



## Selection of feeding sites by horses at pasture: Testing the anti-parasite theory

Geraldine Fleurance<sup>a,\*</sup>, Patrick Duncan<sup>b</sup>, Herve Fritz<sup>b</sup>,  
Jacques Cabaret<sup>c</sup>, Jacques Cortet<sup>c</sup>, Iain J. Gordon<sup>d,1</sup>

<sup>a</sup> *Les Haras Nationaux, Direction des Connaissances, Station Expérimentale des Haras Nationaux, 19370 Chamberet, France*

<sup>b</sup> *Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France*

<sup>c</sup> *INRA, Infectiologie Animale et Santé Publique, 37380 Nouzilly, France*

<sup>d</sup> *The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, United Kingdom*

Accepted 19 November 2006

Available online 15 December 2006

### Abstract

Management of grazed grasslands for production and/or conservation objectives requires a thorough understanding of the choices of feeding sites by herbivores, and of the biological processes involved. Most models of the feeding strategies of herbivores are based on the principle that optimising the intake of energy (or some nutrient) is the primary goal of foragers but other selective forces, such as parasitism, could be important. Gastrointestinal parasites (including cyathostome nematodes) have powerful effects on the fitness of herbivores and may act as a major selection pressure favouring host behaviour that reduces the risk of encountering parasites. Among large herbivores, horses have perhaps the most marked tendency to select particular feeding sites within grasslands. We test here: (1) whether horses select feeding patches with relatively low parasite densities and (2) if their choice is affected by their parasite load. We used 10 two-year old saddle-horses and three periods. In the first period, the horses were under natural parasitism which varied strongly among individuals; in the second period they were all dewormed, and in the third, a sub-set of the horses was experimentally infected with cyathostome larvae. Ninety-eight percent of the infective larvae in the pasture were found <1 m from faeces. The main determinant of the choice of feeding patch by horses was the availability of patches of different parasite risk and grass height. Controlling for availability, the horses used tall grasses (>16 cm) less than expected, whether the grass was contaminated or not, and they selected for short patches >1 m from faeces, where the risk of encountering parasites was low. These results suggest that selection of feeding sites by horses is driven by an interaction between their

\* Corresponding author. Present address: INRA Clermont-Ferrand/Theix, Unité de Recherche sur les Herbivores, 63122 Saint-Genès-Champanelle, France. Tel.: +33 473 62 4652; fax: +33 473 62 4118.

E-mail address: [geraldine.fleurance@clermont.inra.fr](mailto:geraldine.fleurance@clermont.inra.fr) (G. Fleurance).

<sup>1</sup> Present address: CSIRO, Davies Laboratory, PMB PO Aitkenvale, Qld 4814, Australia.

nutritional and anti-parasite strategies: the horses avoid the patches of tall grass which are generally of low quality and areas contaminated by parasite larvae which leads them to prefer the patches of short grass far from faeces. The parasite status of the horses at the time of the experiment had no effect on their feeding choices. However, before concluding that the challenge by cyathostomes has no effect on the selection of feeding sites in horses, it will be necessary to test whether the history of parasitism of the individuals, rather than the current status, is important.

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*Keywords:* Foraging strategies; Horses; Parasite risk; Patch choice

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## 1. Introduction

Grasslands grazed by herbivores generally consist of mosaics of patches of different physical structure and floristic composition. The spatial heterogeneity of the vegetation determines the abundance and quality of food resources for grazing animals (Hodgson, 1990) and has a major influence on biodiversity (Bullock and Mariott, 2000). Management of these grasslands for production and/or conservation objectives, therefore, requires a thorough understanding of the choices of feeding sites by herbivores, and of the biological processes underlying these choices.

The assumption in most optimal foraging models is that optimisation of the intake of energy (or some nutrient) is the primary goal of foragers (Stephens and Krebs, 1986). Nonetheless, other factors, such as the risk of predation or parasitism, are now incorporated into such models, and this improves their predictive powers (Lozano, 1991). Gastrointestinal parasites constitute an important challenge to the performance and even survival of herbivore hosts in both intensive and extensive agricultural systems, as well as in natural ones (Coop et al., 1982; Grenfell, 1992; Gulland, 1992). These parasites impair their host's productivity, mainly by reducing the efficiency of food utilization, particularly the absorption of nutrients (Coop and Kyriazakis, 1999). As a consequence, gastrointestinal parasites could act as a major selection pressure in favour of host behaviour that reduces the risk of encountering infective stages of the life history or, if already parasitized, that reduces the negative impacts of infection (Phillips-Conroy, 1986; Bundy and Golden, 1987; Hart, 1990; Hutchings et al., 2003, 2006).

