SELECTION OF HARDWOOD SAPLINGS BY EUROPEAN ROE DEER: EFFECTS OF VARIATION IN THE AVAILABILITY OF PALATABLE SPECIES AND OF UNDERSTORY VEGETATION

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INTRODUCTION

Damage by ungulates to commercial forestry in northern temperate biomes, principally by browsing shoots of broad-leaved trees in spring and conifers in winter, is an increasingly serious problem because the populations of the principal ungulate species have shown considerable increases in both their range and their densities in recent years (Gill, 1992). Damage can be reduced by shooting the animals, but this is not always possible since in many areas multiple use of the forest requires the maintenance of significant Roe Deer populations (see Cederlund *et al.,* 1998); in these cases methods of damage reduction are of obvious interest.

The most sensitive age classes of trees can be protected successfully by fencing, but this is very costly. Foresters therefore prefer to use natural processes to reduce damage, an essential element of which is the selectivity of feeding by cervids. It is a common observation that damage to plantations varies among tree species: for example, oak (*Quercus* spp.) and hornbeam (*Carpinus betulus*) often suffer most damage, and beech (*Fagus sylvatica*) among the least. Furthermore, damage to young trees often decreases when the abundance of alternative foods increases (see Huss & Olberg-Kalfass, 1922; Roy, 1960; Trichet *et al.*, 1987; Welch *et al.*, 1991). Foresters use their understanding of Roe Deer feeding strategies to reduce damage to plantations by the judicious choice of less preferred species for planting, and also by reducing the apparency of saplings by the management of understory plants. Such techniques are based principally on subjective impressions, as research on the factors affecting food choice by these herbivores has not yet produced the predictive models necessary for planning forestry operations in a quantitative fashion (see Cederlund *et al.*, 1998).

Many forest managers believe that Roe Deer browse individuals of rare tree species more heavily than individuals of abundant ones. It has also been argued

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from a theoretical standpoint that food selection in generalist herbivores such as Roe Deer should be frequency dependent, although two different types of relationships are possible. Firstly, it has been argued that Roe should have a diet with a mixture of plant species in order to satisfy their nutritional requirements and to avoid high intakes of secondary plant metabolites (Crawley, 1983; Lundberg *et al.*, 1990). On this basis a decrease in the availability of a species could lead to an increase in the degree to which it is selected in order to obtain a mixed diet. Secondly, optimal foraging theory leads to the opposite prediction, that herbivores should increase selection for the most profitable prey (plant species) when its abundance increases (Stephens & Krebs, 1986).

Of the European cervids, Roe Deer are the most abundant, with about 5.5 million individuals (Gill, 1990). In a detailed study of Roe Deer food selection in a species-rich deciduous forest edge, chemical characteristics of the plants were found to be the principal determinant of plant species selection, and there was no effect of the relative abundance of the different plant species on the intensity of selection (Tixier *et al.*, 1997). However this study involved many plant species, which differed both in their abundance and in their chemistry, so important effects of abundance on the animal's behaviour could have been obscured. In the experimental study described here, we test three hypotheses as to the direction of frequency-dependent selection: the null hypothesis (H_0) is that food selection is not a frequency-dependent process and that the intensity of selection remains constant when food availability varies; H_1 is that the degree of selection increases as a preferred species becomes rarer (mixed diet hypothesis); and H_2 is that the degree of selection increases with the abundance of a preferred plant species (optimal foraging theory).

Wild Roe Deer are shy animals, and very difficult to observe. We therefore used tame individuals habituated to transport and to the observers. The abundance of young trees was manipulated, first we offered two palatable species in varying proportions and recorded the animals' feeding behaviour. In a second experiment, we observed the feeding behaviour of tame Roe in a commercial plantation where the density of accessible palatable saplings was modified using physical protection and two states of understory vegetation were used, one abundant and one sparse.

METHODS

Experiment 1

We used six tame 1-year-old Roe Deer (1 male, 5 females) which had been bottle reared, and then raised in a large pen with natural forest edge vegetation (see Tixier *et al.*, 1997 for more details). They were therefore thoroughly acquainted with the plants used in these experiments; pellets for goats (ALICOOP-PROXIMA) were provided as a food supplement. During spring the deer were observed in a 0.25 ha enclosed area. We offered them two plant species, hornbeam and dogwood (*Cornus sanguinea*) in varying proportions. At this time of year hornbeam is typically a highly preferred species and dogwood is a principal food, but is neither preferred nor avoided (Tixier *et al.*, 1997). These two species have similar architecture and leaf sizes. They are both high quality food plants for Roe Deer, rich in soluble carbohydrates (4.9 and 6.2 % of dry matter respectively).

