

Effects of Population Density on the Diet of Roe Deer and the Availability of their Food in Chizé Forest

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The diet of roe deer (*Capreolus capreolus*, L.) in winter were studied in Chizé forest (France) with respect to food availability, body weight and fertility. Two areas with different population densities were compared: an un hunted reserve with a roe deer population of over 20 animals per km², and area of similar size where roe deer were hunted and did not exceed 5 animals per km². Analysis of the available forage biomass showed that most of the plants consumed by roe deer are scarce in the reserve. Moreover, assessment of the average diet from analysis of stomach contents indicated a shift in feeding habits with increasing population densities; i.e. the proportion of bramble decreased, that of ivy increased. Roe deer within the reserve were also observed to feed on plant species that are almost totally avoided outside the reserve. Changes in average body weights with increasing population density showed a trend towards weight loss in males, which was reversed only for a short period by a programme of selective shooting. The number of fawns per female markedly decreased with increasing population density.

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1. INTRODUCTION

For several decades populations of roe deer have been increasing in France as in many other European countries. This trend has been expressed by increasing densities and an extension of the geographical range of the species. It is clearly of interest to recognize the density-dependent factors that will constitute the ultimate self-regulatory mechanisms of populations dynamics (Lack, 1954; Wynne-Edward, 1965; Krebs, 1972; Dajoz, 1974; Peek, 1980) and this is particularly true for roe deer as many wildlife managers are questioning the existence of equilibrium populations.

In Federal Republic of Germany and Austria, where roe deer densities are greatly superior to those in France, hunter frequently report seeing animals in poor condition (loss of weight, parasitism, epizootic diseases, declining reproduction rates, etc). The traditional view has been that selective shooting of certain animals would solve the problem, but numerous authors have recently emphasized the necessity for both reducing population numbers and increasing the carrying capacity of their habitats (Eisfeld, 1976, 1982, 1983; Ellenberg, 1978; Bayern & Bayern, 1984; Ueckermann, 1985; Roucher *et al.*, 1985). This idea has developed from empirical considerations, since the effects of density on roe deer have not yet been thoroughly studied.

The Forest of Chizé is particularly suited to such an analysis. One half of the forest is a fenced off national reserve with a density of roe deer approaching 20 animals per km², while hunting rights are leased in the other half and the population here does not exceed 5 animals per km².

The purpose of the present study is to determine the influence of a high population density within the reserve on diet and food availability, and on the related aspects of body weight and fertility.

2. STUDY AREA

Chizé forest is an oak-beech woodland of 48 km² lying on calcareous soil. The "Reserve Nationale de Chasse" (henceforth called the reserve) which occupies 26 km² is managed by the French hunting agency, "Office National de la Chasse" (O.N.C.). The beech (*Fagus sylvatica*) forest is composed of mature high trees and the layer of herbaceous vegetation is dominated by *Ruscus aculeatus*, *Hedera helix*, *Carex* sp. The oak (mainly *Quercus pubescens*) forest has been cut back so as to form coppices with standards associated with a fairly large number of undergrowth species (e.g. *Crataegus monogyna*, *Acer* sp., *Cornus mas* and *C. sanguinea*) and the herbaceous layer is dominated by *Brachypodium pinnatum*.

3. METHODS

3.1. Analysis of Diet

A total of 49 stomach contents were collected between December and March, from 1984/85 to 1986/87. Twenty five came from the reserve and twenty four from outside (animals shot by hunters or run over by cars). Sampling was restricted to winter months because periods with minimal temperatures correspond to critical stages in the animal's physiological cycle (antler growth in males, beginning of the gestation period in females).

Food samples were analysed by washing 100 ml of stomach contents in a 2 mm-mesh sieve, and sorting the different fragments with the aid of a binocular

magnifying glass. Separated categories were oven-dried and each fraction was weighed on a precision balance. The reliability and the limits of this procedure are discussed in Maizeret, 1983.

