Ecology of nematode parasitism in red-legged partridges (Alectoris rufa) in Spain

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Summary

We examined the nematode fauna of 79 shot red-legged partridges (Alectoris rufa) from Southern Spain. Four species (Trichostrongylus tenuis, Heterakis gallinarum, Cyrnea seurati, and Cheilospirura gruveli) were recorded, C. gruveli being identified as the core species of this population. Trichostrongylus tenuis showed higher prevalence and abundance in adults than in juveniles. The infection with C. gruveli increased with age in females but decreased in males. The occurrence of C. gruveli and C. seurati in individual partridges was not independent in juveniles. The C. gruveli population was female-biased, more markedly at high intensities. The presence of spirurid eggs in faeces and C. gruveli females was not independent in juveniles and showed the same trend in adults. The abundance of C. gruveli was positively correlated with the gizzard weight in juvenile partridges. Juvenile females parasitised by C. gruveli had a heavier spleen than those nonparasitised. Adult partridges harbouring C. gruveli were in poorer body condi-tion than those free of the parasite.

Key words: *Alectoris rufa*; *Cheilospirura gruveli*; gamebird; nematode; red-legged partridge; Spain

Introduction

The red-legged partridge (*Alectoris rufa*) is the most abundant wild galliform in the Iberian peninsula. There are about 3 million free-ranging reproductive pairs in Spain, and more than 4 million individuals are hunted yearly. It is believed to have declined considerably in areas of its native range (Gortázar *et al.*, 2002), and helminths have been mentioned as one of the factors involved in the regulation of galliform populations (Hudson *et al.*, 1992). Works regarding the helminth fauna of the red-legged partridge are scarce, and they deal with taxonomic catalogues (Cordero del Campillo *et al.*, 1994), description of species (Illescas and Gómez, 1987), or reports of helminthiasis in farmed individuals (Tarazona *et al.*, 1979). There is no information about the structure, ecology, and host-parasite relationships of the helminth communities of wild red-legged partridge populations. This contrasts with other galliform species, whose helminth ecology has been thoroughly studied (Davidson *et al.*, 1980; Shaw and Moss, 1989; Rizzoli *et al.*, 1997; Holmstad and Skorping, 1998). The availability of such information has fostered the investigations into the role of nematodes in their host's population dynamics (e.g. Hudson and Dobson, 1997).

The present study is part of a long-term investigation on red-legged partridge ecology and diseases. The objectives of this work were to: i) determine the composition of the nematode community of a natural population of this species in the southernmost range of its distribution; ii) investigate characteristics of the ecology of the nematode community, such as species associations, sex ratios, or parasite fecundity; and iii) obtain information on nematode distribution depending on its host's sex and age classes, niche size, or host body condition.

Material and Methods

In November 10th 2000, 79 shot red legged partridges were collected after a driven hunt in Medina Sidonia (Cádiz province, Southern Spain, 05° 58' W, 36° 27' N). Most of the range is devoted to intensive agriculture including large beetroot, wheat and sunflower fields, and only 5 % of the surface is covered by a Termomediterranean scrub of *Pistacia lentiscus* and introduced *Opuntia ficus*. The altitude ranges from 44 to 148 m a.s.l., and the annual rainfall that year was 862 mm.

Partridges were sexed by gonadal observation and aged following Sáenz de Buruaga *et al.* (2001). A "juvenile" partridge was defined as hatched that season. Each bird was measured and weighed, and its internal organs removed and frozen. The tracts were later thawed. Organs were measured following Millán *et al.* (2001). We inspected oesophagus, crop, proventriculus, gizzard, small intestine,

and one of the caeca. Parasites were extracted by washing the content of the digestive tract and scraping the epithelium into a beaker and retrieved under a stereomicroscope. All the nematodes were stored in 70 % alcohol, cleared with lacto-phenol and identified under a microscope, according to López-Neyra (1947), Skryabin (1991), and Anderson (2000). Since the faeces content of the rectum was not enough to allow us to perform a coprological analysis, we include the content of the second caeca. We quantified the excretion of parasitic forms by flotation and count in a MacMaster chamber (Melhorn et al., 1992). Terminology referring to parameters of parasitism is that of Bush et al. (1997). Prevalence was calculated with Quantitative Parasitology 2.0 (Rózsa et al., 2000). Since it was not possible to differentiate Cheilospirura gruveli and Cyrnea seurati excretion forms, worm fecundity (number of eggs/gravid female) was calculated taking into account only those partridges not harbouring C. seurati females. The residual of the regression of body weight on the cube of head and body length was taken as condition index. The data were logtransformed when needed. ANOVA and Mann-Whitney U were used to analyse differences in parasite abundance, egg shedding, body mass, and body condition between groups of partridges. Prevalence relationship were tested using Fisher's exact test. All other correlations were tested using Spearman's Y.

