HELMINTH ASSOCIATIONS IN WHITE-TOOTHED SHREWS *CROCIDURA RUSSULA* (INSECTIVORA: SORICIDAE) FROM THE ALBUFERA NATURAL PARK, SPAIN

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ABSTRACT: The helminths of 218 white-toothed shrews from 29 sites in 2 biotopes in the Albufera Natural Park (Valencia, Spain) were examined from July 1990 to August 1991. An association analysis of helminths occurring at a prevalence of more than 4% was carried out for 4 species of cestodes located in the intestine (*Hymenolepis pistillum*, *H. scalaris*, *H. tiara*, and *Pseudhymenolepis redonica*) and 3 species of nematodes (*Pseudophysaloptera* sp. located in the stomach, *Stammerinema rhopocephala* larvae in the intestine and abdominal cavity, and *Porrocaecum* sp. in the thoracic and abdominal cavities). Bivariate (species pairs) versus multivariate analyses (associations within the entire set of species) were performed of presence–absence and of quantitative records (influence of intensity on associations). The associations were evaluated with respect to the sex and age of the host and to the sampling date and sites. The host and environment played a limited role, and the major determinant of species assemblage was phylogenetic. Positive associations were found among both the cestodes and the nematodes, whereas negative associations were found between cestodes and nematodes. The type of life cycle was probably the second greatest determinant of species associations. Nematodes using shrews as a paratenic host or as their definitive host were both positively associated.

The helminths of the white-toothed shrew have been studied in several parts of Europe, see the review of Vaucher (1971) of European shrews, that of Joyeux and Baer (1936, 1937) in Switzerland, and that of Quentin (1986) in France. In Spain, the helminths infesting these shrews (Mas-Coma and Gallego, 1977; Mas-Coma, 1977, Portolés et al., 1996) have been studied less intensively than those found in other rodents (Mas-Coma and Gallego, 1975; Mas-Coma and Feliu, 1977; Feliu et al., 1997). The Spanish helminth fauna of *Crocidura russula* (Hermann, 1780) identified to date comprises 49 species, i.e., 14, 13, 21, and 1 species of trematodes, cestodes, nematodes, and acanthocephalans, respectively. Thus, the helminth fauna is species rich and is composed of species with different life cycles, but the degree of infestation is low. The helminth fauna in the Albufera Natural Park (on the eastern coast of Spain) compared with other sites studied is characterized by the presence of a single species of trematode and a larger number of nematodes and cestodes (Portoles et al., 1996). The limited number of trematodes is paralleled by the low prevalence of trematode infections in intermediate snail hosts (Toledo et al., 1998).

The assemblage of species may depend on a variety of factors in nature, such as climate (Haukisalmi and Henttonen, 1994 in shrews from Finland), introduction or loss of species as a result of host movements, individual-, age-, or sex-induced host resistance, host feeding habits, and interactions between species. The present study was undertaken entirely within the Albufera Natural Park, therefore climatic conditions were uniform. Slight local variations in the moisture level may affect the presence of shrews because they are found primarily in moist zones (Faus, 1990). Accordingly, sampling in several zones is required to encompass local environmental variability. White-toothed shrews feed on live or, less frequently, dead invertebrates, which are intermediate hosts for cestodes; these shrews also constitute prey for birds and act as paratenic hosts for several nematodes.

Shrews are monogamous, and their movements are limited. Each litter comprises 3–4 progeny, and several generations are usually produced during the breeding period (spring to the end of summer). Postnatal dispersal is low; most juveniles settle within their natal territory or 1 immediately adjacent, and dispersal is restricted to the first litter of juveniles weaned in May (Favre et al., 1997). The movements of young shrews are subsequently also limited. Accordingly, the introduction or loss of helminth species as a result of host movements within a small area is probably negligible. Individual-, sex-, or age-related resistance has not been evaluated in shrews, and this must be done before any study of helminth associations can be undertaken. Interaction between species has been considered to be a major determinant of the host–parasite community structure. Communities display very different organizations: thus out of 50 studied assemblages of fish ectoparasites, ectoparasite species were distributed randomly within 20, whereas they were not distributed randomly in the other 30 (Poulin and Guegan, 2000). Community organization (Holmes and Price, 1986) has been classified as isolationist (a few species independently distributed and low infestation rates) or interactive (interaction plays a key role in determining the structure of the community). Pence (1990) further described the criteria for predicting an isolationist community as a low probability of colonizing the host, a direct life cycle, unsaturated niche use, low species richness, and a small number of high-density species. Some of the characteristics of the helminth community of *C. russula* indicate an isolationist community (direct life cycle, small number of high-density species), whereas others increase the possibility of an interactive community (indirect life cycle, high mean species diversity).