3.2. Analysis of Food Availability

Food availability was compared inside and outside the reserve by estimating available plant biomass (Cibien *et al.*, in prep.) in two representative habitats: a coppice with the standart system of oak stands, and a high beech forest. For each habitat, two sampling areas of similar age and the same form of sylvicultural practice were selected, one within and the other outside the reserve. Presence or absence of characteristic species were sought in each area, according to the procedure defined by Werno (1984), in order to compare plant associations.

Samples were collected in January 1986. Between 15 and 27 plots of 1 m² were surveyed in a 50 m² grid. Within a plot, aerial parts of all green vegetation between ground level and a height of 1.2 m were collected, separated, oven-dried and weighed. The number of plots and their surface areas were calculated according to currently accepted practises for analysis of biomass (Clement & Touffet, 1976; Blair & Grouzis, 1980; Miller *et al.*, 1981; Conroy *et al.*, 1982; Collins & Urness, 1983; Thill, 1984, Wickstrom *et al.*, 1984; Hobbs & Swift, 1985; Hanley & Mackendrick, 1985).

3.3. Chemical Analysis of the Available Food Plants

In order to relate the animals' choice of food to the nutritional quality of the plants, we carried out a chemical analysis of the principal plant species present in Chizé forest during winter months. Seven plant species were collected, each from ten different sites in the forest (*Hedera helix*, *Rubus* sp., *Ligustrum vulgare*, *Rubia peregrina*, *Carex glauca*, *Carex sylvatica*, and *Ruscus aculeatus*).

The method of cellulase digestibility (Jarrige *et al.*, 1970; Martens & Barnes, 1980) was used to evaluate the digestibility of foods. This was preferred to Tilley and Terry's (1963) method which requires rumens fluid. In the present case the rumen fluid could only be collected from shot roe deers and it has been shown that to obtain accurate data, inocula should be collected from animals having been fed a perfectly standardized diet (Church & Peterson, 1960; Bezeau, 1965; Nagy *et al.*, 1967). Crude fiber and nitrogen content of foods as well as nine trace elements were determined by the same analysis.

3.4. Monitoring of Roe Deer Populations in the Reserve

Roe deer have been netted each winter since 1978 by O.N.C. personnel following a standard procedure (310 animals per year on average). Overall densities were estimated from the number of captured individuals divided by the surface area netted (50% of reserve on average). Regular capture also permitted estimation of the mean body weights, the population structure (sex and age ratio) being almost constant (Cabane & Boutin, 1984).

Populations were monitored every September for changes in the number of young per female in order to index breeding success at the end of the summer. The fawns present in a given sector were counted by stalking. On average, 69 groups were observed every year.

4. RESULTS

4.1. Comparison of the Feeding Conditions of Roe Deer within and outside the Reserve

The diet of roe deer in the two study areas (Fig. 1) is characterized by the following observations:

