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Species diversity in gastrointestinal nematode communities of dairy goats: species–area and species–climate relationships

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Summary — Gastrointestinal nematode communities (12 species) of dairy goats were studied in four regions located in the centre of the western part of France. These regions had very similar annual mean temperatures (11 to 12.5 °C) but had rainfall accumulations ranging from 600 to 1 330 mm per year. Breeding management (area of pastures, number of goats in the flock, the age of the farm, and the size of the initial goat population) was investigated only in the driest region. The number of helminth species and Shannon diversity index were positively correlated to the permanent pasture area and negatively to the age of the farm. Evenness was negatively correlated to the age of the farm and increased with the increasing levels of rainfall. The results are interpreted in the following terms: i) large areas of permanent pasture include a large array of environments favourable to the development of the free-living stages of various species of nematodes; ii) age of the farm is unfavourable to the maintenance of all introduced species as the farms are helminth-isolated and infestation can only occur during the grazing season thus imposing the necessity of successive annual recolonization of the pastures; and iii) free-living stages are very susceptible to dryness and survive better in areas with heavy rainfall.

nematode / species diversity / climate / pasture / breeding management

Résumé — **Diversité spécifique au sein des communautés de nématodes chez les chèvres laitières. Relations entre nombre d'espèces, surface de pâturage et climat.** Les communautés

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de nématodes gastro-intestinaux (12 espèces) ont été étudiées chez des chèvres laitières de quatre régions du centre-ouest en France. Ces régions ont des températures moyennes annuelles très voisines (11 à 12,5 °C) mais les pluviométries s'échelonnent de 600 à 1 330 mm par an. Les caractéristiques du mode d'élevage (surface de pâturage, taille du troupeau, ancienneté de la ferme, et nombre de chèvres achetées à la constitution du troupeau) n'ont été recensées que dans les fermes situées dans la région la plus sèche. Le nombre d'espèces et la diversité spécifique étaient positivement corrélés à la surface de pâturages permanents et négativement reliés à l'ancienneté de la ferme. L'équitabilité a été également négativement corrélée à l'ancienneté de la ferme mais augmente avec l'intensité de la pluviométrie. Les résultats sont interprétés de la manière suivante : i) les pâturages permanents couvrent une large palette d'environnements qui permettront le maintien d'espèces parasites dont les exigences au cours de la phase libre sont diversifiées ; ii) les espèces introduites à la création de la ferme devront recoloniser les pâturages à chaque printemps en début de saison de pâture, et l'ancienneté de la ferme correspondra ainsi à des essais annuels successifs de recolonisation, et iii) les stades libres des nématodes sont très sensibles aux conditions de sécheresse, et seules quelques espèces pourront se maintenir dans ce cas, alors que la survie sera bonne pour toutes les espèces dans les zones humides.

nématode / diversité spécifique / climat / pâturage / mode d'élevage

INTRODUCTION

Species–area (Arrhenius, 1921; Preston, 1962) and species–climate relationships (Turner et al, 1987; Currie, 1991) have been extensively studied in plants and free-living animal communities, but very few studies have been made on parasitic helminths in vertebrates (Aho, 1990, in amphibians and reptiles; Fedynich and Pence, 1994, in mallard populations). These studies generally focus on species diversity over a large geographic scale. Descriptive data are available on helminths infecting domestic vertebrate hosts, whose geographic range is extremely large and local conditions extremely diverse. In contrast to the bulk of the descriptive data available, there has been no attempt to relate helminth diversity on domestic hosts to breeding management.

We had the opportunity to study the species diversity in gastrointestinal helminths of domestic goats in relation to environmental factors. The gastrointestinal parasites were well identified, and the breeding management practices were described. High climatic diversity was found in some regions of France, as the annual rainfall accumulations extended from 600 to 1 330 mm. The helminth parasites of goats are

mostly nematodes belonging to the family Trichostrongylidae (Mangeon and Cabaret, 1987; Chartier and Reche, 1992; Cabaret and Gasnier, 1994). These nematodes have a direct life cycle: eggs are passed in the faeces of goats, they develop into infective larvae in the pasture, and ruminants become infected when grazing on infected pastures. The pasture area, one of the main characteristics of breeding management, is the principal factor that accounts for the intensity of the nematode infection (Cabaret et al, 1986) and interferes with species diversity (Cabaret and Gasnier, 1994). In the regions we investigated, the annual temperature was similar in all the farms studied whereas the rainfall accumulations were very different. Climate thus could be assigned to a gradient of rainfall at nearly constant temperature. Our study was simplified by the fact that dairy-goat farms are isolated from the helminthic point of view. Only young uninfected goats or kids are introduced after the establishment of a farm and the observed diversity is the result of the maintenance of the initially introduced species under farm conditions (climate and breeding management). Our objective was to interpret nematode species diversity in relation to the history of the

farm, its husbandry practices and particularly to the pasture area available to goats, and to relate this to the climatic conditions in terms of annual rainfall in a temperate region.

