

High red deer density depresses body mass of roe deer fawns

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Received: 25 July 2009 / Accepted: 24 November 2009 / Published online: 24 December 2009
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Abstract Many previous studies have pointed out that, when resources are limited, the potential for competition should be high among sympatric species that display overlaps in habitat and nutritional niches. However, reliable evidence of competition between red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) has not been yet reported for life history traits directly measuring performance such as body mass, reproduction, or survival. From long-term monitoring of deer populations in the reserve of La Petite Pierre (France), we measured the sex-specific responses of roe deer fawn body mass to changes in red deer density after accounting for possible confounding effects of date of shooting, climatic conditions, and roe deer density. As expected under the hypothesis of competition, red deer density in a given year had a marked negative influence on body mass of roe deer fawns born the same year and the following year. Fawn mass of roe deer males and females responded in similar ways to changes in red deer density. Our study provides the first evidence of a negative response of roe deer performance to high red deer density.

Keywords Inter-specific competition · Herbivores · Density dependence · Individual performance · Sympatric species

Introduction

Interactions among individuals influence population dynamics and thereby species distribution (Begon et al. 2006). For example, on northern European coasts, Brent Geese have better feeding conditions thanks to facilitation by herbivores such as hare, rabbit, cattle and sheep (van der Wal et al. 2000). Competition is expected to be the most common interaction for large herbivores in the absence of large predators (Putman 1996). The most frequent type of competition among large herbivores is exploitation competition (Dolman and Wäber 2008), which occurs when the use of a resource by one individual reduces the availability of that resource to another individual [Johnson et al. (2000) for an example in mule deer *Odocoileus hemionus* and elk *Cervus elaphus*]. Many studies have suggested that, when resources are limited, the potential for competition is high among sympatric species of large herbivores, which often have overlaps in habitats and nutritional niches [Bartos et al. (2002) for white-tailed deer *Odocoileus virginianus*, fallow deer *Dama dama*, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus*; Focardi et al. (2006) for roe deer and fallow deer; Hemami et al. (2004) for roe deer and muntjac *Muntiacus reevesi*; Marshal et al. (2008) for feral ass *Equus asinus* and mountain sheep *Ovis canadensis*].

However, even if competition is possible, deer species of different size can coexist by having different rates of food extraction (Jarman 1974). This corresponds to the Jarman-Bell principle developed to explain the coexistence among African ungulates by a partitioning of food

Communicated by Jörg Ganzhorn.

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resources that differ in fibre content (Perez-Barberia et al. 2008). Therefore, while an intermediate feeder (sensu Hofmann 1989) of large size can consume both highly calorific and poor-quality food, a small-sized concentrate selector (sensu Hofmann 1989) only consumes highly digestible forage (Storms et al. 2008; van Soest 1996). As a consequence, large ungulates may utilize a wider range of habitat types (du Toit and Owen-Smith 1989), whereas small herbivores tend to be more selective (Owen-Smith 2002). Niche differentiation is often the basis for the coexistence of species. However, heterogeneity (over space or time) can have a stabilizing influence on ecological interactions, so when resources become limiting (due for example to seasonality), competition can occur between two species of different size (Begon et al. 2006).

Following the marked increase in deer density during the last 30 years in Western Europe (Andersen et al. 1998; Gill 1990), red deer and roe deer often live in sympatry nowadays [e.g. in more than half of French forests (Office National des Forêts, unpublished data)]. With increasing density of both species the potential for competition is high and could have important implications for managers of multi-species ranches or wildlife reserves (Owen-Smith 2002). Empirical evidence shows differences between red and roe deer in resource selection (Baltzinger 2003; Latham et al. 1999; Staines and Welch 1984; Welch et al. 1990), or a negative correlation between densities of the two species (Latham et al. 1997). However, while introduced muntjac caused decreases of body mass and fertility of native roe deer in eastern England (Hemani 2003 in Dolman and Wäber 2008), inter-specific competition (i.e., the negative impact of one species on the population dynamics of the other) between red deer and roe deer has not been yet demonstrated. One approach to achieve this would be to demonstrate a negative response of roe deer performance to increased red deer density using a long-term monitoring of sympatric populations.