The eggs of many parasites, present in faeces deposited by herbivores on the vegetation, develop into infective, third-stage larvae which migrate onto the surrounding vegetation and are ingested by herbivores (cf. Sykes, 1987). As herbivores do not seem to be able to detect the infective larvae themselves (Cooper et al., 2000), the mechanism involved in reducing parasite infestation could be the avoidance of faeces (Hart, 1990), and this has been observed in many ruminants (Gruner and Sauve, 1982; Forbes and Hodgson, 1985; Hutchings et al., 1998, 1999, 2001, 2002a,b; Cooper et al., 2000). Moreover, the parasite status of individual lambs and sheep has been shown to affect their grazing behaviour, with parasitized animals avoiding contaminated swards to a greater extent than unparasitized ones (Hutchings et al., 1998, 1999, 2001, 2002a,b; Cooper et al., 2000), suggesting that the marginal cost of extra parasites is greater for parasitised than for unparasitised individuals.

Among large generalist herbivores, horses have perhaps the most marked tendency to create and maintain patches of short grass where they concentrate their feeding (70% of their daily foraging time, Putman et al., 1987; Ménard et al., 2002) within a matrix of tall swards contaminated by faeces (Ödberg and Francis-Smith, 1976; Edwards and Hollis, 1982; Putman

et al., 1991). The usual explanation is that this feeding behaviour is an adaptation to reduce infection by gastrointestinal parasites (Taylor, 1954) though this theory has never been tested in the field (Ödberg and Francis-Smith, 1977).

In this study we test these ideas in horses for the first time, using young saddle-horses grazing an heterogeneous pasture. We first characterize the spatial variation in the risk of consumption of infective larvae (i.e. number of infective larvae  $\text{kg}^{-1}$  dry herbage). We then analyse feeding site selection by the horses in relation to their parasite status, the risk of consumption of infective larvae and grass height (which generally plays a major role in determining the selection of feeding patches by herbivores, Black and Kenney, 1984; Arnold, 1987; Illius and Gordon, 1990). We chose to work with young animals, which are more susceptible than adults to the effects of parasites (Giles et al., 1985; Bucknell et al., 1995).

On the basis of the results of the studies on lambs and sheep cited above, we expected that animals with heavier parasite loads would be more sensitive to the risk of further consumption of infective larvae than unparasitized ones. This result may not, however, be general as animals' choices will depend on the marginal cost of extra parasites and the relative nutritional benefits provided by the patches of grass of different height, both of which will vary in different circumstances. We tested whether:

- (a) avoidance of faeces increased with the parasite burden in individuals which are naturally infested (i.e. with adult worms, larvae and intestinal lesions);
- (b) deworming resulted in the animals becoming less sensitive to risk;
- (c) risk avoidance was greater in individuals experimentally infected with small strongyle larvae (cyathostomes), the main parasites affecting horses at pasture (Herd, 1990; Love et al., 1999), compared with uninfected individuals.

## 2. Materials and methods

### 2.1. Experimental design

The experiment was conducted from May to July 2000 at the estate of the National Stud, the Station Expérimentale des Haras Nationaux (Chamberet, France). The experimental pasture (9.14 ha; tall fescue, *Festuca arundinacea*; rye grass, *Lolium perenne*; white clover, *Trifolium repens*; cocksfoot, *Dactylis glomerata*; alfalfa, *Medicago sativa*) was grazed for 2 months before the experiment by 11 parasitized horses of a heavy breed (Breton, eggs per gram of wet faeces =  $555 \pm 495$  S.D., range: 70–1655). This created patches of short grass, and contaminated the pasture with parasites.

The experimental design involved 10 two-year old growing fillies born at the Station Expérimentale (8 Anglo-arabs and 2 French saddle-horses) and of similar body weights ( $453.0 \pm 15.0$  kg S.D.) which had not been treated with anthelmintics since 11 months before the beginning of the experiment. The experimental timetable was divided into:

- (1) Period 1 (9–30 May 2000) when the 10 horses were infested only with naturally acquired parasites. As it was not possible to count adult worms, faecal egg counts (FEC, eggs per gram of wet faeces) were used to estimate the parasite burdens (see Cabaret et al., 1998). FECs were carried out on the faeces taken from the rectum of the animals twice per week. The McMaster technique, modified by Raynaud (1970) (CINa, density =  $1.18\text{--}1.20$ ;  $360 \text{ g l}^{-1}$ ), was used with a minimal detection level of 15 eggs per gram of wet faeces and data were transformed as  $\log(\text{FEC} + 1)$  before statistical analyses. One faecal culture was performed on one sample per individual (Ministry of Agriculture Fisheries and Food, 1986) to determine the parasite genera present (Bevilaqua et al., 1993).