MATERIALS AND METHODS

The farms studied were located in the central part of the western France, and were no more than 220 km apart. Four distinct regions were recognised: Touraine (rainfall 600–650 mm/year; mean temperature 11–11.5 °C; 24 goats necropsied), Plateau Mellois (880 mm/year; 12.1 °C; five goats), Bocage, Plateau de Niort and Plaine de La Mothe-Lezay (960–1 000 mm/year; 11.4–12.5 °C; 16 goats), and Gatine and Entre Plaine et Gatine (1 150–1 330 mm/year; 11.5 °C; ten goats). Breeding management was investigated in Touraine only and included the following factors: the area of permanent (not sown or ploughed for at least 3 years) and temporary (sown with two or three grass species and renewed every year) pastures, the number of goats in the flock, the age of the farm, and the number of goats originally purchased at the establishment of the farm were recorded.

The necropsied goats were adults culled mostly for productivity reasons (poor milk or kid production) from June to November. The technique for recovering the helminths and their identification have been described elsewhere (Chartier and Reche, 1992; Cabaret and Gasnier, 1994). In the Touraine data set, most of the farms (13) were represented by two necropsied goats, although only one goat was obtained in two farms. In the other regions, the goats originated from several farms in each region but no information on breeding management was obtained.

We used the following diversity indices: species richness (number of species, S), Shannon diversity (H' : see Pielou, 1975), and Q-statistics (Kempton and Taylor, 1976). Evenness was measured by the equitability index of Pielou (1975) ($H'/\text{Log}S$), and Alatalo index (Alatalo, 1981). The indices were calculated by means of

the statistical package Biodiv (Baev and Penev, 1993). The relation between the number of species and area was calculated from the original formula of Arrhenius (1921): $(S_i/S_j) = (A_i/A_j)^n$, where S_i correspond to number of species on area A_i , and correspondingly S_j to A_j . The regressions were established by means of the least squares method and the parameter values were controlled by means of resamplings (bootstraps with 500 repeats). Multiple regressions were performed with a Ridge procedure when the independent variables were correlated. One-way analysis of variance or a non-parametric Kruskal and Wallis test (including a bootstrap with 3 000 repeats) were also calculated to evaluate the differences in species diversity between the four regions. All statistical tests were performed with the Simstat software package (Péladeau and Lacouture, 1993).

RESULTS

Helminth communities in the four regions studied

Depending on the region, *Teladorsagia circumcincta* or *Trichostrongylus colubriformis* were the most frequent species in the nematode community (table I). The other species were *Haemonchus contortus*, *Trichostrongylus axei*, *Ostertagia ostertagi*, *Trichostrongylus vitrinus*, *Nematodirus filicollis*, *Nematodirus spathiger*, *Chabertia ovina*, *Oesophagostomum venulosum*, *Cooperia punctata*, *Trichuris ovis*, and *Skrjabinema ovis*.

Breeding management and species diversity in the Touraine region

The breeding management variables taken into account were the following: the area of permanent pasture (range in ha: 0–8.5), the size of flock (7–127 dairy goats), the age of farm (2–25 years) and the number of farms from where the goats were bought at the establishment of farm (range: one to six farms).

Table I. Nematode species proportions in goats from four regions of France.

Nematode	Region			
	Touraine n = 24*	Plateau Mellois n = 5	Bocage, Plaine de Niort Plateau La Mothe Lezay n = 16	Gatine, Entre Plaine and Gatine n = 10
<i>T. circumcincta</i> (%)	75.0	39.6	43.2	33.7
<i>T. colubriformis</i> (%)	21.7	56.4	48.3	58.5
Other species (%)	3.3	4.0	8.5	7.8
Presence of <i>O. ostertagi</i>	Yes	No	Yes	Yes
Presence of <i>Nematodirus</i> sp	Yes	No	No	No
Average number of worms (range)	6 690 (94–17 013)	22 443 (1 580–70 180)	8 836 (240–26 500)	10 446 (120–57 660)

Percentage of a given species in the community: number of a particular species / total number of nematodes \times 100.
* n = number of farms.

