

SPATIOTEMPORAL DISTRIBUTION OF FOUR SPECIES OF CESTODES IN A LANDSCAPE OF MID-ALTITUDE MOUNTAINS (JURA, FRANCE)

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SUMMARY

In eastern France (Jura mountains), from 1985 to 1986 the prevalences of *Taenia taeniaeformis*, *Taenia mustelae*, *Cladotaenia* sp., were studied in rodents from an area of about 1,000 ha. Gradients of prevalence were observed according to habitats and time. Open habitat/close habitat gradients were observed, decreasing for *Taenia taeniaeformis*, increasing for *Taenia mustelae* and *Clado-*

taenia sp. The prevalence of cestodes varied according to time, at the interannual level for *Taenia mustelae*, and at the seasonal level for *Taenia mustelae* and *Cladotaenia* sp., the spring and summer phase of the cycle being critical for the transmission. Results are compared with those obtained on *Echinococcus multilocularis*, in the same study area.

RÉSUMÉ : Distribution spatiotemporelle de quatre espèces de cestodes dans un paysage de montagne de moyenne altitude (Jura, France).

L'infestation des rongeurs par *Taenia taeniaeformis*, *Taenia mustelae*, et *Cladotaenia* sp., a été étudiée dans les régions montagneuses de l'est de la France (Jura) à l'échelle d'un site d'environ 1 000 ha. Des gradients d'infestation ont été observés, fonction de l'espace et du temps. Ces gradients s'établissent des milieux ouverts vers les milieux fermés; dans un sens croissant pour *Taenia mustelae* et *Cladotaenia* sp., décroissant pour *Taenia taeniaeformis*.

En fonction du temps, l'infestation des rongeurs varie; d'une année à l'autre pour *Taenia mustelae*, d'une saison à la suivante pour *Taenia taeniaeformis* et *Cladotaenia* sp., les périodes printanières et estivales étant les plus critiques pour la transmission. Les résultats sont comparés à ceux obtenus précédemment pour *Echinococcus multilocularis* sur le même site.

INTRODUCTION

« The definition of populations is fundamentally neither spatial nor related to time. Nevertheless, the first descriptive characteristics of populations are spatial and related to time » (Legay and Debouzie, 1985).

Studies of species in a heterogeneous habitat must take both these characteristics of populations into account. The scale of the landscape represents one level of heterogeneity. This level offers good opportunities for research in parasite ecology. Such studies are generally carried out as a part of medical or veterinary public health programmes. They are based on stratified sampling of the habitat of parasitized hosts (Rioux *et al.*, 1981) and lead to defining cartography of habitats with high risks of infestation (Dedet, 1977).

The development of control methods against zoonotic parasites such as *Echinococcus multilocularis* Leuckart, 1856, is dependent on an understanding of their life cycles and transmission dynamics in each predator-prey rela-

tionship. These have been studied in four species of larval cestodes of rodents, namely *Taenia taeniaeformis* Batsch, 1786, *Taenia mustelae* Gmelin, 1790, *Cladotaenia cirsi* Yamaguti, 1935, and *Cladotaenia globifera* Batsch, 1786. An important aim was to compare their dynamics with those previously reported for *E. multilocularis* (Delattre *et al.*, 1985, 1988, 1990; Le Pesteur, 1990). Because the movements of definitive hosts (Canidae, Felidae, Mustelidae and Birds of preys) can be extensive, the prevalence data of cestodes in them provides only limited information on focality. As the movements of rodents are generally limited to no more than about one hectare, we have studied the larval phase of these cestodes in them and compared their prevalence between habitats and between seasons. The results are reported in this paper.

MATERIAL AND METHODS

STUDY AREA

The material was collected from an area of about 1,000 ha in the district of Levier (850 m of latitude — Jura, France) near the village of Septfontaine, during two years: 1985-1986. The landscape matrix is permanent grassland (meadows and pastures), divided