The intensity of associations determined under natural conditions may correspond to a mutualistic effect but may also be caused by similarities of life cycle. This means that helminth species associations in natural infestations do not necessarily reflect interactions between parasite species. Associations between helminth species can be estimated pairwise using indices: Pearson's coefficient of correlation, (Barger, 1984) or Spearman's rank correlation, when quantitative data are available, or indices such as the Sokal–Michener, Jaccard, or Dice indices, when only presence–absence data are available. Multivariate

TABLE I. List and characteristics of the helminths recovered in 218 *Crocidura russula* during a 1-yr sampling period (1990–1991) in 2 biotopes of Dehesa zone in the Albufera Natural Park of Valencia, Spain.*

Helminth	Prevalence	No. of worms per host (abundance ± SD)	Parasite location	Host range on the site†	Life cycle
Trematoda					
Brachylaima sp.	1.8	0.03 ± 0.2	Intestine	Cr, Ms, Rr, As	Indirect
Cestoda					
Hymenolepis pistillum (Hp)	23.8	42.0 ± 192	Intestine	Cr	Indirect (insects as intermediary hosts)
Hymenolepis scalaris (Hs)	12.8	0.2 ± 0.8	Intestine	Cr	Indirect (insects as intermediary hosts)
Hymenolepis tiara (Ht)	22.5	0.9 ± 3.0	Intestine	Cr	Indirect (insects as intermediary hosts)
Hymenolepis spp.	11.0	0.2 ± 1.0	Intestine	—	Indirect (insects as intermediary hosts)
Pseudhymenolepis redonica (Pr)	32.6	19.1 ± 119	Intestine	Cr	Indirect (insects as intermediary hosts)
Nematoda					
Calodium splenaecum	1.4	0.01 ± 0.1	Spleen	Cr	Direct?
Calodium soricicola	1.4	0.01 ± 0.1	Liver	Cr	Direct
Aonchotheca europaea	2.7	0.10 ± 0.9	Stomach	Cr	Indirect?
Parastrongyloides winchesi	3.2	0.06 ± 0.3	Intestine	Cr	Direct
Paracrenosoma combesi	0.5	0.00 ± 0.07	Lung	Cr	Indirect
Longistriata sp.	1.4	0.01 ± 0.1	Intestine	Cr	Direct
Porrocaecum sp. (larvae) (P)	35.8	1.5 ± 3.3	Thoracic and abdominal cavities	Cr, Rr, As	Indirect–paratenic host (birds definitive hosts)
Pseudophysaloptera sp. (Pse)	4.1	0.1 ± 0.6	Stomach	Cr	Indirect (insects as intermediary hosts)
Gongylonema sp. aff. *Soricis*	0.9	0.01 ± 0.1	Esophagus	Cr	Indirect (Blattidae as intermediary hosts)
Stammerinema rhopalocephala (larvae) (Sr)	24.8	1.9 ± 10.3	Intestine and abdominal cavity	Cr	Indirect–paratenic host (birds as definitive hosts)

* Unpublished data from E. Portolés.
† Cr, *Crocidura russula*; Ms: *Mus spretus*, Rr: *Rattus rattus*, As: *Apodemus sylvaticus*.

estimates are also available (Cabaret and Hoste, 1998). Positive associations are sometimes linked to the structure of the data (joint presences or absences in hosts) rather than interspecific facilitation (Lotz and Font, 1994), indicating that statistical associations between species must be carefully interpreted in terms of interactions.

In the present study, the helminth associations of crocidurine shrews are described in the light of life-cycle type, biotope, host characteristics, and the prevalence and intensity of infestation, using either presence–absence or quantitative infection data analyzed using bivariate or multivariate procedures. Associations are also evaluated in relation to taxonomic similarities (linked to life cycles) and ecological similarities (in the sense of a "guild" as defined by Root, 1967).

