



## Parasites as secret files of the trophic interactions of hosts: the case of the rufous-bellied thrush

### Los parásitos como archivos secretos en las interacciones tróficas con sus hospederos: el caso del Zorzal Colorado

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**Abstract.** Helminths with heteroxenous cycles provide clues for the trophic relationships of definitive hosts, representing important sources of information for assessing niche overlap between males and females of non-dimorphic species. We necropsied 151 rufous-bellied thrushes (*Turdus rufiventris*) captured in a metropolitan region in southern Brazil to analyze whether the structure of parasite communities is influenced by host sex or age. Most thrushes (93%) were parasitized by at least 1 species. The helminth community of *Turdus rufiventris* was composed of 15 species with prevalences from <1% to 60%. Although the prevalence of *Conspicuum conspicuum*, *Microtetrameres pusilla* and *Aproctella stoddardi* was higher in adults, *Syngamus trachea* was more prevalent in juveniles. Adults showed greater species richness of parasites than juveniles, probably as a consequence of an increase in the opportunities of infection with a larger set of parasites with aging. Adult males and females presented similar species richness of helminths and quite similar communities, allowing us to conclude that they prey upon the same invertebrates, including earthworms, snails, isopods, millipedes, cockroaches and grasshoppers. Therefore, trophic niche overlap between adult males and females is greater than between adults and juveniles.

Key words: *Turdus rufiventris*, passeriform, helminth, diet, dimorphism.

**Resumen.** Los helmintos que presentan ciclos heterogéneos proveen pistas importantes sobre las relaciones tróficas que mantienen con sus hospederos definitivos. Estas pistas son además importantes fuentes de información que permiten evaluar el solapamiento de sus nichos cuando comparamos machos y hembras en especies no dimórficas. Así, se practicaron necropsias en 151 zorzales colorados (*Turdus rufiventris*) que fueron capturados en una región metropolitana al sureste de Brasil, a fin de analizar de qué manera la estructura de la comunidad de parásitos podría estar influenciada por la edad o sexo del hospedero. La mayoría de los zorzales (93%) fueron parasitados por al menos 1 especie. La comunidad de helmintos de *Turdus rufiventris* estuvo compuesta por 15 especies, con prevalencias entre 1% a 60%. Aunque la prevalencia de *Conspicuum conspicuum*, *Microtetrameres pusilla* y *Aproctella stoddardi* fue más alta en adultos, *Syngamus trachea* tuvo una mayor prevalencia en juveniles. Los adultos mostraron una mayor riqueza de parásitos que los juveniles. Probablemente, esto sea consecuencia de una mayor posibilidad de infectarse conforme avanza la edad de los individuos; sin embargo, machos y hembras adultos presentaron una riqueza similar en la concentración de helmintos en comunidades semejantes. Esto podría apoyar a concluir que podrían estar alimentándose del mismo tipo de invertebrados como son: lombrices, caracoles, isópodos, ciempiés, cucarachas y saltamontes. Concluimos que la sobreposición del nicho trófico es mas clara entre machos y hembras adultos que entre los juveniles.

Palabras clave: *Turdus rufiventris*, paseriforme, helmintos, dieta, dimorfismo.

#### Introduction

Parasites are important players in the ecosystem,

but our knowledge of this fascinating and significant biodiversity component is surprisingly poor (Windsor, 1997; McLaughlin, 2001; Hudson et al., 2006). Although actual global species richness for most higher-level taxa or functional groups is unknown, Price (1980) suggests that there are more parasite species than free-living ones. As a result, parasitism is the commonest interspecific interaction

Recibido: 14 octubre 2009; aceptado: 25 marzo 2010

(Poulin and Morand, 2004). Furthermore, species richness of parasites will not be fully known until all hosts have been described and studied (Windsor, 1998).

In addition to the role played in ecosystems, parasites are important sources of data on host behavior and ecology, including trophic relationships. The complex life cycles of parasites may be integrated into intricate food webs and give us clues on food web structure and on the food preferences and foraging strategies of hosts (Marcogliese and Cone, 1997). Diet is a key factor in studies of avian biology and ecology and has been investigated via analysis of stomach contents, forced regurgitation and flushing, fecal samples and direct observation among others (Rosenberg and Cooper, 1990). Considering food digestion time ranges from 45 minutes to 6 hours in birds (Karasov, 1990), the most used method, the analysis of stomach contents, is often inefficient in identifying food remains found in the gut. Consequently, while studies based on gut contents only reflect the last hours of feeding prior to capture, helminths can stay for months or years within a bird host as evidence of long-term trophic relationships. Age and body size can affect the fauna of helminths of a host, revealing ontogenetic changes in feeding behavior (Marcogliese and Cone, 1997).

Therefore, helminths found in the gut and other organs open up a new dimension in the study of avian diet. Because a substantial number of helminths that parasitize birds have a heteroxenous cycle, transmission occurs when the bird (definitive host) preys on an intermediate host infected with the immature stage of the parasite. In this case, the finding of a helminth inside the body of a bird is evidence that the intermediate host belongs in its diet. As a consequence, the more we know about the helminth parasites of a species, the better we will solve its trophic jigsaw.

Several factors determine the structure of parasite communities. Bush (1990) considers the environment as the major determinant of the structure of parasite communities of birds through an influence on the survival and potential transmission of helminths that have direct life cycles or intermediate stages. However, Kennedy et al. (1986) suggest that these factors are related to host traits, such as the complexity of the digestive system, the amount and diversity of food items and host movement. Other factors that can play important roles in the pattern of distribution of helminths among species of hosts include environmental seasonality, and distribution, age, sex (Bush, 1990), and population density (Price, 1990) of the host. Among birds and mammals, for example, the sex of the host can affect parasitism (Isomursu et al., 2006). Many studies have shown that males carry heavier parasite loads than females (Poulin, 1996; Zuk and McKean, 1996;

Schalk and Forbes, 1997; Robinson et al., 2008). Among mammals, this pattern is a product of life history differences between males and females: males tend to demand more energy and resources for growing, whereas females tend to show a greater investment in immunity. Thus, this male bias in parasitism among mammals is associated with sexual size dimorphism (Moore and Wilson, 2002). Among birds, the sex of the host influences parasitism both in species showing body size sexual dimorphism (Robinson et al., 2008) and those non-dimorphic species (Isomursu et al., 2006). Sex-based differences in foraging strategy (Morse, 1990) influence the exposure of hosts to parasites transmitted through the food chain, and appear to be more important than physiological differences in determining male and female parasitism (Robinson et al., 2008).