The results obtained from the necropsies of two goats from the same farm were highly similar (no significant differences between Shannon index of diversity – Wilcoxon test, $P = 0.29$; or Pielou equitability – Wilcoxon test, $P = 0.29$). The relation between the indices of the two goats per farm are shown in figure 1. A significant relationship was found between the estimation of the diversity given by the two goats from one farm ($n = 12$) for Shannon ($R = 0.73$; $P = 0.006$), Pielou ($R = 0.68$; $P = 0.01$) or Alatalo ($R = 0.56$; $P = 0.06$) indices; no significant relation was found for the Q ($R = 0.46$) and Hill ($R = 0.04$) indices.

The following significant regressions (Log: natural logarithm) were established on the 24 necropsied goats:

Q index = $0.89 - 0.005$ size of flock;
 $R^2 = 0.31$ $P = 0.005$

Equitability of Pielou = $0.652 - 0.014$ age of farm;

$R^2 = 0.25$ $P = 0.013$

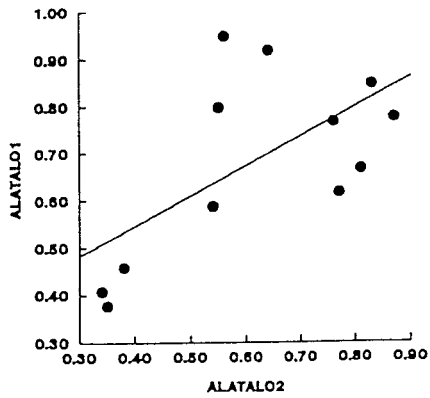
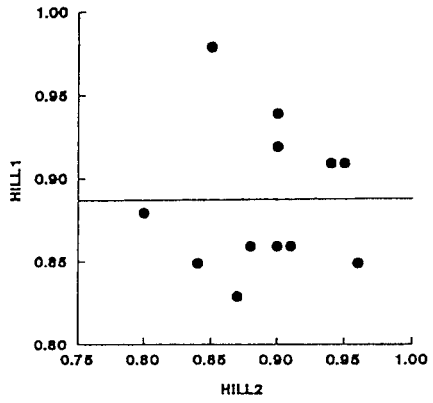
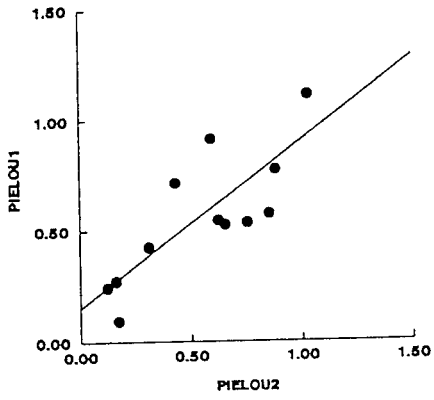
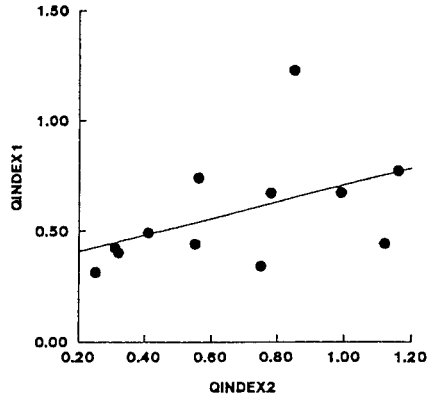
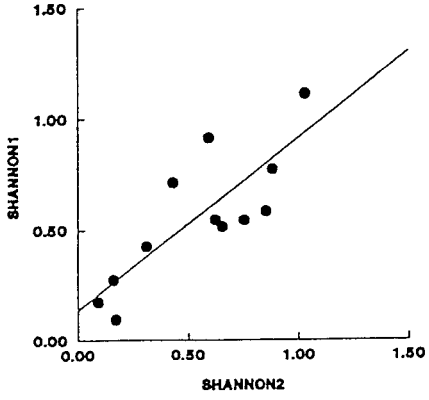
Evenness of Alatalo = $0.857 - 0.013$ age of farm;
 $R^2 = 0.37$ $P = 0.018$

The relationships between Shannon index and breeding management or intensity of infection are shown in figure 2 and correspond to the following significant regressions:

Shannon H' = $0.72 + 0.038$ area of permanent pasture in ha – 0.017 age of farm in years;

$R^2 = 0.42$ $P = 0.007$

Fig 1. Relationship between estimates of diversity (Shannon or Q index) or equitability (Pielou, Hill or Alatalo index) within a pair of goats (coded 1 and 2) from 12 farms.



