Comparative foraging and nutrition of horses and cattle in European wetlands

CATHERINE MENARD*, PATRICK DUNCAN*†, GERALDINE FLEURANCE*‡, JEAN-YVES GEORGES* and MARC LILA§

Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France; †Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France and §Institut National de la Recherche Agronomique, UR889 Unité d'Amélioration des Ressources Fourragères, route de Saintes, 86600 Lusignan, France

Summary

1. Equids are generalist herbivores that co-exist with bovids of similar body size in many ecosystems. There are two major hypotheses to explain their co-existence, but few comparative data are available to test them. The first postulates that the very different functioning of their digestive tracts leads to fundamentally different patterns of use of grasses of different fibre contents. The second postulates resource partitioning through the use of different plant species. As domestic horses and cattle are used widely in Europe for the management of conservation areas, particularly in wetlands, a good knowledge of their foraging behaviour and comparative nutrition is necessary.

2. In this paper we describe resource-use by horses and cattle in complementary studies in two French wetlands. Horses used marshes intensively during the warmer seasons; both species used grasslands intensively throughout the year; cattle used forbs and shrubs much more than horses. Niche breadth was similar and overlap was high (Kulczinski's index 0·58–0·77). Horses spent much more time feeding on short grass than cattle. These results from the two sites indicate strong potential for competition.

3. Comparative daily food intake, measured in the field during this study for the first time, was 63% higher in horses (144 g_{DM} kg $W^{-0.75}$ day^{-1}) than in cattle (88 g_{DM} kg $W^{-0.75}$ day^{-1}). Digestibility of the cattle diets was a little higher, but daily intake of digestible dry matter (i.e. nutrient extraction) in all seasons was considerably higher in horses (78 g_{DM} kg $W^{-0.75}$ day^{-1}) than in cattle (51 g_{DM} kg $W^{-0.75}$ day^{-1}). When food is limiting, horses should outcompete cattle in habitats dominated by grasses because their functional response is steeper; under these circumstances cattle will require an ecological refuge for survival during winter, woodland or shrubland with abundant dicotyledons.

4. Horses are a good tool for plant management because they remove more vegetation per unit body weight than cattle, and use the most productive plant communities and plant species (especially graminoids) to a greater extent. They feed closer to the ground, and maintain a mosaic of patches of short and tall grass that contributes to structural diversity at this scale. Cattle use broadleaved plants to a greater extent than horses, and can reduce the rate of encroachment by certain woody species.

Key-words: diet, food intake, grazing management, habitat selection, herbivory, niche overlap

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Correspondence: P. Duncan, Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France (fax + 33 549 09 6526; e-mail duncan@cebc.cnrs.fr).
‡Present address: Les Haras Nationaux–Direction du Développement, Domaine de la Valade, 19370 Chamberet, France.

Introduction

Equids are generalist herbivores that co-exist with bovids of similar body size in many guilds of grazing herbivores in tropical ecosystems in Africa (Cumming 1982). In temperate ecosystems during the Holocene,

Equus species apparently overlapped extensively with the steppe-living *Bison* species as well as the wild cattle of woodlands (*Bos*; cf. Kurtén 1968). The ecological mechanisms that allow the co-existence in tropical and temperate ecosystems of equids and grazing bovids have been debated. Janis (1976) noted that their very different digestive systems (hindgut, ruminant) could theoretically lead them to adopt different foraging strategies, resulting in niche separation. This 'nutritional model' predicts that the efficient ruminant digestive system allows bovids such as cattle to extract more digestible dry matter than equids from medium-quality grasses (defined by their fibre content). The equid system, in contrast, should allow them to extract more than the bovids from grasses with very high fibre contents because the hindgut digestive system has a higher throughput rate.

It is technically difficult to obtain accurate estimates of daily food intake and digestion for free-ranging animals (Gordon 1995), so few data are available for horses at pasture and for cattle in natural grasslands. Information from single-species feeding trials using stalled animals shows that horses can ingest more dry forage per kg of body weight per day, and extract more nutrients than cattle on all forages (Duncan *et al.* 1990). However, at pasture the low-intake strategy of cattle may allow them to feed more selectively, and they use a wider range of plant species (Krysl *et al.* 1984; Vulink 2001). It is therefore possible that on medium-quality forages at pasture, cattle extract nutrients at a higher rate than do horses, as predicted by the nutritional model.

Equids, unlike ruminants, have two sets of incisors, which could allow them to feed faster than bovids on short grass. Although zebras *Equus burchelli* are medium-tall grass feeders (Bell 1970), horses feed on grass too short for cattle in at least two European grazing systems (cf. Gordon 1989a). Further, ruminants are known to use dicotyledons, which contain more secondary metabolites than graminoids, to a greater extent than horses (Krysl *et al.* 1984). It is therefore possible that the principal mechanism of co-existence is resource partitioning by the use of different plant species, but few comparative data are available to test this hypothesis.

In the context of changing agricultural and conservation policies in Europe, free-ranging herbivores are being used more widely to achieve conservation objectives. Herds of cattle and horses, and to a lesser extent cervids, sheep and geese, are used to maintain open grasslands and marshes and their associated fauna. This is particularly true in wetlands, where succession occurs rapidly. In this context, studies of cattle and horses are of particular interest because the feeding strategies of these species lead them to consume large quantities of the invasive coarse grasses and woody plants, the removal of which is often the object of management. At a different spatial scale, there are initiatives to re-establish natural processes such as plant–herbivore interactions in large areas of artificial ecosystems in Europe, involving the restoration of multispecies grazing

systems with minimal management (WallisDeVries, Bakker & Van Wieren 1998; Bokdam & Gleichman 2000). Both of these management activities, controlling the vegetation and restoring multispecies grazing systems, require a thorough understanding of the comparative foraging and nutrition of cattle and horses. For the former it is necessary to know if the animals use the same or different plants, and for the latter it is necessary to understand the mechanisms that allow them to co-exist. Some of the information can be obtained from studies of these animals in other temperate ecosystems, but comparative studies in wetlands are necessary because wetland plants differ from those of drylands; flooded feeding conditions are risky, as the animals can catch diseases such as foot-rot, and cattle but not horses suffer from liver-flukes. Such studies have been conducted only rarely (Vulink 2001).

In this paper we describe the feeding niches of the two species in wetlands, and test the hypothesis that cattle and horses can co-exist because (i) they use different habitats, at least in the winter; (ii) within habitats horses specialize on graminoids, while cattle use dicotyledons to a greater extent; (iii) horses use short grasslands to a greater extent. We also measured their daily intake of digestible dry matter, and tested the prediction of the nutritional model that cattle achieve higher rates of nutrient extraction from medium-quality forages because their diets are more digestible than those of horses.

We used complementary experimental sites in two internationally important wetlands in France where grazing by horses and cattle is used for conservation management. In the Camargue, free-ranging animals were studied in an extensive year-round grazing system with diverse vegetation including both wetland and dryland habitats, which was ideal for studies of feeding niches but where intake was difficult to measure. Intake and niche overlap were therefore measured in a small-scale experimental set-up in the Marais Poitevin.