- (2) Period 2 (5–19 June 2000), the infestation of adult worms in the horses was reduced using Ivermectin (Oramec<sup>®</sup>) and oral Niclosamide<sup>®</sup> for tapeworms with a naso-gastric tube on 31 May 2000. Ivermectin was chosen because cyathostomes have developed high rates of resistance to all commonly used anthelmintics except the avermectin/milbemycins (Kaplan, 2002). Nonetheless, the horses were not expected to be parasite-free as these avermectin/milbemycins do not eliminate encysted cyathostome larvae completely (Eysker et al., 1992; Klei et al., 1993). Three faecal egg counts were performed per animal on 7, 13 and 19 June to measure the efficacy of the treatment. One blood sample per individual had been tested for liver flukes on 25 May and the results were negative.
- (3) Period 3 (4–18 July 2000), during which the horses were separated into two groups balanced for their FEC when naturally infested and for breed, live-weight, height at withers and paternity (three different fathers). Individuals nos. 1–5 were experimentally infected with 40,000 cyathostome larvae administered with a naso-gastric tube on 4 July (Smith, 1976; Patton et al., 1978; Collobert et al., 1998). Assuming a probability of development of 50% (J. Cabaret, personal observation), this infestation should have led to a normal level of adult worm infestation for naturally infected horses (Ogbourne, 1976; Pecheur et al., 1979; Reinemeyer et al., 1986; Bucknell et al., 1995; Gawor, 1995). In order to maximize the difference in parasite load between the two groups, individuals nos. 6–10 were treated on 4 July with Ivermectin and oral Niclosamide, again using a naso-gastric tube. When ingested by horses, the third stage larvae of cyathostomes migrate into the mucosa and sometimes submucosa of the large intestine where they encyst (Ogbourne, 1978); severe pathogenicity (typhlitis/colitis) is more likely to occur during larval penetration (Murphy and Love, 1997; Thamsborg et al., 1998; Love et al., 1999). In period 3 of our experiment, the penetration and activity in the mucosae constituted the parasitic stress. As the patent period (delay between infection and nematode egg-laying) is over 2 months after infection, no egg was expected to be recovered in period 3. Faecal egg counts (FEC) were performed on 6, 10, 13 and 17 July to measure the effectiveness of the anthelmintic treatment in the unparasitized group. The parasitized animals were handled in the same way and faecal egg counts were carried out every 2 weeks until the 16 October to check the efficacy of the experimental infection with cyathostome larvae (i.e. to verify the development of adults from the larvae).

No studies are available concerning the timing of potential changes in the behaviour of horses following a change in their parasite status. On the basis of the studies conducted in sheep (Kyriazakis et al., 1998; Hutchings et al., 2002a) and cattle (Forbes et al., 2004), where the animals adapted their behaviour to their level of infection in a few days, and, in the case of period 3, because severe pathogenicity of cyathostomes occur generally during larval penetration, the behavioural observations of horses were made about 1 week after each of the treatments.

The experimental pasture was grazed continuously by the 10 animals, including the days between the three experimental periods cited above.

## 2.2. Pasture contamination

Pasture contamination was assessed five times in each period except for the period 3 (one measurement only, because of rain). The number of infective larvae (L3) per kg of dry herbage was measured at different distances from faeces using a modification of the Gruner and Sauve (1982) method: 5 patches of grass contaminated with faeces, and 10 dung piles in each patch, were chosen at random in the pasture. As the majority of larvae are found in the first 30 cm around the faeces (Gruner and Sauve, 1982); one pinch of grass (between thumb and forefinger, about 0.4 g of fresh grass; Ministry of Agriculture Fisheries and Food, 1986) was taken by one person in each quarter of three rings 0–15, 16–30 and 31–100 cm around the faeces (Fig. 1), and then pooled by ring for the 50 dung piles. In each of five patches, three 30 m × 5 m transects (named a–c) were delimited at random 1 m from a faecal pile (Fig. 1). Fifty sampling points (each point was composed of four pinches taken by the same person) were performed in zigzags in each transect (Fig. 1) and samples were pooled through the five patches by transects (a–c) before laboratory analysis. Each grass sample for analysis did not exceed 300 g in order to have a good recovery of the larvae in the herbage (Raynaud and Gruner, 1980). The risk of consumption of infective larvae encountered by the horses when grazing was determined for the