MATERIALS AND METHODS

Host collections

White-toothed shrews were studied in the 21,000-ha Albufera Natural Park (10 km to the south of the city of Valencia, Spain) from July 1990 to August 1991. This park is 1 of the few large wetlands areas remaining in Europe and constitutes a way station for many species of migratory birds, the definitive hosts of parasites that use the shrews as their paratenic hosts. The area studied in the Park (Dehesa) is an 871-ha littoral sandbar separating the inland lake from the Mediterranean Sea. Two

sites were investigated; each enclosed naturally by fireguards and small roads and separated by a distance of 2 km and a 57-m wide canal, to minimize the exchange of rodents or insectivores from 1 biotope to another. The B1 site, 342,536 m² (nearer to the rice paddies, divided into 13 nearly equal sampling areas covering the entire area), was covered with matorrals (*Phillyreo angustifoliae* and *Rhamnus angustifoliae*) with or without myrtle (*Myrtus communis*); some smaller areas were covered with *Teucrium belionis* and *Imperata cylindrica* or replanted with *Eucalyptus* sp. The B2 site, 354,136 m² (nearer to the Albufera Lake and more visited by birds; 16 sampling areas), was covered with similar matorrals. Some of the areas were covered with sedge (*Carex extensae*), reed (*Juncus maritimum*), *Phragmites isiaca*, or *I. cylindrinca* or had been replanted with *Eucalyptus* sp. or *Pinus* sp. The average surface area of a sampling area was approximately 23,000 m², and the maximum distance between areas was 955 m within each biotope (B1 or B2). In each biotope, shrews were trapped every 2 wk. There were 25 sampling periods. At each sampling period, 2 areas were usually inspected using 110 Shermann traps. Each of the 29 sampling areas was sampled from 1 to 3 times during the study.

Parasitological methods

At necropsy, the following organs were examined using a stereomicroscope to identify the parasites: esophagus, stomach, intestines, liver, spleen, lungs, urinary bladder, heart, and abdominal and thoracic cavities. Before identification, nematodes and cestodes were fixed and preserved in 70% alcohol, and trematodes, first, in Bouin solution and then in 70% alcohol. Final preparations of platyhelminths were mounted in toto in Canada balsam after staining (Grenacher boric carmine for trem-
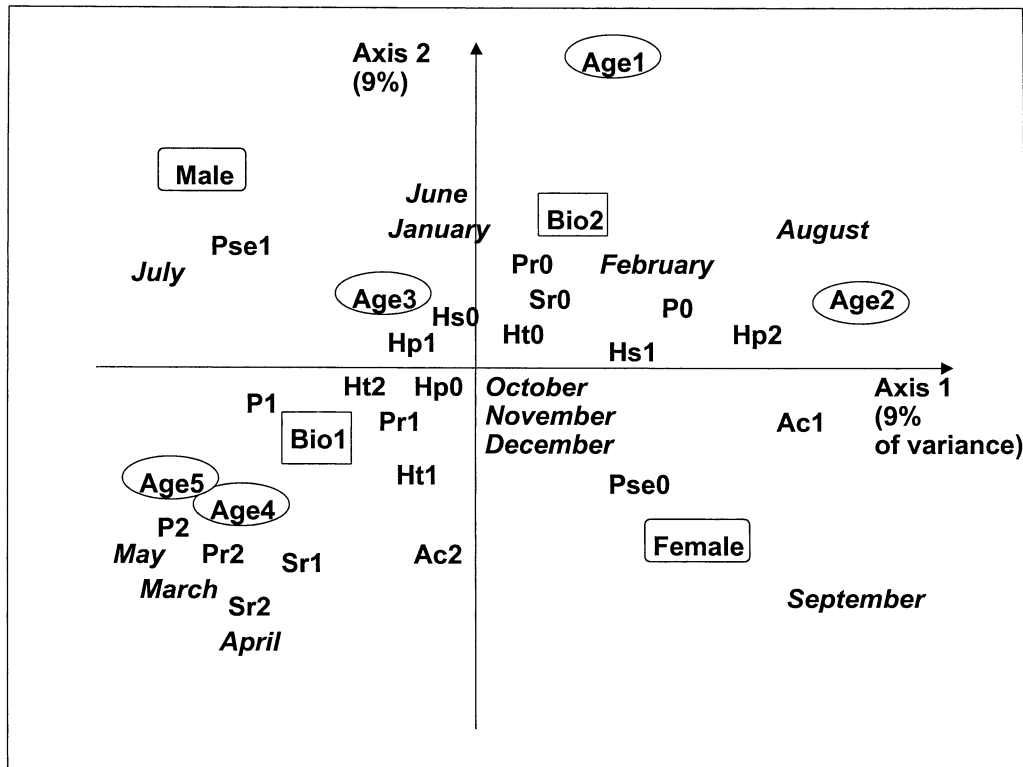
FIGURE 1.   Environment- and host-related factors in helminth infection. The numbers in parentheses represent numbers of worms. Codes: Bio 1 and Bio 2: biotopes 1 and 2, respectively; Age 1 (0–6 wk), Age 2 (6–14 wk), Age 3 (3.5–9 mo), Age 4 (9–14 mo), Age 5 (14–18 mo); Ac1 and Ac2: nonpregnant and pregnant females, respectively; Hp (*Hymenolepis pistillum*): Hp0 (not infected), Hp1 (1–14), Hp2 (15–2,092); Hs (*H. scalaris*): Hs0 (0), Hs1 (1–9); Ht (*H. tiara*): Ht0 (0), Ht1 (1–2) and Ht2 (3–29); Pr (*Pseudhymenolepis redonica*): Pr0 (0), Pr1 (1–5), Pr2 (6–1,525); P (*Porrocaecum* sp.): P0 (0), P1 (1–2) and P3 (3–21); Pse (*Pseudophysaloptera* sp.): Pse0 (not infected) and Pse1 (1–7); Sr (*Stammerinema rhopalocephala*): Sr0 (0), Sr1 (1–2) and Sr2 (3–140).