Study areas and animals

THE CAMARGUE

The study site and the animals

The study was conducted from November 1989 to January 1991, on a 346-ha pasture in the eastern part of the Tour du Valat estate in the east of the Camargue, at the delta of the Rhone river in southern France (42°24′ N, 4°44′ E). The climate is typically mediterranean, varying between subhumid and semi-arid with cool winters. The daily minimum air temperature falls below freezing on average 5 days a month between December and February. Mean monthly evaporation varied from 75 (minimum in spring) to 225 mm (maximum in summer). The mean annual precipitation is 614 mm; rainfall in the year when the data were collected was 531 mm (data from the Tour du Valat meteorological station).

Table 1. Landscape classification of the Camargue study area (from Rogers 1981)

Catena level	Legend	Habitat type	Land facets and dominant plants	Area ha	Area %
Ridge, top	6A	Natural grasslands	Coarse grasslands with shrubs (*Brachypodium phoenicoides*, *Agropyron pungens*, *Phillyrea angustifolia*, etc.)	32	9·3
	6B		Halophyte grasslands (*Halimione portulacoides*, *Limonium vulgare*, *Limonium bellidifolium*, *Medicago* spp., *Phillyrea angustifolia*, etc.)	52	15·0
	OFG	Old-field grasslands	Old-field grasslands (*Poa trivialis*, *Trifolium repens*, *Paspalum paspalodes*, etc.)	21	6·1
	5	Salt flats	Salt flats, with woody and herbaceous halophytes (*Arthrocneum* spp., *Halimione portulacoides*, *Puccinellia distans*, *Juncus subulatus*, etc.)	145	41·9
	4		Lower salt flats (*Arthrocneum glaucum* with no herb layer)	36	10·4
	OFM	Old-field marshes	Old-field marshes, artificially flooded October–June (*Paspalum paspalodes*, *Phragmites australis*, *Alisma plantago-aquatica*, etc.)	9	2·6
	2	Natural marshes	Shallow marshes, flooded for 2–6 months, winter–spring (*Polypogon maritimum*, *Halimione portulacoides*, *Alopecurus bulbosus*, *Aeluropus littoralis*, *Juncus gerardii*, etc.)	25	7·2
Sump, bottom	1		Deep marshes, flooded 9–12 months, autumn–summer (*Bolboschoenus maritimus*, submerged macrophytes, and some *Phragmites australis*)	26	7·5
Totals				346	100

The experimental herd consisted of breeding mares and cows, and their offspring. The mares were all of the Camargue breed (*c.* 400 kg after foaling), while the cows belonged to three ancient breeds also adapted to extensive grazing: Camargue, Fighting bull (*toro de lidia*) × Camargue crosses and *Aure et Saint Girons*, weighing up to 300, 400 and 600 kg, respectively.

There were 15 females of each species aged 3–15 years, matched between species for age and parity, and between four and 12 1- and 2-year-olds of each species. A stallion and a bull were introduced each spring so that births occurred between late February and early May simultaneously for both species. The numbers were managed so that there was always enough forage; supplementary food was not provided.

The vegetation and its management

The study area contained a wide range of semi-natural habitats (grasslands, salt flats and wetlands) and abandoned arable fields (Bassett 1978). It was typical of the eastern Camargue and had affinities with four phytosociological orders, *Thero–Brachypodietalia*, *Salicornietalia*, *Juncetalia maritimi* and *Phragmitetalia*, which are important components of mediterranean halophytic vegetation. The area was classified into landscape units and mapped by Rogers (1981) (Table 1; plant nomenclature follows Tutin *et al.* 1964–80).

In the grasslands, growth is usually halted by the summer water deficit as well as by low temperatures in winter (Duncan 1992). In the wetlands, growth occurs from March to September–October. In a previous study (Duncan 1983), the standing crop of green herbaceous

plants varied from nil in the lower salt flats, to an average value of 600 g_{DM} m^{-2} (DM, dry matter) in the deep marsh in summer. Most of the values for the average standing crop of green matter in the different land facets were below 250 g_{DM} m^{-2}.

Management of the range during this study was limited to irrigation of the old-fields. The old-field marshes, managed as feeding habitats for waterbirds, were maintained under water (0–30 cm) from October to July. Thereafter, they were kept damp by flooding about once a month, when the soil became cracked. The old-field grasslands were kept damp in the same way, by irrigation in the warm seasons (May–September).

THE MARAIS POITEVIN

The study site and the animals

The data presented here were collected on the communal grazing land of the Commune of Magnils-Reigniers (Vendée, France; 46°28′ N, 1°10′ W) near the mouth of the Sèvre Niortaise river, during the grazing seasons (May–October) of 1998 and 1999. This area is part of one of the major wetlands of the country, the Marais Poitevin (Duncan *et al.* 1999). This common has been used for centuries for a mixed grazing system with horses, cattle and domestic geese (*Anser*). Major parts of the Marais Poitevin have been drained since the 12th century for arable farming, but flood expansion areas have typically been kept as commons for summer grazing (May–November; Amiaud 1998). The climate is oceanic with seasonal precipitation that peaks in winter (mean monthly values between October

Table 2. Experimental set-up in the Marais Poitevin site. (a) The plots: these were single species (E2 and E2d for horses; B2 and B2d for cattle) or mixed species (EB). (b) Plant species composition of the three communities in the study site. The species are ordered in relation to their contribution to the biomass (Amiaud 1998)

(a)

Year	Plot	Number of animals	Age (years)	Area (ha)	Mean biomass (kg ha^{-1})
1998	E2	2	3–6	2	770
	E2d	2	3–5	2	780
	B2	2	2	1	890
	B2d	2	2	1	980
	EB	6	2–7	4	610
1999	E2	2	2	2	490
	E2d	2	2–4	2	680
	B2	2	2	1	430
	B2d	2	2	1	440
	EB1	4	2	2	970
!!!!	EB2	4	2	2	940

(b)

Community	Dry	Intermediate	Wet
	Hordeum secalinum	*Juncus gerardii*	*Agrostis stolonifera*
	Agrostis stolonifera	*Carex divisa*	*Glyceria fluitans*
	Lolium perenne	*Hordeum secalinum*	*Juncus articulatus*
	Bromus commutatus	*Agrostis stolonifera*	*Eleocharis palustris*
	Cynodon dactylon	*Elymus repens*	*Oenanthe fistulosa*
	Cynosorus cristatus	*Alopecurus bulbosus*	*Trifolium fragiferum*
	Elymus repens	*Bromus commutatus*	*Ranunculus sardous*
	Juncus gerardii	*Hordeum marinum*	*Potentilla anserina*
		Lolium perenne	

and January are 85–90 mm, and 42 mm in July). The 30-year mean annual precipitation at the northern edge of the Marais Poitevin is 810 mm and average annual evapotranspiration is 760 mm (data from Météo-France).

