Abomasal Parasites in Wild Sympatric Cervids, Red Deer, *Cervus elaphus*, and Fallow Deer, *Dama dama*, from Three Localities across Central and Western Spain: Relationship to Host Density and Park Management

Mónica Santín-Durán
*United States Department of Agriculture*

José M. Alunda
*Universidad Complutense de Madrid*

Eric P. Hoberg
*United States Department of Agriculture, eric.hoberg@ars.usda.gov*

Concepción de la Fuente
*Universidad Complutense de Madrid, cfuente2@vet.ucm.es*

Follow this and additional works at: [http://digitalcommons.unl.edu/parasitologyfacpubs](http://digitalcommons.unl.edu/parasitologyfacpubs)

Part of the Parasitology Commons
ABOMASAL PARASITES IN WILD SYMPATRIC CERVIDS, RED DEER, CERVUS ELAPHUS AND FALLOW DEER, DAMA DAMA, FROM THREE LOCALITIES ACROSS CENTRAL AND WESTERN SPAIN: RELATIONSHIP TO HOST DENSITY AND PARK MANAGEMENT

Mónica Santín-Durán*, José M. Alunda, Eric P. Hoberg†, and Concepción de la Fuente‡
Departamento de Sanidad Animal, Facultad de Veterinaria, Universidad Complutense de Madrid, Madrid 28040, Spain. e-mail: cfuentet2@vet.ucm.es

ABSTRACT: A survey of abomasal parasites in cervids from Central Spain was conducted at 3 sites, Quintos de Mora (Toledo), Maluénitez de Arriba (Cáceres), and La Herguijuela (Cáceres). Commonly occurring helminths belonged to 3 polymorphic species of the Ostertagininae: Spiculopteragia asymmetrical, S. quadrispiculata, and O. kolchida, and O. drozdii. Ostertagia rycikovi, Trichostrongylus axei was found in very few cases. Ostertagia drozdii/O. rycikovi and the minor male morphotype, S. quadrispiculata, are reported for the first time in red deer from Spain. The 3 ostertaginnae species are also reported for the first time in fallow deer from Spain. These 3 species of Ostertagininae are primarily parasites of cervids, and nematode species characteristic of domestic ruminants were not present. Prevalence of infection by gastrointestinal parasites in cervids was high, ranging from 97.5 to 100%, across the 3 areas sampled. Mean intensity of infection and abundance showed a positive relationship to the population density of red deer. Helminth burdens were higher in fallow deer than in the sympatric red deer and may reflect the gregarious social structure and different foraging patterns of fallow deer.

Red deer (Cervus elaphus) are the most abundant and widely distributed cervids in Spain, and during recent years, the populations of this cervid have increased (Tellería and Sáez-Royuela, 1984). Expanding populations can likely be attributed to increasing habitat availability with the concurrent and progressive abandonment of many rural settlements, a growing concern with the conservation of wildlife resources, and the use of management practices that include the alternative for exploitation of free range for domestic livestock. In this regime of ecological transition, protocols for parasitological survey and inventory were used to contribute to a definitive knowledge of helminth biodiversity in cervids from Spain (e.g., Santín-Durán et al., 2001, 2002). A need for basic biodiversity information is the main reason for addressing such timely issues as the influence of management and farming practices for wild and semidomestic ruminants (Drozd, 1995), interfaces or sympatry for abomasal parasites in 2 species of wild cervids (red deer and fallow deer, Dama dama) at 3 localities in central (Quintos de Mora, Toledo) and western Spain (Maluénitez de Arriba and La Herguijuela, Cáceres); collections at Quintos de Mora followed a complete annual cycle. A comparative framework for this study emphasizes the different management conditions (wild fauna exclusively in Quintos de Mora vs. extensive grazing of wild and domestic fauna in 2 localities in Cáceres) and practices for land use (conservation vs. hunting) as potential determinants of the parasite fauna of red and fallow deer.

MATERIALS AND METHODS

Study areas

Quintos de Mora (Toledo) (Fig. 1): The study area comprised a government-owned and -managed park of 6,864 ha (Quintos de Mora, Toledo) located in Central Spain (39°25’N, 4°04’W). The park exhibits considerable habitat heterogeneity and is partitioned into 2 main areas including a plain, 800 m above sea level (asl) crossed by the Navas River and a surrounding mountainous region with a maximum elevation of 1,235 m asl. The climate is Mediterranean, with a dry season from June to September (rainfall ca. 14 mm; temperature ca. 24 °C) and a wet season with maximum rainfall in winter and spring (rainfall ca. 33 mm; temperature ca. 10 °C). Vegetation includes an overstory with Pinus pinea, P. pinaster, Quercus rotundifolia, Quercus faginea as the predominant trees and a shrub-based understory including Arbutus unedo, Phyllirea angustifolia, Cistus ladanifer, and Erica spp. in varying stages of succession (Alvarez et al., 1991). Several species of large wild mammals are found within the park boundaries, including red deer, fallow deer, roe deer (Capreolus capreolus), muntlon (Ovis musimon), and wild boar (Sus scrofa). Red and fallow deer are by far the most abundant,
with populations of *C. elaphus* estimated at approximately 2,100 individuals (density = 0.3 deer/ha), and about 200 fallow deer (0.03 deer/ha) (Álvarez, 1988). Populations of all ungulates are essentially wild, and treatment with anthelmintics or other veterinary health measures have not been undertaken. There is no domestic animal in this area, and the population of cervids is isolated by a continuous wall surrounding the entire park.