The rufous-bellied thrush (*Turdus rufiventris* Vieillot, 1818) is a non-sexually dimorphic passeriform. Male and female rufous-bellied thrushes are visually indistinguishable, a characteristic that hampers sex comparisons in studies on the ecology and behavior based on field observations of unmarked and unsexed individuals. This bird is found in woodlands and on city streets and gardens, where it is well-adapted to human contact (Efe et al., 2001; Fontana, 2001). In forests it often occupies the intermediate stratum of the canopy, whereas the ground is highly used in city gardens (Belton, 1994), where it feeds on fruits and invertebrates such as insects and earthworms (Efe et al., 2001; Fontana, 2001). This thrush is a resident species in the State of Rio Grande do Sul (hereafter RS), Brazil (Belton, 1976), and is a member of the avifauna of the city of Porto Alegre at least since the 1920's, when it used to be found in areas less populated by humans; currently, it is among the commonest species of urban birds and shows a more homogeneous pattern of city occupation (Fontana, 2005).

Passeriform birds are parasitized by trematodes, digeneans, cestodes, acanthocephalans and nematodes (Borgstede et al., 2000). Interspecific differences in the fauna of helminths are evidence of differences in habitat use, food preferences and resource partitioning and interactions with intermediate hosts (Ching, 1993). *Turdus rufiventris* is known to host only 5 helminth species: the digeneans *Conspicuum conspicuum* (Faria, 1912) Bhalerao, 1936 (Travassos et al., 1969), *Lutztrema obliquum* (Travassos, 1917) Travassos, 1941 (Travassos et al., 1969; Fabio and Ferreira, 1999) and *Prosthogonimus* sp. (Travassos et al., 1969) and the nematodes *Tetrameres pusilla* (Travassos, 1915) Chabaud, 1975 and *Tetrameres* sp. (Vicente et al., 1995).

In this paper we describe the structure of the helminth community of rufous-bellied thrushes living in the metropolitan region of Porto Alegre, State of Rio Grande

do Sul, Brazil, analyze whether sex and age influence the structure of the parasite community of individual hosts, and discuss what helminths reveal about host ecology and behavior.

## Materials and methods

A total of 151 rufous-bellied thrushes were collected using mist nets in the metropolitan region of Porto Alegre, RS (29°50'57"-30°09'25"S, 50°01'20"-51°18'45"W), Brazil, between March 2003 and March 2006. The technique for euthanasia involved an overdose with gaseous anesthetic (Gaunt and Oring, 1999). Necropsy of birds and processing of helminths follow Amato et al. (1991). Voucher specimens were deposited in the Coleção Helmintológica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil (see Table 1).

Sex identification was based on gonadal analysis during necropsy, whereas juveniles were identified by the presence of bursa of Fabricius, an organ that is atrophic in adults (Proctor and Lynch, 1993). All individuals were weighed with an accuracy of 1g using 60g Pesola© scales before necropsy.

Data on parasite infrapopulations were used to calculate prevalence, range and mean intensity of infection and mean abundance (Bush et al., 1997). In addition, helminths were classified based on their importance value (I) into dominant ( $I \geq 1.0$ ; species characteristic of the community), codominant ( $0.01 \leq I < 1$ ; contributes significantly to the community, but to a lesser degree than dominants), subordinate ( $0 < I < 0.01$ ; uncommon and although it breeds and develops in the host, it does not contribute significantly to the community) or unsuccessful pioneer ( $I = 0$ ; has access to the host, but does not develop or reproduce, contributing little to the community because it is characteristic of another host species) (Thul et al., 1985).

A species accumulation curve (Santos, 2003) was used to evaluate whether the observed species richness of helminths was representative of the actual fauna of helminths of rufous-bellied thrushes. Shannon's index of diversity of the helminth community was calculated using the natural logarithm ( $\log_e$ ) in the formula (Brower and Zar, 1984) and compared using the *t* test. The similarity of the parasite communities of adult males and females was assessed qualitatively using the Jaccard's index of similarity (Magurran, 1988), as performed by Brasil and Amato (1992), and quantitatively using the Morisita-Horn index of similarity (Magurran, 1988).

The prevalence and the intensity of infection of each

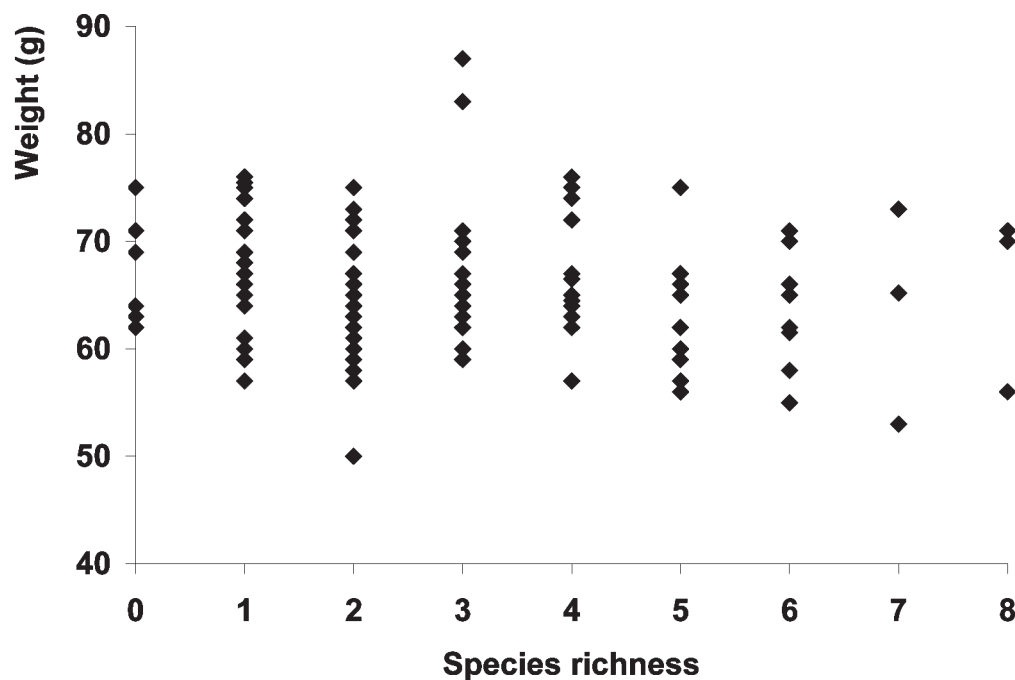
helminth species was compared between adults and juveniles and between adult males and females. Data on prevalence were compared using the G-test with Yates correction by organizing the number of positive and negative necropsies in each class into 2x2 contingency tables, whereas the intensity of infection was compared using the Mann-Whitney U test. Linear regression was applied to evaluate whether species richness of parasites (independent variable) compromises the health of hosts estimated by a proxy measure, body weight (dependent variable).