This study was conducted as part of an experiment to compare the effects of cattle and horses on vegetation dynamics (Amiaud 1998). On an area of 20 ha, nine fenced plots of 1–4 ha contained horses and cattle alone and mixed, at densities from one to four individuals ha^{-1} (Table 2). The plots were chosen to be as similar as possible in terms of geomorphology and plant communities. For this study we used seven plots, either single species (horses: E2, E2d; cattle: B2, B2d) or mixed species (EB in 1998; EB1 and EB2 in 1999); seasonal biomass densities in these plots ranged from 430 to 980 kg ha^{-1} (Table 2). The animals were all growing non-lactating females aged from 2 to 7 years; the horses were of a local draught breed (Mulassier Poitevin; live weight 410–850 kg) and the cattle were of the Charolais beef breed (310–570 kg).

The vegetation and its management

The grasslands comprised three plant communities (Table 2): (i) wet grasslands in shallow natural drainage channels, which are flooded from late autumn to spring and usually remain damp in summer; (ii) dry grasslands on the top of the catena; and (iii) intermediate grasslands on the slopes, the soils of which are saline (Amiaud

1998). These short–medium height grasslands had sward surfaces of 3–90 cm (measured by a drop disc; Stewart, Bourn & Thomas 2001) and the mean biomasses in the different vegetation communities varied between 200 and 650 g$_{DM}$ m^{-2} at the peak (June) and 70–250 g$_{DM}$ m^{-2} in October. The forage was of medium quality, with average neutral detergent fibre (NDF) values (in clipped samples taken to mimic feeding animals) ranging between 48% and 64% in different months and plant communities, and with protein values between 9% and 25%.

Methods

DESCRIPTION OF THE FEEDING NICHES

Landscape facets were used for the Camargue (Table 1) as this is known to be an appropriate scale for animals of this size (Duncan 1983). The herds were visited on foot and the use of habitats determined from scan samples of the individual animals (Altmann 1974). There was an equal number of visits per daylight hour in each month (with a maximum of two per day). The results of two series of observations over 24-h showed that daytime and 24-h data provided similar estimates of overlap, 0·91 vs. 0·92 in August 1989 and 0·79 vs. 0·77 in June 1990: we considered that the evaluation of ecological overlap from daytime data in this study area was likely to reflect the overlap over the 24-h. The year was divided into four seasons: autumn (September, October, November),

winter (December, January, February) spring (March, April, May) and summer (June, July, August). The sample size was taken as the number of visits, to avoid pseudoreplication.

The plants used in the Camargue by eight cows and eight mares that could be approached to within 5 m were determined by bite counts (60–150 per individual per season) and allocated to one of the plant species listed in Table 1. It was not always possible to allocate each bite to a single plant species when they were feeding on dryland swards, so the bites were in some cases allocated to the categories coarse grasses (the genera of perennial grasses, *Brachypodium*, *Dactylis*, *Agropyron*, etc.) and herb-rich grassland (a mixture of annual and perennial grasses, forbs).

In the Marais Poitevin, the behaviour of individuals was recorded using scan sampling at intervals of 5 min when following individuals, 15 or 30 min when observing a set of animals. We did two 24-h observations in the months of May, July and October 1998 and June and September 1999. We noted the position of the animals in the plot, their feeding activity, the plant community and the height of the surface of the sward they were feeding on, using a drop disc. As the behaviour of the individuals in the same plot was not independent, to avoid pseudoreplication we used average values for each plot for all analyses. The feeding times were calculated per month, then averaged per season, summer (May, June, July) and autumn (September, October). These were the same as the seasons for the Camargue study, except that no data were available for August and November, and May was added to the summer as the observations were made in the last half of the month.

Four measures of habitat use and selection were employed.

1. Use (p_i). The percentage of all feeding observations that were recorded in the *i*th facet.

2. Selection (S_i). Hunter's (1962) index of selection was used:

$$S_i = p_i/A_i$$

where A_i is the percentage of the study area covered by the *i*th habitat. This index varies from 0 (total avoidance) through 1 (no selection) to higher values indicating increasing degrees of selection.

The use of such indices for comparing the selection of food items has been questioned for a variety of reasons (Johnson 1980). We used Hunter's index in this comparative study because the habitats were equally available to the two species.

3. Niche breadth. Simpson's index was used (Begon, Harper & Townsend 1996):

$$D = \frac{1}{\sum_{i=1}^{n} P_i^2}$$

where *n* is the total number of categories available.

4. Niche overlap (α_{hc}). Kulczinski's index (Oosting 1956) was used:

$$\alpha_{hc} = \sum_{i=1}^{n} \min(p_{ih}, p_{ic})$$

where p_{ih} and p_{ic} are the proportion of the total resource use by horses and cattle, respectively, allocated to the *i*th category of a given resource dimension (e.g. coarse grassland). This index measures the proportion of the diets that is identical, and assumes values between 0 (total niche separation) and 1 (total overlap).

Overlap at the two levels of spatial organization, which were of course nested, was calculated according to the principles in May (1975) as the product of overlap at the two levels.

DAILY FOOD INTAKE

Food intake was measured in the Marais Poitevin as:

$$DMI = F/(1 - DMD)$$

where *DMI* is the dry matter intake (g kg $W^{-0.75}$ day^{-1}, where W is the live weight and day^{-1} is per day), *F* is the weight of faeces produced over 24-h (g) and *DMD* is the dry matter digestibility expressed as a proportion. *F* was estimated by collecting the total amount of faeces produced twice a day over 4 successive days in plots initially cleared of faeces. When parts of plots were flooded, we followed individual animals continuously over 24 h in order to collect faeces as they were produced. The time of production was also recorded so that the weight of faeces that fell into water could be determined using the relationship between the time since the last defecation and the weight of the following one [the equations for the individuals concerned were: (i) a horse, $F = 12·4t + 965$, $r^2 = 0·80$; (ii) a cow, $F = 5·31t + 490$, $r^2 = 0·69$; *F* is in grams and *t* in minutes].

The dry matter digestibility (*DMD*) was calculated using published equations:

horses: $DMD\,(\%) = 73·4 - 178·72/Nf$
(Mesochina *et al.* 1998)

$r^2 = 0·65$, r.s.d. = 0·038, $P < 0·001$, $n = 27$,
where Nf = faecal nitrogen
(percentage, within the range 7–21%)
r.s.d. = residual standard deviation

cattle: $DMD\,(\%) = 86·6 - 0·485 \times NDFf$
(Duncan *et al.* 1990)

$r^2 = 0·355$, $P < 0·001$, $n = 54$, where $NDFf$ = faecal neutral detergent fibre
(percentage, within the range 43–69%)

Nitrogen and NDF were analysed from samples of dry faeces at the Institut National de la Recherche Agronomique (INRA UR 889, Lusignan, France).

To compare the nutrient extraction rates between horses and cattle, we calculated the daily digestible dry matter intake (*DDMI*; g_{DM} kg $W^{-0.75}$ day^{-1}):

$$DDMI = DMI \times DMD$$

The quality of the forage eaten was estimated by hand-picking samples of forage, mimicking the animals as far as possible using a pair of scissors. Nitrogen and NDF values were determined as above.