Shannon $H' = -0.95 - 0.35 \text{ Log (age of farm) } + 0.21 \text{ Log (worms) } + 0.20 \text{ Log (size of flock);}$
 $R^2 = 0.58 \quad P = 0.0007$

In addition, for farms with more than 1 ha of permanent pasture (pp), the following relation was established:

Shannon $H' = -0.28 - 0.31 \text{ Log (age of farm) } + 0.20 \text{ Log (worms) } + 0.21 \text{ Log (Log pp);}$
 $R^2 = 0.77 \quad P = 0.002$ (established on 13 necropo-
 sited goats)

The breeding management variables were often significantly interrelated (ie, age of farm and number of goats in the flock: $R = -0.47$, age of farm and number of farms from which goats originated at establishment of farm: $R = -0.47$). The indices of diversity or evenness were also significantly related (H' and evenness of Pielou, $R = 0.78$; evenness of Alatalo and Pielou, $R = 0.91$).

Species and area relationship in the Touraine region

The pasture area is composed of permanent (not sown or ploughed for at least 3 years) or tempo-

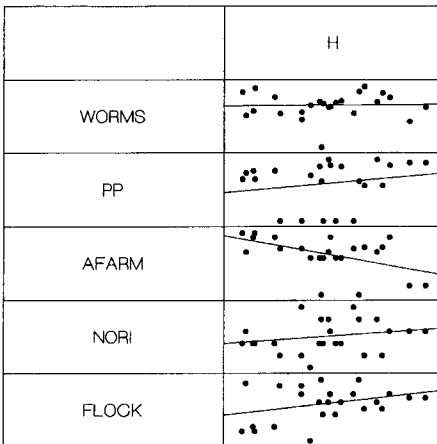


Fig 2. Relationships between Shannon index (H') and number of worms (Log worms), hectares of permanent pasture (Log pp), age of the farm (Log Afarm), number of farms from which the goats were bought (Nori), and flock size (Log Flock).

rary (sown with two or three species of grass and renewed every year) pastures. The total pasture area was not significantly correlated to the number of species ($R = -0.11$). Conversely, a significant relationship was found between the diversity estimates and the area of permanent pasture:

$\text{Log (number of species)} = 1.37 + 0.08 \text{ Log (area of permanent pasture in ha);}$
 $R^2 = 0.28 \quad P = 0.01$

In 12 cases, no temporary pasture was available and the number of species (log nsp) could be significantly regressed to the surface of permanent pasture (log pp):

$\text{Log nsp} = 1.13 + 0.30 \text{ Log pp;}$
 $R^2 = 0.51 \quad P = 0.008$

The situation was more complex in the 12 other cases when permanent (pp) and temporary pastures (tp) were available in the farms, as shown from a Ridge regression :

$\text{Log nsp} = 1.52 + 0.01 \text{ Log pp} - 0.09 \text{ Log tp;}$
 $R^2 = 0.54 \quad P = 0.08$

$\text{Log DSP} = -0.069 + 0.225 \text{ LogDHA}$

$R=0.57 \quad n=156 \quad P<0.001$

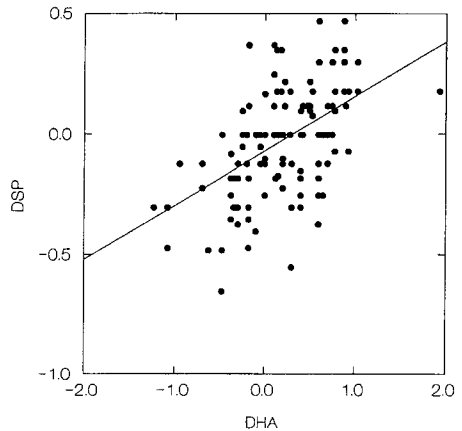


Fig 3. Linear relation between the number of species ($\text{DSP} = \text{Log}(S_i/S_j)$), ratio of the number of species S in goats from i and j farms) and the area ($\text{DHA} = \text{Log}(A_i/A_j)$), ratio of areas A of permanent pastures in ha in farms i and j), established on all i and j pairs ($N = 156$).