They are higly digestible (in vitro digestibility: 79.7 and 81.8 % of dry matter) but hornbeam is a little more fibrous (lignocellulose: 19.5 % versus 14.6 % of dry matter) and contains less protein than dogwood (13.1 % versus 20.3 % crude protein). Plants were attached in groups of 10 branches of similar size on a wooden frame. During each test three observers recorded the duration of feeding events on each branch for each animal. The intake rate does not differ between dogwood and hornbeam and depletion rate appears to be very similar between these two species (C. Richard, unpublished data), so we used feeding time as an estimator of food consumption. Seven tests were conducted with different proportions of hornbeam and dogwood (8/2, 7/3, 7/3, 5/5, 3/7, 3/7, 2/8); the tests ended when the animals stopped feeding, or when the observers considered that depletion of the preferred species meant that there was no longer enough to give the animals a choice.

The data were expressed as the relative consumption of hornbeam and dogwood (% C_h and % C_d), and their relative abundance (proportion of branches, % A_h and % A_d). The effects of individual, and of the covariate plant availability, on plant consumption were tested using analysis of covariance (SAS Institute Inc.1989). A graphical analysis, similar to that used by Lundberg *et al.* (1990), was performed with relative consumption ($\log (C_h + 1 / C_d + 1)$) expressed as a function of relative abundance ($\log (A_h + 1 / A_d + 1)$). The regression parameters were estimated: the intercept is a measure of selectivity and the slope a measure of the degree of frequency-dependence. When the intercept is > 0, then the relative consumption is greater than the relative abundance and the plant species is preferred; a negative value of the intercept shows avoidance and a value of zero indicates no selection. We tested for selection for hornbeam by comparing the intercept with zero (no selection), and for frequency-dependence by comparing the slope to 1.0 (no effect of availability on selection).

EXPERIMENT 2

Also in spring, we used a 6-year-old mixed-species plantation of hardwood saplings in the Chizé forest, containing beech (*Fagus sylvatica*), oak (*Quercus robur/pedunculata*) and sycamore (*Acer pseudoplatanus*); the lines of saplings were separated by mown strips (Fig. 1). The understory vegetation was composed principally of shrubs (*Ruscus aculeatus, Prunus spinosa, Rubus* sp., *Crataegus monogyna, Ligustrum vulgare, Acer monspessulanum*) and a creeper (*Clematis vitalba*) with a herb-layer composed of grasses, sedges and ivy (*Hedera helix*). Four pens of 400 m^2 were used (P_1 to P_4), with an average of 50 beech, 10 oak and 11 sycamore saplings in each pen. The relative availability of oak saplings was varied by protecting some of the saplings with plastic tubes, and the understory vegetation was kept in one of two states of abundance, dense and sparse, by cutting it mechanically at a height of 10 cm in the pens where the sparse state was required. The relative abundance of each species of sapling was estimated by taking account their volume, since this varied greatly between species (e.g. the sycamore was tall and narrow, the oak was small and broad). Each plant was allocated to a volume class (Table I); the relative abundance (A_i) of each species (i) was then calculated according to the formula:

$$A_i = (n_1 *12.5 + n_2 *50 + n_3 *87.5)/(n_1 + n_2 + n_3)$$

where n_1 to n_3 are the numbers of plants of the "i"th species in each volume class.

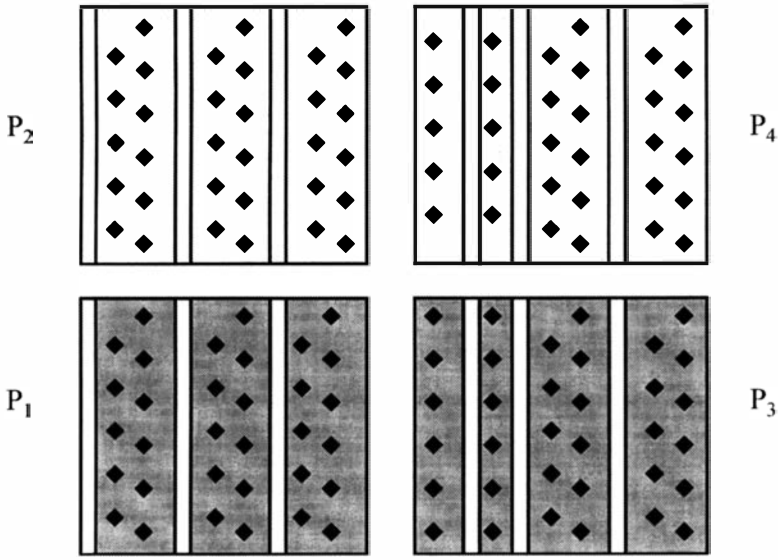

Figure 1. — Map of the experimental pens in the plantation: P_1 and P_3 have dense understory vegetation (indicated by shading), P_2 and P_4 have sparse understory vegetation (cut at 10 cm). Diamonds indicate the lines of saplings.