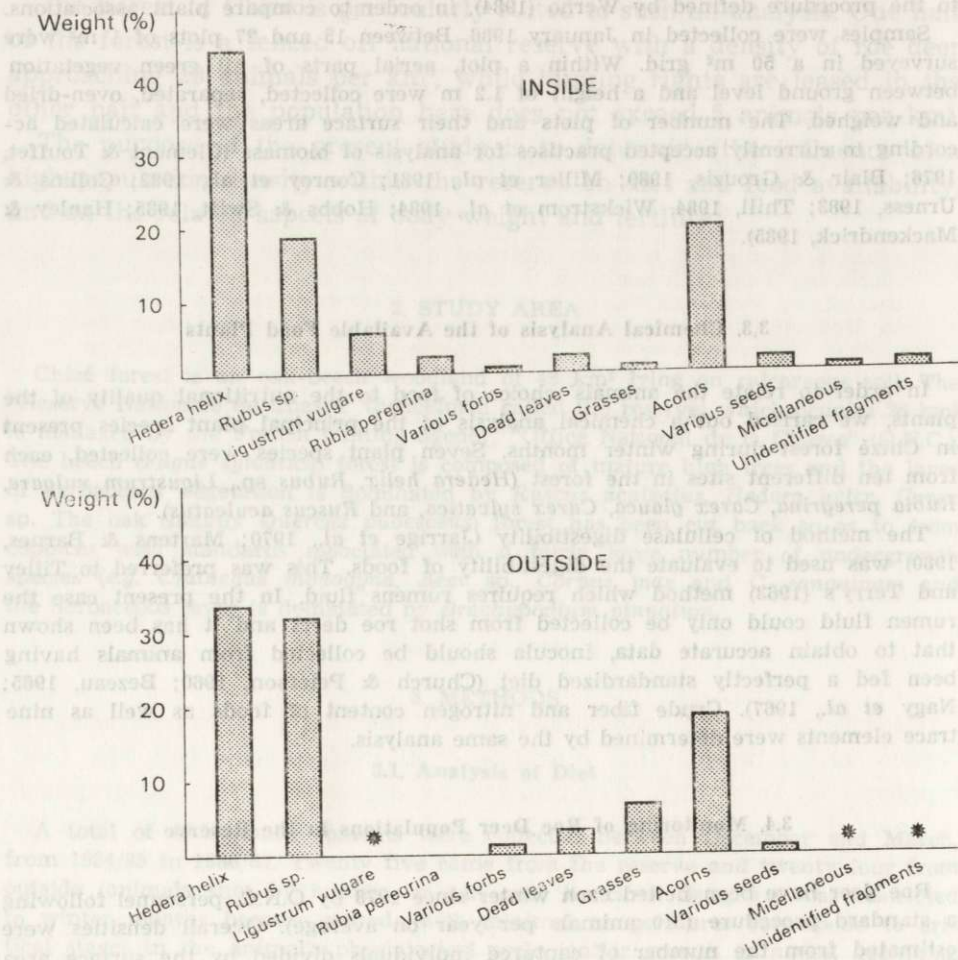


Fig. 1. Analysis of stomach contents collected inside and outside the reserve (*=traces).

a) Almost equal proportions of bramble (34%) and ivy (32%) were consumed outside the reserve. Other plant species were poorly represented, except acorns, which made up almost 20% of the average diet. Two samples only contained large quantities of cultivated grasses taken by animals from farmlands abutting the forest edge.

b) Bramble constituted 19.1% of the average weight of diet within the reserve representing a significantly smaller proportions (*t* test, $p < 0.01$) compared to the diet of animals living outside the reserve. This difference was compensated by an increase in the relative proportion of