*Maluénez de Arriba* (Cáceres): Maluénez de Arriba is a private hunting area of 1,305 ha located in western Spain (Cáceres) (39°50′N, 0°59′W). The park has 2 parts: a plain and a mountainous area. Vegetation includes *Q. rotundifolia* and *Q. alba* as the predominant trees, and some shrub species, i.e., *A. unedo, P. angustifolia*, and *E. spp.* There is a resident population of *C. elaphus* of about 800 individuals (0.6 deer/ha). In this area, cattle (*B. taurus*) have been sharing pastures with wild ruminants (400 females and 150 males, plus the young fawns of about 800 individuals as the predominant trees, and some shrub species, i.e., *A. unedo, P. angustifolia*, and *E. spp.* There is a resident population of *C. elaphus* of about 800 individuals (0.6 deer/ha). In this area, cattle (*B. taurus*) have been sharing pastures with wild ruminants (400 females and 150 males, plus the young fawns of the year) for several years.

*La Herguijuela* (Cáceres): La Herguijuela is also a private hunting area on 2,402 ha located in western Spain (Cáceres) (39°51′N, 5°55′W). Terrain at this site is comparable with that of Maluénez (see above); accordingly, vegetation is also very similar. In this area, the population of red deer is approximately 424 individuals (0.1 deer/ha); deer share common pastures with cattle and sheep (*Ovis aries*).

**Animals studied**

At Quintos de Mora (Toledo), a total of 147 red deer and 17 fallow deer were collected and examined for parasites. Collections were made on a monthly basis during an annual cycle extending from October 1994 to September 1995. Three age groups were considered (<1 yr, 1–2 yr, adult deer). During each month, at least 3 animals per age group and sex (only in adult deer) were sampled. This study reports analyses of parasites in 81 adult red deer (39 males and 42 females) and 16 male fallow deer. Results of collections from other age classes will be considered in subsequent analyses that focus on the annual cycle.

At Cáceres, 52 adult red deer (22 males and 30 females) were collected from Maluénez de Arriba, and 13 adult male red deer were collected from La Herguijuela during the hunting season (fall 1999).

**Necropsy procedures**

All animals were subjected to standard necropsy procedures. Each abomasum was ligated in situ from the small intestine and omasum, removed, and processed for recovery and enumeration of adult nematodes (MAFF, 1971). Abomasal contents and washes were combined and aliquoted, with 2 × 10% duplicate aliquots being collected and preserved in ethanol (70%) or fixed in phosphate-buffered formalin (5%). Abomasal digestion for recognition of possible populations of arrested fourth-stage larvae for respective species of ostertagiines was not conducted. The total number of worms of each species was calculated by identifying and counting male and female worms in a 10% aliquot of the contents from each animal.

**Identification of nematodes**

Specimens were studied as temporary whole mounts cleared in phenol–alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with interference contrast light microscopy. Male specimens were identified according to Drózdz (1965), Jančev (1979), Lichtenfels et al. (1988), and Hoberg et al. (1993). Female specimens of Ostertagininae were identified on the basis of the structure of the synloph and the esophagus (e.g., Lichtenfels and Hoberg, 1993; M. Santín-Durán, E. P. Hoberg, and A. Abrams, unpubl.). Concepts for polymorphism among species in the Ostertagininae were adopted following Lancaster and Hong (1981), Lichtenfels and Hoberg (1993), and Drózdz (1995), and counts of major and minor morphotypes for males of respective species were combined for calculations of intensity and abundance. Although a consistent convention for the taxonomy of di-morphic and polymorphic ostertagiines remains to be articulated (Hoberg et al., 1999), taxonomy in this study follows the structure in which the major morphotype is listed first followed by the minor; e.g., *O. drozdzii*.*O. ryjikovi.* Representative specimens of these nematodes were deposited in the U.S. National Parasite Collection (from *C. elaphus*: USNPC 91176, 91274, 91275, 91278, 91279, 91285, 91286, 91290, 91291, 91294, 91297, 91301–91304, 91305–91310, 91313, 91314, 91321, 91435, 91436, 91439–91441, 91444, 91445, 91447, 91448, 91450–91453, 91455, 91458, 91459, 91462, 91463, 91466, 91468, 91470–91472, 91475, 91476, 91478–91480, 91485–91487, 91491, 91493–91496, 91500, 91501; from *D. dama*: USNPC 93566–93583) at the Animal Parasitic Diseases Laboratory, USDA, ARS Beltsville, Maryland, and in the Departamento de Sanidad Animal, Facultad de Veterinaria, Universidad Complutense de Madrid (UCM), Madrid, Spain.