There were no clear differences in the animals' behaviour between the single- and multispecies plots: as there were not enough data on the multispecies ones to analyse them separately, we combined the data in all the analyses. Where the distributions of the data permitted, we used parametric analyses, after arcsine transformation for proportions, using Systat (SPSS 1998).

Results

FEEDING NICHES

Habitat use in the Camargue

Both species used all the vegetation types for feeding (Fig. 1a,b), and allocated over 40% of their time to marshes in summer (horses over 65%), while in winter they both spent about three-quarters of their time in the grasslands, the horses principally in the heavily grazed old-fields, the cattle in the natural grasslands. The two species had similar niche breadths, which varied between 3·1 and 5·3, and were highest in spring and lowest in winter (Table 3).

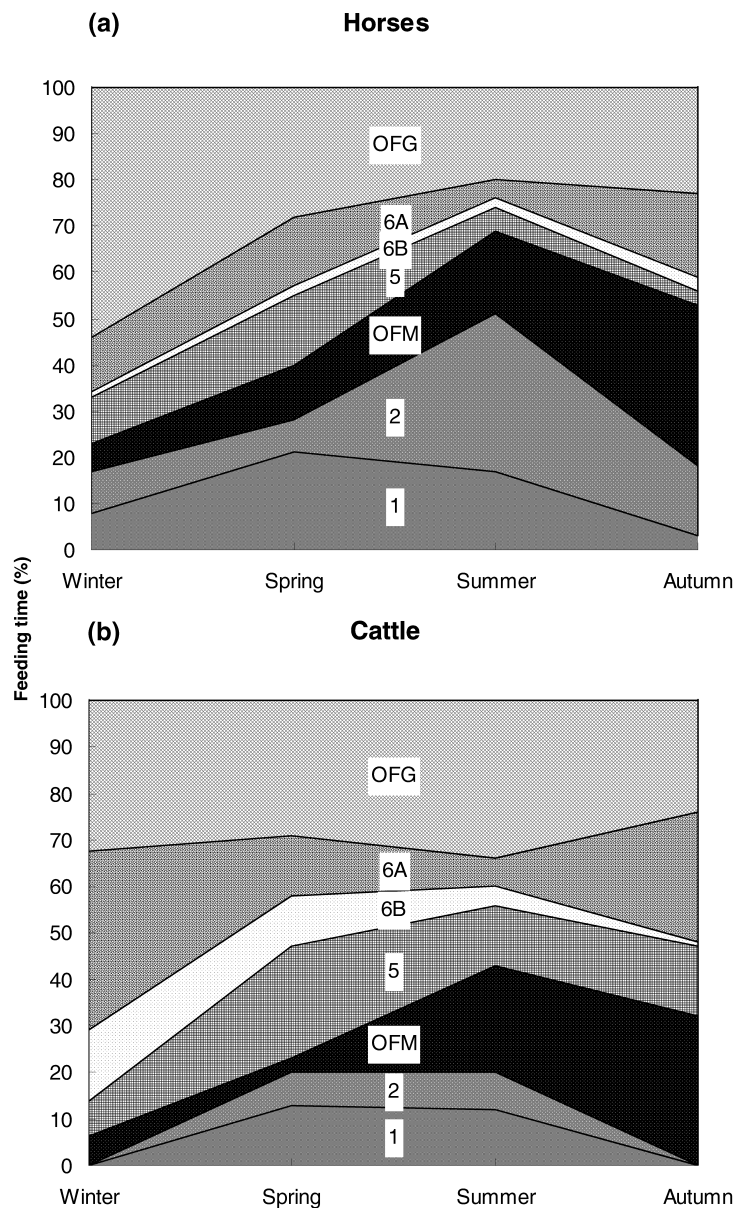The old-field grasslands and marshes, which together covered less than 10% of the area, were used for

(a)   **Horses**

(b)   **Cattle**

Fig. 1. Use of the habitats by horses (a) and cattle (b) for feeding in the Camargue. Habitats: salt flats = 5; grasslands = 6A, 6B, OFG; marshes = OFM, 2, 1. See Table 1 for details.

Table 3. Niche breadth in habitat use by horses and cattle in the Camargue (Simpson's index)

	Niche breadth	
	Horses	Cattle
Winter (December, January, February)	3·1	3·8
Spring (March, April, May)	5·3	5·2
Summer (June, July, August)	4·5	4·7
Autumn (September, October, November)	4·3	3·8
Year-round	5·5	5·2

46% and 49% of the annual grazing time of the horses and the cattle. These habitats maintained the highest densities and biomasses in each season (median = 225 kg ha^{-1}, compared with 20 kg ha^{-1} for the natural habitats).

Both horses and cattle showed significant selection for old-field grasslands in all seasons (Table 4). The horses, in addition, selected one or more marsh types (old-field, shallow or deep marshes) in the three warmer seasons, spring to autumn, while cattle showed significant selection for only one marsh type (old-field marshes) in two seasons, summer and autumn.

In autumn and winter, cattle but not horses showed significant selection for natural coarse grasslands in addition to the old-field grasslands (Table 4). Horses therefore selected more marsh types, and for more of the year, than did cattle. In spite of these differences in foraging behaviour, overlap in habitat use between the two species was high in the warmer seasons (0·69–0·81); in winter this dropped to 0·58.

In winter the principal food plants of both species were grasses (coarse grasses and *Paspalum paspaloides*), herb-rich swards, *Halimione portulacoides* and some *Arthrocnemum*. The cattle, but not the horses, also ate *Phillyrea angustifolia* (> 10% of the winter diet in natural grasslands), *Limonium vulgare* (flowers) and whole plants of the conspecific *L. bellidifolium*. Overlap in plant use in the different habitats was high (0·84–0·98). In spring, monocotyledons again dominated the diets

of both species (coarse grasses, *Bolboschoenus maritimus*, *Paspalum paspaloides*, *Juncus gerardii*, *Alopecurus bulbosus* and *Phragmites australis*) and both species used herb-rich swards and *Halimione portulacoides*. When feeding in marshes, where there were few species and virtually no dicotyledons, the diets of the two species were very similar, although the cattle ate *Typha angustifolia* and *Alisma plantago-aquatica* which the horses did not (overlap 0·84–0·98). In the grasslands, especially the old-fields, there was a significant difference in plant use, with the horses eating more coarse grasses and the cattle more herb-rich swards and clover (χ^2, $P < 0.05$; overlap = 0·62). In summer and autumn the same species were used (except for *Halimione portulacoides* and *Juncus gerardii*) and the overlap was 0·80–0·98, except in the old-field grasslands where the difference between the diet of the two species involved the same species as in spring (χ^2, $P < 0.05$; overlap = 0·50, 0·52 in summer and autumn, respectively).