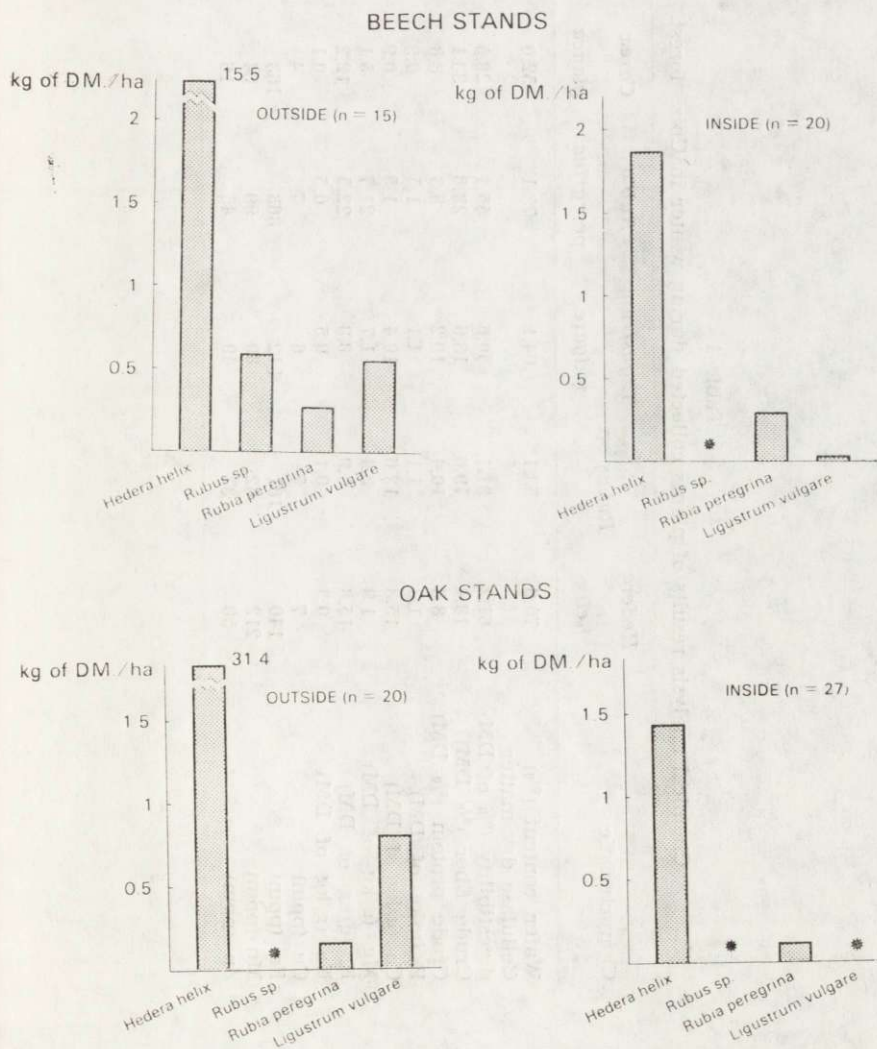


Fig. 2. Biomass of the principal food species of roe deer (*=traces).

Table 1
Chemical analysis results of plants collected during winter in Chizé forest.

Characteristic	<i>Hedera</i>	<i>Rubus</i> sp.	<i>Ligustrum</i>	<i>Rubia</i>	<i>Carex</i>	<i>Carex</i>	<i>Ruscus</i>
	<i>helix</i>		<i>vulgare</i>	<i>peregrina</i>	<i>glauca</i>	<i>sylvatica</i>	<i>aculeatus</i>
Water content (%)	70.6	53.1	64.1	73.1	52.0	59.9	49.2
Cellulase dry matter digestibility (% of DM)	61.2	31.1	50.6	55.1	28.5	37.6	48.4
Crude fiber (% DM)	18.4	19.6	13.6	23.8	28.1	24.3	31.9
Crude protein (% DM)	8.8	10.4	10.2	8.3	8.8	9.6	9.4
P (g/kg of DM)	1.2	1.1	1.1	1.5	0.9	1.1	0.9
Ca (g/kg of DM)	15.3	13.6	10.4	1.5	0.9	1.1	10.3
Mg (g/kg of DM)	1.9	3.4	1.7	1.5	5.1	5.8	1.2
K (g/kg of DM)	15.8	5.9	8.8	21.7	12.2	10.5	8.8
Na (g/kg of DM)	0.3	0.1	0.5	0.5	0.1	0.3	0.1
Cu (ppm)	7	7	6	7	4	4	4
Fe (ppm)	140	161	112	863	163	408	80
Mn (ppm)	212	62	80	99	64	97	78
Zn (ppm)	58	37	49	45	16	19	55

ivy and by the presence of such species as *Rubia peregrina* and *Ligustrum vulgare*, which were not consumed outside the reserve.