Variables with sample sizes  $\geq 20$  were tested for normality using a D'Agostino Pearson test, whereas those variables with sample sizes from 10 to 19 were tested using a D'Agostino test (Ayres et al., 2005). Variables with a normal distribution were tested using the parametric Student *t* test when variances were similar, and using a Z test when variances differed. In the absence of a normal distribution and when transformations were not capable of normalizing the data, non-parametric tests were used. Unless otherwise stated a significance level of 5% was used for all tests. When multiple tests were performed on the same variable, the significance level was adjusted following Leigh and Jungers (1994). Tests were performed using BioEstat 4.0 (Ayres et al., 2005), Systat 5.0 (Wilkinson, 1990), and PAST 1.81 (Hammer et al., 2001).

## Results

A total of 140 out of the 151 necropsied rufous-bellied thrushes (92.7%) were parasitized by at least 1 helminth species. The helminths recorded (N= 2 387 specimens) belonged to Nematoda (56%), Digenea (20%), Eucestoda (17%) and Acanthocephala (7%), showing a mean intensity of infection of 15.8 helminths per host. The helminth community was composed of 15 species (Table 1) and had a Shannon's index of diversity of  $H' = 2.139$ . The species accumulation curve indicates that such species richness is representative of the fauna of helminths of rufous-bellied thrushes. After finding the 15<sup>th</sup> species of helminth in the 52<sup>nd</sup> necropsied specimen, no new species were found in the last 99 necropsies. Species richness of parasites per individual host ranged from 0 to 8, showing an average richness of 2.92 species/host. Nine species were classified as dominant, 5 as codominant, and only 1 as subordinate in the helminth community of *T. rufiventris* (Table 1).

Adult weight ranged from 50 to 87 g (mean= 65.6, s.d.= 6.3, n= 115), it did not differ between the sexes (males: mean= 64.9, s.d.= 5.3, n= 63; females: mean= 66.6, s.d.= 7.2, n=52;  $H = 2.1087$ , d.f. = 1,  $p = 0.1465$ ) and



**Figure 1.** Relationship between body weight in grams (independent variable) of adult rufous-bellied thrushes (*Turdus rufiventris*) and species richness of parasites (dependent variable).

was not affected significantly by the species richness of parasites ( $F$  [regression]= 2.1716,  $p= 0.1395$ , Fig. 1). An analysis of the influence of the abundance of each species of parasite (independent variable) on the weight of adults ( $n= 115$ , dependent variable) suggests that an increase in the frequency of *Fernandezia spinosissima* (Linstow, 1894) López-Neyra, 1936 ( $F= 5.2646$ ,  $p= 0.0222$ ,  $r^2= 4.45\%$ ), *Wardium fernandensis* (Nybelin, 1929) ( $F= 4.2604$ ,  $p= 0.0388$ ,  $r^2= 3.63\%$ ) and *Cardiofilaria* sp. ( $F= 5.2620$ ,  $p= 0.0223$ ,  $r^2= 4.45\%$ ) relates to a decrease in individual weight. Considering that these coefficients of determination are very low (<5%), an analysis of the influence of the intensity of infection with each species on the weight of thrushes was performed. The weight of thrushes was not related to the intensity of infection with *W. fernandensis* ( $F= 2.9341$ ,  $p= 0.0943$ ,  $r^2= 9.48\%$ ,  $n= 30$ ) or *Cardiofilaria* sp. ( $F= 3.2000$ ,  $p= 0.1048$ ,  $r^2= 26.23\%$ ,  $n= 11$ ), but the intensity of infection with *F. spinosissima* affected the weight of thrushes ( $F= 7.1635$ ,  $p= 0.0359$ ,  $r^2= 54.42\%$ ,  $n= 8$ ). Excluding the single outlier from the sample (18 *F. spinosissima* specimens in a 55 g thrush), however, results in a marginally significant relationship ( $F= 6.3425$ ,  $p= 0.0525$ ,  $r^2= 55.92\%$ ,  $n= 7$ ). The abundance and intensity of infection of none of the other 12 species presented a significant relationship with the weight of

adult thrushes.

Adult males and females showed similar species richness of parasites, which ranged from 0 to 8 species (males: mean= 3.0, s.d.= 2.0,  $n= 63$ ; females: mean= 3.2, s.d.= 2.0,  $n= 53$ ; Student's  $t$  test:  $t= 0.6105$ , d.f.= 114,  $p= 0.5427$ ), and quite similar helminth communities, both qualitatively (Jaccard's index of similarity= 92.9%) and quantitatively (Morisita-Horn index of similarity= 84.6%). However, the diversity of the helminth community of adult males ( $H^*= 2.225$ ) was higher than that of adult females ( $H^*= 1.801$ ;  $t= 9.7061$ ,  $p<0.0001$ ).

The species richness of parasites of juvenile males ranged from 0 to 5 species (mean= 2.4, s.d.= 1.5,  $n= 19$ ), whereas in juvenile females it ranged from 1 to 5 (mean=2.3, s.d.=1.5,  $n=16$ ). Species richness of parasites was similar between juvenile males and females ( $t= 0.2340$ , d.f.= 33,  $p= 0.8164$ ). Compared to adults, juveniles showed a lower species richness of parasites (adults: mean= 3.1, s.d.= 2.0,  $n= 116$ ; juveniles: mean= 2.3, s.d.= 1.5,  $n= 35$ ;  $Z= 2.5505$ ,  $p= 0.0108$ ).

The prevalence of a few parasite species also differed between adult and juvenile thrushes (Table 2). Whereas adults showed a higher prevalence of *C. conspicuum* (64.66% vs. 42.86%), *Microtetrameres pusilla* (37.07% vs. 14.29%) and *Aproctella stoddardi* Cram, 1931 (26.72% vs.