Results

Composition of the nematode community

We recorded a total of four nematode species. Their prevalence, abundance and range of parasitation, and the number of nematode species by host sex and age are reflected in Table 1.

Nematode ecology

Adult partridges harboured more nematode species than juveniles (Two way ANOVA, $F_{1.75} = 5.44$, P < 0.05). These differences were more marked in females, as shown by the interaction between sex and age (Two way-ANOVA, $F_{1,75} = 5.44$, P < 0.01). Trichostrongylus tenuis showed higher prevalence ($\chi^2 = 10.30$, df = 1, P < 0.01) and abundance (Two way-ANOVA, $F_{1.75} = 12.59$, P < 0.001) in adults than in juveniles. Despite the absence of age-related differences in the infection with C. gruveli, a sex by age interaction was found (Two ways-ANOVA, $F_{1.70} = 4.87$, P < 0.05). The abundance increased with age in females but decreased in males. Although the differences were not significant, the infestation of partridges with Cyrnea seurati also followed this pattern. In fact, the occurrence of C. gruveli and C. seurati in individual partridges was not independent in juveniles ($\chi^2 = 9.74$, df = l, P < 0.01). With the exception of C. gruveli in adult males, all the nematodes presented aggregated distributions.

The female-to-male sex ratio among the *C. gruveli* population was 1.86 ± 1.87 (adults: 1.56 ± 1.75 ; juveniles: 2.14 ± 1.97). We found a positive relationship between the intensity of infection and female-to-male sex ratio of *Cheilospirura gruveli* ($r_s = 0.33$, n = 45, P < 0.05).

Results regarding the distribution of *C. gruveli* specimens depending on their sex are reflected in Table 2. No differences were found among host age and sex classes. However, as in the total parasite count, an age by sex interaction was found in the distribution of *C. gruveli* females (Two ways-ANOVA, $F_{1.74} = 7.20$, P < 0.01). The *C. gruveli* egg excretion and the fecundity of the females are also reflected in Table 2. No other helminth excretion form was detected during the faecal analysis. The presence of *C. gruveli* eggs in faeces and *C. gruveli* females was not indepen-

 Table 1. Prevalence (Confidence Intervals in parenthesis), mean abundance (mean ± SD.), and range of each species, and number of nematode species retrieved by host sex and age in 79 red-legged partridges (Alectoris rufa) from Medina Sidonia (Southern Spain)

		Adults		Juveniles		Sex	Age	Age *Sex
	-	Males (n=20)	Females (n=14)	Males (n=20)	Females (n=25)	-	Ð	5
Trichostrongylus	Р	0.20 (0.06-0.44)	0.36 (0.13-0.65)	0.05 (0.01-0.32)	0	ns	< 0.01	
tenuis								
	Α	0.20 ± 0.41	0.36 ± 0.49	0.05 ± 0.22	0	ns	< 0.001	ns
	R	0-1	0-1	0-1	-			
Heterakis	Р	0.05 (0.01-0.32)	0.21 (0.05-0.51)	0.05 (0.01-0.32)	0.04 (0.00-0.20)	ns	ns	
gallinarum								
	А	0.05 ± 0.22	0.42 ± 1.09	0.05 ± 0.22	0.04 ± 0.2	ns	ns	ns
	R	0-1	0-4	0-1	0-1			
Cyrnea seurati	Р	0.15 (0.03-0.38)	0.29 (0.08-0.58)	0.35 (0.15-0.60)	0.28 (0.12-0.49)	ns	ns	
	Α	0.55 ± 1.67	0.86 ± 1.83	0.95 ± 1.61	0.64 ± 1.22	ns	ns	ns
	R	0-7	0-6	0-5	0-4			
Cheilospirura	Р	0.75 (0.51-0.91)	0.93 (0.66-0.99)	0.85 (0.62-0.97)	0.60 (0.39-0.79)	ns	ns	
gruveli								
.,	А	4.25 ± 4.06	11.64 ± 20.71	11.00 ± 17.11	5.00 ± 8.57	ns	ns	< 0.05
	R	0-14	0-80	0-68	0-37			
No species		1.15 ± 0.58	1.78 ± 0.80	1.25 ± 0.85	0.88 ± 0.83	ns	< 0.05	< 0.05