We therefore used fawn body mass to assess the response of roe deer to changes of red deer density. Fawn body mass at the onset of the winter is a reliable measure of roe deer performance both at the individual (Pettorelli et al. 2002) and at the population scale (Gaillard et al. 1996; Myrsterud and Ostbye 2006). Fawn body mass changes correspond to an indicator of ecological change (sensu Morellet et al. 2007) of roe deer populations. In particular, roe deer fawn body mass is highly sensitive to changes in population density (e.g., Kjellander et al. 2006), in climate in spring-summer (Toïgo et al. 2006), and in habitat quality both within (Pettorelli et al. 2001, 2003) and among populations (Pettorelli et al. 2006). If red deer negatively influence roe deer performance as predicted under the hypothesis of competition, we should expect a negative relationship between red deer density and body mass of roe deer fawns. Moreover, roe deer is a slightly dimorphic

species in which adult males are only slightly larger than adult females [25 vs. 23 kg (Andersen et al. 1998)]. We thus expected that males and females should respond in a similar way to changes in red deer density.

Study area

The La Petite Pierre National Hunting and Wildlife Reserve (“La Petite Pierre” hereafter) is a 2,674-ha unfenced forest located in northeast France (48.5°N, 7°E), in the Vosges mountains. The mean elevation is 300 m a.s.l. and the climate is continental with oceanic influences, involving cool summers and mild winters (mean January and mean July temperatures are 0.6 and 18.4°C, respectively, data from Météo France, Phalsbourg weather station, 10 km from La Petite Pierre). Vegetation has a low nutritional quality for large herbivores like red and roe deer. Indeed, the soil is made up of sandstone and is thereby not highly fertile. Previous studies on the red deer population showed that density-dependent responses of life history traits occurred (Bonenfant et al. 2002), suggesting that resources were limiting when red deer density was high. The forest is structured with even-aged tree stands and includes approximately equal proportions of broadleaved (mainly beech *Fagus sylvatica*) and coniferous species [mainly silver fir *Abies alba*, Norway spruce *Picea abies*, and Scots pine *Pinus sylvestris* (Hamann et al. 1997)]. During the last 30 years, areas of forest management remained approximately identical (Office National des Forêts, unpublished data). The only change involved regenerating trees that have doubled in number within the last 20 years (Table 1). The forest has changed from a rich understorey to stands of tall trees with little understorey, thus has become poorer for deer from a resource viewpoint. However, since the end of 1990s, managers have created some openings to increase vegetation biomass and thereby deer food resources. In addition, hurricane Lothar hit the forest in December 1999 and swept away 480 ha of mature forest, generating several wind-throws up to 50 ha in size (Storms et al. 2006). Lothar thus led to increased resource availability for roe deer (Widmer et al. 2004) without impacting negatively on survival or reproduction (Gaillard et al. 2003). All the three species of large ungulates present on the reserve are hunted, with an average of 40 red deer, 50 roe deer and 150 wild boar, *Sus scrofa*, harvested every year.

Materials and methods

Roe deer data

We collected data on harvested roe deer during each year’s hunting season (1979–2007). We recorded the sex of each deer harvested and distinguished fawns from older roe deer

Table 1 Model selection for the ANOVA on body mass of roe deer fawns. Red deer density effects are shown: immediate (*Red deer density*), and 1-year lag (*Red deer density 1*). Models are ranked according to their Akaike Information Criterion (AIC) weights (*w*)