Four combinations of oak frequency were studied with dense understory vegetation, 4.7, 5.2, 9.0 and 15.9 % oak, and four with sparse, 5.6, 6.4, 11.8 and 17.7 % oak. The abundance of the understory vegetation was not quantified, but even in the sparse state it was far more abundant than the saplings.

Two tame 1-year-old Roe Deer, a male and a female, which were not used in Experiment 1, were transported daily to this site and the feeding time of each animal on each plant species was noted by two observers over 8 sessions per animal. A third observer recorded the relative abundance of the saplings. The time spent on each species of sapling was expressed as percentage of the total time spent feeding.

TABLE I

The volume classes used to estimate the relative abundance of the saplings. % volume occupied refers to a cylinder whose height was 1.2 m, and radius 1.0 m.

Class	% of volume occupied	Average
1	< 25 %	12.5 %
2	25-75 %	50 %
3	> 75 %	87.5 %

The results were analysed using linear regressions of the consumption of oak on its frequency, with and without understory vegetation. We tested for an effect of the abundance of understory vegetation by comparing the intercepts; and for frequency-dependency by comparing the slopes with 1.0.

RESULTS

EXPERIMENT 1

Analysis of variance showed that the covariate (regressor) "abundance" explained 48 % of the variance in consumption ($F_{1.29} = 6.90$, $p = 0.0001$, Fig. 2), and an "individual" effect was also significant ($F_{5.29} = 4.57$, $p = 0.039$). The interaction between the regressor and the factor individual was not significant, showing no differences between the slopes of the individuals. This analysis shows that relative consumption is linearly related to relative abundance, and that after taking into account the effect of abundance, there remain small, but significant differences between individuals in the values of the intercepts.

The positive intercept was significantly different from zero (0.444, $t = 4.25$, $p = 0.0001$) indicating that hornbeam was selected relative to dogwood. The slope was 1.002, indicating that the degree of selection remained constant in spite of the sharp increase in the relative abundance of the preferred plant. The null hypothesis was therefore accepted, and the two frequency-dependence hypotheses rejected.

EXPERIMENT 2

Figure 3 shows the average consumption of the saplings (oak, sycamore, beech) and of the shrubs and forbs with and without understory vegetation. In both cases the main food item was understory shrubs (more than 49 %) while beech and sycamore were practically not eaten (less than 2 %). When understory vegetation was sparse, the Roe consumed less shrubs and more oak; the consumption of forbs, beech and sycamore remained about the same.

The relationship between oak consumption and its availability, with dense and sparse understory vegetation, is shown in Figure 4. The lower intercept observed with dense understory vegetation shows that consumption of oak relative to other plants decreased when understory vegetation was abundant. The slopes of the two regressions with dense and sparse understory vegetation were not significantly different from each other ($F_{1.4} = 1.54$, $p > 0.05$), or from 1.0 (both $p > 0.05$): selection for oak did not vary with its relative abundance.

DISCUSSION

In both the experiments, Roe Deer increased their relative consumption of preferred food plants as their relative availability increased, however, the degree of selection was independent of availability. The somewhat crude measure of relative availability in the second experiment could have introduced some error, and may have obscured important relationships. It would have been more accurate to use