The principal difference between the diets of horses and the cattle was therefore that the cattle ate more broadleaved plants, especially *Phillyrea angustifolia* in winter, and herb-rich swards and clovers in the warmer seasons. The clovers were of higher quality than the perennial monocotyledons of the wetlands and drylands, which formed a greater part of the diets of horses (crude protein content in summer, 22·1% vs. 13·5–17·5% for six species of perennial monocotyledons).

When the data on habitat and plant use were combined (Table 5), the niche breadth was similar to that obtained from habitat use alone (Table 3). Overlap in winter was identical (0·58), and in the warm seasons overlap declined to 0·63–0·77.

Plant community use in the Marais Poitevin

The horses selected wet and intermediate grasslands ($S = 1.56 + 0.55$ and $S = 1.45 + 0.62$, respectively, with $n = 24$ days of observations; Fig. 2) rather than the upper dry grassland, which they tended to avoid ($S = 0.51 + 0.23$, $n = 24$). The cattle used the three

Table 4. Selection or avoidance of the habitats in the Camargue. Significant values of the index are shown (selection, $P_i > 1.0$; avoidance, $P_i < 1.0$; $P_i = 2.8$ means that deep marshes were used more than twice as much as expected in the 26 ha of this habitat, see the Methods of analysis; χ^2 tests, $P < 0.05$ of the null hypothesis that a habitat was used as expected on the basis of its area)

		Marshes			Salt flats		Grasslands		
		Deep	Shallow	Old-field	Lower	Rich	Old-field	Halophyte	Coarse
Winter (December, January, February)	Horses				0·0	0·2	8·9		
	Cattle	0·0	0·0		0·0	0·3	5·6		3·5
Spring (March, April, May)	Horses	2·8		4·7	0·0		4·8		
	Cattle				0·0		4·9		
Summer (June, July, August)	Horses	2·1	4·8	6·9	0·0	0·1	3·4		
	Cattle			8·8	0·0	0·3	5·6		
Autumn (September, October, November)	Horses		2·1	13·5	0·0	0·2	3·9		
	Cattle	0·0		12·4	0·0	0·3	4·1		3·1

Table 5. Niche breadth for habitat × plant use (Simpson's index) and overlap for horses and cattle in the Camargue (Kulczinski's index)

	Niche breadth		Overlap
	Horses	Cattle	Horses/cattle
Winter (December, January, February)	3·33	2·77	0·58
Spring (March, April, May)	4·04	5·39	0·77
Summer (June, July, August)	4·12	4·54	0·63
Autumn (September, October, November)	3·31	3·24	0·73
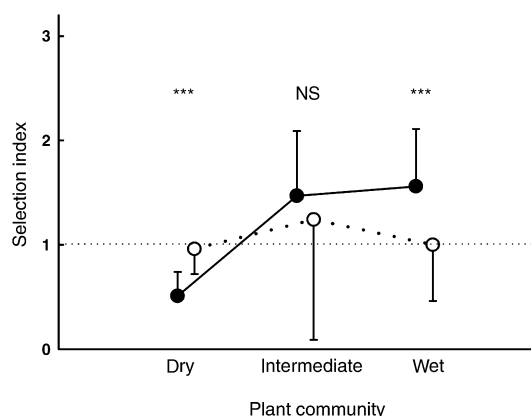
Fig. 2. Selection of plant communities in the Marais Poitevin by horses (filled circles) and cattle (open circles) (*t*-test: ***P < 0·001; NS, non-significant; *n* = 48 plots × months × sessions). Selection index: 0–1·0 = avoidance, 1·0 = used as available, 1·0–∞ = selected.

Table 6. Feeding time budgets (percentage of the 24-h) of horses and cattle in the Marais Poitevin. There were significant effects of species and season (two-way ANOVA: $r^2 = 0·79$; species: $F_{1,50} = 138·5$, $P < 0·001$; season: $F_{1,50} = 42·0$, $P < 0·001$; interaction non-significant)

Season	Month	Cattle	Horses
Summer	May	32·1 ± 2·1	55·3 ± 1·7
	June	36·2 ± 5·5	57·0 ± 5·4
	July	39·2 ± 3·7	49·9 ± 9·2
Autumn	September	40·2 ± 4·9	63·5 ± 4·8
	October	48·3 ± 6·7	71·4 ± 5·5

Table 7. Digestibility of dry matter (mean percentage ± SD) in the diets of horses and cattle. There were significant effects of species and season, with the values for horses declining more than for cattle in autumn (two-way ANOVA: $r^2 = 0·74$; species: $F_{1,72} = 101·3$, $P < 0·001$; season: $F_{1,72} = 13·4$, $P < 0·001$; species × season: $F_{1,72} = 2·9$, $P = 0·027$)

Season	Month	Horses		Cattle	
Summer	May	61 ± 1	$n = 4$	63 ± 2	$n = 4$
	June	57 ± 2	$n = 10$	60 ± 1	$n = 8$
	July	53 ± 3	$n = 8$	60 ± 3	$n = 8$
Autumn	September	55 ± 1	$n = 8$	61 ± 1	$n = 8$
	October	56 ± 2	$n = 8$	59 ± 1	$n = 8$

preferred grasses 9–16 cm in height, and both species tended to avoid taller grass (> 25 cm). The results for the month of June, when there was the greatest range of grass height, are shown in Fig. 3c. As a consequence of this preference for short grass, the horses spent over four times as much time as the cattle on lawns, the sward surfaces of which were < 5 cm (Fig. 4). The feeding niches of the horses and cattle were therefore somewhat different: the horses selected wetter communities and shorter swards than the cattle.

FEEDING TIME AND DAILY FOOD INTAKE

The horses foraged for 50% longer than the cattle, with 54% and 36% of their time spent feeding in summer, respectively (Table 6), increasing to 68% and 45%, respectively, in autumn.

The estimated digestibility of the cattle diets was higher than that of the horses, as predicted (Table 7). The values for both species were highest in May, and the decline in the digestibility of the horse diets was greater than for cattle, as there was a significant species–month interaction.