Model	<i>P</i>	AIC	Δ AIC	<i>w</i>
Julian date + Gausson index + Sex + Red deer density + Red deer density 1	6	1,200.27	0.0000	0.1753
Julian date + Gausson index + Sex \times Red deer density + Red deer density 1	7	1,200.65	0.3764	0.1378
Julian date + Roe deer density + Gausson index + Sex + Red deer density + Red deer density 1	7	1,200.72	0.4461	0.1331
Julian date + Gausson index + Sex + Red deer density 1	5	1,201.49	1.2181	0.0998
Julian date + Roe deer density + Gausson index + Sex \times Red deer density + Red deer density 1	8	1,201.22	0.9495	0.0976
Julian date + Gausson index + Red deer density + Sex \times Red deer density 1	7	1,201.91	1.6415	0.0732
Julian date + Roe deer density + Gausson index + Sex + Red deer density 1	6	1,202.71	2.4350	0.0519
Julian date + Roe deer density + Gausson index + Red deer density + Sex \times Red deer density 1	8	1,202.53	2.2592	0.0507
Julian date + Gausson index + Sex \times Red deer density + Sex \times Red deer density 1	8	1,202.64	2.3691	0.0480
Julian date + Gausson index + Sex \times Red deer density 1	6	1,203.23	2.9605	0.0399
Julian date + Roe deer density + Gausson index + Sex \times Red deer density + Sex \times Red deer density 1	9	1,203.22	2.9443	0.0337
Julian date + Roe deer density + Gausson index + Sex \times Red deer density 1	7	1,204.56	4.2873	0.0195
Julian date + Gausson index + Red deer density + Red deer density 1	5	1,205.15	4.8744	0.0160
Julian date + Roe deer density + Gausson index + Red deer density + Red deer density 1	6	1,205.80	5.5273	0.0111
Julian date + Gausson index + Red deer density 1	4	1,206.69	6.4217	0.0077
Julian date + Roe deer density + Gausson index + Red deer density 1	5	1,208.09	7.8179	0.0037
Julian date + Sex + Red deer density 1	4	1,213.64	13.3649	0.0002
Constant model	1	1,329.50	129.2289	0.0000

using dental eruption (Flerov 1952). We also measured eviscerated body mass of roe deer harvested. We focused on individuals ($n = 332$) harvested between August and February. During this time period, body growth is linear (Hewison et al. 2002). We thus measured the average mass gain of roe deer fawn by regressing body mass on the date of shooting (using the Julian date). We did not include the hunting season 1990–1991 because only one fawn was shot.

Climatic data

Spring-summer conditions influence vegetation development, and thereby food resources available for fawns and their mothers, and are of prime importance for adult females in an income breeder such as roe deer (Andersen et al. 2000). In addition to fawn body mass, spring-summer climatic conditions have been reported to influence fawn survival (Gaillard et al. 1997) and early growth (Gaillard et al. 1993). On the other hand, winters are quite mild and are not likely to constitute a limiting factor of deer populations. Thus, based on previous studies of variation in body mass of roe deer fawns in other populations with similar characteristics (Gaillard et al. 1997; Toïgo et al. 2006), we used the mean temperature and total rainfall of the spring of birth (i.e. April, May and June preceding the hunting season) as a climatic driver. We calculated the Gausson index as a measure of water available for vegetation in spring. The Gausson index is calculated as the amount of precipitation minus twice the mean temperature and has been previously

shown to be related to ungulate performance (Gaillard et al. 1997; Garel et al. 2004; Toïgo et al. 2006).

Population density

We used the abundance index (AI) method (Caughley 1977) to assess changes in population density of deer throughout the study period. We applied this method to road counts. We counted deer at night when driving a car along a road twice a month between February and April. We sampled deer along three independent roads of variable length. We counted both deer species from 1978 to 2007 using a powerful spotlight (100 W). As the number of deer observed increased with road length we expressed the count in terms of number of deer seen per kilometre. We used the mean number of deer seen per kilometre in a given year as the measure of deer density (see Garel et al. 2010; Fig. 1). This AI method based on road counts provided reliable estimates when compared to line-transect methods for counting red deer in Spain (Acevedo et al. 2008).

Statistical analysis

We performed the analysis on 337 roe deer less than 1 year of age. We used the median date of shooting (7 December) as the first Julian date. As variances of male and female body mass were similar ($F = 0.182$; $df = 1, 330$; $P = 0.66$) we tested immediate and delayed possible effects of red deer density on fawn roe deer body mass.

