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Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus* (L.) in an agroecosystem of the Ile-de-France

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Abstract

The diets of the European hare (*Lepus europaeus* Pallas) and wild rabbit (*Oryctolagus cuniculus* L.) in an agrosystem of Ile-de-France are compared. The results are based on analysis of faeces collected at least monthly at 4 sites over one or two annual cycles.

Hares and rabbits had very similar diets. Grasses made up the base of their diet (50 to 100 % of the fragments found in the faeces) of which wheat was the preferred food item throughout the year. Their diet was more varied in summer and fall, and included maize, inflorescences of grasses, and various dicotyledons, as well as *Equisetum arvense* for the hare. The difference between two species' food choices are related to the behaviour of food selection: the proximity of food resources to the warrens for the rabbits and, on a larger scale, the repartition of fields for the hare.

These results show that the rabbit is a generalist compared with the hare which is more selective. Although feeding on the same plants in certain seasons, the two Lagomorphs exploit different areas, and are therefore unlikely to compete for food under these circumstances.

Introduction

The European hare (*Lepus europaeus*) and the gray partridge (*Perdix perdix*) are the main game species of the agroecosystems of Ile-de-France. In spite of this and the determining role of diet on the status and management of the hare population, its diet has not yet been studied in France. Our current knowledge is essentially based on the works of MATUSZEWSKI (1966), BRÜLL (1976), STEINECK (1978), HOMOLKA (1982, 1983, 1987a, 1987b), and of FRYLESTAM (1986), which were carried out under different climatic conditions, particularly during winter snow cover.

Another lagomorph, the wild rabbit (*Oryctolagus cuniculus*) is equally associated to these agroecosystems, when uncultivated zones exist close enough to allow installation of warrens. Their diet in uncultivated areas has been the subject of numerous publications (GILLHAM 1955; COOKE 1974; CHAPUIS 1981; BHADRESA 1982), but few deal with their dietary preferences in cultivated areas (TURCEK 1959; CHAPUIS 1981, 1982; HOMOLKA 1987b, 1988).

On the other hand, following the drop in rabbit populations resulting from the introduction of the virus myxomatosis, MOREL (1956), MOORE (1956), ROTHSCHILD (1961), ROTHSCHILD and MARSH (1956, 1958) noted a general increase in hare populations. In 1960–1970, while rabbit populations were recovering (TROUT et al. 1976; ARTHUR et al. 1980), a decrease in the number of hares was recorded (BROEKHUIZEN 1975; TAPPER and PEARSON 1984). Different hypotheses were proposed to explain the nature of these interrelations: behaviour, parasitic and pathological interactions, food competition, intensification of farming (MOORE 1956; BROEKHUIZEN 1975; BROEKHUIZEN and KEMMERS 1976). BARNES and TAPPER (1986) recently refuted some of these hypotheses, notably the

food competition. On the contrary, in agroecosystems of Czechoslovakia, HOMOLKA (1987b) states that "hares and rabbits are evident trophic competitors exploiting similar trophic supplies during the greatest part of the year".

In this paper I analyze the diet of these lagomorphs in an agroecosystem of Ile-de-France (Paris region), which is favorable to the hare, though the rabbit is also found locally here. Their utilization of trophic resources is compared in order to evaluate the possibility that they could compete for food.

Study area

Situated 18 km southeast of Paris (48°44' N, 2°11' E) the study area consists of 200 hectares of heavily cultivated land on siliceous-clay silt. The climate is oceanic with continental tendencies and some years it is marked by a 15 day period of light snow cover in January/February which does not, however, prevent access to the herb layer.