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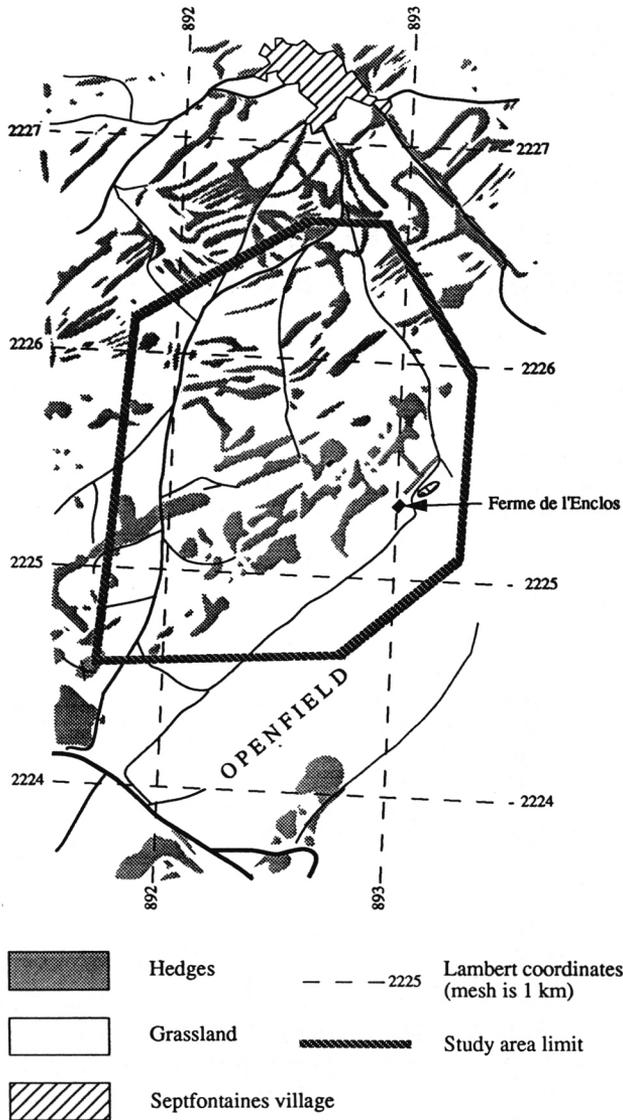


FIG. 1. — Map of the study area.

by a hedgerow network, that we'll name « bocage » (Gouly, 1991) (Fig. 1).

Six types of habitat were used to describe the elements of the landscape. These were 1) meadows (68 % of the study area); 2) pastures, grazed by cattle, with their number decreasing from the village to the openfield (17 %); 3) ploughed fields, representing a very low percentage of the study area (less than 1 %); 4) fields borders; 5) edges, these were diverse, especially those between two open habitats, such as meadow/ploughed field, border of a road in a field, meadow/pasture, etc. (6 %); 6) hedgerows and groves, where deciduous trees were dominant (8 %).

TRAPPING

Sampling was carried out four times each year (April, June, August and October). Rodents were captured with INRA trap lines (Spitz *et al.*, 1974). Each line, about 100 m length, involved 34 traps with a regular interval of 3 m between each. From April 1985

	Hedgerow	Edges	Meadow	Pasture	Field border	Ploughed field	Total
<i>Microtus agrestis</i>	36 ← 1 à 4 ind./ha →	9	2				47
<i>Clethrionomys glareolus</i>	321 ← 1 à 40 ind./ha →	17	5	4	2		349
<i>Pitymys subterraneus</i>	35 ← 1 à 10 ind./ha →	37		2	1		75
<i>Apodemus sp.</i>	172 ← 1 à 10 ind./ha →	29	9	6	14		230
<i>Microtus arvalis</i>	24 ← 5 à 240 ind./ha →	413	1061	368	535	119	2520
Trap lines	40	35	60	27	30	5	

Fig. 2. — Number of captures and number of trap lines. Estimations of densities are obtained from the number of capture per line multiplied by correcting factors (Spitz *et al.*, 1974).

to October 1986, 19,700 m of trap lines were laid. During each sampling period of 3 days, about 25 lines were set up, and traps were patrolled every day, so that the sampling pressure is 2,550 trapping days, at less. Each type of habitat was sampled according to its importance in area (Fig. 2). For each season, trap lines were at the same place, but were changed from one season to another, in order to avoid overtrapping. Captures allowed us to establish an abundance index as a mean number of captures per line and per habitat. These indexes can be transformed into densities using correcting factors established by Spitz *et al.* (1974).

Intensive trapping was performed 3 times on quadrats including hedges or groves in order to catch almost all accessible rodents. A total of 939 traps were laid (330, 420, 189). Those data will be used separately, in chapter "Prevalence/Habitat relationships" only.