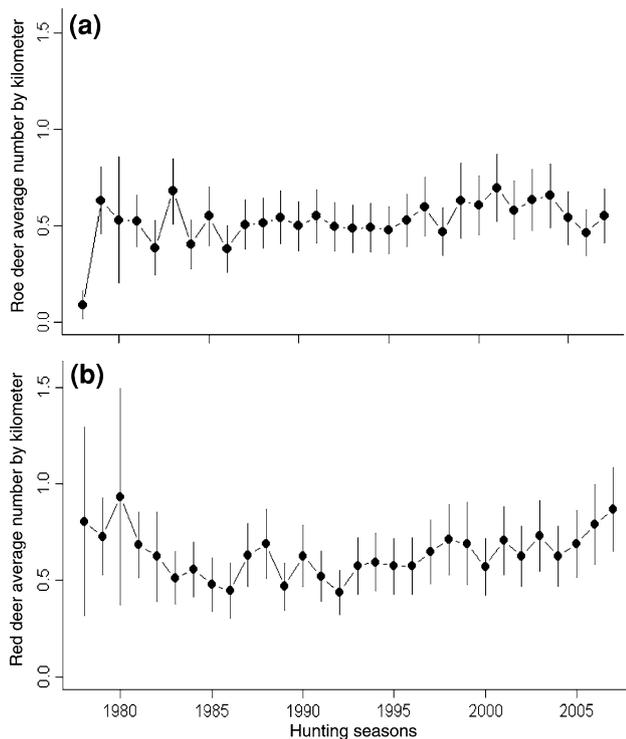


Fig. 1 Mean annual numbers of **a** roe deer and **b** red deer estimated by road counts. Points represent predictions of number of individuals per hunting season with SEs indicated by error bars

We used linear models to analyse variation in fawn roe deer body mass. We included Julian date (to account for confounding effects of growth) and the Gausse index (to account for possible confounding effects of weather) as covariates when modelling the effects of red deer density on body mass of roe deer fawns. As no correlation occurred between red deer and roe deer abundances ($\rho = 0.096$, $P = 0.611$), we also included roe deer density (to account for possible confounding effects of intra-specific competition) as a covariate in the models.

We used AIC as a procedure of model selection (Burnham and Anderson 2002). We selected the model with the lowest AIC (best compromise between precision that decreases with an increasing number of parameters and accuracy that increases with an increasing number of parameters). We also calculated AIC weights (w_i) as a measure of the likelihood that a given model is the best among the set of models fitted. We performed all statistical analyses using R software [(Crawley 2007); version 2.7 (R Development Core Team 2008)].

Results

The selected model (Table 1) included additive effects of sex (males were heavier than females by

0.359 ± 0.178 kg), Julian date (increase of 12 ± 2 g/day), Gausse index (slope of -0.018 ± 0.004), and red deer density both in the same (slope of -1.76 ± 0.99) and the previous year (slope of -1.81 ± 0.95). When red deer density changed from high (0.8 deer/km) to low (0.4 deer/km), the body mass of roe deer fawns increased from 8.25 to 8.95 kg and from 7.89 to 8.59 kg for males and females, respectively, during the same year (Fig. 2a), and from 8.27 to 8.99 kg and from 7.90 to 8.63 kg for males and females, respectively, the following year (Fig. 2b). The selected model did not include an effect of roe deer abundance on body mass of roe deer fawns. When adding such an effect of roe deer abundance to the best model, the negative influence of red deer density persisted, whereas no effect of roe deer abundance occurred. As red deer and roe deer abundance varied independently throughout the study period, we can confidently interpret these results as demonstrating a negative effect of red deer abundance on body mass of roe deer fawns.

Discussion

Our study provides the first empirical evidence of a response of roe deer performance to changes in red deer density. As predicted, red deer density had a negative influence on body mass of roe deer fawns born the same year and the following year (Fig. 2a, b). Such results support our first prediction of a marked negative impact of red deer density on roe deer performance. In mammals, density-dependent responses occur in most life history traits, including juvenile body mass [see Fowler (1987) and Bonenfant et al. (2009) for reviews]. The effects we reported here for red deer density are thus similar to those reported in previous studies of density dependence [see Kjellander et al. (2006) for a case study on roe deer fawns], so that we can interpret the negative impact of red deer density we report here as inter-specific density dependence.