Table II. Mean values of diversity indices in the four climatic regions in relation to rainfall levels.

	Region				Statistical significance
	Touraine	Plateau Mellois	Bocage, Plaine de Niort, Plateau La Mothe, Lezay	Gatine Entre Plaine and Gatine	
Shannon H'	0.57	0.61	0.68	0.71	NS ($P = 0.41$)
Pielou equitability	0.44	0.52	0.61	0.64	S ($P < 0.05$)
Species richness	4.1	3.2	3.1	3.5	NS ($P = 0.13$)

Statistical significance obtained from analysis of variance.

In all cases, the number of species was positively correlated to the area of permanent pasture available and only this type of pasture will be considered hereafter. Utilizing the values determined using the Arrhenius formula, a highly significant relation was established between Log (ratio of the number of species in goats from i and j farms, respectively S_i and S_j) and Log (ratio of areas of permanent pastures in farm i and j , respectively A_i and A_j), as shown in figure 3. The r value for 500 bootstrap repeats was 0.51; the constant term of linear regression and slope respectively ranged from -0.098 to -0.033 and from 0.15 to 0.27, at $P = 0.05$. When we took A_j as 1 ha (A_1), and S_j as the number of nematode species expected for farms where goats are grazed on 1 ha of permanent pasture, the Arrhenius formula became:

$$\text{Log}(S_i) = \text{Log}(S_j) + n \text{Log} A_i$$

The intercept constant in regression corresponded to Log (number of species on flock grazed on 1 ha), and n , the slope, was the exponent of the power function in the Arrhenius equation. The calculated regression was:

$$\text{Log}(S_i) = 1.04 + 0.30 \text{Log} pp$$

($n = 24$; $R = 0.60$; $P = 0.002$)

where the bootstrap confidence intervals (2 000 repeats; $P = 0.05$) were 0.82–1.26 and 0.12–0.48 for the intercept and the slope of the regression line respectively.

Species and rainfall in four regions

The data are shown in table II. The results showed that the Shannon H' (non-significantly) and Pielou equitability (significantly) increased (one-way ANOVA: $P < 0.05$; Kruskal and Wallis test where P ranges from 0.002 to 0.13 according to bootstrap resamplings) with intensity of annual rainfall, whereas the species richness fluctuated randomly from one region (with particular rainfall) to another. Equitability was significantly related to rainfall on the set of the 55 necropsied goats using Log-transformed data: Log (equitability of Pielou) = $-6.22 + 0.81 \text{Log}(\text{rainfall/year in mm})$;

$$R^2 = 0.13 \quad P = 0.007$$

The various bootstrap samples (500, 1 000 and 2 000 repeats) gave to similar values of R^2 (0.10).

DISCUSSION

Choice of diversity indices

A huge amount of literature has been devoted to the choice of a diversity index in free-living organisms (among others: Hill, 1973; Pielou, 1975; Kempton and Taylor, 1976; Routledge, 1979; Alatalo, 1981). Figuratively, we may consider N_0 = number of all species (species rich-

ness), N_1 ($\exp H'$, with $H' = -\sum p_i \text{Log } p_i$, p_i is the frequency of species i in the sample) as the number of 'abundant' species and N_2 ($1/\sum p_i^2$) as the number of 'very abundant' species. Most indices are sensitive to the few commonest species, the number of which may fluctuate erratically from year to year or from site to site but the Q index (Kempton and Taylor, 1976) should not suffer from these disadvantages. Evenness can be defined as $\log N_1/\log N_0$ (Pielou, 1975), N_2/N_1 (Hill, 1973) or $(N_2 - 1)/(N_1 - 1)$ (Alatalo, 1981) and it depends on the species richness and sampling size. In our study, two species (*T. circumcincta* and *T. colubriformis*) were very abundant and the sampling size represented more than a hundred worms identified per host. The diversity indices (H' as well as the number of species) were related to the pasture areas; the only exception was the Q index which was related to the number of goats in the flock. H' was positively related to the area of natural pasture (source of variability) and negatively related to age of the farm. The infective larvae survive for long periods on pasture and several species are able to overwinter there. Natural pasture are not altered and thus infective larvae may survive and possibly infect hosts and maintain diversity. Goats are treated with anthelmintics and then kept indoors during winter and each spring they acquire anew (or not) the species present on a farm, and thus maintain (or not) the species' diversity. We retained H' as a particularly pertinent index of diversity as it was related to the main factors that may affect the level of diversity. Equitability of Pielou or that of Alatalo were highly related and were both negatively correlated with the age of the farm (a factor that probably reduced diversity). For this reason we retained only the Pielou equitability because it has been largely used in previous studies.