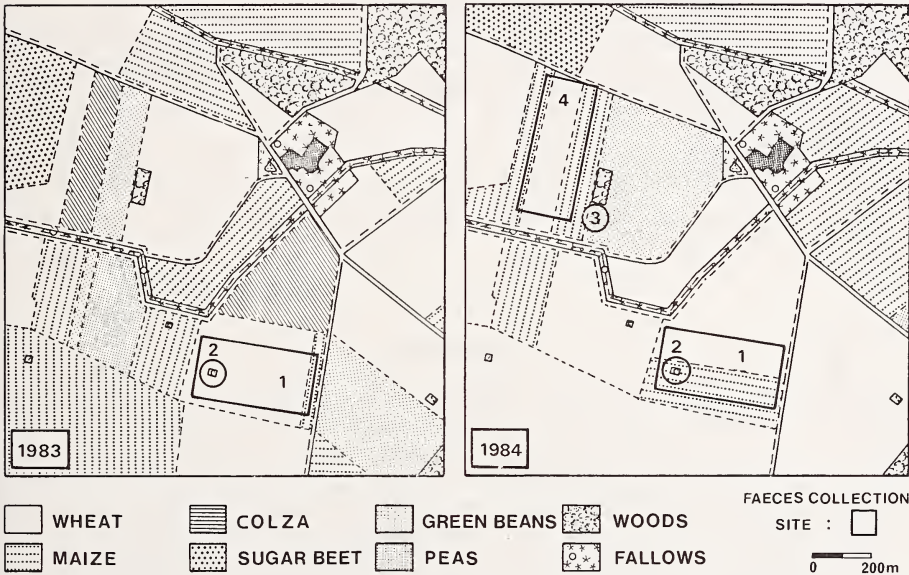


Fig. 1. Distribution of the cultivated plots in June 1983 and June 1984, and localization of faecal collection sites for the hare and rabbit

The study area (Fig. 1) consists of 3 to 15 hectares fields cultivating mainly winter wheat (*Triticum sativum*) (40 to 50 % of the study area depending on the year), maize (*Zea mays*) (30 %), peas (*Pisum sativum*) (10 %) and, less commonly, oilseed rape (*Brassica napus*) (up to 10 %), sugar beet (*Beta vulgaris*) (5 %) and green beans (*Phaseolus vulgaris*) (3 %). The uncultivated zones (isolated woods, access roads, fallows) cover only small surfaces. About 15 adventive species (*Solanum nigrum*, *Equisetum arvense*, *Polygonum* spp.) are well represented on the cultivated plots. Roadside vegetation is primarily graminaceous (*Lolium multiflorum*, *Phleum pratense*, *Poa* spp.) with a few dicotyledons (*Trifolium pratense*, *Achillea millefolium*, *Ranunculus repens*). In the fallows (banks of ditches), the herb layer is mainly composed of *Agropyrum repens*, *Phalaris arundinacea*, *Urtica dioica*, the shrub layer of *Salix* spp. and *Prunus spinosa*. A few fruit trees, *Pirus malus*, *Cerasus avium*, are also found. The wooded zones which offer protection to the warrens are dominated by trees, mainly *Fraxinus excelsior*, *Quercus pedunculata* and *Cerasus avium*, by *Sambucus nigra*, *Prunus spinosa*, *Ligustrum vulgare* and *Crataegus monogyna* for the shrub layer, and by *Urtica dioica*, *Rubus* sp., *Hedera helix* and *Galium aparine* for the herb layer.

Hares occupy the entire study area; the sites for faeces collection were therefore selected according to the localisation of rabbits (Fig. 1). In the first year, samples were taken from two sites (1, 2) in one zone; in the second year two others were added (3, 4) in another zone. Based on home ranges of

approximately 2 ha for the rabbit (from 1.2 to 2.7 ha in the same habitat: ARTHUR (1989) and 30 ha for the hare (from 16 to 38 ha according to the habitat: PTELOWSKI 1972; SCHNEIDER 1978; BROEKHUIZEN and MAASKAMP 1982; RICCI 1983, HOMOLKA 1985), cultivated species available per site were as follows: site 1 (hare): wheat and maize, to which were added oilseed rape, peas, and green beans in 1983; site 2 (rabbit): wheat, maize; site 3 (rabbit): peas, maize and wheat; site 4 (hare): wheat, maize, sugar beet, peas.

Material and methods

The hare's and rabbit's diets were analyzed by a previously tested method of microscopic identification of epidermal fragments in faeces (CHAPUIS 1980). The samples were collected on surfaces of 0.3 ha for the rabbit (sites 2 and 3) and 3 ha for the hare (sites 1 and 4). The collection periodicity varied from 15 days to one month depending on the season, from February 1983 to February 1985 at sites 1 and 2, and from January 1984 to January 1985 at sites 3 and 4. Each sample was comprised of 15 to 20 fecal pellets taken from a maximum number of pellet groups. I identified 350 to 400 fragments (from 0.25 to 2 mm in size) per sample, distributed among 100 microscopic fields (20 fields/slide). The results are expressed in percentage of relative abundance.