For the principal plant species eaten by roe deer the differences in biomass between the two study plots (Fig. 2) show a significantly lower

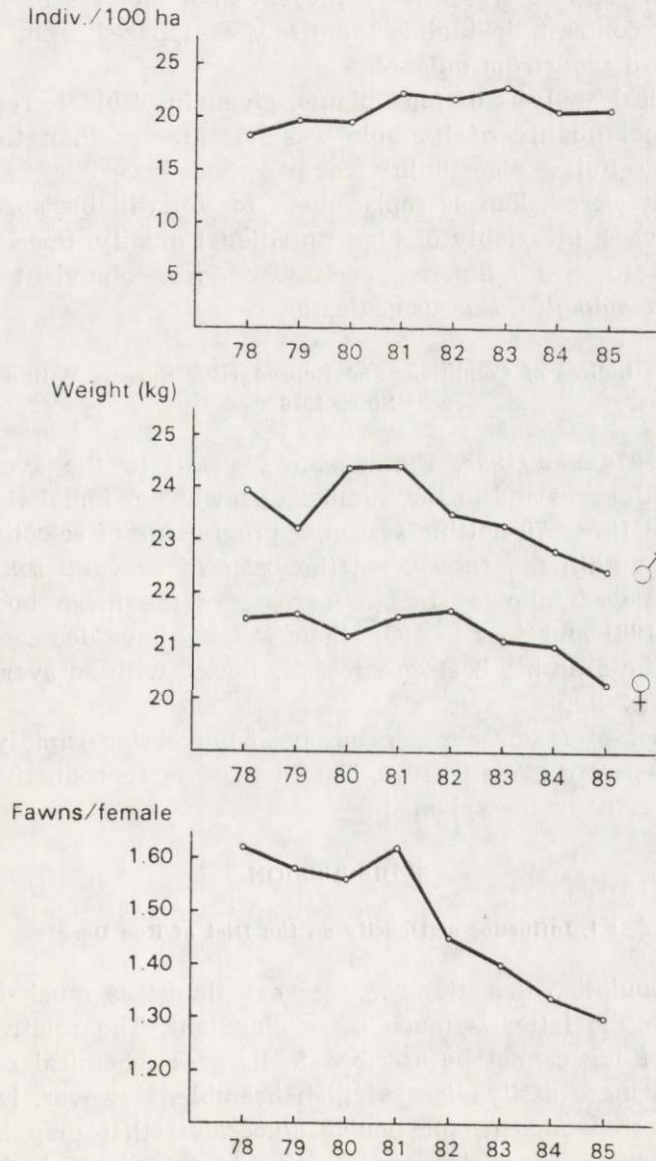


Fig. 3. Changes in the roe deer population in Chizé forest between 1978 and 1985: Densities (A); average body weights of males and females (B); number of fawns per female (C).

representation within the reserve (t test, $p < 0.01$) for all species except *Rubia peregrina*. This species constituted only 2.6% of the average diet and therefore was subject to little pressure from browsing. Availability of ivy was particularly diminished within the reserve (t test, $p < 0.01$). However, this species was always present at a biomass of 1–2 kg/ha. Bramble, in contrast, had almost entirely disappeared from within the reserve, as had *Ligustrum vulgare*.

The chemical analysis of food plants, given in Table 1, revealed that the nutritional quality of bramble was not greater than that of ivy; moreover its cellulase digestibility was two times lower.

Plants that were taken as replacement for unavailable species within the reserve were invariably of high nutritional quality. Species of lower nutritional value were ingored, even when very abundant e.g. *Carex glauca*, *Carex sylvatica*, *Ruscus aculeatus*.

4.2. Changes in Indices of Conditions and Reproductive Success Within the Reserve Since 1978

Between 1978 and 1985, Fig. 3 shows a fall in the average body weight of both sexes and in the number of fawns per female.

During the 1978–79 netting season, a programme of selective removal was applied within the reserve on the basis of age and sex. Although this measure was followed by an increase in the mean body weights of bucks in 1981 and does in 1982, their weights have decreased steadily ever since. The drop has been greatest for bucks, with an average weight loss of almost 2 kg.

The number of fawns per doe has been decreasing rapidly since the first estimates were made in 1978. The increase of reproductive performance in 1981 remains unexplained.