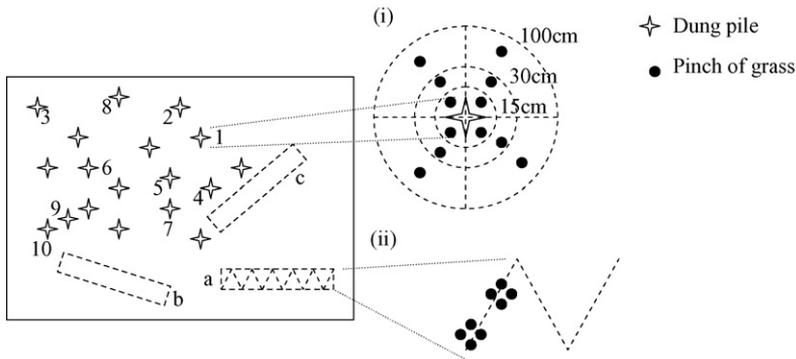


Fig. 1. Sward sampling for measuring the density of infective larvae. (i) In a patch contaminated with faeces: one pinch of grass was taken in each quarter of the three rings (0–15, 16–30 and 31–100 cm) surrounding 10 dung piles chosen at random. (ii) In a patch >1 m from a dung pile (transects a–c): 50 sampling points, composed of four pinches, were performed in zigzags in each 30 m × 5 m transect.

different distance classes from faeces (0–15 cm, 16–30 cm, 31–100 cm and >1 m) from the density of infective larvae which were present (number of larvae per kg of dry herbage). Infective larvae in the grass were extracted, identified and counted by the Laboratoire Vétérinaire Départemental de Corrèze (France). The larvae were extracted from the grass after it had been soaked for one day in a bucket and then sieved. After collection on a 20 µm sieve the larvae were concentrated by floatation in magnesium sulfate ( $d = 1.29$ ) for counting and genera identification (see Gruner and Raynaud, 1980). Transformations to  $\log(\text{infective larvae } L3 + 1)$  were performed to normalise the data before statistical analyses.

### 2.3. Grazing behaviour

The horses were first accustomed to grazing the pasture and direct observations were used to measure diet selection as it has been successfully done in previous studies conducted on different species of herbivores including horses (Dumont et al., 1995; Gillingham et al., 1997; Tixier et al., 1997; Ménard et al., 2002). Several days were set aside before each observations period in order to get the horses accustomed to the close and continuous presence of the observer, using a lamp at night. The behaviour of the horses was recorded using scan sampling (Altmann, 1974) at 30 min intervals during three 24 h cycles for each of the three periods. When an individual was recorded as feeding (i.e. prehending food, biting, chewing or swallowing), the observer, situated level with the horses' hindquarters, but to one side, counted five bites keeping their eye on the exact location of the last bite. Once the animal moved forward enough (>3 m) from the bite location, the observer moved to the location of the bite and measured the grass height (measured with a drop disc, i.e. a sliding square of polystyrene (100 cm<sup>2</sup>; 2.7 g; Stewart et al., 2001) and the distance class from the closest faeces (0–15 cm, 16–30 cm, 31–100 cm and >1 m, measured with a folding ruler). The horses were very tame and the observer was extremely careful never to force the animals to move away from its chosen feeding patch. The relative availability of the different grass heights and distances from the closest faeces were assessed in each period by systematic observations every 10 m on parallel transects covering the entire pasture (about 860 sample points per period).

### 2.4. Statistical analysis

The data were grouped into classes for statistical analyses, for grass heights (1–4, 5–8, 9–16, 17–24, 25–32, 33–40, 41–48, 49–56, 57–64, 65–72, 73–80, 81–88 and >88 cm). After arcsine transformation for proportions (Sokal and Rohlf, 1995), analysis of variance was conducted using Systat (SPSS, 1998), as the assumptions for parametric tests were met. In each period, we first calculated the number of feeding observations expected, on the basis of areas, for the different combinations of grass height and risk of

consumption of infective larvae classes, assuming that the animals were distributing their feeding behaviour randomly in relation to the availability of grass height and risk of consumption of infective larvae classes in the pasture ('available'). This variable was first fitted in a general linear mixed model (GLIMMIX procedure) adapted to Poisson distributions (PROC MIXED; SAS, 1999); we then fitted 'parasite status' as  $\log(\text{FEC} + 1)$  in the first period, where the FEC value was the mean of the six samples taken from each individual in periods 1 and 2; and parasitized versus unparasitized in the third period. The other variables were then fitted in the following order: 'risk' (i.e. risk of consumption of infective larvae, with two modalities high/low), 'height class' (i.e. grass height in 13 classes, see above), risk  $\times$  height, parasite status  $\times$  height, parasite status  $\times$  risk, parasite status  $\times$  height  $\times$  risk to test whether they had an effect on the distribution of horses grazing behaviour. 'Date', 'individual' and their interaction were included as random effects: this procedure generates a more powerful analysis by ensuring that variance due to these variables is taken into account in the analysis, and not simply included in the error term.