atodes or chlorhydric carmine hydrochloride for cestodes). Nematodes were studied as wet mounts, first in water and then in lactophenol. The numbers of parasites (nematodes and trematodes) or scolices (cestodes, except for *Pseudhymenolepis redonica*) were enumerated.

Statistical methods

The indices of similarity (see L. Legendre and P. Legendre, 1979) are numerous. We used 1 that includes double absences (Sokal and Michener, 1958), and another that excluded double absences; the former gives equal weight to each data pair (Jaccard, 1908), and the latter gives extra weight to the cooccurrence of 2 species within a host (Dice, 1945). A distance measure based on $1 -$ coefficient of correlation was used for quantitative data; values ranged from 0 (full positive association) to 2 (full negative association). Correspondence analyses were performed with STAT-ITCF software (1988), using simple (helminth data) or multiple (helminth, environment, and host) correspondence analyses (CAs). The Euclidean distances between species (dCApa and dCAq, for presence–absence data and qualitative data fell into 3 classes of data, respectively) were derived from CAs in a manner similar to that described in Cabaret and Hoste (1998) for principal component analyses. They were scaled so that their absolute values could be compared. Principal component analysis on standardized data was also performed using the same software. In the present study, CAs (able to handle categorical data) were preferred to principal component analyses (used for quantitative data) because we could compare associations on the basis of presence–absence or parasite numbers arranged into classes using the same type of analysis. The Mantel test (1967) was used to compare distance matrices established by several indices of association. One-way analyses of variance were standard.

RESULTS

Insectivores and rodents collected

Crocidura russula accounted for 38.3% of the total insectivores; the rodents included (569), *Apodemus sylvaticus* 44.1%, *Rattus rattus* 10.0%, and *Mus spretus* 7.6%. The *M. spretus* was relatively more frequent at the B1 site, whereas all the other species were recorded more often at the B2 site. The average weight of the *C. russula* caught was 8.8 g (SD = 3.4), and the mean age according to I. E. Vesmanis and A. Vesmanis (1979) was 3.5–9 mo.

Characteristics of infestation

One species of trematode, 4 species of cestode, and 10 species of nematode were found (Table I). Practically all these helminth species are specific for *C. russula*, and the majority had indirect life cycles. The prevalence of most of the species found was very low, and only those for which the prevalence was more than 4% were taken into consideration. The abundance was low in most cases, except for *Hymenolepis pistillum* and *P. redonica*. For these 2 parasites, most of the worms were concentrated in a few hosts, as shown by the large variance–mean ratio.

TABLE II. Pairwise associations between parasite species infesting shrews: distances based on dCApa for the presence–absence or $(1 - r)$ and (dCAq) of abundance data divided into 3 classes and their similarities (Sokal–Michener, Jaccard, or Dice indices).