P-prevalence; A-abundance; R-range

		Ad	ults	Juveniles			Age	Age*
		Males	Females	Males	Females		0	Šex
Parasite sex		n=20	n=14	n=20	n=25			
Males	Р	0.65 (0.41-0.84)	0.71 (0.42-0.92)	0.70 (0.46-0.88)	0.40 (0.15-0.59)	ns	ns	
	А	2.15 ± 2.45	3.64 ± 5.22	4.00 ± 7.67	1.88 ± 3.63	ns	ns	< 0.05
Females	Р	0.70 (0.45-0.88)	0.86 (0.57-0.98)	0.85 (0.62-0.97)	0.56 (0.35-0.76)	ns	ns	
	Α	2.10 ± 2.40	8.00 ± 15.60	7.00 ± 10.06	3.04 ± 5.20	ns	ns	< 0.01
Immatures	Р	0	0	0	0.08 (0.01-0.26)			
	Α	0	0	0	0.08 ± 0.27			
Eggs/g		n=15	n=8	n=13	n=15			
faeces								
	Р	0.40 (0.16-0.68)	0.25 (0.25-0.80)	0.54 (0.25-0.80)	0.33 (0.11-0.61)	ns	ns	
	А	81.8 ± 192.7	115.7 ± 324.4	207.1 ± 336.6	108.2 ± 291.6	ns	ns	ns
Fecundity		n=11	n=7	n=10	n=7			
	Μ	82.8 ± 202.5	131.3 ± 347.1	38.5 ± 43.0	51.7 ± 63.0	ns	ns	ns
	R	0-675.6	0-918.6	0-120.7	0-132.3			

Table 2. Prevalence (Confidence Intervals in parenthesis) and mean abundance (mean \pm SD.) of males, females, and egg shedding; and mean (\pm SD.) and range of fecundity of *Cheilospirura gruveli* by host sex and age in 79 red-legged partridges (*Alectoris rufa*) from Medina Sidonia (Southern Spain)

P-prevalence; A-abundance; M-mean; R-range

dent in juveniles ($\chi^2 = 13.59$, P < 0.001), and tended to be related also in adults ($\chi^2 = 3.6$, P = 0.06). We found no differences among age and sex-classes in *C. gruveli* female fecundity. However, the range was markedly wider in adult than in juvenile partridges. We also found no relationships between *C. gruveli* abundance and female fecundity.

Host-parasite relationships

Gizzard weight was positively correlated with *C. gruveli* abundance in juveniles ($r_s = 0.68$, n = 45, P < 0.001). No other relationship was found between any species and its niche. Young females parasitised by *C. gruveli* had a heavier spleen (2.37 ± 2.16 g, n = 15) than those non-parasitised (0.38 ± 0.37 g, n = 10, Mann-Whitney U, Z = -3.30, P < 0.001). Adult partridges harbouring *C. gruveli* were in poorer body condition than those free of the parasite (Mann-Whitney U, Z = -2.20, P < 0.05).

Discussion

Composition of the nematode community

All nematodes found were previously reported parasitising the red-legged partridge (Cordero del Campillo *et al.*, 1994). The gizzard worm *Cheilospirura gruveli* can be considered to be the core species of this population of partridges. This species was considered by Tarazona *et al.* (1979) as the most common parasite of wild partridges. Since only one of the caecum was analysed, the prevalence of caecal nematodes might be slightly higher than observed. Either way, the prevalence and abundance found here are far from these reported in other galliforms (e.g. Davidson *et al.*, 1991). The intensive agriculture practices carried out in the area may be unfavourable for *T. tenuis* transmission. *Heterakis gallinarum* is rare in wild red-legged partridge populations (Millán *et al.*, in eval.).

Nematode ecology

Age-related differences in *T. tenuis* were also observed in other galliforms (Shaw and Moss, 1989; Davidson *et al.*, 1991). These have been attributed to the shorter length of exposure of juvenile birds compared with adults, and the time required for helminth development (Davidson *et al.*, 1980). To Shaw and Moss (1989), the differences they found in red grouses (*Lagopus lagopus scoticus*) were probably due to the longevity of *T. tenuis*, the little or no immunity to reinfection that grouses have, and the fact that intensity-dependent processes are unimportant in regulating this parasite.

No differences were found in C. gruveli parasitisation among age and sex classes. Blakeney and Dimmick (1971) found that Cheilospirura spinosa was more prevalent among adult bobwhites (Colinus virginianus). However, as observed in bobwhites (Moore et al., 1987), red-legged partridges form mixed sex and age coveys in late summer and remain in these groups until spring. These birds of various sex and age-classes move and forage together, and it is probable that they are exposed equally to parasitic infective forms. Surprisingly, we found that C. gruveli abundance increased with age in females but decreased in males. To Davidson et al. (1991), which also reported such finding in the infestation of bobwhites with Heterakis isolonche and Cyrnea colini, factors responsible for these differences are unknown. The reproductive effort of females may affect their susceptibility to parasites (Holmstad and Skorping, 1998; but see Poulin, 1996).