Daily faecal production varied by a factor of three, between 31 and 101 g_{DM} kg $W^{-0.75}$ in horses and 14–47 g_{DM} kg $W^{-0.75}$ in cattle. The estimation of daily intake was therefore much more sensitive to variations in faecal production than to diet digestibility, as this varied only between 53% and 61% in horses and 59% and 63% in cattle. There was no significant difference between years (1998 May, July, October, and 1999 June, September); both species ate more in autumn than in summer
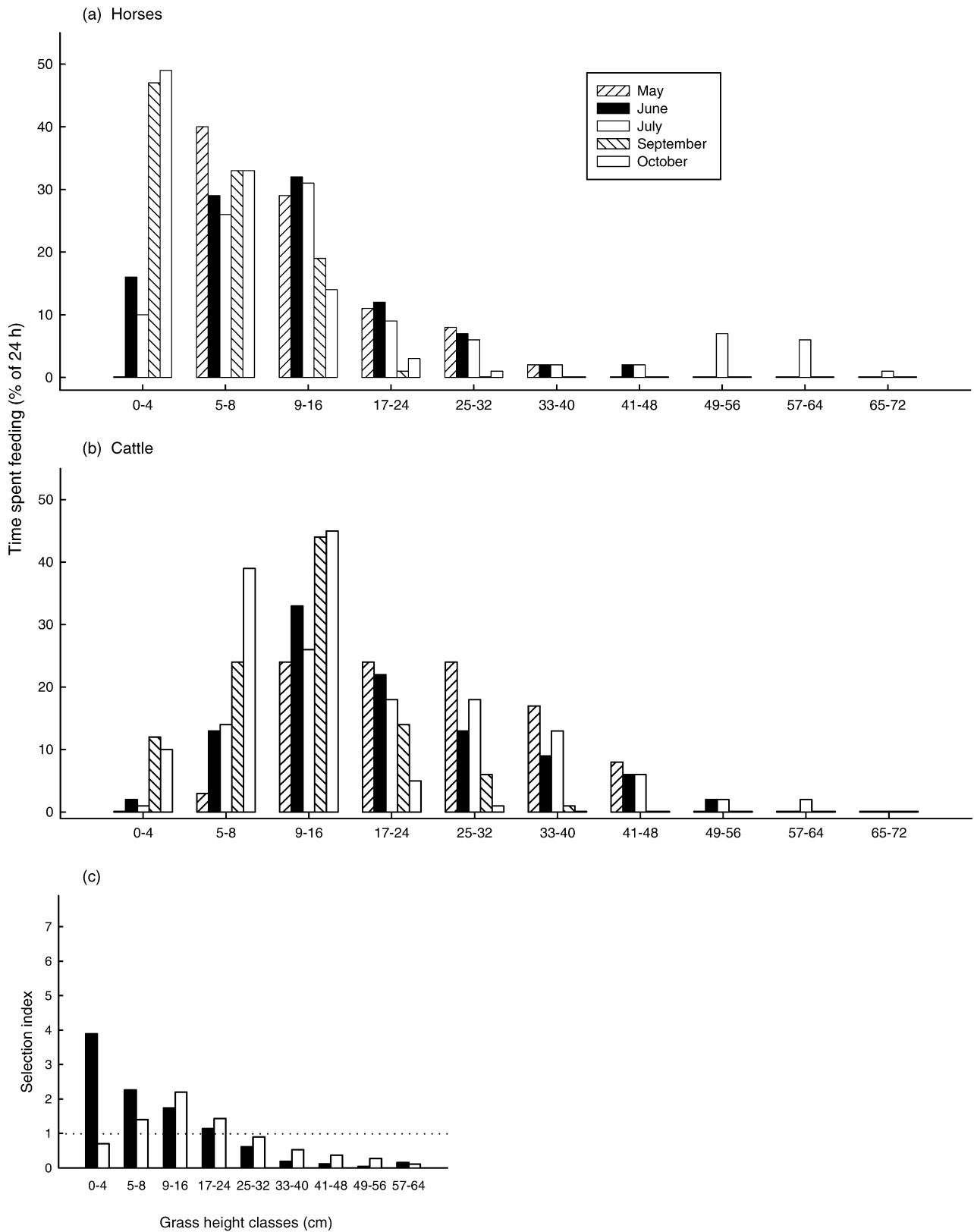
grasslands according to their availability (*S* close to 1·0). The selection indices of the two species differed significantly for two of the three plant communities (wet: $t = -3·567$, $P = 0·001$; dry: $t = 6·597$, $P < 0·001$; but not for intermediate: $t = -0·838$, $P = 0·408$). None the less, the overlap in the use of the three plant communities by horses and cattle in the Marais Poitevin was high (summer: 0·76 + 0·14, *n* = 5; autumn: 0·75 + 0·04, *n* = 6).

There were differences in the use of swards of different height: the horses' modal height class was 5–16 cm in summer, 0–4 cm in autumn (Fig. 3a), for the cattle it was 9–16 cm or taller (Fig. 3b). The horses showed strong selection for grasses shorter than 5 cm, the cattle

Fig. 3. Use of grass height classes by (a) horses and (b) cattle in the Marais Poitevin. The selection indices are shown in (c) for the month with the greatest range of heights available, June 1999, for horses (solid bars) and cattle (white bars). The proportions of time spent by each species on each height class differed significantly from the proportions of the area covered by the height classes in each of the four plots per species (selection index: 0–1 = avoidance, 1–∞ = selection; χ² tests: $n = 100$; $P < 0.001$ in each plot).
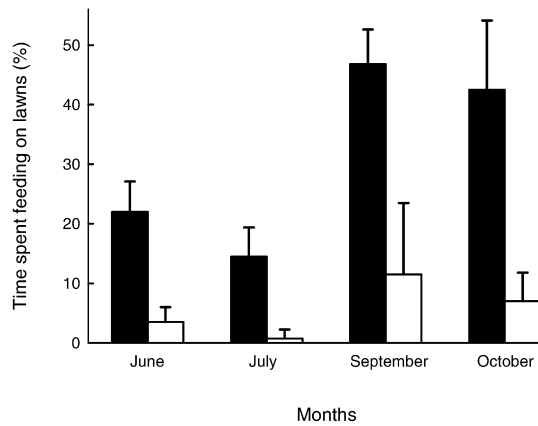
Fig. 4. Proportion of time spent feeding on lawns (sward surface < 5 cm) by horses (solid bars) and cattle (white bars) in mixed species plots in the Marais Poitevin; the areas covered by lawns in the plots were similar (5–8%). Two-way ANOVA: species × month, $F_{4,45} = 44.1$, $P < 0.001$; effect of species, $F_{1,49} = 132$, $P < 0.001$; effect of month, $F_{3,49} = 12.6$, $P < 0.001$; the interactions were not significant.

(Fig. 5) and the horses ate more than the cattle in each month (on average 63% more). The seasonal pattern of daily nutrient extraction followed that for intake, and was unrelated to the fibrosity of the forage: the horses extracted significantly more nutrients than the cattle in all months except July (two-way ANOVA species × month: $r^2 = 0.84$; effect of species: $F_{1,64} = 126$, $P < 0.001$; effect of month: $F_{4,64} = 49$, $P < 0.001$; the interaction was also significant, but explained only 6.6% of the variance).

Discussion

FEEDING NICHES AND THEIR OVERLAP

In the Camargue, where the animals had a wide choice of different habitats year-round, both species used all habitats in the warmer seasons (spring, summer and autumn) and they concentrated their feeding in the drier

habitats where some plant growth occurred in winter. Both species therefore had broader feeding niches in the warmer seasons. Horses selected old-field grasslands and all the marsh habitats strongly in the Camargue, and in the Marais Poitevin they selected the wettest habitat. Cattle preferentially used old-field grasslands year-round in the Camargue, and old-field marshes in summer and autumn. The three grasslands were used as available in the Marais Poitevin. These basic seasonal patterns are similar to those in other areas (Putman 1986; Gordon 1989a), although horses sometimes prefer grasslands, and not marshes, year-round (e.g. in Oostvaardersplassen, an artificial polder in the Netherlands; Vulink & Van Eerden 1998).