Species pairs* Association	Similarity indices			Distances		
	Sokal–Michener	Jaccard	Dice	dCApa	$(1 - r)$	dCAq
Hp–Ht	0.74	0.22	0.36	0.17	0.97	0.22
Hp–Hs	0.71	0.15	0.26	0.10	0.78	0.29
Hp–Pr	0.61	0.19	0.32	0.27	1.08	0.56
Hp–P	0.53	0.13	0.23	0.56	1.07	0.73
Hp–Sr	0.62	0.13	0.23	0.47	1.03	0.56
Hp–Pse	0.74	0.03	0.07	0.27	1.02	0.27
Ht–Hs	0.77	0.19	0.32	0.05	0.93	0.12
Ht–Pr	0.65	0.18	0.31	0.16	0.97	0.54
Ht–P	0.63	0.20	0.33	0.43	0.99	0.48
Ht–Sr	0.72	0.14	0.24	0.43	1.04	0.34
Ht–Pse	0.78	0.21	0.04	0.17	1.05	0.05
Hs–Pr	0.62	0.15	0.27	0.21	0.94	0.44
Hs–P	0.62	0.13	0.24	0.47	1.05	0.42
Hs–Sr	0.68	0.09	0.17	0.43	1.04	0.27
Hs–Pse	0.81	0.24	0.05	0.17	1.04	0.12
P–Sr	0.67	0.29	0.45	0.45	0.85	0.15
P–Pse	0.63	0.05	0.09	0.43	0.98	0.44
Sr–Pse	0.75	0.04	0.07	0.28	1.04	0.29
Pr–P	0.57	0.25	0.41	0.45	0.99	0.60
Pr–Sr	0.58	0.16	0.28	0.58	1.00	0.52
Pr–Pse	0.61	0.01	0.02	0.30	0.99	0.56
Average (SD)	0.67 (0.08)	0.15 (0.08)	0.23 (0.13)	0.34 (0.14)	0.99 (0.07)	0.38 (0.19)

* Cestodes: Hp (*Hymenolepis pistillum*), Hs (*H. scalaris*), Ht (*H. tiara*), and Pr (*Pseudhymenolepis redonica*). Nematodes: P (*Porrocaecum* sp.), Pse (*Pseudophysaloptera* sp.) and Sr (*Stammerinema rhopalocephala*).

Species proportions in relation to host and environment

One-way analysis of variance (ANOVA) (biotope being the studied factor) showed that the helminth fauna (proportion of species, arc sine transformed) was the same for biotopes Bio1 and Bio2 ($P = 0.20$). The age of the shrew was a major factor in the log-transformed values of species abundance (*H. pistillum*, $P < 0.001$, higher values at age 2; *H. tiara*, $P = 0.06$, higher values at age 4 and 5; *Porrocaecum* sp., $P < 0.001$, higher values at age 4 and 5). In itself, season was not an important source of variation for the proportion of species but was related to the age ($P = 0.01$) or weight ($P < 0.01$) of the hosts. The sex of the host shrews was not linked to any significant variation of helminth infections, except in the case of *Pseudophysaloptera* sp.; males were more heavily infected with this species than females ($P < 0.01$). The results from multiple CAs are shown in Fig. 1. Environmental and host descriptors were used to construct the analysis, and the parasitological data were used as supplementary variables (they were identified post hoc on the graph derived from the environment–host data). The variables that were located in the same part of the graph were associated positively (see age 4 and age 5 and the March, April, May samplings), whereas those that were located in widely separated parts of the graph were associated negatively (male vs. female); variables located at 90° sites were independent (Bio2 and female for example). The older shrews (age category 4 and 5) in March, April, and May clearly harbored a heavier load of *P. redonica*, *Porrocaecum* sp. larvae, and *Stammerinema rhopalocephala*, whereas younger shrews were more heavily infested with *H. pistillum*. Males were infested more intensely with *Pseudophysaloptera* sp. than females. However, the asso-

ciation between environment and species was low because only 18% of variance was recorded on the first 2 axes. At the scale we investigated parasites of *C. russula*, the associations of species may also be determined by other nonenvironmental factors. The results from ANOVA and CAs are somewhat similar because neither indicates any strong relationships between host environment and species association.