**Data and statistical analyses**

The prevalence, abundance, and mean intensity were calculated as specified in Margolis et al. (1982). The frequency of each species, i.e., (number of nematodes, males and females, of 1 species/total number of nematodes of all species) × 100, was established for each animal on the basis of all the worms found in the aliquot; a mean frequency was calculated from all deer infected. In the same manner, the ratio of major- and minor morphotype for the pair of males representing each species of ostertagine and the percentage of females of each species were calculated.

Data were analyzed at the UCM Computing Center (CPD) using BMDP Statistical Software (Dixon, 1993). Statistics included parametric (Student’s *t*-test, analysis of variance) and nonparametric tests (correlation, X²). Welch test (alternative *t*-test) was used to compare means when standard deviations were not equal between compared groups. Duncan and Tukey multiple comparison tests were performed when the *P* value was less than 0.05. The term significant refers to statistical significance at *P* ≤ 0.05.

**RESULTS**

**Red deer**

*Quintos de Mora*: Adult nematodes were found in the majority of abomasum examined (97.5%), with an overall abundance of 545.8 ± 549.97 nematodes/deer and a mean intensity of 559.6 ± 457.34 nematodes/deer infected. No sex-related differences were observed in prevalence (males: 97.4%; females: 97.6%), abundance (males: 600.51 ± 490.14; females: 495 ± 429.73), or mean intensity (males: 616.31 ± 486.55; females: 507.07 ± 427.8).

Nematodes belonged to 4 species, i.e., *Spiculopteragia asymmetricalis*, *S. quadrirupedalis*, *O. leptospicularis*/*O. kolchida*, *O. drozdzii*.*O. ryjikovi*, and *Trichostrongylus axei*. Whereas Ostertagininae were prevalent and abundant, *T. axei* was found only...
Prevalence of infection with abomasal nematodes was very high; *Spiculopteragia asymmetrical*/*S. quadrispiculata* was the most common species in both sexes. However, the prevalence of *O. leptospicularis/O. kolchida* in male hosts was significantly higher than in females ($P = 0.0001$). *Ostertagia drozdzii/O. ryjikovi* was not present in female red deer and was seldom found in males (18%). Also, a low prevalence was observed for *T. axei* in males and females (ca. 17%).

Abundance and mean intensity of abomasal infection, including all species and for *S. asymmetrical/S. quadrispiculata*, differed significantly between male and female red deer (Table III). For *O. leptospicularis/O. kolchida*, the differences were only significant for abundance ($P = 0.0011$) when male and female hosts were compared, but not for intensity. There was no difference in the distribution of *T. axei* between males and females.

In the abomasum of infected red deer, the mean percentages that each species represented were: *S. asymmetrical/S. quadrispiculata*, 91.63 ± 10.37; *O. leptospicularis/O. kolchida*, 6.66 ± 8.96; *O. drozdzii/O. ryjikovi*, 0.08 ± 0.30; and *T. axei*, 1.54 ± 5.20. The mean percentage of *S. asymmetrical/S. quadrispiculata* was significantly greater in females (94.77 ± 9.5) in females vs. 85.50 ± 10.47 in males ($P = 0.0126$), whereas the opposite was observed for *O. leptospicularis/O. kolchida* (10.26 ± 8.81 in males vs. 3.93 ± 8.37 in females) ($P = 0.0119$).

In the species of ostertagiines, the relative abundance for major morphotypes represented in the total for males of each species was similar to that observed at other sites: *S. asymmetrical*/*S. quadrispiculata* (n = 50) 84.46 ± 9.79%, *O. leptospicularis/O. kolchida* (n = 26) 89.35 ± 21.80%, and 100% for *O. drozdzii/O. ryjikovi* (n = 3). In female red deer, we found a

### Table I. Average percentage (±SD) that different Ostertagiinae represented for the total abomasal worm burdens in infected adult red deer from Quintos de Mora.