This method has been evaluated elsewhere (WESTOBY et al. 1976; CHAPUIS 1980; HOLECZEK et al. 1982). To minimize the problems of underestimation of certain food items, many authors (STEWART 1967; BARKER 1986) recommend applying correction factors. As my aim was to compare the diets to two species having the same digestive mechanisms and to study the evolution of their food preferences over the seasons depending on food availability, I didn't consider it necessary to calculate and apply these correction factors.

Further observation of browsing traces showed that all species noted as having been consumed were also found in the faeces. This suggests that the method of fecal analysis did not lead to major biases here.

For comparisons I used the overlap index C of ZARET and RAND (1971) and the diversity index I of SHANNON and WEAVER (1949).

Results

Hare's feeding

At site 1 (Fig. 2), starting in October, the hare's most important food source was wheat germinated from winter crops. In June the leaves were left in favor of the ears which were ingested until August. If ploughing did not immediately follow harvesting, young shoots of grains left on the ground were consumed, before the appearance of the young shoots on neighboring fields resulting from the fall sowing. This was reflected by the predominance of this cereal in their diet during the two study years. In summer, feeding was more varied with consumption of maize during the first two months following germination (maximum 40 % in June 1983 and 30 % in August 1984) and consumption of *Equisetum arvense* (30 % maximum in July/August). Various dicotyledons (*Matricaria discoidea*, *Polygonum* spp.) and graminea (*Lolium multiflorum*, *Poa* spp.) were ingested in small amounts, especially in June and September–October, periods when the leaves of wheat had dried out or were unavailable. Even though the field was close to the site of faeces collection in 1983, pea plants were rarely consumed. A maximum of 8.6 % was recorded in May upon apparition of the young shoots and grain in October (5 %) upon germination of fallen grains. The green bean plant was ingested only in July (4.2 %) when the first leaves appeared.

The hare's diet at site 4 (Fig. 3) was very similar to that in site 1. The only differences were related to a lesser consumption of *Equisetum arvense*, and to a greater proportion of various graminea at the onset of summer, essentially *Lolium multiflorum* found along roads. The leaves and roots of beet were virtually not consumed (maximum 1 % in November).