### 3. Results

#### 3.1. The parasites in the pasture and in the horses

As expected, small strongyles dominated the community of larvae in the pasture (Table 1). Across the sward as a whole, the density of larvae showed strong spatial variability, with some patches of the pasture with less than 50 larvae per kg of herbage, and others with thousands. There was, as expected, a clear effect of faecal piles: the number of infective larvae (L3) were significantly lower  $> 1$  m from the faeces ( $40 \pm 14$  L3  $\text{kg}^{-1}$  DM S.E.,  $n = 31$ ) than for each of the closer distances (0–15 cm,  $1704 \pm 254$  L3  $\text{kg}^{-1}$  DM S.E.,  $n = 11$ ; 16–30 cm,  $829 \pm 112$  L3  $\text{kg}^{-1}$  DM S.E.,  $n = 11$ ; 31–100 cm,  $387 \pm 71$  L3  $\text{kg}^{-1}$  DM S.E.,  $n = 11$  (one-way anova:  $F_{3,60} = 51.853$ ,  $p < 0.0001$ )). The differences between the three closest distance classes were not significant but the variance was high. The risk encountered by the horses feeding  $> 1$  m away from the faeces was, therefore, classed as "low" and the risk when they were grazing in one of the three other classes as "high". The proportion of the pasture affected by faeces (i.e. the area of sward  $< 1$  m from faeces) varied between 24 and 38% during the three experimental periods.

The height of the grass varied among periods (one-way anova:  $F_{2,2585} = 45.104$ ,  $p < 0.0001$ ) with lower values in the first (natural infestation,  $32 \pm 19$  cm S.D.,  $n = 867$ ) and in the last periods (one-half of the horses experimentally infected,  $30 \pm 25$  cm S.D.,  $n = 864$ ) compared to the second one (the horses dewormed,  $40 \pm 25$  cm S.D.,  $n = 857$ ). There was no correlation

Table 1

Relative abundance of the different genera of strongyle nematode infective larvae (percentage of the total population) on the experimental pasture (all periods) and in the horses (period 1)

	Pasture (%)	Horses (%)
<i>Cyathostominae</i> small strongyles or cyathostomes		
<i>Cyathostomum</i> sp.	59.4	66.7
<i>Gyalocephalus</i> sp.	11.8	6.4
<i>Poteriostomum</i> sp.	7.8	9.2
<i>Strongylinae</i> large strongyles		
<i>Strongylus vulgaris</i>	10.6	10.0
<i>Oesophagodontus</i> sp.	8.7	4.5
<i>Strongylus equinus</i>	1.5	0.2
<i>Triodontophorus</i> sp.	0.2	3.0

The classification follows Lichtenfels (1975) and Bevilacqua et al. (1993).

between grass height and distance from faeces in the second and third periods (Spearman,  $p > 0.3$ ,  $n > 850$ ), and a weakly positive one in the first period (Spearman correlation coefficient,  $r = 0.218$ ,  $p < 0.001$ ,  $n = 867$ ).

The 10 horses initially had very different rates of excretion of parasite eggs (one-way anova:  $F_{9,50} = 42.64$ ,  $p < 0.001$ , small and large strongyles combined), which varied between 80 and 1175 eggs  $g^{-1}$  of faeces (mean value: 574 eggs  $g^{-1}$ ) (Fig. 2). Small strongyles represented between 69 and 100% of the nematode populations of the different horses, and small and large strongyles were significantly correlated (Spearman:  $r = 0.80$ ,  $p < 0.01$ ,  $n = 10$ ). The genus *Cyathostomum* was the commonest in the faeces (Table 1). No eggs were found in the 10 animals during the second period, confirming the efficacy of the anthelmintic treatments (Fig. 2). In the third period, one-half of the individuals were successfully experimentally infected with larvae, as shown by the production of eggs measured during the following weeks (Fig. 2). Time spent foraging was unaffected by differences in parasite status (on average 59% of the 24 h, one-way anova,  $F_{1,28} = 0.852$ ,  $p = 0.364$ ) and no clinical symptoms of infection were apparent in the horses.