In the marshes the diets were very similar, but in the grasslands the cattle ate a wider range of plants than the horses, including the abundant evergreen shrub *Phillyrea angustifolia* and many other dicotyledons, especially clovers. Many of these plants contain secondary compounds (e.g. heterosids in *Phillyrea*; Touati 1985) that may have different effects on ruminants and hind-gut fermenters. Horses are generally monocotyledon specialists (Hansen & Clark 1977; Olsen & Hansen 1977; Krysl *et al.* 1984), although they do broaden their diets considerably when food is sparse (Putman 1996).

The main determinant of habitat use by horses in semi-natural habitats seems to be the availability of green plant tissues (Duncan 1983; Gordon 1989b). In the Camargue during the growing season the highest densities of green plant tissues are found in the marshes. In the winter the aerial parts of the emergent plants of the wetlands die, so no green tissues are available at all, whereas many of the plants in grasslands keep growing through the winter in these mediterranean and atlantic climates. The grasslands of artificial polders such as Oostvaardersplassen are sown with pasture grasses (e.g. *Dactylis*, *Festuca*), which are of much higher quality than natural plants. These results suggest that, in horses, the function of habitat selection, like diet selection (Vulink 2001), is to maximize their intake of digestible
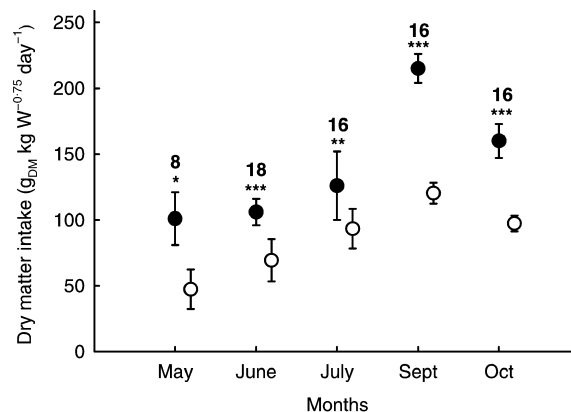
Fig. 5. Dry matter intake (g_{DM} kg $W^{-0.75}$ day^{-1}) by horses (solid circles) and cattle (open circles) in 5 months in 1998 (May, June, October) and 1999 (July, September). The number of days when intake was measured is given for each month. Two-way ANOVA: species × month, $r^2 = 0.89$; effect of species, $F_{1,64} = 238$, $P < 0.001$; effect of month, $F_{4,64} = 7.05$, $P < 0.001$; the interaction was significant, but explained only 3% of the variance. Significant differences between species within months are indicated: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
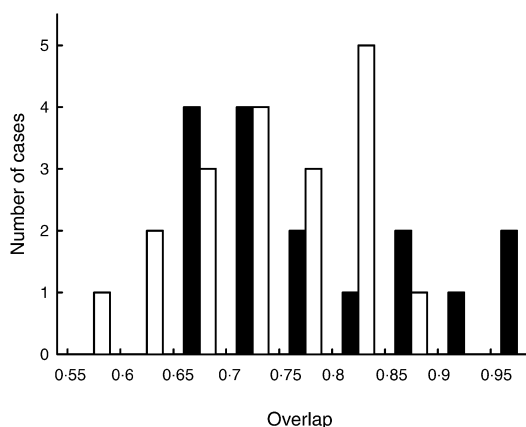
Fig. 6. Overlap in the diets of equids and bovids in four temperate (solid bars) and tropical (open bars) ecosystems (Kulczinski's index, the proportion of the diets that is identical). Each case is a site × season. Data from Gwynne & Bell (1968), Stewart & Stewart (1970), Owaga (1975), Hansen & Clark (1977), Olsen & Hansen (1977), Sinclair (1977), Krysl *et al.* (1984) and Putman (1996).

nutrients. The patterns of habitat use by horses in European wetlands therefore appear to be determined by an interaction of the amount and the quality of green plant tissues available.

Cattle have a similar diet selection strategy (maximizing nutrient intake; Vulink & Drost 1991) but use the resources differently because they are less constrained by secondary metabolites (so are able to use dicotyledons to a greater extent) but more constrained by plant height (so are unable to use short grasslands). The feeding niches of horses and cattle therefore differ, especially in winter, but overlap between the two species was great (> 50% in both areas, all seasons and across two spatial scales; Table 5). A similar conclusion was reached in another study of horses and cattle in a European wetland where 'On average differences in botanical composition between diets of horses and cattle were small ...' (Vulink 2001). More generally, high levels of diet overlap are typical for equids and grazing bovids in a wide range of temperate and tropical ecosystems, from deserts to forests (median = 0·73; Fig. 6). However, in two systems with heavy grazing pressure, overlap in winter was low (New Forest, 0·23 Pianka's index, Putman 1996; Isle of Rum 0·23, Schoener's index, Gordon & Illius 1989) because the cattle abandoned completely the very short high-quality grasslands. They were apparently excluded by the horses, whose twin sets of incisors enable them to have a steeper functional response than cattle for instantaneous intake (Gross *et al.* 1993), and they can maintain this difference for daily intake by their long 24-h feeding times (up to 75%; Mesochina 2000).

The horses in the Marais Poitevin preferred short grass (< 5 cm sward surface), where they established and maintained grazing lawns. They spent up to 70% of their grazing time on these (as in other areas; Odberg & Francis-Smith 1976; Putman 1986) and apparently

improve the quality of their diet (crude protein 38% higher; Fleurance, Duncan & Mallevaud 2001). Cattle feed on the patches of taller grasses avoided by the horses and, at a coarser spatial scale, horses and cattle may occupy different parts of wet grasslands (Putman, Fowler & Tout 1991). The feeding niches of the two species therefore differ, as predicted in the first hypothesis.

COMPARATIVE NUTRITION

The feeding times in the Marais Poitevin (for mares 54% in summer and 68% in autumn, for cows 36% and 48%, respectively) were within the normal range observed in other extensive grazing systems (mares 50–68%, Duncan 1992; cows 17–54%, Arnold & Dudzinski 1978). The animals in these experimental conditions therefore had time budgets typical for their species.

The estimated digestibility of the diets (53–61% for horses and 59–63% for cattle) was average for the species (40–70% horses, 40–75% in cattle; Duncan *et al.* 1990), which shows that the animals were feeding on medium-quality forage. The cattle digested their food to a greater extent than the horses, as predicted.

The cattle ate $46 \pm 15 - 119 \pm 8$ g_{DM} kg $W^{-0.75}$ day^{-1}, consistent with the results of other studies of cattle at pasture and in stalls (e.g. 43–114 g_{DM} kg $W^{-0.75}$ day^{-1}; Dulphy *et al.* 1994). The highest values were observed in autumn: food intake by cattle increases with increasing requirements for maintenance, growth and reproduction, and with the quality of the forages. In this study intake was not correlated with forage quality (NDF, nitrogen) and the cause of the increase in autumn, when the availability of the food was low and its digestibility declining, is unknown.