<table>
<thead>
<tr>
<th></th>
<th>Spiculopteragia asymmetrical</th>
<th>Ostertagia leptospicularis</th>
<th>Ostertagia drozdzii</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>S. quadrispiculata</em></td>
<td><em>O. kolchida</em></td>
<td><em>O. ryjikovi</em></td>
</tr>
<tr>
<td>Males (38)*</td>
<td>88.74 ± 12.45</td>
<td>9.53 ± 11.99</td>
<td>1.73 ± 3.07</td>
</tr>
<tr>
<td>Females (41)</td>
<td>89.68 ± 18.01</td>
<td>9.02 ± 16.98</td>
<td>1.29 ± 3.36</td>
</tr>
<tr>
<td>Total (79)</td>
<td>89.23 ± 15.5</td>
<td>9.27 ± 14.7</td>
<td>1.51 ± 3.21</td>
</tr>
</tbody>
</table>

* In parentheses, number of animals sampled.

### Table II. Prevalence (%), abundance (±SD), and mean intensity (±SD) of Ostertagiinae in adult red deer from Quintos de Mora.

<table>
<thead>
<tr>
<th></th>
<th>No. of animals parasitized</th>
<th>Prevalence</th>
<th>Abundance (±SD)</th>
<th>Mean intensity (±SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spiculopteragia asymmetrical/<em>S. quadrispiculata</em></td>
<td>Males 38</td>
<td>97.4</td>
<td>528.7 ± 437.3</td>
<td>542.6 ± 434.4</td>
</tr>
<tr>
<td></td>
<td>Females 40</td>
<td>95.2</td>
<td>440.7 ± 366.4</td>
<td>462.7 ± 361.5</td>
</tr>
<tr>
<td></td>
<td>Total 78</td>
<td>96.3</td>
<td>483.1 ± 402</td>
<td>501.7 ± 398.1</td>
</tr>
<tr>
<td>Ostertagia leptospicularis/<em>O. kolchida</em></td>
<td>Males 28</td>
<td>71.8</td>
<td>58.7 ± 88.7</td>
<td>81.8 ± 95.5</td>
</tr>
<tr>
<td></td>
<td>Females 27</td>
<td>64.3</td>
<td>46.7 ± 97.9</td>
<td>72.6 ± 114.7</td>
</tr>
<tr>
<td></td>
<td>Total 55</td>
<td>67.9</td>
<td>52.5 ± 93.2</td>
<td>77.3 ± 104.5</td>
</tr>
<tr>
<td>O. drozdzii/<em>O. ryjikovi</em></td>
<td>Males 15</td>
<td>38.5</td>
<td>13.1 ± 23.5</td>
<td>34 ± 27.2</td>
</tr>
<tr>
<td></td>
<td>Females 12</td>
<td>28.6</td>
<td>7.6 ± 19.5</td>
<td>26.7 ± 29.3</td>
</tr>
<tr>
<td></td>
<td>Total 27</td>
<td>33.3</td>
<td>10.2 ± 21.6</td>
<td>30.7 ± 27.9</td>
</tr>
</tbody>
</table>
significant differences between sexes (P ≤ 0.05).

Comparison of collection sites

A comparison, considering data from red deer for the 3 study areas, is shown in Table IV. Prevalence of infection for abomasal nematodes exhibited no difference across the 3 sites. In contrast, mean intensity of infection was significantly higher in Maluénuez de Arriba than in the other areas; Quintos de Mora and La Herguijuela did not differ. Three species of ostertagiines were represented, but all species were not present at each site; T. axei was sporadic in its occurrence.

Some differences in the specific composition of the infections were evident because at La Herguijuela only 2 species, S. asymmetrica and O. leptospicularis/O. kolchida, were identified. The prevalence of O. leptospicularis/O. kolchida was significantly lower in red deer at La Herguijuela than in the other 2 parks. Ostertagia drozdzi/O. ryjikovi was significantly more prevalent at Quintos de Mora than at Maluénuez de Arriba. In contrast, for T. axei we found significantly lower prevalence at Quintos de Mora than at Maluénuez de Arriba (P = 0.0001).

Significant differences were found in the intensity of infection for S. asymmetrica/S. quadrispiculata among red deer from the 3 areas studied (P < 0.001). The intensity of infection for O. leptospicularis/O. kolchida was greater at Maluénuez de Arriba than at Quintos de Mora and La Herguijuela and that from O. drozdzi/O. ryjikovi was greater, but not significantly so, at Quintos de Mora than at Maluénuez de Arriba. Trichostrongylus axei only occurred with a moderate mean intensity at Maluénuez de Arriba, and it was found sporadically in Quintos de Mora. There were significant differences in the percentage of S. asymmetrica/S. quadrispiculata in abomasum of red deer among areas studied (P < 0.01), and O. drozdzi/O. ryjikovi showed a lower percentage in Maluénuez de Arriba (P = 0.0001).