INRA traps are suitable for catching small species of rodents weighing less than 50 g. Hence, only a few young of *A. terrestris* were captured, and this did not allow us to estimate the prevalence of cestodes in this species.

The relative age of the rodents was established by weighing the dry crystalline lens (Martinet, 1966; Le Louarn, 1971; Bourlière and Spitz, 1975).

Rodents were dissected and their liver examined for cysts macroscopically. Both species of *Cladotaenia* were pooled because of difficulties in differentiating the one from the other. Generally, this method did not permit diagnosis of the very early stages of infestation. In this study, the rodents which were old enough to have macroscopically detectable cysts were called « detectable parasite rodents ». For each species of rodent and cestode, the « detectable parasite rodents » category was defined from the minimal weight of the crystalline lens below which no infested rodent could be observed (Delattre *et al.*, 1985).

RESULTS

RODENT POPULATION KINETICS

Six species of rodents were captured: 2,520 *Microtus arvalis*, 349 *Clethrionomys glareolus*, 230 *Apodemus sp.*, 24 *Arvicola terrestris*, 75 *Pitymys subterraneus*, 47 *Microtus agrestis*. The general rough spatial distribution of the main

species are illustrated in Figure 2. Populations showed seasonal and inter annual variations of abundance. In our study (1985-1986) the variations in the number of each population were synchronous and the level of abundance of rodents was high. Specific seasonal variations were noted (low spring level/high autumn level). Average densities of 1986 were half those of 1985.

Analysis of variance of crystalline lens weights showed that the mean age of populations did not vary significantly and greatly according to habitats, and did not vary from one year to another. In spring, populations showed a high proportion of old animals which had survived the winter. From spring, populations progressively got younger until the autumn, when nearly the whole population was composed of animals born during the year (Fig. 6).

HOST-PARASITE RELATIONSHIPS

The number of rodents with detectable cysts, age structures and species of cestode are correlated in Figures 3 and 4. *Cladotaenia* sp. infested mainly *C. glareolus* and *Apodemus* sp., rodents of close habitats. *T. taeniaeformis* mainly parasitized *P. subterraneus*, *M. agrestis* and *M. arvalis*, rodents of open habitats and borders. The prevalence of *T. mustelae* was high for *C. glareolus*, *P. subterraneus* and *M. agrestis*, i. e. rodents of close habitats and borders.

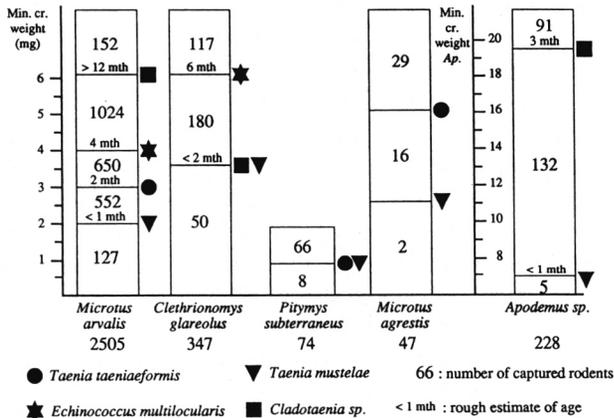


FIG. 3. — Minimum crystalline lens weights (mg) of the infested rodents according to the different species of cestodes (rodents whose crystalline lens weight is over the limit are considered as « detectable parasite rodents »).

PREVALENCE/HABITAT RELATIONSHIPS

Taenia taeniaeformis showed increasing prevalences from close habitats to open habitats, whereas *T. mustelae* showed a reverse gradient (fig. 5).

Cladotaenia sp. needed close habitats as 38 of the 39 cases were recorded in these habitats. Half of the captures of