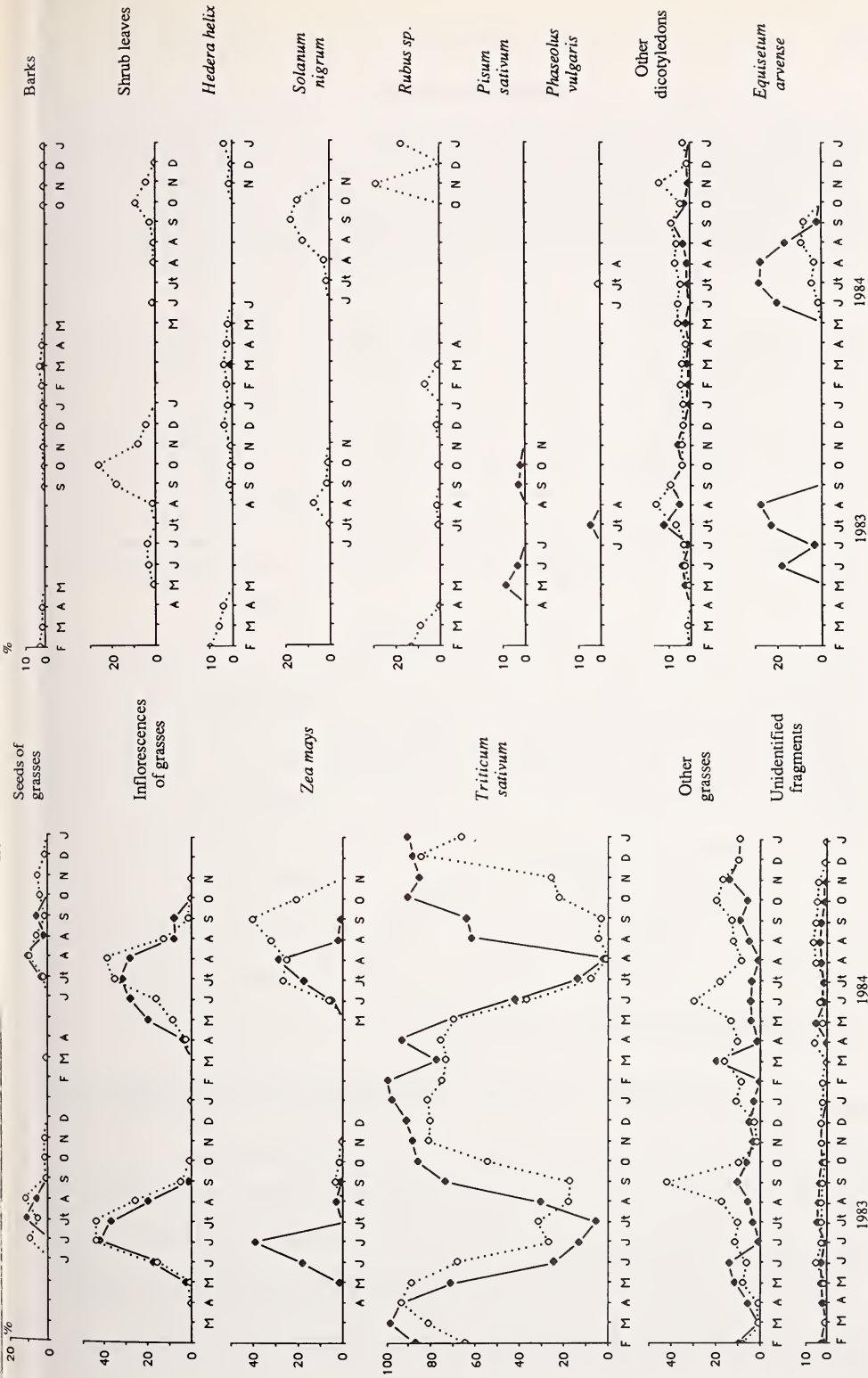


Fig. 2. Evolution of the diet of the European hare (solid symbols) and the wild rabbit (open symbols) from February 1983 to January 1985 at sites 1 and 2

Wild rabbit's feeding

The rabbit's diet at site 2 (Fig. 2) was very similar to that of the hare: wheat was preponderant in winter, spring and fall. In summer rabbits mainly fed on inflorescences of graminea (wheat) and leaves of maize, in different proportions according to the year. Maize and its adventice plant *Equisetum arvense*, were ingested in 1984 at a time when the field was in the immediate vicinity of the warrens, but were ignored by the rabbits in 1983 because of the field's distance (approx. 100 m from the warrens). The grain teguments