Bivariate versus multivariate analysis of presence–absence data: interrelations in species associations

The matrix of distances between Sokal–Michener, Jaccard, and Dice bivariate indices (Table II) were compared using a Mantel test. They were not significantly correlated. Conversely, the distance matrix derived from CA on presence–absence data (dCApa) was related to Sokal–Michener distances ($P = 0.03$). The univariate Sokal–Michener and dCApa indices were calculated including joint absences, which may explain their similarity. The fact that the multivariate (all species associations) and 1 univariate index (paired species) are closely correlated, indicates that the presence of any particular species of helminth is probably not related to the presence or absence of any other helminth species.

Multivariate analysis of categorical versus quantitative data: species abundance and associations

The associations were related to taxonomic groups. The cestodes were usually positively associated, and the nematodes were also positively associated (Fig. 2A–C). This was found for all analyses. The mean distances gained from dCApa and dCAq
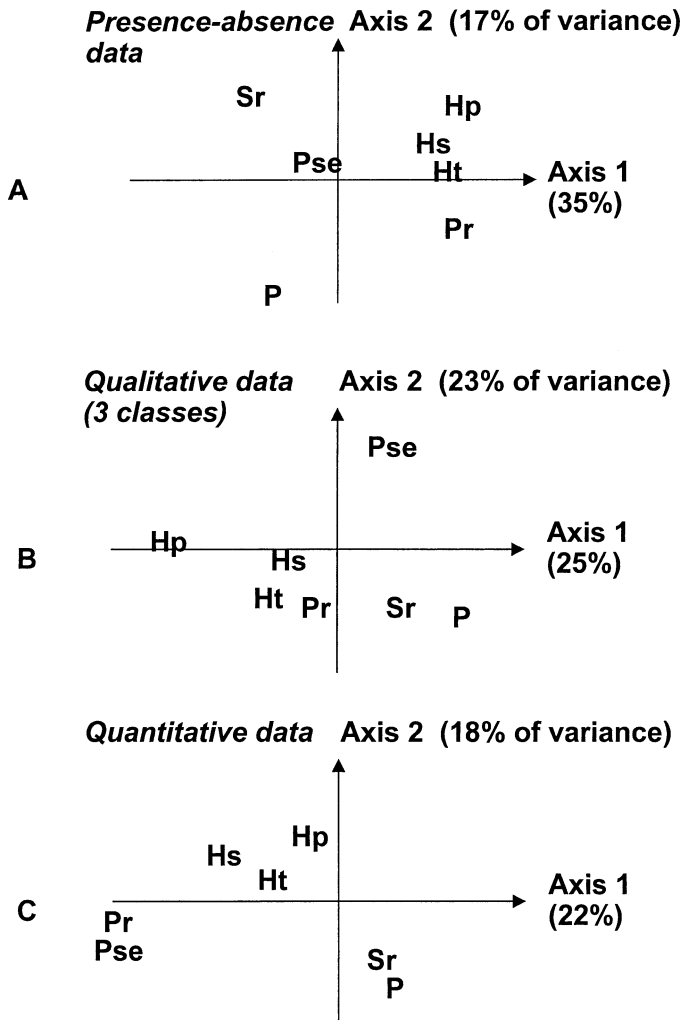
FIGURE 2. Associations between species using simple CA based either on presence–absence data (**A**) or abundance data divided into 3 classes (**B**) as in Fig. 1, or principal component analysis of abundance data (**C**). Cestodes: Hp (*Hymenolepis pistillum*), Hs (*H. scalaris*), Ht (*H. tiara*), and Pr (*Pseudhymenolepis redonica*). Nematodes: P (*Porrocaecum* sp), Pse (*Pseudophysaloptera* sp), and Sr (*Stammerinema rhopalocephala*).

were of the same magnitude (Table II). However, these distances were slightly different when comparing the t2 set of distances obtained from Fig. 2A and B (Mantel test: $P = 0.09$); the value $P > 0.05$ indicates that differences are statistically significantly different, i.e., that the 2 sets of distances were not statistically related. The differences were related to the associations of *H. pistillum* with other cestodes (mean dCApa = 0.18 and mean dCAq = 0.36). A similar finding was observed for the associations of *P. redonica* with other cestodes (mean dCApa = 0.21 and mean dCAq = 0.51). Thus, the distances were greater than expected from presence–absence data. These 2 cestodes were the most abundant species, which could indicate that abundance might interfere with the degree of positive associations. The dCAq values differed from the bivariate estimates (Mantel test: $P = 0.15$), with $P > 0.05$ indicating that the differences are statistically different. This suggests that spe-

cies associations based on pairs of species or on all species associations could lead to slightly different interpretations when qualitative data divided into 3 classes of infection are examined.