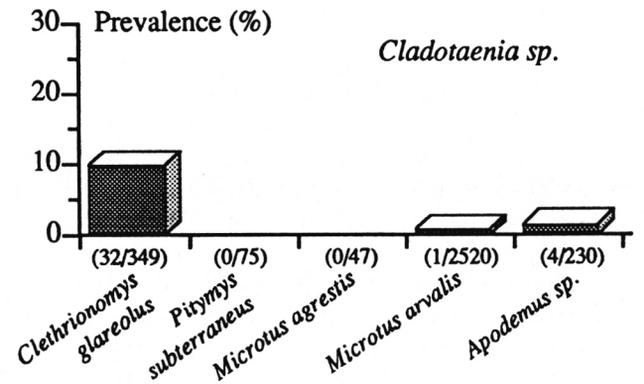
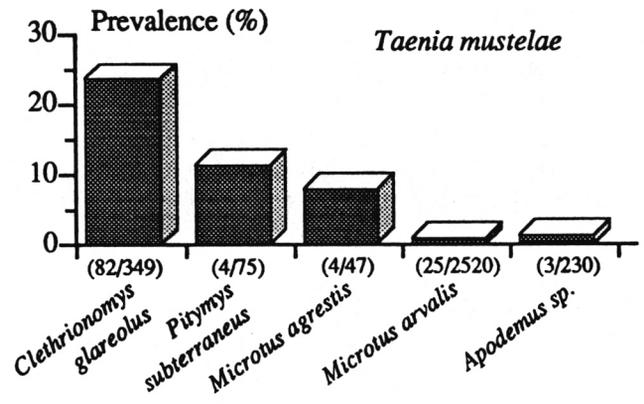
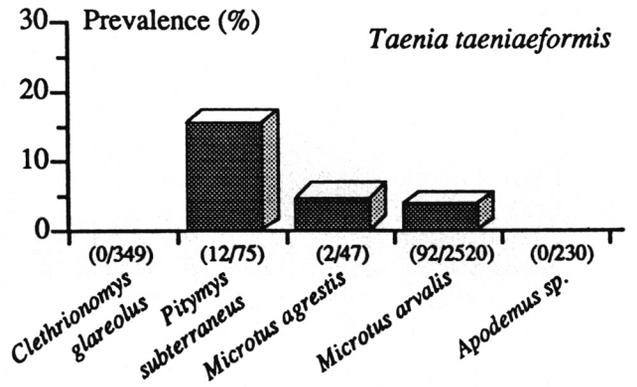


FIG. 4 — Prevalence of different species of cestodes in their intermediate hosts (= number of infested rodents/total number of rodents).

infested rodents were concentrated in two trap lines only. One was located in a grove of deciduous trees, north-east of the « Ferme de l'Enclos », and the other in a hedge near a highway suggesting a clustered distribution of this cestode.

Using intensive trapping within quadrats including close habitats, it was possible to determine the distribution of *T. mustelae* locally in *C. glareolus*. The prevalence in close habitats (non-significant differences between deciduous trees/coniferous trees) was 11.2 % (16/143), in the bor-

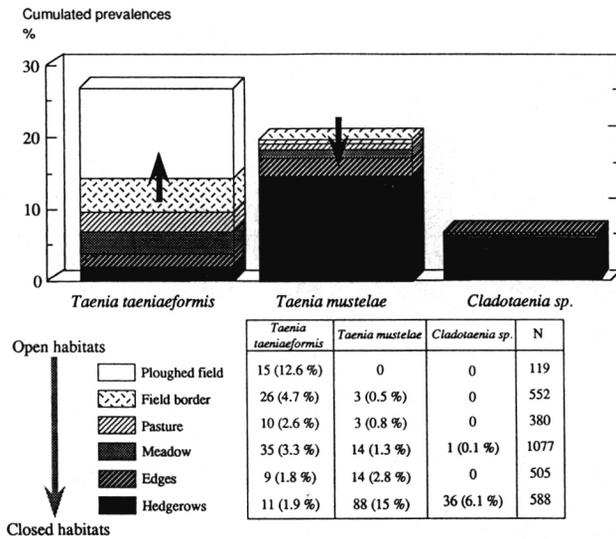


FIG. 5. — Cumulated prevalences according to each species of cestodes and to habitats (N = total number of rodents; columns indicates the number of infested rodents and, between parentheses, the prevalences).

ders of close habitats 2.8 % (1/36), and in meadows 2.7 % (5/185). Thus, the open habitat/close habitat gradient of prevalence was confirmed ($p < 0.008$).

PREVALENCE/TIME RELATIONSHIPS

Figure 6 shows the age pattern of the host population according to cestode species and seasons.