**Table 1.** Prevalence, intensity of infection (mean  $\pm$  standard deviation), abundance (mean  $\pm$  standard deviation) and importance value of each helminth parasite species of rufous-bellied thrushes (*Turdus rufiventris*) in the metropolitan region of Porto Alegre, State of Rio Grande do Sul, Brazil (N= 151 necropsied birds)

<i>Táxon</i>	<i>Prevalence (%)</i>	<i>Intensity (mean <math>\pm</math> SD)</i>	<i>Abundance (mean <math>\pm</math> SD)</i>	<i>Importance value (I)</i>	<i>CHIOC accession number</i>
<b>Digenea</b>					
Brachylaimidae					
<i>Brachylaima</i> sp.	0.66	3 (3.00)	0.02 $\pm$ 0.24	0.003 (S)	37272
Eucotylidae					
<i>Tamerlania inopina</i>	4.64	1-10 (3.71 $\pm$ 2.93)	0.17 $\pm$ 2.34	0.18 (CD)	37271
Dicrocoeliidae					
<i>Conspicuum conspicuum</i>	59.60	1-20 (2.42 $\pm$ 2.34)	1.44 $\pm$ 2.16	19.35 (D)	36508
<i>Lutztrema obliquum</i>	13.91	1-47 (11.10 $\pm$ 12.92)	1.54 $\pm$ 6.09	4.83 (D)	37270
<b>Eucestoda</b>					
Davaineidae					
<i>Fernandezia spinosissima</i>	7.95	1-17 (3.25 $\pm$ 4.77)	0.26 $\pm$ 1.56	0.46 (CD)	
Dilepididae					
<i>Dilepis undula</i>	30.46	1-17 (3.48 $\pm$ 3.78)	1.06 $\pm$ 2.62	7.26 (D)	37266, 37267
Hymenolepididae					
<i>Wardium fernandensis</i>	25.83	1-27 (5.49 $\pm$ 6.46)	1.42 $\pm$ 4.05	8.23 (D)	37269
<b>Acanthocephala</b>					
Plagiorhynchidae					
<i>Lueheia inscripta</i>	40.40	1-17 (2.64 $\pm$ 2.69)	1.07 $\pm$ 2.14	9.69 (D)	37273a, 37273b
<b>Nematoda</b>					
Capillariidae					
<i>Aonchotheca</i> sp.	1.99	1-8 (3.33 $\pm$ 4.04)	0.07 $\pm$ 0.66	0.03 (CD)	
Thelaziidae					
<i>Oxyspirura petrowi</i>	9.93	1-12 (4.60 $\pm$ 3.50)	0.46 $\pm$ 1.75	1.02 (D)	35672
Tetrameridae					
<i>Microtetrameres pusilla</i>	31.79	1-13 (3.83 $\pm$ 2.88)	1.22 $\pm$ 2.41	8.71 (D)	35673
Onchocercidae					
<i>Aproctella stoddardi</i>	20.53	1-13 (3.55 $\pm$ 2.96)	0.73 $\pm$ 1.96	3.36 (D)	35674
<i>Cardiofilaria</i> sp.	7.28	1-7 (3.18 $\pm$ 1.94)	0.23 $\pm$ 0.97	0.38 (CD)	35677
Strongyloididae					
<i>Strongyloides oswaldoi</i>	27.81	1-166 (20.55 $\pm$ 30.90)	5.72 $\pm$ 18.61	35.75 (D)	35675
Syngamidae					
<i>Syngamus trachea</i>	7.95	2-36 (5.17 $\pm$ 9.74)	0.41 $\pm$ 2.99	0.73 (CD)	35676

SD = standard deviation; importance value: D = dominant; CD = codominant; S = subordinate

**Table 2.** Prevalence of helminth species in juvenile, adult male and adult female rufous-bellied thrushes, *Turdus rufiventris*. Significant differences between classes in bold. For all *G* tests: d.f.= 1

Taxon	Prevalence (%)			<i>G</i> test (Yates)	
	Juveniles (N=35)	Males (N=63)	Adults (N=116) Females (N=53)	Juveniles x Adults	Adult males x Adult females
<i>Brachylaima</i> sp.	2.9	0	0	G=0.3420, p=0.5587	---
<i>Tamerlania inopina</i>	0	4.8	7.5	G=1.3362, p=0.2477	G=0.0556, p=0.8136
<i>Conspicuum conspicuum</i>	42.9	63.5	66.0	<b>G=4.3727, p=0.0365</b>	G=0.0082, p=0.9277
<i>Lutztrema obliquum</i>	5.7	19.0	13.2	G=1.9731, p=0.1601	G=0.3567, p=0.5504
<i>Fernandezia spinosissima</i>	8.6	3.2	13.2	G=0.0412, p=0.8392	G=2.8154, p=0.0934
<i>Dilepis undula</i>	20.0	31.7	35.8	G=1.8421, p=0.1747	G=0.0721, p=0.7882
<i>Wardium fernandensis</i>	25.7	33.3	17.0	G=0.0408, p=0.8399	G=3.2774, p=0.0702
<i>Lueheia inscripta</i>	62.9	27.0	41.5	G=8.2510, p=0.0041	G=2.1075, p=0.1466
<i>Strongyloides oswaldoi</i>	14.3	28.6	35.8	G=3.6136, p=0.0573	G=0.4061, p=0.5240
<i>Aonchotheca</i> sp.	5.7	1.6	0	G=1.0427, p=0.3072	G=0.0075, p=0.9309
<i>Oxyspirura petrowi</i>	2.9	19.0	3.8	G=1.9120, p=0.1667	<b>G=5.4166, p=0.0199</b>
<i>Microtetrameres pusilla</i>	14.3	31.7	43.4	<b>G=5.9618, p=0.0146</b>	G=1.2115, p=0.2710
<i>Aproctella stoddardi</i>	0	22.2	32.1	<b>G=14.4167, p=0.0001</b>	G=0.9658, p=0.3257
<i>Cardiofilaria</i> sp.	0	11.1	7.5	G=3.0976, p=0.0784	G=0.1126, p=0.7372
<i>Syngamus trachea</i>	22.9	3.2	3.8	<b>G=9.3577, p=0.0022</b>	G=0.1135, p=0.7362

0%), juveniles showed a higher prevalence of *Syngamus trachea* (Montagu, 1811) Chapin, 1925 (22.86% vs. 3.45%). However, the intensity of infection of all species of parasites found in both adult and juvenile individuals was similar between these classes (Table 3).

The prevalence of parasite species was more similar between adult males and females than between adult and juvenile individuals (Table 2). Only *Oxyspirura petrowi* Skrjabin, 1929 was more prevalent in males (19.05%) than in females (3.77%). The intensity of infection of adult male and adult female thrushes with each species of parasite also was similar (Table 4).