Species–area relationship

Arrhenius (1921) first stated that the number of plant species increases continuously as the area increases. Preston (1962) observed a similar relationship in the land birds of England and

Wales; the mammals and birds of East Indies or Madagascar; and the birds, amphibians and reptiles of the West Indies. Three hypotheses have been advanced to account for the significant positive correlation observed between number of species and area (Connor and McCoy, 1979): the 'habitat–diversity' hypothesis (when the amount of area sampled is increased, new habitats with their associated species are encountered), the 'area-per-se' hypothesis (which de-emphasises the importance of habitat and explains the species number as a function of immigration and extinction rate), and the 'passive sampling hypothesis' (larger areas harbour larger samples than smaller ones, and thus apparently contain more species). The exponent of the power function was approximately 0.25 in the data presented by Preston (1962). It was higher for the intestinal helminth species of amphibians and reptiles: 0.27–0.67 (with the exception of Iguanidae: 0.11) as recorded by Aho (1990). The areas were much larger (North America) than the ones we considered in our work (up to several hectares) and may account for the difference in exponent value. The exponent of the power function was 0.22 in our case and was very similar to that recorded in free-living organisms, possibly indicating that diversity tended to be rather controlled during the free-living stages on pasture rather than on the parasitic stages in host. The small differences in diversity recorded between the two goats supported to the very limited influence of host on nematode diversity, at least under our conditions. The fact that only the area of permanent pasture (and not the temporary pasture area) was positively correlated with species diversity deserves explanation in the light of the 'habitat–diversity' theory for diversity. The use of temporary pastures results in high levels of disturbance for nematodes (the pastures are ploughed before being sown, destroying the remaining larvae, are used for a shorter period than permanent pastures and are eventually cut for hay or silage production, thus destroying the majority of larvae) and also provide a uniform environment for nematodes during the grazing season (few grass species are sown). Our results

(diversity increases as permanent pasture area increases) are apparently consistent with the intermediate disturbance hypothesis (highest diversity is expected at intermediate levels of disturbance: Petraitis et al, 1989). If the disturbance is too mild (uniformity of plant species and biomass on temporary pasture), nematode communities are dominated by a few species, and if the disturbance is too harsh (chaotic events for larval populations on temporary pastures), only a few species of nematodes will resist the disruption according to the theoretical model of Petraitis et al (1989). The natural pastures correspond to an intermediate level of disturbance and consequently to a larger number of species. The relationship between species and area for permanent pastures is also in agreement with the widely held view that larger areas will include a greater range of different environments (Bell et al, 1993), and possibly permit the maintenance of a larger array of species, each having different requirements.

Species and rainfall

According to Kates (1950), optimal survival levels for infective third-stage L3 are different: warm and humid for *H contortus*, *O venulosum* and *T colubriformis*, whereas *T circumcincta*, *O ostertagia* and *Nematodirus* sp survive best under cold and humid conditions. It has also been shown that the faecal water contents plays an important role in the development of the eggs emitted in faeces into L3 (Rossanigo and Gruner, 1995): optimal faecal water contents were 55% (*O ostertagia*), 60% (*T circumcincta* and *C ovina*), 65% (*T vitrinus* and *T colubriformis*), and 70% (*H contortus*). These optimal faecal water contents are higher than that usually recorded in fresh faeces: a humid environment should, therefore, hinder desiccation or even increase the moisture content in the faeces. The intensity and frequency of rainfall, the source of the moisture, should thus play a role on the optimal development and survival of the free living stages of these nematodes. Higher rainfall levels should result in a higher moisture con-

tent of the faeces (where eggs are located) and herbage (where L3 are located), thus providing an opportunity for the development and survival of all the species, which in turn should result in an increase of equitability of nematode infection, ie, balanced proportions of all species. This was corroborated by a relationship between rainfall and equitability in our samples.

The species diversity or equitability, although dependent on the available area of permanent pasture or climatic conditions, were not completely explained by those two factors as shown by the coefficient of determination. Factors relating to breeding management (other than those related to pastures: size of flock for example) and farm history (age of farm) also account in part for the species diversity and equitability recorded.

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