No rodents born after the winter seemed to be infested with *T. taeniaeformis* before October (Fig. 6a). The minimum duration of larval development given by Hutchinson (1958) was about one month. The weights of crystalline lens of the two youngest infested *M. arvalis* in October was 3,8 and 3,2 mg. The age of both rodents did not exceed one month. Thus the infestation season seemed to be from September to March. *P. subterraneus* showed the same distribution. The only infestations in *M. agrestis* were observed in April in old animals. These results are consistent with those on *M. arvalis* and *P. subterraneus*. Parasite prevalence in rodents having survived the winter (crystalline lens weight > 3,5 mg) and which were captured in April, was higher than that of the same cohort captured in summer and autumn (9.9 and 4 %, respectively; $p < 0.05$): the survival of *M. arvalis* infested with *T. taeniaeformis* seemed to be low compared to that recorded for *E. multilocularis*, and for which reverse proportions have been reported (Delattre *et al.*, 1988). *P. subterraneus* showed the same trends even though the numbers were too low to be statistically significant.

Infestation with *Cladotaenia sp.* (Fig. 6b) only studied for the Bank Vole (*C. glareolus*) showed the same temporal distribution pattern as *T. taeniaeformis*. Laboratory

studies of Freeman (1959) recorded that the development of a visible cyst takes two or three weeks. This result and the fact that the first cases of infestation were recorded in August show that the infestation season extends from July to March. The results obtained from a small number of infested *M. arvalis* and *Apodemus sp.* are in keeping with this conclusion. On the other hand, the temporal distribution of infested *C. glareolus* showed great inter-annual variations of prevalence: 27 of the 32 infested rodents were captured in 1985 ($p < 0.05$).

Unlike the other species, the prevalence of *T. mustelae* seemed to be more regular throughout the year, at least in *C. glareolus* and in *M. arvalis* (Fig. 6c). The minimal age at which the parasite could be detected was very low (age of rodents less than one month). This would be expected if there was a very rapid development of the cyst.

DISCUSSION

Delattre *et al.* (1988, 1990) showed large variations in the prevalence of *E. multilocularis*, with the best habitat for infection being the borders of ploughed fields or other areas where below ground survival of *E. multilocularis* eggs is possible. The spatial distribution of the prevalence of *T. taeniaeformis* was similar to that of *E. multilocularis*. In contrast *T. mustelae* showed a reverse gradient. Freeman (1959) and Leiby and Dyer (1971) reported that receptivity to cestodes varied according to rodent species and even rodent strains. Most rodents species did not occupy all the habitats of the study area. For example, *C. glareolus* is almost absent in the grasslands and *M. arvalis* was very seldom observed in the hedges of the bocage. In these cases, it was impossible to separate variations in the prevalence related to interspecific differences of sensitivity from those related to the distribution of rodent species in different habitats. Accepting the existence of both hypotheses, we pooled the results of each rodent species. Based on these pools, gradients of prevalence between open habitats and close habitats appeared in all the cases.

The prevalence of cestodes varied according to time at the inter annual level with *T. mustelae* at least. At the seasonal level, all species of cestodes showed interseasonal variations of prevalence. The summer phase of the cycle was critical for *E. multilocularis* (Delattre *et al.*, 1988), *T. taeniaeformis* and *Cladotaenia sp.* It was difficult to interpret results for *T. mustelae*, although it may be assumed that there are specific periods of infestation.

We are aware these results integrate the result of the action of numerous factors that we cannot separate. Biogeographical and mesoclimatological factors being involved on this scale, factors that determine the transmission dynamics of each host-parasite system include the following:

- 1) microclimatological conditions supporting egg-survival probably represent the most critical point of the cycle. This