Considering the relative abundance of male morphotypes within respective species of ostertagiines, few differences were noted. The percentage of S. asymmetrica morphotype did not show differences among areas studied. However, the O. leptospicularis morphotype was more prevalent in hosts from Quintos de Mora than from Maluénuez de Arriba (98.64 ± 7.93 vs. 89.35 ± 21.80) (P = 0.0425). The minor morphotype associated with O. drozdzi was not found at Maluénuez de Arriba.

Fallow deer

Sampling of fallow deer occurred at Quintos de Mora where they are sympatric with red deer. Adult nematodes were recovered from 13 of 16 abomasas studied, and prevalence of infection (81.3%) did not differ significantly from that found in red deer from the same locality (Tables IV, V). Prevalence of S. asymmetrica/S. quadrispiculata was slightly greater in red deer, whereas fallow deer showed a higher, although not significantly different, prevalence of O. drozdzi/O. ryjikovi. However, prev-

### Table III. Prevalence (%), abundance (±SD), and mean intensity (±SD) of the species found in abomasum of male and female red deer from Maluénuez de Arriba.

<table>
<thead>
<tr>
<th></th>
<th>Prevalence</th>
<th>Abundance (±SD)</th>
<th>Mean intensity (±SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spiculopteragia asymmetrical/S. quadrispiculata</td>
<td>100</td>
<td>1094.5 ± 960.47*</td>
<td>1094.5 ± 960.47*</td>
</tr>
<tr>
<td>Ostertagia leptospicularis/O. kolchida</td>
<td>95.45*</td>
<td>107.27 ± 102.92*</td>
<td>112.38 ± 102.56*</td>
</tr>
<tr>
<td>O. drozdzi/O. ryjikovi</td>
<td>18.18</td>
<td>1.82 ± 3.95</td>
<td>10</td>
</tr>
<tr>
<td>Trichostrongylus axei</td>
<td>18.18</td>
<td>45.91 ± 149.97</td>
<td>252.5 ± 296.47</td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>1251.4 ± 1106.5*</td>
<td>1251.4 ± 1106.5*</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. asymmetrica/S. quadrispiculata</td>
<td>96.67</td>
<td>605.67 ± 529.75*</td>
<td>626.55 ± 526.41*</td>
</tr>
<tr>
<td>O. leptospicularis/O. kolchida</td>
<td>36.67*</td>
<td>20.33 ± 51.76*</td>
<td>55.45 ± 75.01</td>
</tr>
<tr>
<td>O. drozdzi/O. ryjikovi</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>T. axei</td>
<td>16.67</td>
<td>7.33 ± 32.79</td>
<td>44 ± 76.03</td>
</tr>
<tr>
<td>Total</td>
<td>96.67</td>
<td>633.67 ± 543.9*</td>
<td>655.52 ± 539.96*</td>
</tr>
</tbody>
</table>

* Significant differences between sexes (P ≤ 0.05).
<table>
<thead>
<tr>
<th>Area</th>
<th>Quintos de Mora</th>
<th>Malánez de Arriba</th>
<th>La Herguijuela</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence of abomasal infection</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spiculopteragia asymmetrica / S. quadrispiculata</td>
<td>98.08%</td>
<td>61.5%</td>
<td>98.08%</td>
</tr>
<tr>
<td>Ostertagia leptospicularis / O. kolchida</td>
<td>67.9%</td>
<td>7.69%</td>
<td>61.54%</td>
</tr>
<tr>
<td>Ostertagia leptospicularis / O. ryjikovi</td>
<td>0%</td>
<td>0%</td>
<td>7.69%</td>
</tr>
<tr>
<td>Total</td>
<td>97.5%</td>
<td>17.3%</td>
<td>100%</td>
</tr>
<tr>
<td>Mean intensity of abomasal infection</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. leptospicularis / O. kolchida</td>
<td>82.84 ± 95.8%</td>
<td>9.38 ± 95.8%</td>
<td>91.63 ± 105.7%</td>
</tr>
<tr>
<td>O. drozdzi / O. ryjikovi</td>
<td>0%</td>
<td>0%</td>
<td>6828.4%</td>
</tr>
<tr>
<td>Total</td>
<td>89.23%</td>
<td>77.3%</td>
<td>104.5%</td>
</tr>
<tr>
<td>Percentage of each species in the total burden</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. asymmetrica / S. quadrispiculata</td>
<td>89.23%</td>
<td>15.5%</td>
<td>91.63%</td>
</tr>
<tr>
<td>O. kolchida</td>
<td>9.27%</td>
<td>6.66%</td>
<td>8.96%</td>
</tr>
<tr>
<td>O. drozdzi / O. ryjikovi</td>
<td>6.15%</td>
<td>3.21%</td>
<td>0.30%</td>
</tr>
<tr>
<td>T. axei</td>
<td>1.54%</td>
<td>1.54%</td>
<td>1.54%</td>
</tr>
<tr>
<td>Percentage of the major morphotype</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. asymmetrica / S. quadrispiculata</td>
<td>89.79%</td>
<td>84.46%</td>
<td>85.7%</td>
</tr>
<tr>
<td>O. drozdzi / O. ryjikovi</td>
<td>2.57%</td>
<td>9.79%</td>
<td>21.8%</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Species diversity**