## Discussion

The fauna of helminths of rufous-bellied thrushes was known from opportunistic reports to comprise only 5

species (Travassos et al., 1969; Vicente et al., 1995; Fabio and Ferreira, 1999). Our study increased it to 16 species, elevating the diversity of parasites of *T. rufiventris* to the level found in intensively studied congeneric species, the North American *Turdus migratorius* Linnaeus, 1766 (e.g., Webster, 1943; Slater, 1967; Cooper and Crites, 1976a, 1976b; Ching, 1993) and the European *Turdus merula* Linnaeus, 1758 (e.g., Pojmanska, 1969; Schmidt, 1975; Machalska, 1980; Okulewicz and Wesoowska, 2003; Misof, 2005). Whereas the former is known to be parasitized by 6 nematode species, 3 cestodes, 1 digenean and 1 acanthocephalan, the latter is host to 7 nematodes, 4 digeneans, 3 cestodes and 1 acanthocephalan. The proportion of individuals parasitized by at least 1 species of helminth was also similar among these 3 thrushes: *T. rufiventris* (92.7%, this study), *T. migratorius* (93.5%, Slater 1967) and *T. merula* (82.0% based on fecal sample screening, Misof, 2005).

The fauna of parasites of *T. rufiventris* largely

**Table 3.** Intensity of infection of adult and juvenile rufous-bellied thrushes, *Turdus rufiventris*, with each species of helminth found in both classes. Values represent mean parasite load per positive host  $\pm$  standard deviation [and range] and sample size for each age class. The result of the Mann-Whitney (U) test and the respective probability (p) are also shown

<i>Taxon</i>	<i>Adults</i>	<i>Juveniles</i>	<i>Mann-Whitney</i>
<i>Conspicuum conspicuum</i>	2.27 $\pm$ 1.46 [1-9] 75	3.20 $\pm$ 4.77 [1-20] 15	U=568.0, p=0.950
<i>Lutztrema obliquum</i>	11.90 $\pm$ 13.34 [1-47] 19	3.50 $\pm$ 2.12 [2-5] 2	U=24.0, p=0.547
<i>Fernandezia spinosissima</i>	4.00 $\pm$ 5.36 [1-17] 9	1.00 $\pm$ 0 [1] 3	U=21.0, p=0.121
<i>Dilepis undula</i>	3.33 $\pm$ 3.96 [1-17] 39	4.29 $\pm$ 2.69 [1-8] 7	U=89.5, p=0.137
<i>Wardium fernandensis</i>	4.70 $\pm$ 5.79 [1-25] 30	8.11 $\pm$ 8.15 [2-27] 9	U=80.0, p=0.061
<i>Lueheia inscripta</i>	2.85 $\pm$ 3.18 [1-17] 39	2.27 $\pm$ 1.49 [1-7] 22	U=407.0, p=0.726
<i>Strongyloides oswaldoi</i>	21.51 $\pm$ 32.62 [1-166] 37	13.40 $\pm$ 11.72 [2-28] 5	U=89.5, p=0.907
<i>Aonchotheca</i> sp.	8.00 [8] 1	1.00 $\pm$ 0 [1] 2	U=2.0, p=0.157
<i>Oxyspirura petrowi</i>	4.79 $\pm$ 3.56 [1-12] 14	2.00 [2] 1	U=9.5, p=0.558
<i>Microtetrameres pusilla</i>	3.86 $\pm$ 2.93 [1-13] 43	3.60 $\pm$ 2.61 [1-7] 5	U=107.5, p=1.000
<i>Syngamus trachea</i>	2.00 $\pm$ 0 [2] 4	6.75 $\pm$ 11.85 [2-36] 8	U=10.0, p=0.180

**Table 4.** Intensity of infection of adult male and female rufous-bellied thrushes, *Turdus rufiventris*, with each species of parasite. Values represent mean parasite load per positive host  $\pm$  standard deviation [and range] and sample size for each sex class. The result of the Mann-Whitney (U) test and the respective probability (p) are also shown

<i>Taxon</i>	<i>Adult males</i>	<i>Adult females</i>	<i>Mann-Whitney</i>
<i>Tamerlania inopina</i>	5.33 $\pm$ 4.16 [2-10] 3	2.50 $\pm$ 1.00 [1-3] 4	U=3.0, p=0.271
<i>Conspicuum conspicuum</i>	2.28 $\pm$ 1.62 [1-9] 40	2.26 $\pm$ 1.29 [1-6] 35	U=736.5, p=0.685
<i>Lutztrema obliquum</i>	10.83 $\pm$ 10.01 [1-31] 12	13.71 $\pm$ 18.56 [1-47] 7	U=45.0, p=0.799
<i>Fernandezia spinosissima</i>	2.00 $\pm$ 1.41 [1-3] 2	4.57 $\pm$ 6.02 [1-17] 7	U=7.5, p=0.878
<i>Dilepis undula</i>	2.60 $\pm$ 2.14 [1-9] 20	4.10 $\pm$ 5.20 [1-17] 19	U=196.0, p=0.860
<i>Wardium fernandensis</i>	4.71 $\pm$ 5.83 [1-25] 21	4.67 $\pm$ 6.04 [1-20] 9	U=91.5, p=0.887
<i>Lueheia inscripta</i>	3.06 $\pm$ 4.18 [1-17] 17	2.68 $\pm$ 2.21 [1-8] 22	U=207.5, p=0.531
<i>Strongyloides oswaldoi</i>	14.39 $\pm$ 20.79 [1-90] 18	28.26 $\pm$ 40.26 [1-166] 19	U=212.0, p=0.212
<i>Oxyspirura petrowi</i>	5.08 $\pm$ 3.68 [1-12] 12	3.00 $\pm$ 2.82 [1-5] 2	U=16.5, p=0.404
<i>Microtetrameres pusilla</i>	4.80 $\pm$ 3.58 [1-13] 20	3.04 $\pm$ 1.96 [1-7] 23	U=288.5, p=0.146
<i>Aproctella stoddardi</i>	3.86 $\pm$ 3.78 [1-13] 14	3.29 $\pm$ 2.17 [1-8] 17	U=123.5, p=0.855
<i>Cardiofilaria</i> sp.	3.57 $\pm$ 1.99 [1-7] 7	2.50 $\pm$ 1.92 [1-5] 4	U=9.5, p=0.385
<i>Syngamus trachea</i>	2 $\pm$ 0 [2] 2	2 $\pm$ 0 [2] 2	U=2.0, p=1.000

reflects its diet, which is composed of invertebrates such as earthworms, terrestrial snails, terrestrial isopods, millipedes, cockroaches and grasshoppers (Table 5). Therefore, the low prevalence shown by some species of helminths can be related to several non-mutually exclusive factors, including (a) a low natural infection of intermediate hosts, (b) a low availability of intermediate hosts or (c) a low consumption of particular intermediate hosts by the birds. Research on the density of intermediate hosts and their relationships with parasites are important for reaching a better understanding of this multispecies interaction. It is also critical to take into account the variety of life cycles shown by helminths. For example, the filariids *A. stoddardi* and *Cardiophilaria* sp. are transmitted by vectors and the strongyloidid *Strongyloides oswaldoi* Travassos, 1930 has a monoxenous (without intermediate host) cycle.