### 3.2. Feeding behaviour of naturally infected individuals

The availability of the different types of feeding sites (classes of grass height and risk of consumption of infective larvae) was a prime determinant of the feeding sites by the horses ( $F_{1,1256} = 843.7$ ,  $p < 0.0001$ ). After taking the availability of the different types of feeding sites into account, selection of feeding sites was still strongly influenced by the risk of consumption of infective larvae ( $F_{1,1256} = 231.6$ ,  $p < 0.0001$ ), grass height ( $F_{1,1256} = 215.6$ ,  $p < 0.0001$ ) and their interaction ( $F_{1,1256} = 26.6$ ,  $p < 0.0001$ ), but the horses with the highest excretion rates did not spend more time grazing low risk areas ( $F_{1,1256} = 1.12$ , ns). The horses used the tall grass (i.e.  $> 16$  cm; Fig. 3A) less than expected, selecting strongly grass of 5–16 cm height where the risk of consumption of infective larvae was low.

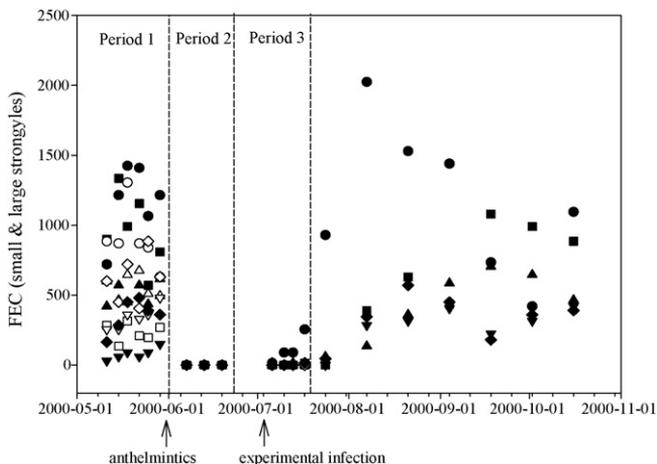


Fig. 2. Changes in the FEC of the 10 individuals throughout the whole experiment (one symbol per individual). For the all figure, the five individuals experimentally infected in period 3 are in black while the five individuals dewormed in period 3 are in white. Period 1, 10 horses naturally infected; period 2, 10 individuals dewormed (symbols are superimposed); period 3, 5 individuals experimentally infected with cyathostome larvae, 5 individuals dewormed (some symbols are superimposed). The FEC of the five individuals experimentally infected with cyathostome larvae in period 3 were measured until 16 October to check the efficacy of the experimental infection.