Multispecies assemblages of ostertagine nematodes are the rule in cervids, consistent with observations from our study. Most species of abomasal nematodes recovered in this study have been reported previously in red deer from Spain. *S. asymmetrical S. quadrispiculata* has been observed in red and roe deer, *O. leptospicularis/O. kolchida* only in red deer, and *T. axei* has been found in a wide range of hosts, including red deer (Cordero del Campillo et al., 1994; Ortiz et al., 1996; García-Romero et al., 2000). However, this is the first report in Spain for *O. drozdzi/O. ryjikovi*, but it has been reported in red deer from other European countries (Jančev, 1979; Ambrosi et al., 1993; Rehbein and Haupt, 1994; Drózd et al. 1997). Moreover, as far as we know, this is the first study of abomasal nematodes in fallow deer from Spain and, thus, the collection of *S. asymmetrical S. quadrispiculata, O. leptospicularis/O. kolchida, and O. drozdzi/O. ryjikovi* constitutes new host records for the country.

Very few reports have been published on the relative abundance of major and minor morphotypes for males among species of Ostertaginae (Drózd et al., 1987, 1992; Hoberg et al., 1999), and most observations have been limited to faunas in domestic ruminants. In our case, we found different ratios characteristic for each genus and species of the subfamily, and no variation was observed to be related to the sex of the hosts. The only exception was the apparent increase among older animals in the relative abundance of the minor morphotype for *O. drozdzi/O. ryjikovi*. Drózd et al. (1987) also found an increase of the minor phenotype for *S. spiculoptera/S. mathevosiani* associated with age of host in roe deer but not for *O. leptospicularis/O. kolchida*. In addition, when the ratios for male morphotypes among respective species of ostertagines in sympatric cervids from Quintos de Mora were compared, a greater percentage of major forms of *S. asymmetrical S. quadrispiculata* and *O. drozdzi/O. ryjikovi* were found in fallow deer.
Perhaps this may be related to fallow deer being the principal cervid host for *S. asymmetrical/S. quadrispicularis* and *O. drozdzi/O. ryjikovi* (Drózdz, 1995).

There is also evidence that the ratio of major:minor morphotypes may be altered seasonally or through senescence of the entire population in a host; for example, consider *Teladorsagia boreoarcticus*, where the percentage of the minor morphotype may exceed 50% of the total population late in the winter (Hoberg et al., 1999; E. Hoberg and S. Kutz, unpubl. data). Host species and age, seasonal effects, and population senescence may serve as determinants in the maintenance of a balanced species diversity and specificity among species of some ostertagiines, but the biological significance of this phenomenon remains elusive.

Nematode species identified in this study are typical parasites of cervid hosts (Drózdz, 1965; Janče, 1979; Govorka et al., 1988), except for *T. axei*, a common gastrointestinal nematode of a variety of ruminants, including deer, and some monogastric animals. Although *O. leptospicularis/O. kolchida* is a typical cervid parasite, it has also been found associated with *O. ostertagii/O. lyrata* in cattle, where it can be a significant pathogen (Dunn, 1983; Hoberg et al., 1993). *Ostertagia drozdzi/O. ryjikovi* as well as *S. asymmetrical/S. quadrispicularis* are considered typical parasites of fallow deer (Kotrla and Kotrlý, 1975; Janče, 1979), and the former has only been reported in other hosts (red deer and goat, *Capra hircus*) when fallow deer were sympatric and sharing common pasture (Rehbein and Haupt, 1994; Drózdz et al., 1997).

It is important to emphasize that there was no contact between cervids and domestic ungulates in Quintos de Mora (Toledo), but contact was the usual situation at both Maluénuez de Arriba and La Herguijuela (Cáceres). Even so, no notable difference was observed for faunal diversity among areas, and no species typical of domestic ruminants, except *T. axei*, was found at Maluénuez de Arriba and La Herguijuela. No evidence of parasite switching between cervids and bovids was obtained from our results, in contrast to reports by Lanfranchi et al. (1985) and Batty et al. (1987). The possibility of cross-transmission for gastrointestinal nematodes among domestic and wild ruminants is a controversial issue, and such species typical of domestic ruminants as *O. ostertagii/O. lyrata*, *Teladorsagia circumcincta/T. trifurcata/T. daviani*, and *Haemonchus contortus* have been reported in cervids sharing pastures with cattle, sheep, and goats (Barth and Matzke, 1984; Zaffaroni et al. 1997, 2000). It should be noted that evolving concepts for species diversity and specificity among species of *Teladorsagia* and *Haemonchus* may alter our understanding of host associations for abomasal nematodes (Hoberg et al. 1999, 2004; Liegnel et al., 2002).