The relationship between the size and age of hosts and the species richness of helminths in the infracommunity and the component community is a major issue in parasite ecology (Bush, 1990, Simberloff and Moore, 1997, but see Poulin and Morand, 2004). Studies have shown that lowly pathogenic intestinal parasites cause a marked weight loss

in hosts by strongly changing their energy flow (Connors and Nickol, 1991). Despite the assumption that parasites compromise the health of the host, the species richness of parasites found in the specimens necropsied in the current study did not show a significant relationship with adult weight. This likely absence of influence of species richness of parasites on host morbidity suggests that helminths found in the population of rufous-bellied thrushes do not show intensities of infection high enough to compromise the health of individuals, though histopathological analyses were not conducted.

The higher species richness of parasites of adults in comparison with juvenile thrushes is compatible with an increase in the opportunities of infection with a large number of parasites as an effect of age as suggested by Dogiel (1964 apud Simberloff and Moore, 1997). This hypothesis is based on the assumption that the older the host, the longer its exposure to a greater number and diversity of prey species, vectors, eggs and infectant larvae. This relationship can also explain the higher prevalence of some parasite species (*C. conspicuum*, *M. pusilla*, *A. stoddardi* and, possibly, *S. oswaldoi* and *Cardiophilaria* sp.)

**Table 5.** Potential intermediate hosts for the helminths of rufous-bellied thrushes, *Turdus rufiventris*, in the metropolitan region of Porto Alegre, RS, Brazil.

<i>Taxon</i>	<i>Intermediate host</i>	<i>Reference(s)</i>
<b>Digenea</b>		
<i>Brachylaima</i> sp.	Terrestrial mollusk	Yamaguti 1975
<i>Tamerlania inopina</i>	Terrestrial mollusk	Kingston 1965
<i>Conspicuum conspicuum</i>	Terrestrial mollusk (1 <sup>st</sup> IH) Terrestrial isopod (2 <sup>nd</sup> IH)	Patten 1952
<i>Lutztrema obliquum</i>	Terrestrial mollusk (1 <sup>st</sup> IH) Millipede (2 <sup>nd</sup> IH)	Krissinger 1984
<b>Eucestoda</b>		
<i>Fernandezia spinosissima</i>	Unknown	
<i>Dilepis undula</i>	Earthworm	Rysavy 1973
<i>Wardium fernandensis</i>	Insect (beetle and grasshopper)	Mourad 1967
<b>Acanthocephala</b>		
<i>Lueheia inscripta</i>	Insect (American cockroach)	Acholonu 1976
<b>Nematoda</b>		
<i>Aonchotheca</i> sp.	Earthworm	Moravec et al. 1987, Anderson 2000
<i>Oxyspirura petrowi</i>	Insect (cockroach)	Fielding 1926,1927, Anderson 2000
<i>Microtetrameres pusilla</i>	Insect (grasshopper)	Cram 1934, Quentin et al. 1986
<i>Syngamus trachea</i>	Earthworm (PH)	Wehr 1937, Anderson 2000

1<sup>st</sup> IH=first intermediate host, 2<sup>nd</sup> IH=second intermediate host, PH=paratenic host



observed in adults. The adult-juvenile difference in the prevalence of *C. conspicuum* and *M. pusilla* can be related to the aforementioned factors or to actual differences in food preference. Diet composition is a better candidate for explaining the higher percentage of *S. trachea* in juveniles (22.86% vs. 3.45% in adults). The highest intensity of infection with *S. trachea* (36) was found in a fledgling individual. Because *S. trachea* presents a heteroxenous cycle and can be transmitted directly to the definitive host via ingestion of eggs or of a paratenic host (an earthworm, for example), it is reasonable to suggest that parents can offer earthworms to nestlings.

On the other hand, age is a better variable for explaining the pattern of infection seen with *S. oswaldoi*, since this monoxenous parasite species depends on the contact of a host with its larvae to be transmitted. In this case, time of exposition is critical. But, the lack of difference between adults and juveniles in the intensity of infection of all species of parasites does not support Dogiel's (1964) hypothesis. This interpretation is based on the rationale that if age affects the probability of infection with a greater number of species, it also should influence the intensity of parasite infection.

The high qualitative and quantitative similarity between the helminth communities of adult males and females permits the conclusion that they prey upon the same invertebrates and highlights a wide overlap in the animal dimension of the trophic niches of males and females. These findings are compatible with Schoener's (1974) ecological postulate that body size influences how species exploit resources. The few differences in prevalence, however, suggest subtle differences in preference for particular food items by males and females. The higher prevalence of *O. petrowi* in adult males (19.05% vs. 3.77% in females), for example, may derive from a higher consumption of cockroaches.

In sum, parasites proved to be important tools for contributing to our knowledge on the trophic interactions between definitive and intermediate hosts, an approach particularly promising for non-dimorphic or secretive species, whose field observations on unmarked individuals is difficult or produces limited data. Future studies may integrate modern techniques of DNA fingerprinting for sexing marked individuals with methods of behavioral observation for comparing microhabitat selection, foraging techniques and diet composition of male and female rufous-bellied thrushes.

## Acknowledgements

We thank Luis Cláudio Muniz Pereira, Carla Suertegaray Fontana and Inga Ludmila Veitenheimer Mendes for their comments on this research; Philip J. Scholl for reviewing the English version; the Federal University of Rio Grande do Sul for logistical support; the IBAMA and SMAM for the federal and municipal licenses to collect the birds. CCM also thanks Júlio César, Gabriel and Ana Beatriz for their support and help in all steps of this project, and the Higher Education Authority (CAPES) and the Brazilian National Research Council (CNPq) for the doctoral scholarship. This research comply with current Brazilian laws (federal and municipal licenses, respectively, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis/IBAMA #051/2002/RS, 005/2004/RS and 004/2005/RS, and Secretaria Municipal do Meio Ambiente/SMAM #176/04 and 049/05) and were approved by the Commission of Research Ethics of the Universidade Federal do Rio Grande do Sul.