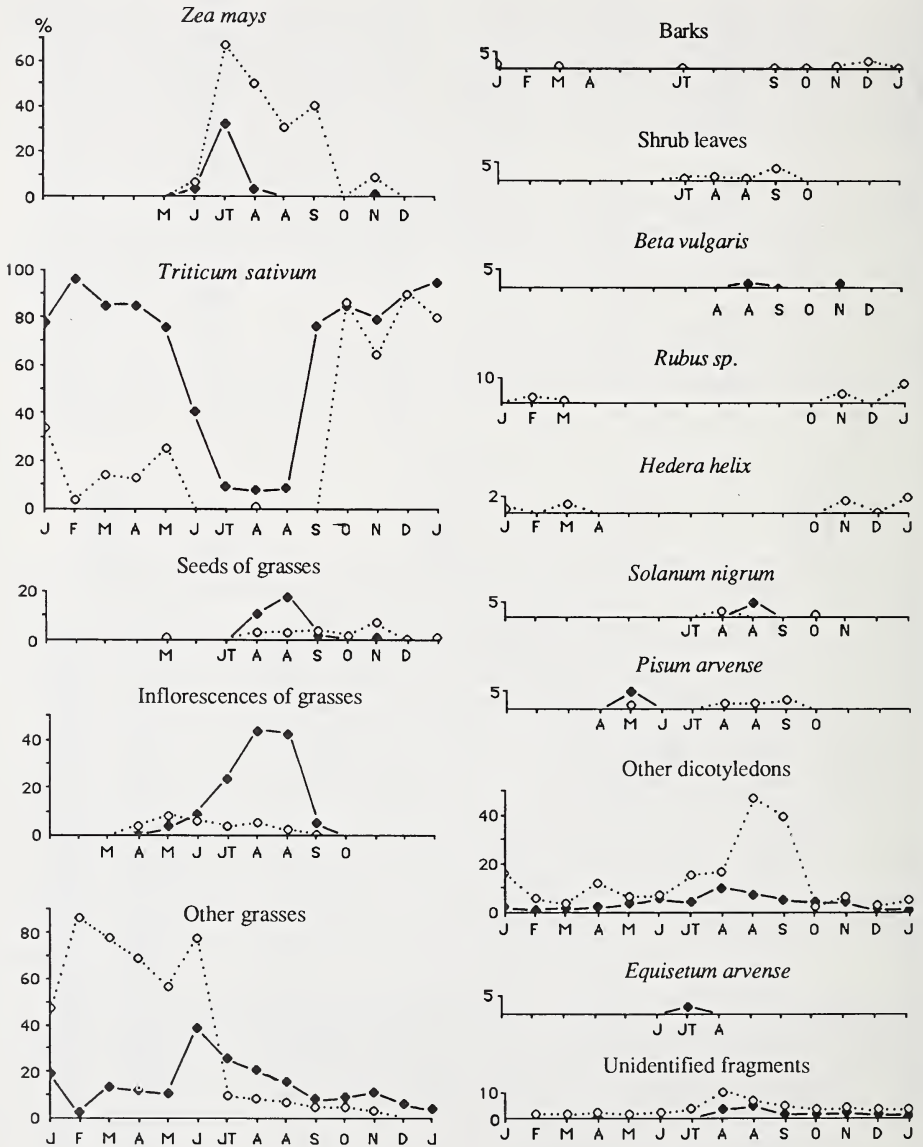


Fig. 3. Evolution of the diet of the European hare (solid symbols) and the wild rabbit (open symbols) from January 1984 to January 1985 at sites 3 and 4

present in the faeces collected from October to December 1984 correspond mainly to the consumption of maize issued from cut or fallen stalks and ears left over from harvesting. Because of the drying out of wheat leaves and before the appearance of new shoots, the rabbit's diet was more varied at the beginning and end of summer. It consisted mainly of maize, wheat ears, and various grasses (*Lolium multiflorum*, *Phleum pratense*, *Poa trivialis*), of *Solanum nigrum* (foliage, flowers and seeds) and of other various dicotyledons. Fall was marked by the consumption of shrub leaves (*Prunus spinosa*, *Cerasus avium*, *Crataegus monogyna*), and in winter other underwood species (*Hedera helix*, *Rubus* sp.) were ingested along with small proportions of shrub bark.

At site 3 (Fig. 3), the absence of wheat on fields next to the warrens explains the consumption from January to June of grasses found on the access road situated at more than 100 m from the warrens. Nevertheless the rabbits cross the abandoned ditches, dry for most of the year, to feed on wheat. From October on, when newly sown wheat replaces the peas, the rabbits fed almost exclusively on this cereal, and did so until the end of the study. During summer the rabbits fed on maize, from its germination in June until September. At this time, various adventive dicotyledons were also ingested, especially in August and September. Among the other available species, the rabbits ate peas plants from a field adjacent to the woods (maximum 2.4 % only, in September), and in fall-winter, underwood species (bramble, ivy, shrub leaves and bark). As for site 2, consumption of gramineae grains (maize) was noted from August 1984 to January 1985.