In our study, we provide only limited evidence for acquisition of gastrointestinal nematodes from domestic hosts as indicated by the occurrence of *T. axei* in red deer, otherwise, our data are consistent with a level of independence between wild and domestic faunas. Increasingly, however, with the advent of ecological perturbation linked to global environmental change and the breakdown in isolating mechanisms between faunas, heightened levels of reciprocal exchange, dissemination, and emergence may be predicted with unknown outcomes for both domestic and wild ungulates (Hoberg, 1997; Daszak et al., 2000; Hoberg et al., 2001, 2003).

Richer nematode communities have been reported from other areas of Europe, but it could be related to co-occurrence of red deer with other sympatric cervids and bovids and not with domestic ruminants (Drózdz et al., 1992, 1997). Among studies reporting greater species richness, only 2 or 3 nematodes are responsible for the abomasal infections among cervids, and these are always typical components of fauna restricted to deer (e.g., Dunn, 1965; Rossi et al., 1997; Zaffaroni et al., 1997). Such observations do not reduce the importance of understanding the influence of ecotones or interfaces between managed and natural ecosystems on helminth diversity in cervids and bovids (Hoberg et al., 2001). Notably, translocation and introduction remain as major determinants of parasite faunal diversity. A primary example is seen in the widespread occurrence, host switching, and dissemination of *Ashworthius sidemi* in western Europe coinciding with the introduction of sika, *C. nippon*, from Eurasia (Fért et al., 2000); this haemonchine has yet to be recognized in Spain.

### Quantitative faunal comparisons

It is challenging to directly compare both qualitative and quantitative aspects of our studies with results of previous research because many of these investigations of cervid parasites failed to consider the concept of polymorphism for ostertagine males. Thus, even in recent literature, respective major and minor morphotypes of single species are referred to different genera or as discrete congenic species (e.g., Ambrosi et al., 1993; Mason, 1994; Rehbein and Haupt, 1994; García Romero et al., 2000). Such practices continue even when the concept of polymorphism has been clearly demonstrated across the continuum from comparative morphology to multilocus analyses of DNA sequences (Lancaster et al., 1983; Lichtenfels et al., 1988; Andrews and Beveridge, 1990; Hoberg et al., 1993; Drózdz, 1995;
Drozdz Ç et al., 1994, 1997; Rossi et al., 1997; Garcia-Romero observed among domestic ruminants (Suárez et al., 1991; infection that is usually considered moderate relative to levels approaching 100%, has been a common observation in all parasite differences is available (physiology, ecology, or immunology), not been conducted, no information on the reason for these ryjikovi in fallow deer. Because experimental infections have

abomasal nematodes occurred at Malueñez de Arriba (0.6 red
danger for red deer and domestic ungulates including cattle and sheep. However, a concurrent study of the fauna typical in do-
mertic ungulates was not conducted, but it is predicted that for
conducted for reindeer and ostertagiines at Svalbard in the Arctic (see Albon et al., 2002).

No definite pattern of sex-related parasitism (prevalence and intensity) was demonstrated in this study. Differences between sexes have been described (Bye and Halvorsen, 1983; Barth and Matzke, 1984) and have been attributed to hormone levels usually during breeding (Dobson, 1964; Grossman, 1985; Zuck and McKeen, 1996). Male deer are usually more heavily parasitized than the females (Dunn 1965, 1983; Battly et al., 1987; Ambrosi et al., 1993; Poulin, 1996; Rossi et al., 1997), whereas in other reports no evidence of this difference was obtained (Zaffaroni et al., 1997; Halvorsen and Bye, 1999); studies should be examined in the context of seasonal effects and the timing of collections. We found significantly higher burdens in male deer at Maluéñez de Arriba and Quintos de Mora, but the differences were not significant in the latter locality.

The greater parasite burdens found in fallow deer than those from the sympatric red deer in Quintos de Mora could be related to the feeding behavior of the hosts. The former are grazers that depend more on the pastures; in contrast, red deer are primarily browsers, with only 25% of total food intake being represented by grasses and forbs (Alvare, 1990). In addition, fallow deer are highly gregarious (Soriguer et al., 1994), which further contrasts with red deer. Interestingly, these results are in sharp contrast to the results obtained by Drozdz Ç et al. (1997), and the primary difference between the respective studies is that sympatric cervids were farmed and confined and at relatively high densities, rather than wild and completely free ranging.