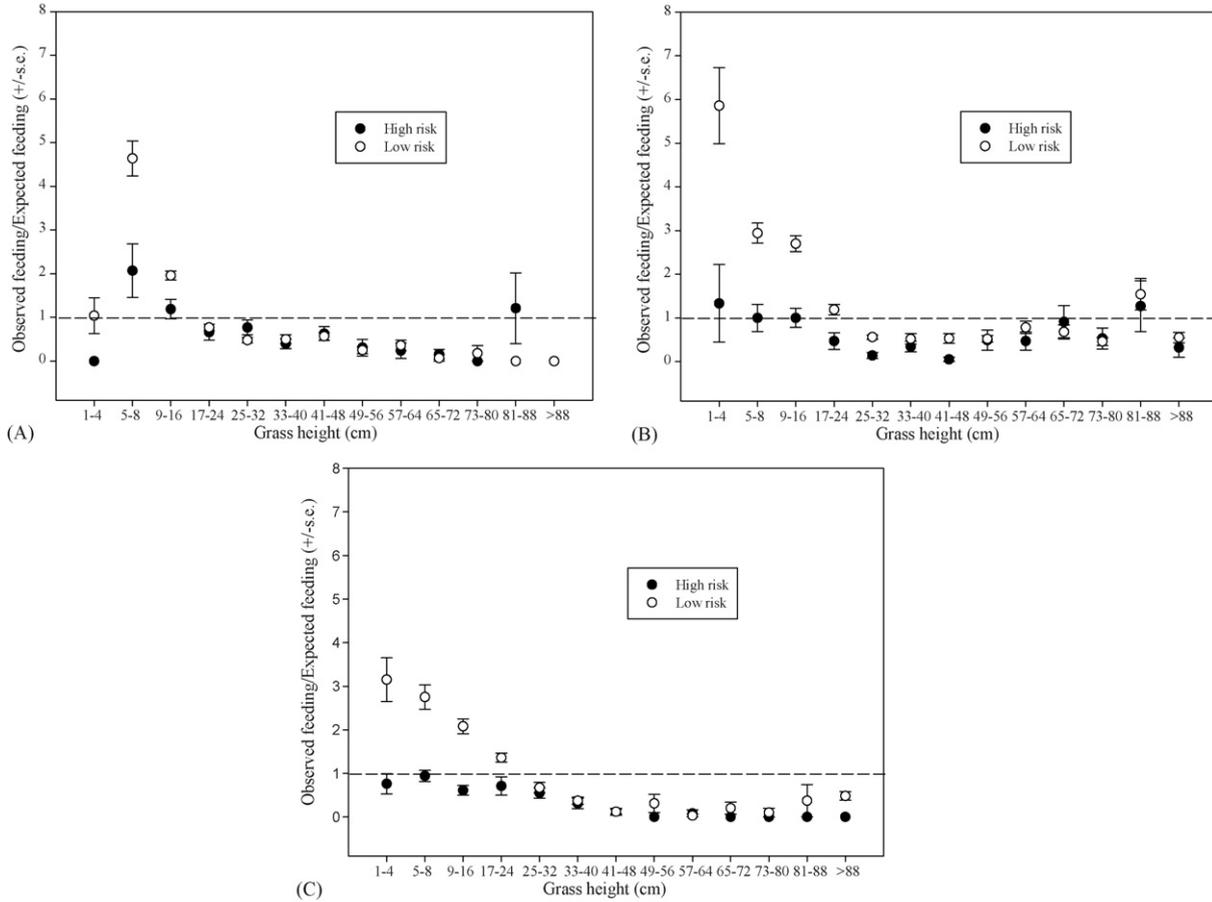


Fig. 3. Feeding site selection for different grass heights: the ratio of observed to expected under the hypothesis of random use (i.e. the availability of the different combinations of the 13 grass heights classes and the two level of risk of consumption of infective larvae: low (>1 m from faeces); open circles and high (<1 m from faeces); solid circles  $n = 10$ ). Ratio: <1, avoidance; 1, used as expected; >1, used more than expected. (A) Naturally infected individuals = period 1. (B) Dewormed individuals = period 2. (C) One-half of the individuals experimentally infected, one-half of the individuals dewormed = period 3.

### 3.3. The effect of deworming

As in the first period, after taking into account the effect of availability ( $F_{1,1412} = 560.0$ ,  $p < 0.0001$ ), the horses' foraging was still strongly influenced by the risk of consumption of infective larvae and they never used feeding sites within 1 m of faeces more than expected ( $F_{1,1412} = 192.1$ ,  $p < 0.0001$ ; Fig. 3B). Grass height explained a large part of the variance in the selection of feeding sites by the horses, with tall grass (i.e. >16 cm) used very little ( $F_{1,1412} = 132.8$ ,  $p < 0.0001$ ; Fig. 3B). The interaction between risk and height was significant, as the horses selected short grass only where it was >1 m away from a faecal pile ( $F_{1,1412} = 12.5$ ,  $p < 0.001$ ; Fig. 3B).

### 3.4. The effect of artificial infection

As in the two first periods, the choice of feeding sites by the horses was partly explained by availability ( $F_{1,1350} = 992.7$ ,  $p < 0.0001$ ); and the effects of risk of consumption of infective larvae ( $F_{1,1350} = 126.8$ ,  $p < 0.0001$ ) and grass height ( $F_{1,1350} = 308.5$ ,  $p < 0.0001$ ) were strong. All the horses, whatever their parasite status ( $F_{1,1350} = 0.08$ , ns), used contaminated areas and patches of tall grass relatively little (Fig. 3C). The interaction between grass height and risk of consumption of infective larvae was nearly significant ( $p = 0.06$ ), and, as in the period during which the horses were dewormed, the horses selected short grass only when the risk of parasitism was low.

## 4. Discussion

Small strongyles dominated the nematode communities, as is usually the case in grasslands grazed by horses (Herd, 1990; Love et al., 1999); *Cyathostomum* was the commonest genus. Ninety-eight percent of the infective larvae were found less than 1 m from faeces: this was expected as the capacity of the larvae of these nematodes to disperse from faecal deposits is limited (Herd and Willardson, 1985). The variability in each of the three closest distance classes from faeces (0–15, 16–30 and 31–100 cm) was high, perhaps because the age of the faecal piles differed as shown in cattle (Gruner and Sauve, 1982).

The heterogeneity of the pasture in terms of sward structure was consistent with previous observations on grasslands grazed by horses (e.g. Ménard et al., 2002), with mean values of grass heights comprised here between 30 and 40 cm and standard deviations between 19 and 25 cm. The correlation between the two variables, parasite risk and grass height was nonexistent or weakly positive, perhaps because where the risk of consumption of infective larvae was low (i.e. at distances >1 m from a faecal pile), grass height was very variable. The principal determinant of the choice of feeding sites by these horses was their availability (i.e. the abundance of patches of different risks of consumption of infective larvae and different heights in the pasture), as has been observed in cattle (Illius et al., 1987). After taking availability of the different types of feeding site (risks of consumption of infective larvae and grass heights) into account, the animals avoided patches near faeces, as in ruminants (Gruner and Sauve, 1982; Forbes and Hodgson, 1985; Hutchings et al., 1998, 1999; Ezenwa, 2004). Studies of horses have provided contrasting results: Ödberg and Francis-Smith (1977) offered horses the choice of cut grass from lawns and roughs, with and without faeces and showed that the horses ate grass cut from both areas equally but refused both when a faecal bolus was present. Medica et al. (1996) on the other hand showed that horses defecated and fed on both lawns and roughs (tall grass areas), but only under very high stocking densities.