## Literature cited

- Acholonu, A. D. 1976. Helminth fauna of saurians from Puerto Rico with observations on the life cycle of *Lueheia inscripta* (Westrumb, 1821) and description of *Allopharynx puertoricensis* sp.n. Proceedings of the Helminthological Society of Washington 43:106-116.
- Amato, J. F. R., W. A. Boeger and S. B. Amato. 1991. Protocolos para Laboratório – Coleta e Processamento de Parasitos de Pescado. Imprensa Universitária, Universidade Federal Rural do Rio de Janeiro, Seropédica. 81 p.
- Anderson, R. C. 2000. Nematode Parasites of Vertebrates: Their Development and Transmission. CABI Publishing, Wallingford. 650 p.
- Ayres, M., M. Ayres Jr., D. L. Ayres and A. S. Santos. 2005. BioEstat 4.0. Aplicações estatísticas nas áreas das Ciências Biológicas e Médicas. Sociedade Civil Mamirauá, Belém. 324 p.
- Belton, W. 1976. Alguns aspectos da migração e distribuição das aves no Estado do Rio Grande do Sul, Brasil. Iheringia 5:69-80.
- Belton, W. 1994. Aves do Rio Grande do Sul: Distribuição e Biologia. Editora Unisinos, São Leopoldo. 584 p.
- Borgstede, F. H. M., A. Okulewicz and J. Okulewicz. 2000. A study of the helminth fauna of birds belonging to the Passeriformes in the Netherlands. Acta Parasitologica 45:14-21.
- Brasil, M. C. and S. B. Amato. 1992. Faunistic analysis of the helminths of sparrows (*Passer domesticus* L., 1758) captured in Campo Grande, Rio de Janeiro, RJ. Memórias do Instituto Oswaldo Cruz 87:43-48.
- Brower, J. E. and J. H. Zar. 1984. Field and Laboratory Methods

- for General Ecology. Wm. C. Brown Company Publishers, Dubuque. 226 p.
- Bush, A. O. 1990. Helminth communities in avian hosts: determinants of pattern. *In* Parasite communities: patterns and processes, G. W. Esch, A. O. Bush and J. M. Aho (eds.). Chapman & Hall, New York. P. 197-232.
- Bush, A. O., K. D. Lafferty, J. M. Lotz and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83:575-583.
- Ching, H. L. 1993. Helminths of varied thrushes, *Ixoreus naevius* and robins *Turdus migratorius*, from British Columbia. *Journal of the Helminthological Society of Washington* 60:239-242.
- Connors, V. A. and B. B. Nickol. 1991. Effects of *Plagiorhynchus cylindraceus* (Acanthocephala) on the energy metabolism of adult starlings, *Sturnus vulgaris*. *Parasitology* 103:395-402.
- Cooper, C. L. and J. L. Crites. 1976a. Community ecology of helminth parasitism in an insular passerine avifauna. *Journal of Parasitology* 62:105-110.
- Cooper, C. L. and J. L. Crites. 1976b. A check list of the helminth parasites of the robin, *Turdus migratorius* Ridgway. *The American Midland Naturalist* 95:194-198.
- Cram, E. B. 1934. Orthopterans and pigeons as secondary and primary hosts, respectively, for the crow stomach-worm *Microtetrameres helix* (Nematoda: Spiruridae). *Proceedings of the Helminthological Society of Washington* 1:50.
- Efe, M. A., L. M. Mohr and L. Bugoni. 2001. Guia Ilustrado das Aves de Porto Alegre. PROAVES, SMAN, COPELUL, CEMAVE, Porto Alegre. 144 p.
- Fabio, S. P. and I. Ferreira. 1999. Parasitismo por *Lutztrema obliquum* (Travassos, 1917) (Digenea, Dicrocoeliidae) em *Turdus albicollis* (Vieillot, 1818), sabiá-coleira, da Ilha da Marambaia, Rio de Janeiro. *Contribuições Avulsas sobre a História Natural do Brasil, Série Zoologia* 4:1-3.
- Fielding, J. W. 1926. Preliminary note on the transmission of the eyeworms of Australian poultry. *Australian Journal of Experimental Biology and Medical Science* 3:225-232.
- Fielding, J. W. 1927. Further observations of the life history of the eyeworm of poultry. *Australian Journal of Experimental Biology and Medical Science* 4:273-281.
- Fontana, C. S. 2001. Aves. *In* Flora e Fauna do Parque Natural Morro do Osso Porto Alegre/RS, S. R. Mirapalmete (coord.). SMAM, Porto Alegre. p. 82-95.
- Fontana, C. S. 2005. A ornitofauna de Porto Alegre no Século XX: status de ocorrência e conservação. *Comunicações do Museu de Ciência e Tecnologia da PUCRS, Série Zoologia* 18:161-206.
- Gaunt, A.S. and L. W. Oring. 1999. Guidelines to the Use of Wild Birds in Research. The Ornithological Council, Washington. 115 p.
- Hammer, Ø, D. A. T. Harper and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm). 27.IX.2006
- Hudson, P. J., A. P. Dobson and K. D. Lafferty. 2006. Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology and Evolution* 21:381-385.
- Isomursu, M., O. Rätti, P. Helle and T. Hollmén. 2006. Sex and age influence intestinal parasite burden in three boreal grouse species. *Journal of Avian Biology* 37:516-522.
- Karasov, W. H. 1990. Digestion in birds: Chemical and physiological determinants and ecological implications. *Studies in Avian Biology* 13:391-415.
- Kennedy, C. R., A. O. Bush and J. M. Aho. 1986. Patterns in helminth communities: why are birds and fish different? *Parasitology* 93:205-215.
- Kingston, N. 1965. On the morphology and life cycle of the trematode *Tanaisia zarudnyi* (Skrjabin, 1924) Byrd and Denton, 1950, from the ruffed grouse, *Bonasa umbellus* L. *Canadian Journal of Zoology* 43:935-969.
- Krissinger, W.A. 1984. The life history of *Lutztrema monenteron* (Price and McIntosh, 1935) Travassos, 1941 (Trematoda: Dicrocoeliidae). *Proceedings of the Helminthological Society of Washington* 51:275-281.
- Leigh, S. R. and W. L. Jungers. 1994. A re-evaluation of subspecific variation and canine dimorphism in woolly spider monkeys (*Brachyteles arachnoides*). *American Journal of Physical Anthropology* 95:435-442.
- Machalska, J. 1980. Helminth fauna of the genus *Turdus* L., examined during their spring and autumn migration. I. Digenea. *Acta Parasitologica Polonica* 27:153-172.
- Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton. 179 p.
- Marcogliese, D. J. and D. K. Cone. 1997. Food webs: a plea for parasites. *Trends in Ecology and Evolution* 12:320-325.
- McLaughlin, J. D. 2001. EMAN – Protocols for Measuring Biodiversity: Parasites of Birds. Canadian Society of Zoologists, Montreal. 84 p.
- Misof, K. 2005. Eurasian blackbirds (*Turdus merula*) and their gastrointestinal parasites: a role for parasites in life-history decisions? *Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn*. 115 p.
- Moore, S. L. and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* 297:2015-2018.
- Moravec, F., J. Prokopic and A. V. Shlikas. 1987. The biology of nematodes of the family Capillariidae Neveu-Lemaire, 1936. *Folia Parasitologica* 34:39-56.
- Morse, D. H. 1990. Food exploitation by birds: some current problems and future goals. *Studies in Avian Biology* 13:134-143.
- Mourad, A. R. 1967. Beetles as intermediate hosts of cestodes of the family Hymenolepididae. *Folia Parasitologica* 14:379-380.
- Okulewicz, J. and M. Wesoowska. 2003. Rediscovery of *Leyogonimus postgonoporus* (Neiland, 1951) (Trematoda,