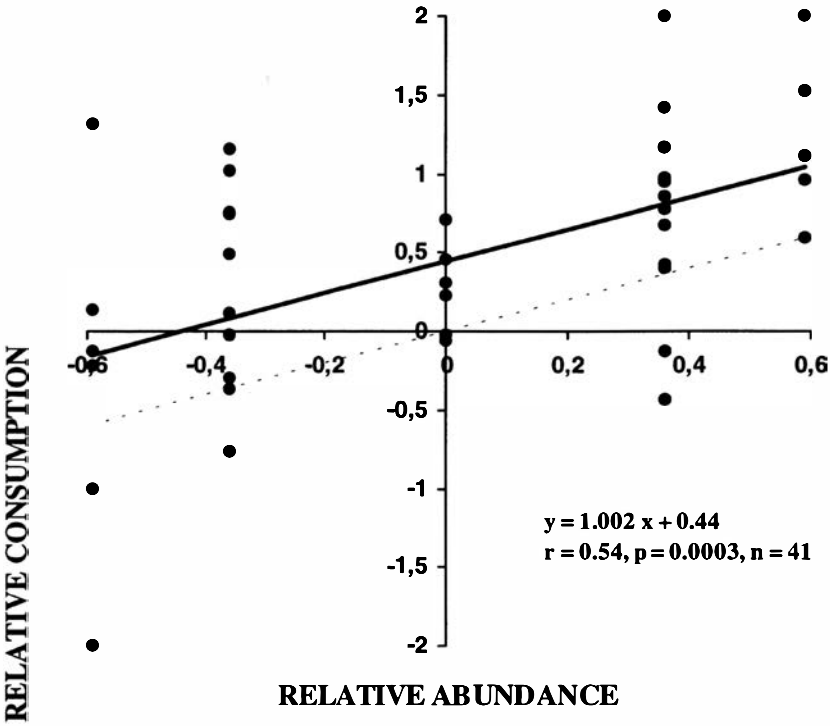

Figure 2. — Regression of the relative consumption of hornbeam in Experiment 1 ($\log(C_h + 1 / C_d + 1)$) on its relative abundance ($\log(A_h + 1 / A_d + 1)$). Hornbeam and dogwood were offered in varying proportions to six tame Roe Deer (individual points, and the heavy line). The dotted line is the null hypothesis, no selection and no frequency-dependency.

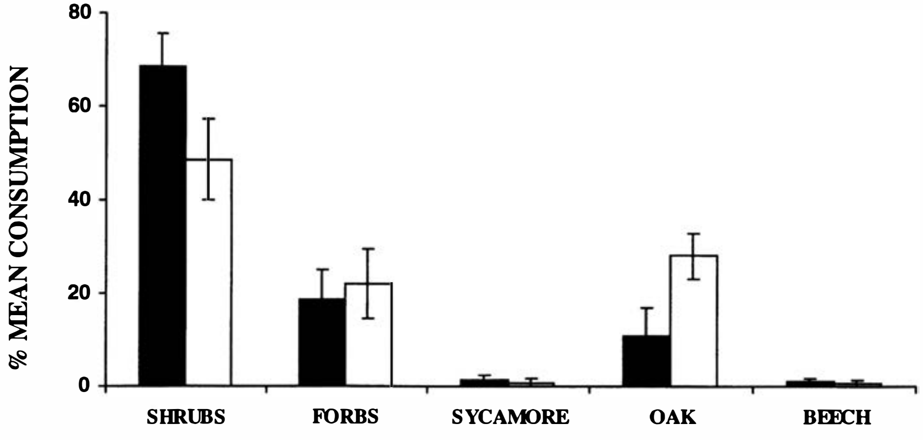

Figure 3. — Mean consumption (%) and confidence limits of saplings (oak, beech, sycamore), shrubs and forbs by two Roe Deer. Understory vegetation was dense (shaded bars) or sparse (open).

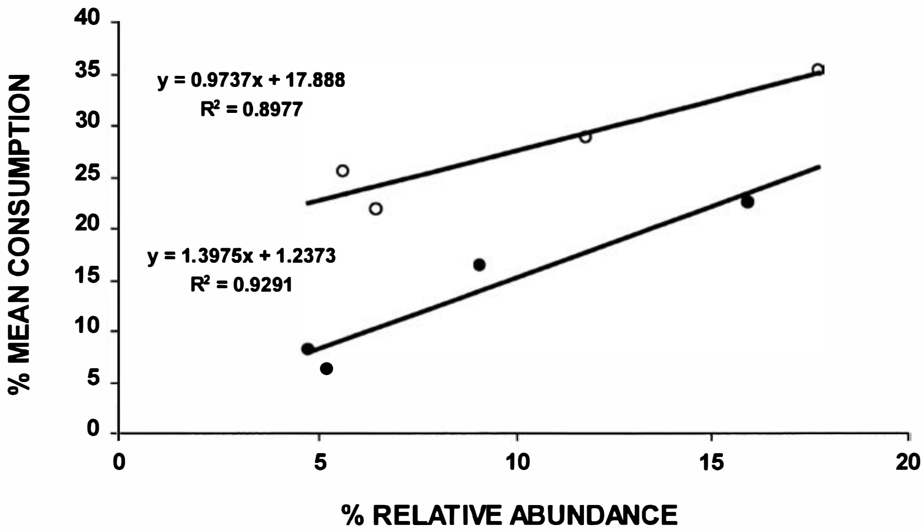

Figure 4. — Oak tree consumption by two tame Roe Deer in relation to the availability of oak relative to the other saplings. Understory vegetation was dense (black circles), or sparse (open circles).

destructive sampling methods, which was not possible here. However, in view of the absence of any suggestion of an effect of frequency-dependent selection, we do not expect that our conclusion would be modified had we done so.