The parasite burden of individual horses seemed to have no effect on their feeding behaviour, since:

- in the first period the animals reduced their use of patches near faeces and the taller swards (>16 cm) to the same extent, regardless of their parasite burden in spite of the fact that the FECs were highly variable among individuals;
- the horses did not become less risk averse (i.e. spend more time feeding at <1 m from faeces) in the second period, when their parasite load was strongly reduced by treatment with anthelmintic drugs (they did not become more risk averse either);
- in the third period, the horses reduced their use of grass near faeces and selected short grass to the same extent, whether they were experimentally infected with cyathostome larvae or not.

The differences in the mean values did not even go in the direction of the predictions. We cannot exclude the possibility that horses may respond later than ruminants to a change in their parasite status as the life cycles of their nematodes differ and that the observations came too early in periods 2 and 3, and/or that the level of experimental infection was too low in period 3. Nonetheless, one-half of the individuals remained dewormed in both periods 2 and 3 and never changed their behaviour. Moreover, the lack of any effect of the parasite burden of horses in period 1 when the natural infection was highly variable between individuals is also different from previous observations in ruminants (Hutchings et al., 2002a,b) and consistent with the results obtained in the two following periods. The parasite burden of individuals will affect their foraging decisions only if they are able to evaluate their parasite status. It is possible that horses cannot, but this is unlikely as lambs appear to be able to do so: foraging decisions in ruminants are influenced by the parasite burdens they carry, with parasitized individuals avoiding swards contaminated by faeces more strongly than uninfected ones (Hutchings et al., 1998, 2001, 2002a,b; Cooper et al., 2000). A lack of any effect of the parasite status on feeding behaviour has also been found in other horses (Fleurance et al., 2005) and also in reindeer (van der Wal et al., 2000). It is, however, possible that the history of parasitism is an important determinant of their behaviour, a hypothesis which should be tested with foals which are naïve to parasites.

The horses used the taller grass (>16 cm) much less than expected, whatever the risk of consumption of infective larvae, which is typical for horses in temperate grasslands (Ödberg and Francis-Smith, 1977; Edwards and Hollis, 1982; Putman, 1986; Fleurance et al., 2001; Ménard et al., 2002). This is consistent with the Forage Maturation Hypothesis (Fryxell, 1991) which argues that herbivores should select swards of intermediate, not high, biomass to maximise the daily intake of digestible nutrients because of the inverse relationship between the abundance and the quality of plant tissues. However, we have shown elsewhere (Fleurance, 2003) that horses select shorter grass than expected if they were simply maximising rates of nutrient intake. In the study reported here, short patches (<16 cm) were eaten approximately according to their abundance in the pasture where the risk of consumption of infective larvae was high (with two exceptions; Fig. 3A, classes 1–4 and 5–8 cm), but these patches were selected strongly when the risk of consumption of infective larvae was low (again with one exception; Fig. 3A, class 1–4 cm): this interaction between sward height and risk of consumption of infective larvae, which was highly significant in the first two periods and close to significance in the third, suggests that the risk of parasitism stopped the horses from selecting patches of short grass which were close to faecal piles, and may have led them to overselect the patches of short grass far from faeces. Feeding patch selection in horses therefore, does reduce the risk of consumption of larvae, and it appears to be driven by an interaction between their nutritional and anti-parasite strategies.

## 5. Conclusion

The horses avoided the patches of tall grass, whether they were contaminated or not, and selected patches of short grass far from faeces where the risk of consumption of infective larvae was limited. This behaviour appears to be driven by an interaction between nutritional and anti-parasite strategies: the horses avoid patches of tall grass generally of low quality and it appears that the parasites led them to overselect the patches of short grass far from faeces. Their parasite status at the time of the experiment had no effect on their feeding choices, however the history of parasitism of these individuals may be important. Further investigation of the relationships between parasite risk, nutritional characteristics of swards and foraging behaviour is needed to test the generality of these conclusions.

## Acknowledgements

This work was funded by les Haras Nationaux, Direction du Développement. Particular thanks to the colleagues from the experimental farm of the French National Stud at Chamberet for their technical help and Bartek Kapron and Aline Paula Reis who helped with the observations.

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