Roe deer are income breeders, as they do not store energy reserves (Andersen et al. 2000). As a consequence, roe deer are especially sensitive to changes in resource availability because they have to continuously find food to avoid starvation. Indeed, at Chizé, another study area in western France, both fawns (Pettorelli et al. 2001) and adults (Pettorelli et al. 2002) are heavier in the forest stand where plant species preferred by roe deer in spring are most abundant. However, the availability of resources depends on seasons and on the number of individuals of sympatric populations that use these resources (Storms et al. 2008). As both species can occupy the roe deer dietary niche (Storms et al. 2008), red deer can consume all resources available for roe deer when red deer density is high relative to that of roe deer. Body mass of juveniles is affected by

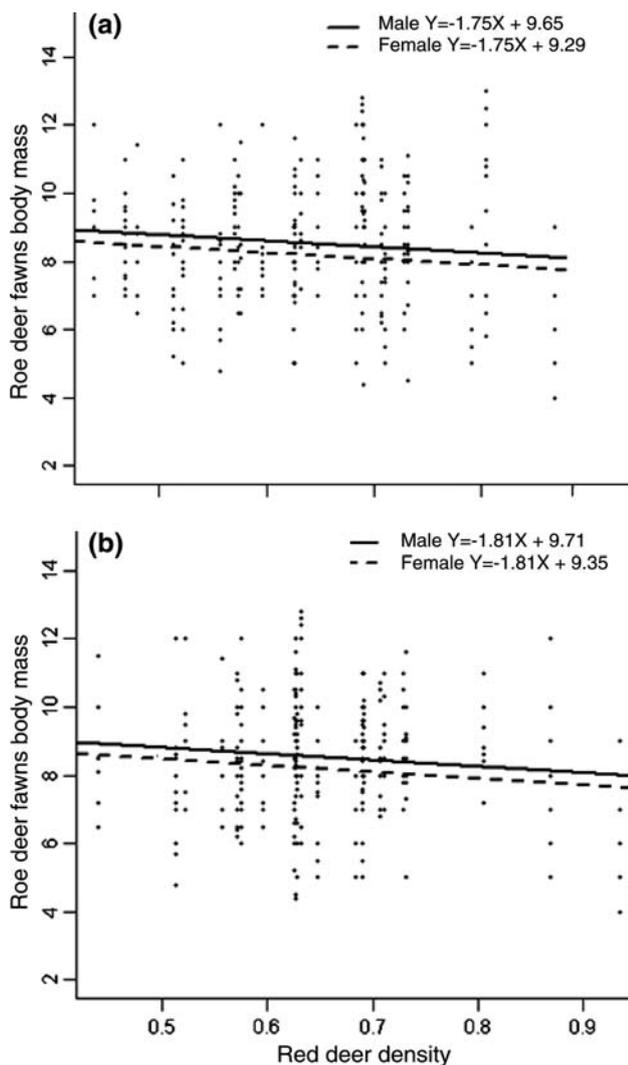


Fig. 2 Relationship between red deer density (number of deer per kilometre) and fawn roe deer mass **a** the same year and **b** the following year. Predictions of the average model for males (solid line) and females (dashed line)

cohort and mother characteristics in several ungulates like bighorn sheep (Portier et al. 1998), Soay sheep *Ovis aries* (Milner et al. 2000), and red deer (Clutton-Brock et al. 1988). When roe deer females have low energetic resources available during gestation, fawn roe deer should be lighter at birth. Growth rates in roe deer fawns are high [about 150 g/day during first 3 weeks of life (Gaillard et al. 1993)], so that about 65% of adult mass is usually reached at 8 months of age. As roe deer fawns spend their first year of life within the maternal home range, mothers with a poor-quality home range should produce lighter fawns at the onset of winter. Spring summer forage plays a major role because of the high energetic needs of lactation and the strong effect of summer nutrition on growth (Therrien et al. 2007). In the study area, the vegetation dynamic is

slow (Office National des Forêts, unpublished data), so that mothers with a poor-quality home range would not have a high-quality home range the following year because red deer density had decreased. After a negative impact of red deer on vegetation, it takes time for roe deer to find vegetation of suitable quality again, which accounts for the observed delay of their response. Therrien et al. (2007) showed that when resource availability declines and intra-specific competition increases, maternal care in white tailed deer decreases. The same situation could occur in the case of inter-specific competition and resource partitioning.