Interspecific comparison

The fact that every food item cannot be determined down to the species level implies that the indexes do not give an absolute quantification of the diversity and the competition level between the two species, in terms of resource allocation. Nevertheless, relative variations of these indexes indicate the seasonal variations of food habits and of the overlap of their diets. The diversity indexes of the hare and rabbit diets show similar evolution over the seasons for the four sites (Fig. 4). Low in winter, these indexes increase in spring until

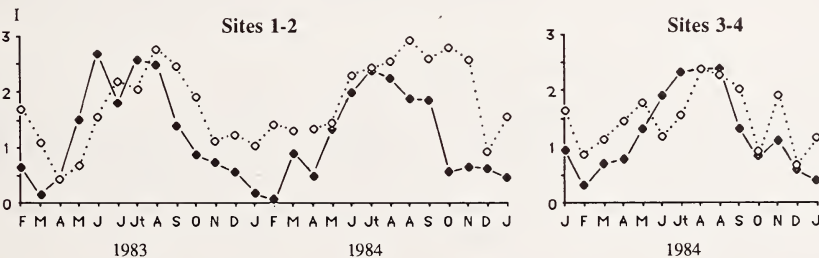


Fig. 4. Evolution of the diversity index I (SHANNON and WEAVER 1949) of the diets of the European hare (solid symbols) and the wild rabbit (open symbols) at sites 1-2 and 3-4

reaching a maximum in June-July for the hare and August-September for the rabbit. During fall-winter they decrease more rapidly for the hare than for the rabbit. The main differences between their diets are found during the seasons when the rabbits consume a greater variety of plants than do the hares. The differences recorded for the rabbit (site 1) from 1983 to 1984 are linked to the availability of food in the vicinity of the warrens (presence of wheat in 1983 and maize in 1984).

The comparison of overlap index C (Fig. 5) shows that at site 1-2 the two species used the same food resources during winter and spring. The index decreased in summer and fall, notably in 1984 where $C < 0.6$ from August to November, indicating a very small overlap

of the diet (BROWN and LIEBERMAN 1973). At site 3–4 the index reveals the use of different resources from January to September, with nonetheless a great similarity of species consumed in June–July. From October to the end of this study, their diets were very similar (mainly wheat).

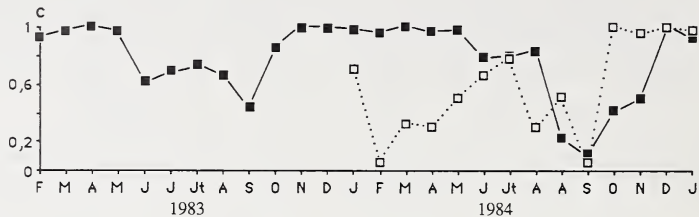


Fig. 5. Evolution of the overlap index C (ZARET and RAND 1971) of the diet of the European hare and the wild rabbit at sites 1–2 (solid symbols) and 3–4 (open symbols)

Discussion

In the study area, as in most other habitats, hares and rabbits fed essentially on grasses (50 to 100 % of the fragments found in the faeces). Among these, the leaves of wheat constituted the base of their diet from October to May. The rest of the year they consumed ears of wheat, leaves of maize, and various dicotyledons found in the fields and along the access roads. One adventive fern, *Equisetum arvense*, was particularly sought out by the hare.

Considering the availability of food resources, these results agree with the observations of other authors, particularly those of HOMOLKA (1983) on the hare and of CHAPUIS (1982, 1986) and HOMOLKA (1988) on the rabbit, in cultivated zones. However, BRÜLL (1976) and FRYLESTAM (1986) noted a significant consumption of oilseed rape by the hare (15 to 39 % of the epidermis found in the stomachs collected in winter). Oilseed rape (variety "Bienvenu") occupied 10 % of our territory in 1983 and was completely ignored by the hare. This divergence of results could be due to difficulties in identifying rape leaf epidermes in faeces. More likely, it should be related to the presence of large surfaces of winter wheat, preferred to the crucifer. For the rabbit the oilseed rape was too far from the warrens and was therefore unaccessible. Even in other situations, this crucifer is usually ignored by the rabbit or ingested in small proportions (CHAPUIS 1982). On the other hand, contrary to observations in Eastern Europe (TURCEK 1966; KALUZINSKI 1976; SZUKIEL 1976; HOMOLKA 1982), the hare did not use woods and thickets for feeding purposes in this study area. A constant winter snow cover in the East's more continental climate, which prevents access to the herbaceous layer explains this difference in diet.