DISCUSSION

Environment did not play a large role in the helminth fauna established in the *C. russula* from Albufera Park. This is possibly due to the uniformity of the environment at the scale investigated. Although biotopes B1 and B2 could be differentiated by the presence of birds (more numerous in B2), which are the definitive hosts for most of the nematodes found in *C. russula*, the B2 biotope did not contain many nematodes (Fig. 1). The fact that sampling areas within a given biotope did not affect assemblages of species is not surprising because the environment was very similar and shrew migrations occurred among these sampling areas (Favre et al., 1997). The presence or abundance of parasites was somewhat modified by the age or sex of the shrews but only to a limited extent. The role of host characteristics (age and sex) on parasite abundance and assemblage remained slight, as already shown in other host–parasite groups (Sasal et al., 1999) and accounted for 5–12% of the variance in canonical analyses. Environment was not a decisive factor in determining the presence or absence of parasite species because the 2 axes in multiple CA accounted for only 18% of the variance. No correction for the environment was therefore necessary when investigating associations between species.

The relative abundance of a parasite species within a community may depend on density-dependent processes and interactions or on functional–ecological or phylogenetic constraints. Brooks (1980), Price (1987), and Rohde (1989) have suggested for a variety of reasons, e.g., history, turnover of parasites, and accumulation without saturation in host species, that parasite communities are noninteractive. Rohde et al. (1998) indicated that 70% of the studied parasite assemblages in fish were not interactive. The community organization of parasites has been identified as isolationist, i.e., independently distributed species have been identified (Kennedy et al. [1986] in fish and Goater et al. [1987] in salamanders) but also as interactive, where interaction plays a role in determining the structure of the community, i.e., Goater and Bush (1988) in birds, and Lotz and Font (1991), in bats. Pence (1990) described further the criteria for predicting an isolationist (noninteractive) community. There was a low probability of colonizing the host, direct life cycles, unsaturated niches, low species richness, and small number of high-density species. The helminth community of shrews was characterized by species with a low probability of colonizing the host (low prevalence) and low species richness (7 species), even if we only consider species with prevalence of more than 4.0%, and small number of high-intensity species (*H. pistillum* and *P. redonica*). Presence–absence data (which are not much affected by density dependence) yield more similar association patterns (except in the case of *P. redonica* and *Pseudohymenolepis* sp.) than quantitative data (which are affected to a greater extent by density dependence). We may expect that density does not play an active role in association patterns, e.g., that niche use is not saturated. According to Pence (1990), this should be an isolationist community. We may thus view the shrew community, as proposed by Pence (1990), as being noninteractive

(isolationist). Haukisalmi and Henttonen (1994), studying the habitat segregation of helminths in other species of shrews, noted the small size of helminths, their low degrees of aggregation in hosts, and large intestinal space, factors that could explain why regulatory effects due to space or niche are not important.

The major determinant of helminth assemblages in shrews is phylogenetic or functional. Nematodes, for example, engulf their food and are grouped together, as opposed to the cestodes, which are absorbers. The cestodes of *C. russula* thus constitute a guild because they are ecologically similar, especially in the way they use resources. They all live in the intestine, *C. russula* is their only definitive host, and they have indirect life cycles involving insects. They all belong to the Hymenolepididae and, therefore, are also phylogenetically closely related. The *Hymenolepis* spp. was always closely associated (Fig. 2A–C), whatever the analysis. Moreover, *P. redonica* was also more loosely associated with the *Hymenolepis* spp., suggesting that phylogenetic similarity was possibly an important determinant in structuring the assemblage of cestode species. The nematodes (ingestor guild) were conversely more diverse with respect to their life cycles (indirect, and in several species, the shrews were used as paratenic hosts), location in the host (stomach, intestine, abdominal or thoracic cavities), host specificity, and phylogeny (they belong to the Physalopteridae, Acuariidae, or Ascarididae). Among the 3 species of nematodes, *Pseudophysaloptera* sp., which has an indirect life cycle but does not use shrews as a paratenic host, is located in the stomach and is associated with both nematode and cestode species. Helminth species associations in shrews are apparently influenced mainly by phylogeny and only secondarily by life-cycle similarities.

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