The horses ate $101 \pm 20 - 215 \pm 11$ g_{DM} kg $W^{-0.75}$ day^{-1} (i.e. 63% more than cattle), which is high compared with published studies of stalled geldings (65–115 g_{DM} kg $W^{-0.75}$ day^{-1}; Duncan 1992; Dulphy *et al.* 1994) but consistent with data on horses with high requirements (e.g. lactating mares, 155–188 g_{DM} kg $W^{-0.75}$ day^{-1}, and breeding and growing mares at pasture, 155–197 g_{DM} kg $W^{-0.75}$ day^{-1}; Duncan 1992; Fleurance, Duncan & Mallevaud 2001). The highest intakes were also observed in autumn: food intake by horses does not appear to vary with diet quality (Duncan 1992), and the high values observed for growing and lactating horses suggest that the principal determinant of daily intake in horses is the animals' requirements: why these should be higher in autumn is unknown.

The horses therefore ate much more than the cattle (+63%), so much so that even on these medium-quality forages the horses acquired more digestible nutrients per day. These comparative nutritional data, obtained from animals at pasture for the first time, therefore do not support the second hypothesis, and suggest that equids achieve higher nutrient extraction rates than bovids on all forages, at pasture as in stalls (Duncan *et al.* 1990; Illius & Gordon 1992).

COMPETITION AND CO-EXISTENCE OF EQUIDS AND BOVIDS IN NATURAL ECOSYSTEMS

The nutritional model proposed to explain the co-existence of equids and grazing bovids (Janis 1976) assumed that bovids extract more nutrients per day than equids on medium-quality forage, so the results reported here do not support it. However, further data are clearly needed from temperate ecosystems in winter, when low food availability may limit the rate of intake by horses, and from tropical ecosystems, where the grasslands often have low basal cover and may be less favourable for equids. The energy costs of the high-intake strategy of the equids at pasture also need to be evaluated.

The data on feeding niches in this and two other ecosystems support the alternative mechanism that could explain co-existence of these animals, resource partitioning, for the cattle have a refuge in the form of a wide range of dicotyledonous plants that the horses avoid. None the less, these studies show that there are high levels of niche overlap: although the ecological significance of such overlap is controversial (Tokeshi 1999), these results suggest that there is potential for strong competition between horses and cattle. Negative effects of the presence of horses on the life-history traits of cattle (or vice versa) have not been demonstrated, perhaps because in the systems where most of the work has been done, ecological processes are masked by cultural ones. None the less, the circumstantial evidence is that competition does indeed occur (Putman 1996). In one European grazing system, Oostvaardersplassen in the Netherlands, cattle and horses are being allowed to come to equilibrium with the vegetation (Vulink & Van Eerden 1998). In this artificial polder, where most of the food of the animals is medium-quality grasses, the intrinsic rate of population increase is significantly higher in the horses (koniks, 1984–2000, $r = 0.25$) than the Heck cattle ($r = 0.21$, $P < 0.01$; Vulink 2001; T. Vulink, personal communication). We predict that when this system comes to equilibrium the horses will outcompete the cattle. If this is so, in natural ecosystems cattle should persist only if there are adequate amounts of broadleaved plants unavailable to horses, or if high predation on horses limits their numbers. This hypothesis is currently being tested for zebras and grazing bovids in an African ecosystem.

THE IMPACT OF GRAZING AND WETLAND MANAGEMENT

The densities and biomass of the animals in the natural habitats of the Camargue (< 0.25 individuals ha⁻¹, median biomass 20 kg ha⁻¹) were low but within the range of biomasses in near-natural temperate multi-species grazing systems cited in WallisDeVries (1998; 8–67 kg ha⁻¹). The old-field habitats in the Camargue, however, carried densities and biomass about 10 times as high as the natural habitats (*c.* one individual ha⁻¹

and 250 kg ha⁻¹). The plants that naturally colonized these abandoned arable fields were intensively used throughout the year, and the old-field marshes, maintained by an appropriate artificial flooding regime, were the preferred habitat in autumn when use of the natural marshes declined as the reeds became overmature. Old fields can therefore be used to create good grazing with minimal management, and thus greatly increase the carrying capacity of grazing systems in this area. This can provide important flexibility for management in the Camargue, and perhaps elsewhere in the mediterranean region where fresh water is available for pastoral and wildlife management. There is no evidence for interference competition between horses and cattle, and their slightly different feeding niches mean that the two species together use the vegetation, to some extent, in a complementary manner.

The high ecological overlap between horses and cattle shown by this and the other studies cited above means that these animals can be considered broadly as alternative tools for the management of marshes. Where the objective of management is to control the development of the vegetation in marshes, the feeding strategy of horses means that this can be achieved with fewer horses and less management than with cattle. Horses seek out the areas most productive of green biomass, which leads them to use marshes preferentially for most of the year, and they did so to a greater extent in both the Camargue and the Marais Poitevin, although not in the artificial polders of the Netherlands (Vulink 2001). Where the objective of management is to restore a natural guild of grazers, these results suggest that cattle will require an ecological refuge for survival in winter, in the form of large areas of woodland and shrubland with dicotyledonous plants not used by equids.

In spite of the low densities in the Camargue, the impact of horses and cattle on the vegetation of the marshes was strong: they maintained short reed beds of *Phragmites australis* and *Bolboschoenus maritimus* (Duncan 1992), as in other grazed European wetlands (Van Deursen & Drost 1990). In old-field marshes, which tend to become colonized by ruderal species such as *Typha angustifolia* and *Alisma plantago-aquatica*, the more catholic feeding behaviour of cattle means that they maintain open habitats that would become closed under grazing by horses alone (Mesléard, Grillas & Lepart 1991).

The impact of the two species on grassland vegetation differs more sharply: two principles are involved, first the creation and maintenance of grazing lawns is much stronger under horse than cattle grazing, and secondly, cattle are better able to use plants with secondary metabolites than are horses. In many grasslands removal of grazing leads to a rapid decline in plant species diversity as competitive perennial grasses exclude other species (Bakker & Van Wieren 1998). A relatively high biomass of cattle is required to maintain plant diversity in such grasslands (in the Marais Poitevin, > 700 kg ha⁻¹ for 5 months), but horses maintain grazing

lawns whatever their densities, so some diversity is maintained at a wide range of stocking levels (300–900 kg ha^{-1}; Amiaud 1998). In the longer term, grasslands in most wetlands are invaded by woody plants, in the Camargue by the shrub *Phillyrea*. Horses do not eat this plant so their impact on its abundance is negligible. Cattle, however, when maintained at high densities, can be effective at controlling the cover and height, if not the number of individuals, of this species (Strasberg 1987). In the Netherlands the same principle holds: grasslands grazed by horses are colonized rapidly by *Sambucus nigra*, but the process is much slower under cattle grazing (Vulink 2001).

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