Ferretti et al. (2008) showed that fallow deer are able to exclude roe deer from natural feeding sites through behavioural intolerance. In the same way, Latham (1999) concluded after comparing resource use by roe deer with that of sympatric large herbivores that roe deer are particularly sensitive to competitive displacement by other deer species. Johnson et al. (2000) argued that exploitation competition could occur between mule deer and elk. Elk has a wider feeding niche than mule deer, which shows an opposite resource selection. Recently, based on an observed increase in similarity between red and roe deer diets in winter, Storms et al. (2008) speculated in the context of the optimal foraging theory that resources were not limiting and that any exploitation competition between red and roe deer was unlikely. However, low resource diversity in winter could lead red and roe deer to consume similar items but in lower quantities. In addition, Storms et al.'s (2008) study took place after hurricane Lothar that occurred in December 1999 and led to improve resource availability for deer. We thus suggest that competition is likely to have occurred between red and roe deer in our study area. However, the intensity of competition was higher during the first years of the study than later on. Population abundances of both roe deer and red deer are mostly controlled by harvest at La Petite Pierre. However, during the first years of the study the hunting bags of red deer (limited upwards by hunting quotas) were too low to prevent an increase in population size. As a consequence, red deer density was high; this compromised natural forest regeneration, and likely prevented roe deer from increasing in numbers despite low hunting quotas for this latter species. As a consequence of low forest productivity, foresters asked for marked increases in red deer hunting bags. Roe deer hunting bags did not change throughout the study period. Hence, in the late 1970s and early 1980s, roe deer density was low while red deer density was high. From the available evidence, it thus seems most likely that the slackening of competition did allow roe deer to increase in numbers in the mid-1980s. To assess further the life history consequences of competition for roe deer, the relationship between litter size or recruitment of roe deer and red deer density should be investigated. As fecundity is highly

sensitive to density dependence, changes in habitat quality, and female body mass, we expect litter size to decrease when food availability decreases, as has often been reported for roe deer (Gaillard et al. 1998).

Finally, the red deer density affected male and female roe deer identically. As predicted, the body mass of roe deer fawns decreased linearly with increasing red deer density in a similar way for both sexes. Males only showed a slight trend to be more sensitive than females to changes in red deer density the year before. This is in accordance with the weak intensity of sexual selection in roe deer (Gaillard et al. 1993).

Linking nutritional ecology and population dynamics is a major challenge in ecology (Mysterud et al. 2001) but is necessary to allow us to understand mechanisms of potential competition or negative interactions between two sympatric species. Many studies have quantified density-dependent responses of life history traits of large herbivores [see Fowler (1987); Bonenfant et al. (2009) for reviews]. However, according to our knowledge, this study is the first to report a negative impact of the density of red deer on the performance of roe deer.

Acknowledgements Funding was provided by the Office National de la Chasse et de la Faune Sauvage (ONCFS). The national reserve is managed by the ONCFS and the Office National des Forêts. We are grateful to wildlife technicians, foresters and many volunteers for help in counts. We are also grateful to hunters for having taken measurements on roe deer fawns. We thank Christophe Bonenfant, Mathieu Garel, and the members of the GROS research group for stimulating discussions. Finally, we thank Atle Mysterud and one anonymous reviewer for their comments.