Overall, the abomasal parasite fauna of both red deer and fallow deer in central and west Spain were characterized by relatively low diversity. There was minimal variation among the 3 sites, and there was no apparent effect related to common grazing for red deer and domestic ungulates including cattle and sheep. However, a concurrent study of the fauna typical in dom-
cestic ungulates was not conducted, but it is predicted that for some species such as O. leptospicularis/O. kolchida, cervids could serve as a source of infections for domestic stock in areas of sympathy. Further studies of this cervid fauna will include

Species found in fallow deer, i.e., S. asymmetrical/S. quadrispiculata, O. leptospicularis/O. kolchida and O. drozdzi/O. ryjikovi, were present in red deer and are typical of cervid hosts. Spiculopteragia asymmetrical/S. quadrispiculata had the higher percentage in abomasas of infected animals (as in red deer). However, in fallow deer, the percentage of O. drozdzi/O. ryjikovi was greater than in red deer, whereas O. leptospicularis/O. kolchida occurred sporadically. Our results agree with those of Drozdz Ç et al. (1997) who also found the 2 species in sympatric cervids, red and fallow deer, but as in this study, with different percentages; S. leptospicularis/O. kolchida and O. asymmetrical/S. quadrispiculata and O. drozdzi/O. ryjikovi in fallow deer. Because experimental infections have not been conducted, no information on the reason for these differences is available (physiology, ecology, or immunology), although fallow deer are considered the principal hosts for the latter ostertagiines.

A high prevalence of infection by abomasal nematodes, approaching 100%, has been a common observation in all parasite surveys carried out among cervids, with a mean intensity of infection that is usually considered moderate relative to levels observed among domestic ruminants (Suárez et al., 1991; Drozdz Ç et al., 1994, 1997; Rossi et al., 1997; García-Romero et al., 2000; Hoberg et al., 2001). Although most deer were infected in this study, abundance and intensity were variable; such may represent variation linked to seasonal effects, which will be examined in a subsequent comparative framework.

An overdispersed pattern was observed for the distribution of all species of ostertagiines in red deer from Quintos de Mora. Thus, although prevalence of infection was near 100%, relatively few hosts harbored infections of great intensity. Aggregation of parasite infrapopulations is the rule rather than the exception (Anderson, 1978, 1982), including those in wild hosts (Grenfell et al., 1995). In addition, this population model is frequently found among parasites with direct life cycles in which infective stages are passively ingested by the host; in this case, while grazing.

There was a direct relationship between host density and parasite burdens in red deer. Greatest intensity of infection for abomasal nematodes occurred at Maluéñez de Arriba (0.6 red deer/ha), whereas the lowest helminth burdens were documented at La Heruguijuela (0.1 red deer/ha). Differences among sites were also observed when collection data were corrected for the season of collection at respective localities. In this instance, comparisons were solely on the basis of hosts sampled in the same period of the annual cycle (fall), and at Quintos de Mora during this season, abundance and mean intensity were 463 nematodes/deer. These empirical data are consistent with theoretical predictions about the positive linkage of host density with the intensity infection and abundance of parasites (Anderson and May, 1978; Arneberg et al., 1998). Drozdz Ç et al. (1994) observed peak levels of intensity of infection for abomasal nematodes before culling of an expanding population of red deer in Poland. Suárez et al. (1997) noted higher parasite burdens in farmed deer maintained at high densities compared with wild populations. In addition, Eve and Kellogg (1977) have established a correlation between intensity of infection and local population density for hosts in studies of white-tailed deer (Odocoileus virginianus). Such empirical observations are important in establishing an understanding of positive feedbacks between density for hosts and parasites, linkages to habitat structure and stability, and the regulation of populations of wild ungulates (Grenfell, 1992; Arneberg et al., 1998). Currently, there are no data available from boreal systems to demonstrate regulatory effects of parasites on host populations through fecundity or other effects such as those demonstrated for reindeer and ostertagiines at Svalbard in the Arctic (see Albon et al., 2002).
an examination of the seasonal effects on the diversity and distribution of abomasal nematodes. Such a biodiversity survey and inventory serves as a baseline for documenting faunal stability and transition in a regime of global change (e.g., Hoberg et al., 2003).

ACKNOWLEDGMENTS

We deeply thank Instituto Conservación de la Naturaleza (ICONA) and the Spanish Ministry of Science and Technology (BOS2003-09027-CO-03) for partial financial support of this project. Cooperation of J. M. Sebastián and C. Rodríguez was critical. Warden services and J. M. San Miguel, I. Domínguez, A. López, A. González, and M. Carballo helped us in the collection of red deer and sampling for parasites. Some laboratory studies by M.S.-D. with E.P.H. were conducted at the U.S. National Parasite Collection, and we wish to thank P. Pilitt and A. Abrams for their assistance in preparation of specimens.

LITERATURE CITED


—. 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology 85: 373–398.