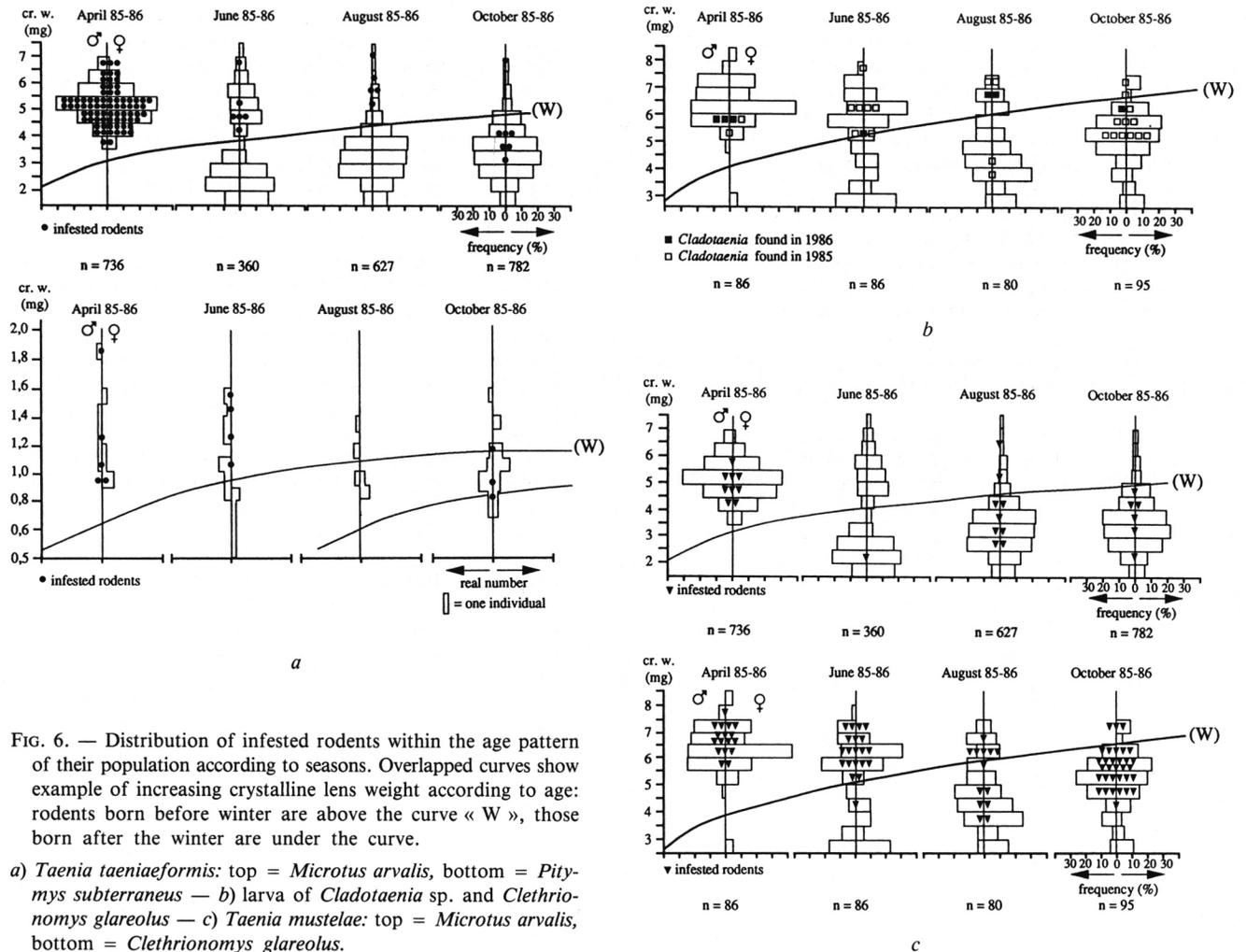


FIG. 6. — Distribution of infested rodents within the age pattern of their population according to seasons. Overlapped curves show example of increasing crystalline lens weight according to age: rodents born before winter are above the curve « W », those born after the winter are under the curve.

a) *Taenia taeniaeformis*: top = *Microtus arvalis*, bottom = *Pitymys subterraneus* — b) larva of *Cladotaenia* sp. and *Clethrionomys glareolus* — c) *Taenia mustelae*: top = *Microtus arvalis*, bottom = *Clethrionomys glareolus*.

can be modified by man on a limited (= local) scale (e. g. ploughed fields for *E. multilocularis* and *T. taeniaeformis*);

2) defecation behaviour and movements of definitive hosts can also be important. The high prevalence of *Cladotaenia* sp. under a tree and a hedge can be related to their use by birds of prey as a roost. The same kind of relationship can be established between the foraging strategies of predators and the aggregated distribution of parasites. Further observations were noted to support this:

— *T. taeniaeformis*: differences in prevalence were recorded inside the bocage. Predators seemed to concentrate their hunting effort within specific areas over about 1 ha although we were unable to separate these areas from unfrequented ones according to landscape criteria (Herschmidt, 1984; Giraudoux, 1991),

— the high prevalence of *T. mustelae* in close habitats can be related to the preference of Mustelidae for this kind of habitats;

3) the longevity of the tapeworm in definitive hosts may be a critical factor determining the parasite survival within

unfavorable seasonal conditions of egg-survival (e. g. in late spring and summer);

4) spatial distribution and density of rodents can determine the level of transmission;

5) genetic structure of host and parasite populations can be more or less favourable for transmission.

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