The occurrence of *C. gruveli* and *C. seurati* was not independent. Both parasites are heteroxenous, but the arthropods used as intermediate hosts are unknown (Cordero del Campillo and Rojo, 1999). This association may be attributable to the use of the same vectors (Davidson *et al.*, 1991). Both *Cyrnea* and *Cheilospirura* belong to the order Spiru-

rida, and, in North America, *Cyrnea colini* and *Cheilospirura spinosa* use grasshoppers species as intermediate hosts (Anderson, 2000). Homstad and Skorping (1998) found that a willow ptarmigan (*Lagopus lagopus*) with a high intensity of one parasite species was more likely to have high intensities of other parasites. To them, this could be caused by individual differences in exposure and susceptibility, parasite interactions, or sampling artefacts.

Aggregated distribution of parasites are typical within animal populations (Shaw and Dobson, 1995). Aggregation is considered a function of heterogeneity in host behaviour. exposure, and susceptibility, host defensive capabilities, and aggregated spatial patterns of infective-stage distribution (Anderson and Gordon, 1982; Hudson and Dobson, 1997). The absence of aggregation is generated by different factors, such as parasite mortality, density-dependent processes, or parasite-induced host mortality (Anderson and Gordon, 1982). Since we found some relationship between body condition and parasite burden in adults, the absence of aggregation in adult males may suggest parasiteinduced host mortality in this class of partridges. However, such mortality would also affect adult females. Therefore, other factors, such as the reduction in the degree of heterogeneity in the infection rate (for example, unmated adult males of partridges form groups during spring and summer), or the action of acquired immunity, which are more marked in older hosts (Anderson and Gordon, 1982), may be involved. Moreover, sex-related differences in the susceptibility to helminths have been reported (e.g. Gray, 1972). Nevertheless, as pointed out by Anderson and Gordon (1982), small sample sizes may affect the results in field studies of natural populations of hosts and parasites.

Adult nematode sex ratio is usually female-biased (Poulin, 1997). In polygamous mating, the maximum mean number of mated female occurs for a female biased sex-ratio (May and Woolhouse, 1993). *C gruveli* population was less female-biased at low intensities. The reasons for this finding are not clear, since the opposite was expected: female-biased sex ratios are favoured when intensity of infection is low to avoid inbreeding or increase probability of mating (see revision in Poulin, 1997).

C. gruveli female burden and egg shedding were correlated, markedly in juveniles. These age-related differences may be explained by the ageing of the parasites (see below). Although the accuracy of egg counts as indicators of the number of adult worms is discussed (Solomons and Scott, 1994), this suggests that the coprological analysis may be a good indicator of C. gruveli prevalence. C. gruveli fecundity range was markedly wider in adult than in juvenile partridges. In some nematode species, the ageing of parasites is cited as one of the reasons of the decrease in worm fecundity (Shaw and Moss; 1989). Nothing is known about that in C. gruveli. However, adult partridges could harbour both young and old worms, which may explain the dispersion of the data. We did not find density dependence in worm egg production. However, as observed by Mc-Callum and Scott (1994), their detection in field studies is complicated by its large variability.

Host-parasite relationships

Such juveniles with heavier gizzards harboured a higher parasite burden. Other authors did find correlations between size of helminth communities and gut size (Simberloff and Moore, 1997). This relationship was not found among adult partridges. Such differences between ageclasses could be related with transitory inflammatory response in young individuals.

Parasitised juvenile females had a heavier spleen. Parasites can affect the size of immunopoyetic organs such as the spleen (Moller *et al.*, 1999). In fact, splenomegaly is a common symptom of parasitic diseases in birds, including intestinal nematodes (John, 1995). In addition, we also found a relationship between *C. gruveli* burden and body condition in adult partridges. Since parasites have recently been found involved in the regulation of some galliform populations (e.g. Hudson *et al.*, 1992; Rizzoli *et al.*, 1997), more research is needed in order to establish the role of this species in wild red-legged partridge populations.

The age and gender-related differences in *C. gruveli* ecology found in the present study suggest changes in the host-parasite relationship along the partridges' life which may be related with the time of exposure and physiological peculiarities of each group. The results suggest that more research is needed in order to establish the actual role of *Cheilospirura gruveli* in red-legged partridge population dynamics.

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