5. DISCUSSION

5.1. Influence of Density on the Diet of Roe Deer

At low population densities roe deer eat almost as much bramble as ivy, although the latter is much more abundant. The relatively poorer palatability of ivy cannot be ascribed to its gross chemical composition, because it is more easily digested than bramble. However, ivy contains some toxic compounds (in particular glucosides) that may be harmful to roe deer above a certain concentration in the diet (Lieutaghi, 1969; Debelmas & Delaveau, 1978). The low intake of privet can probably be explained in the same way (presence of saponins according to Jean-Blain & Grisvard, 1973).

Within the reserve where population density has been maintained at levels often exceeding 20 animals per km², the most frequently eaten plant species, in particular bramble, have become relatively scarce. It should be noted, however, that bramble is probably under-represented by the analysis of biomass because it grows best at the edge of the forest. Bramble was nevertheless overbrowsed which explained its almost complete absence from the survey plots within the reserve, so that deer were forced to eat twice as much ivy as bramble.

The nutritional consequences of such shifts in the composition of the diet are unfortunately difficult to assess with certainty. They appear to depend to a large extent on the concentration of secondary plant compounds. The chemical constituents of the plant species discussed here are not well known and little is understood of their physiological effects on cervids. The only indications of possible toxicity come from veterinary surveys which indicate that cattle are prone to poisoning after ingestion of either of these plant species (Jean-Blain, 1978).

A limited availability of some food plants within the reserve may also have affected the energy budget of roe deer. The biomass of potentially consumable plant species is seven times less abundant inside the reserve for beech and twenty times less for oak. Thus, it is likely that roe deer within the reserve would have to move greater distances than those living outside in order to ingest the same quantity of food. In particular, the role of bramble needs more thorough investigation as it makes up nearly 20% of the diet even though it grows only in specific locations within the reserve.

5.2. Influence of Population Density on the Growth of Roe Deer

The management programme in 1978—79 caused an increase in the average body weight of roe deers. However, it was apparent for the next two years that the improvement was not permanent. This finding suggests that one-off selective shooting is not sufficient when the density is too high relative to the carrying capacity of the habitat.

The number of fawns per doe fell to an unusually low level (1.3) in 1985, compared to values from the literature which are usually around 1.8 (Strandgaard, 1972; Ellenberg, 1973; Eiberle, 1979). Even in 1978 when observations began, the effects of over population must already have been marked, as the observed number of fawns per doe was then only 1.62.

These results imply either a decrease in the fertility rate of does or an increase in fawn mortality. A lower fertility rate could be a simple effect of stress caused by too high a density of territorial adults. How-

ever, experiments have shown that roe deer which are fed artificially, can be maintained at very high population levels, and at a normal growth rates (Bayern & Bayern, 1984). In respect of post-natal mortality, Aucher (1985) has shown that predation by foxes is unlikely to be a significant cause of mortality in Chize forest, as fawns remains are rarely found in predators faeces. On the other hand, Boutin (1986) mentions some cases of mortality by coccidiosis among juveniles but this may be a secondary effect of limited food availability following from concomitant changes in physiological conditions.

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WPLYW ZAGĘSZCZENIA POPULACJI SARN NA SKŁAD I DOSTĘPNOŚĆ ICH POKARMU W LASACH CHIZÉ

Streszczenie

Badano skład pokarmu zimowego i jego dostępność oraz wagę ciała i płodność sarn w lasach Chizé (Francja) na 2 terenach o różnym zagęszczeniu populacji: rezerwat (ponad 20 osobników/km²) i obszar gdzie prowadzono polowania (do 5 osobników/km²).

Oceniono biomasa najważniejszych gatunków roślin zjadanych przez sarny (Ryc. 2) oraz ich skład chemiczny (Tab. 1). Analiza treści żwaczy wykazała, że wraz ze wzrastającym zagęszczeniem populacji zmniejszał się udział jeżyny w diecie, a wzrastał bluszczu; oraz, że zjadane były gatunki roślin, których uprzednio sarny nie wybierały (Ryc. 1).

Wraz ze wzrastającym zagęszczeniem populacji malał średni ciężar ciała samców, a znacznie obniżała się średnia liczba potomstwa przypadającego na samice (Ryc. 3).