References

- Acevedo P, Ruiz-Fons F, Vicente J, Reyes-Garcia AR, Alzaga V, Gortazar C (2008) Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *J Zool* 276:37–47
- Andersen R, Gaillard JM, Liberg O, San Jose C (1998) Variations in life history parameters. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 285–307
- Andersen R, Gaillard JM, Linnell JDC, Duncan P (2000) Factors affecting maternal care in an income breeder, the European roe deer. *J Anim Ecol* 69:672–682
- Baltzinger C (2003) Sélection des sites de repos par le cerf (*Cervus elaphus*) et le chevreuil (*Capreolus capreolus*) en forêt tempérée de moyenne montagne. PhD thesis, Ecole Nationale du Génie Rural, des Eaux et des Forêts, Paris
- Bartos L, Vankova D, Miller KV, Siler J (2002) Interspecific competition between white-tailed, fallow, red, and roe deer. *J Wildl Manage* 66:522–527
- Begon M, Townsend CR, Harper JL (2006) *Ecology from individuals to ecosystems*. Blackwell, Oxford
- Bonenfant C, Gaillard JM, Loison A, Klein F (2002) Sex- and age-dependent effects of population density on life history traits of red deer (*Cervus elaphus*) in a temperate forest. *Ecography* 25:446–458
- Bonenfant C, Gaillard JM, Coulson T, Festa-Bianchet M, Loison A, Garel M, Loe LE, Blanchard P, Pettorelli N, Owen-Smith N, Du Toit J, Duncan P (2009) Empirical evidence of density-dependence in population of large herbivores. *Adv Ecol Res* 41:313–357
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference, a practical information theoretic approach*. Springer Science, New York
- Caughley G (1977) *Analysis of vertebrate populations*. Wiley, Chichester
- Clutton-Brock TH, Albon SD, Guinness FE (1988) Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) *Reproductive success*. University of Chicago Press, Chicago, pp 325–343
- Crawley MJ (2007) *The R book*. Wiley, Chichester
- Dolman PM, Wäber K (2008) Ecosystem and competition impacts of introduced deer. *Wildl Res* 35:202–214
- du Toit JT, Owen-Smith N (1989) Body size, population metabolism and habitat specialization among African large herbivores. *Am Nat* 133:736–740
- Ferretti F, Sforzi A, Lovari S (2008) Intolerance amongst deer species at feeding: roe deer are uneasy banqueters. *Behav Processes* 78:487–491
- Flerov KK (1952) Fauna of USSR. In: *Mammals*, vol 1, No 2. New Series 55. Academy of Sciences of the USSR, Moscow, USSR
- Focardi S, Aragno P, Montanaro P, Riga F (2006) Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography* 29:407–417
- Fowler CW (1987) A review of density dependence in population of large mammals. In: Genoway HH (ed) *Current mammalogy*. Plenum, New York, pp 401–441
- Gaillard JM, Delorme D, Jullien JM (1993) Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* 94:57–61
- Gaillard JM, Delorme D, Boutin JM, van Laere G, Boisaubert B (1996) Body mass of roe deer fawns during winter in 2 contrasting populations. *J Wildl Manage* 60:29–36
- Gaillard JM, Boutin JM, Delorme D, van Laere G, Duncan P, Lebreton JD (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* 112:502–513
- Gaillard JM, Liberg O, Andersen R, Hewison AMJ (1998) Population dynamics of roe deer. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 309–336
- Gaillard JM, Duncan P, Delorme D, van Laere G, Pettorelli N, Maillard D, Renaud G (2003) Effects of hurricane Lothar on the population dynamics of European roe deer. *J Wildl Manage* 67:767–773
- Garel M, Loison A, Gaillard JM, Cugnasse JM, Maillard D (2004) The effects of a severe drought on mouflon lamb survival. *Proc R Soc Lond Ser B* 271:471–473
- Garel M, Bonenfant C, Hamann JL, Klein F, Gaillard JM (2010) Are abundance indices derived from spotlight counts reliable to monitor red deer populations? *Wildl Biol* 16(1) (in press)
- Gill RMA (1990) *Monitoring the status of European and North American cervids*, Nairobi, Kenya
- Hamann JL, Klein F, Saint-Andrieux C (1997) Domaine vital diurne et déplacements des biches (*Cervus elaphus*) sur le secteur de la Petite Pierre (Bas Rhin). *Gibier Faune Sauvage* 14:1–17
- Hemami MR, Watkinson AR, Dolman PM (2004) Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer

- (*Capreolus capreolus*) in a lowland commercial pine forest. For Ecol Manage 194:49–60
- Hewison AJM, Gaillard JM, Angibault JM, van Laere G, Vincent JP (2002) The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. J Zool 257:303–309
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443–457
- Jarman PJ (1974) Social organization of antelope in relation to their ecology. Behaviour 48:215–267
- Johnson BK, Kern JW, Wisdom MJ, Findholt SL, Kie JG (2000) Resource selection and spatial separation of mule deer and elk during spring. J Wildl Manage 64:685–697
- Kjellander P, Gaillard JM, Hewison AJM (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521–530
- Latham J (1999) Interspecific interactions of ungulates in European forests: an overview. For Ecol Manage 120:13–21
- Latham J, Staines BW, Gorman ML (1997) Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. J Zool 242:681–704
- Latham J, Staines BW, Gorman ML (1999) Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. J Zool 247:409–418
- Marshal JP, Bleich VC, Andrew NG (2008) Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. Wildl Biol 14:228–236
- Milner JM, Pemberton JM, Brotherstone S, Albon SD (2000) Estimating variance components and heritabilities in the wild: a case study using the “animal model” approach. J Evol Biol 13:804–813
- Morellet N, Gaillard JM, Hewison AJM, Ballon P, Boscardin Y, Duncan P, Klein F, Maillard D (2007) Indicators of ecological change: new tools for managing populations of large herbivores. J Appl Ecol 44:634–643
- Mysterud A, Ostbye E (2006) Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway. Wildl Biol 12:321–329
- Mysterud A, Perez-Barberia FJ, Gordon IJ (2001) The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia 127:30–39
- Owen-Smith N (2002) Adaptive herbivore ecology. Cambridge University Press, Cambridge
- Perez-Barberia FJ, Perez-Fernandez E, Robertson E, Alvarez-Enriquez B (2008) Does the Jarman-Bell principle at intra-specific level explain sexual segregation in polygynous ungulates? Sex differences in forage digestibility in Soay sheep. Oecologia 157:21–30
- Pettorelli N, Gaillard JM, Duncan P, Ouellet JP, van Laere G (2001) Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. Oecologia 128:400–405
- Pettorelli N, Gaillard JM, van Laere G, Duncan P, Kjellander P, Liberg O, Delorme D, Maillard D (2002) Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. Proc R Soc Lond Ser B 269:747–753
- Pettorelli N, Gaillard JM, Duncan P, Maillard D, van Laere G, Delorme D (2003) Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology 84:3307–3316
- Pettorelli N, et al. (2006) Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112:565–572
- Portier C, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Yoccoz NG (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). J Zool 245:271–278
- Putman R (1996) Competition and resources partitioning in temperate ungulate assemblages. Chapman & Hall, London
- Staines BW, Welch D (1984) Habitat selection and impact of red (*Cervus elaphus* L.) and roe (*Capreolus capreolus* L.) deer in a Sitka spruce plantation. Proc R Soc Edin Sec B 82:303–319
- Storms D, Said S, Fritz H, Hamann JL, Saint-Andrieux C, Klein F (2006) Influence of hurricane Lothar on red and roe deer winter diets in the Northern Vosges, France. For Ecol Manage 237:164–169
- Storms D, et al. (2008) Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Wildl Biol 14:237–250
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://R-project.org>
- Therrien JF, Côté SD, Festa-Bianchet M, Ouellet JP (2007) Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behav Ecol Sociobiol 62:193–199
- Toïgo C, Gaillard JM, van Laere G, Hewison M, Morellet N (2006) How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography 29:301–308
- Van der Wal R, Van Wijnen H, Van Wieren S, Beucher O, Bos D (2000) On facilitation between herbivores: how brent geese profit from brown hares. Ecology 81:969–980
- Van Soest PJ (1996) Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biol 15:455–479
- Welch D, Staines BW, Catt DC, Scott D (1990) Habitat usage by red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer in a Scottish Sitka spruce plantation. J Zool 221:453–476
- Widmer O, Said S, Miroir J, Duncan P, Gaillard JM, Klein F (2004) The effects of hurricane Lothar on habitat use of roe deer. For Ecol Manage 195:237–242