- Stomylotrematidae) in Central Europe. *Acta Parasitologica* 48:233-236.
- Patten, J. A. 1952. The life cycle of *Conspicuum icteridorum* Denton and Byrd, 1951, (Trematoda: Dicrocoeliidae). *Journal of Parasitology* 38:165-182.
- Pojmanska, T. 1969. *Leucochloridium perturbatum* sp. n. (Trematoda: Brachylaimidae), morphology, individual variability and life cycle. *Acta Parasitologica* 16:153-178.
- Poulin, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist* 147:287-295.
- Poulin, R. and S. Morand. 2004. *Parasite Biodiversity*. Smithsonian Books, Washington. 216 p.
- Price, P. W. 1980. *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton. 237 p.
- Price, P. W. 1990. Host populations as resources defining parasite community organization. In *Parasite communities: patterns and processes*, G. W. Esch, A. O. Bush and J. M. Aho (eds.). Chapman & Hall, New York. p. 23-40.
- Proctor, N. S. and P. J. Lynch. 1993. *Manual of Ornithology: avian structure & function*. Yale University Press, New Haven. 340 p.
- Quentin, J. C., C. Seureau and S. D. Kulo. 1986. Cycle biologique de *Tetrameres (Microtetrameres) inermis* (Linstow, 1879) nématode Tetrameridae parasite du Tisserin *Ploceus aurantius* au Togo. *Annales de Parasitologie Humaine et Comparée* 61:321-332.
- Robinson, S. A., M. R. Forbes, C. E. Hebert and J. D. McLaughlin. 2008. Male-biased parasitism by common helminthes is not explained by sex differences in body size or spleen mass of breeding cormorants *Phalacrocorax auritus*. *Journal of Avian Biology* 39:272-276.
- Rosenberg, K. V. and R. J. Cooper. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13:80-90.
- Rysavy, B. 1973. *Ensiella tetraedra* (Savigny)(Oligochaeta), a new intermediate host of the cestode *Dilepis undula* (Schrank, 1782). *Folia Parasitologica* 20:16.
- Santos, A. J. 2003. Estimativas de riqueza em espécies. In *Métodos de Estudos em Biologia da Conservação e Manejo da Vida Silvestre*, Jr. L. Cullen, R. Rudran and C. B. Valladares-Pádua (eds.). Editora da Universidade Federal do Paraná, Curitiba. p. 19-41.
- Schalk, G and M. R. Forbes. 1997. Male biases in parasitism of mammals: effects of study type, host age, and parasite taxon. *Oikos* 78:67-74.
- Schmidt, G. D. 1975. *Sphaeroirostris wertheimae* sp. n., and other Acanthocephala from vertebrates of Israel. *Journal of Parasitology* 61:298-300.
- Schoener, A. P. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Simberloff, D. and J. Moore. 1997. Community ecology of parasites and free-living animals. In *Host-Parasite Evolution: general principles and avian models*, D. H. Clayton and J. Moore (eds.). Oxford University Press, Oxford. p. 174-197.
- Slater, R. L. 1967. Helminths of the robin, *Turdus migratorius* Ridgway, from Northern Colorado. *American Midland Naturalist* 77:190-199.
- Thul, J. E., D. J. Forrester and C. L. Abercrombie. 1985. Ecology of parasitic helminths of wood ducks, *Aix sponsa*, in the Atlantic flyway. *Proceedings of the Helminthological Society of Washington* 52:297-310.
- Travassos, L., J. F. T. Freitas and A. Kohn. 1969. Trematódeos do Brasil. *Memórias do Instituto Oswaldo Cruz* 67:1-886.
- Vicente, J. J., H. O. Rodrigues, D. C. Gomes and R. M. Pinto. 1995. Nematóides do Brasil. Parte IV: Nematóides de Aves. *Revista Brasileira de Zoologia* 12:1-273.
- Webster, J. D. 1943. Helminths from the robin, with the description of a new nematode, *Porrocaecum brevispiculum*. *Journal of Parasitology* 29:161-163.
- Wehr, E. E. 1937. Observations on the development of the poultry gapeworm *Syngamus trachea*. *Transactions of the American Microscopical Society* 56:72-77.
- Wilkinson, L. E. 1990. *Systat*. Systat Inc, Evanston. 677 p.
- Windsor, D. A. 1997. Stand up for parasites. *Trends in Ecology and Evolution* 12:32.
- Windsor, D. A. 1998. Most of the species on Earth are parasites. *International Journal for Parasitology* 28:1939-1941.
- Yamaguti, S. 1975. *A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates*. Keigaku Publishing Co, Tokyo. 590 p.
- Zuk, M. and K. A. McKean. 1996. Sex differences in parasite infections: patterns and processes. *International Journal for Parasitology* 26:1009-1024.