These experiments were of short duration (< 2 hours), so it is possible that the animals would make different foraging decisions if they were offered these choices over long periods. However, the conclusions of these experiments concur with those of a more extensive study of Roe feeding in a complex natural habitat, which showed that the degree of selection for a species was not related to its abundance across a large number of plant species (Tixier *et al.*, 1997). We therefore expect that the conclusion will prove robust over longer time scales, as in the study of another generalist browser, the Moose (*Alces alces,* Danell & Ericson 1986; Lundberg *et al.*, 1990).

The results of the study of Moose suggested that they select on the basis of plant (patch) size: this was not the case in our experiments, since in the first experiment the branches were of the same size, and in the second we used plant volume as a measure of plant abundance, thus taking plant size into account. These results indicate that, at least in the conditions of these experiments, the selection of saplings reflects deer preferences which depend on the food value of the plants (Tixier *et al.* 1997), and not their relative size or availability.

Though the degree of selection remains constant, the use of saplings of preferred tree species (and therefore damage) can be reduced by making them less apparent. An increase in the availability of other food resources, such as those provided by understory vegetation, is a useful technique (see also Demolis & Jamey, 1988) that is even more effective if understory species preferred by Roe occur in the plantations. Furthermore, understory vegetation which includes spiny species such as *Prunus, Crataegus* and especially brambles can provide physical protection in addition to reducing the apparency of saplings of commercial value (cf. Trichet *et al.*, 1987). These three effects, dilution, attraction and dissuasion can provide a basis for management strategies that use existing woody vegetation to reduce damage to saplings in plantations.

Saplings in competition with grasses do grow more slowly than on bare soils (Collet *et al.*, 1996), and the effect of competition with shrubs and brambles, though less than with grasses (Frochot *et al.*, 1995) is still considerable. There is also an effect of competition on the growth-form of oak saplings: a shrub understory induces a considerable reduction in diameter, and an improvement in growth in height compared to a grass understory (Frochot *et al.*, 1995). The financial consequences of such effects have not yet been quantified: this is clearly a necessary step in comparing this approach to the protection of saplings with the traditional methods based on fencing. As the total cost of understory management is less than the cost of fencing (Demolis & Jamey, 1988) this approach holds promise.

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SUMMARY

Feeding by Roe Deer (*Capreolus capreolus*) in European commercial forests has important financial costs. Oak (*Quercus robur, Q. pedunculatus*) and hornbeam (*Carpinus betulus*) are commonly among the preferred species, and suffer high levels of damage. In this paper we test the hypothesis that selection is frequency-dependent. In one experiment, hornbeam was offered together with dogwood (*Cornus sanguinea*) in proportions varying from 2/8 to 8/2: hornbeam was preferred and the degree of preference was not affected by its relative abundance. In a second experiment the Deer were offered oak, beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*) in more natural conditions with sparse or dense understory vegetation. The consumption of oak decreased when the understory vegetation was dense; but its availability relative to the other saplings had no effect on the degree of preference. Food selection in Roe Deer appears not to be frequency-dependent. Some conclusions for the management of hardwood plantations are drawn.

RÉSUMÉ

L'alimentation du chevreuil (*Capreolus capreolus*) dans les forêts européennes de production a des conséquences financières importantes. Le chêne (*Quercus robur, Q. pedunculatus*) et le charme (*Carpinus betulus*) font partie des espèces communément consommées et souffrent de niveaux de dégâts élevés. Dans cet article, nous testons l'hypothèse que les préférences alimentaires du chevreuil dépendent de la fréquence de présence des espèces. Dans la première expérience, le charme et le cornouiller (*Cornus sanguinea*) sont offerts en proportions variables de 2/8 à 8/2 : le charme est préféré et le degré de préférence n'est pas affecté par son abondance relative. Dans la deuxième expérience, le chêne, le hêtre (*Fagus sylvatica*) et l'érable (*Acer pseudoplatanus*) sont offerts dans des conditions plus naturelles (plantation) avec une végétation d'accompagnement abondante ou rare. La consommation de chêne diminue quand la végétation d'accompagnement est abondante ; mais son abondance relative par rapport aux autres plants n'a pas d'effet sur le degré de préférence. La sélection alimentaire chez le chevreuil n'apparaît pas être dépendante de la fréquence des espèces : certaines conclusions sont tirées pour la gestion des plantations forestières.

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