At the study sites the monthly evolution of the diet of these two lagomorphs reveals some discrepancies at certain seasons, showing their different utilization of food resources. Since the morphological and physiological features of the two species are quite similar, the differences observed in their diet can be explained by their behaviour. For example at site 3 (Fig. 3) rabbits usually did not move further than 100 m to feed on wheat, which is still a preferred species (CHAPUIS 1982, 1986). In the same way, in August and September, they only ate the young wheat sprouts (from fallen grains after harvest) near their warrens. When wheat is no longer available, rabbits vary their diet. In summer, they fed on grasses and dicotyledons growing on access roads, on maize and, especially at site 1, on weeds such as *Solanum nigrum*. In fall, they ingested shrub leaves (*Prunus spinosa*, *Cerasus avium*, *Crataegus monogyna*) and in winter, underwood plants (*Rubus* sp., *Hedera helix*). In comparison, the hares cover larger areas and thus have a different diet at certain

seasons. They ate more wheat than rabbits, particularly in summer and fall, when young shoots were available. Maize was only consumed during June and July but *Equisetum arvense*, a scarce and localized species, was actively sought after from June to August (site 2). In fall, soon after wheat seedling time, hares fed almost exclusively on this crop until early summer. At this time, they discarded leaves and fed upon ears.

These results show that the two lagomorphs are selective herbivores, choosing precise foods, according to what is available in their feeding area. These choices are closely related to the phenological stage of plant species.

On the other hand, these results strengthen WESTOBY (1974) and BELOVSKY (1978) statement i.e. herbivores become "specialists" when food is abundant and "generalists" when food resources are limited. Because of the different behaviour of these two lagomorphs in the study area, this "specialist" tendency is more marked for the hare, whose foraging area is larger. This species also makes better use of the trophic potentialities of its habitat in adapting its foraging movements to the crops' phenology. Therefore, the hare can be more selective than the rabbit, whose feeding area is limited to the vicinity of its warren. This is why at certain seasons, the rabbit has to diversify its diet and, in that way, adopts a more "generalist" behaviour earlier than the hare (Fig. 2 and 3).

Although the results are close to those of HOMOLKA (1987b), an interpretation leads to the opposite conclusion: in the type of agroecosystem studied here, the two species do not compete for food. Even if their diets overlap at certain seasons, the plants eaten during these periods are in fact available in excess. Moreover, the two lagomorphs do not exploit the same surfaces.

These results clearly demonstrate that hares and rabbits have different trophic niches in this type of habitat. They also reinforce BARNES and TAPPER (1986) assumption that the current decline of hares is not due to the increasing rabbit populations but to changes in farming practises. Moreover, the characteristics of new varieties of cultivated species could affect wild animal populations. For example, increasing cultivation of a new variety (00) of colza (*Brassica napus*) could be responsible for the mortality of the roe deer (*Capreolus capreolus*) in Austria (ONDERSCHEKA et al. 1987). Current studies in Europe are testing this assumption for the hare. However, preliminary results indicate that colza "00" does not seem to be directly responsible for the mortality of hares.

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Zusammenfassung

Vergleich der Nahrungsspektren von zwei sympatrischen Hasenartigen, *Lepus europaeus* (Pallas) und *Oryctolagus cuniculus* (L.) in einem Agrosystem der Ile-de-France

Die Nahrung des Feldhasen (*Lepus europaeus*) und des Wildkaninchens (*Oryctolagus cuniculus*) wird in Ackerland der Ile-de-France verglichen. Dazu wurden in monatlichem Abstand an vier Stellen Kotproben über 1–2 Jahre gesammelt und analysiert. Danach ist die Nahrung von Hase und Kaninchen sehr ähnlich. Gräser, und davon vor allem Weizen, bilden 50–100 % der Fragmente in den Faeces. Im Sommer war die Nahrung vielfältiger als im Winter und enthielt dann Mais, Grasblüten, verschiedene Kräuter und beim Hasen Ackerschachtelhalm (*Equisetum arvense*). Die Unterschiede in der Nahrung beruhen vor allem auf dem größeren Aktionsradius des Hasen und seinem Aufenthalt auf Feldern. Im Vergleich zum Kaninchen ist der Hase hier eher ein Nahrungsspezialist. Obwohl Hase und Kaninchen zu manchen Jahreszeiten dieselben Pflanzenarten fressen, besteht zwischen ihnen wahrscheinlich doch kaum Konkurrenz um Nahrung, weil sie diese unterschiedlichen Standorten entnehmen.

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