawns with slow early body development cannot compensate for their small mass. This cohort effect (sensu Albon et al. 1992) is expected to markedly affect pop- ulation dynamics and managers should consider its long-term consequences. The study also gives managers a clearer ex- ample of the pitfalls in using the concept of absolute density for defining population manage- ment objectives: The population density in TF during the 18 years of population monitor- ing was about the same as the peak density in CH. The mean winter mass of fawns was about 3-4 kg higher in the richer site (TF), and density-dependent responses occurred in the poorer site (CH).

Lastly, we suggest that monitoring winter mass of roe deer fawns is a useful indicator of pop- ulation performance. Owing to difficulties in assessing and interpreting trends in population size of roe deer (Strandgaard 1972, Gaillard 1985), such biological indicators could be partic- ularly useful for managers.

LITERATURE CITED


