

# Biased sex ratio and niche restriction in *Baruscapillaria obsignata* (Madsen 1945) (Nematoda, Capillariidae) from *Columba livia* (Aves, Columbidae)

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## Abstract

In the present study populations of the avian nematode species *Baruscapillaria obsignata* are described from *Columba livia*. Male and female individuals were obtained from 27 birds, fixed in alcohol/formalin/acetic acid (AFA) and preserved in 70% ethanol. Nematodes were identified and then counted under a stereoscopic microscope. *Baruscapillaria obsignata* were much more frequent in the anterior third of the small intestine, and females were more abundant than males in all infra populations. The prevalence was 55.6%, mean intensity was 11.8 (median 11.0; range 1–31) and abundance 6.56. In the present study, we observed an aggregated distribution of parasite infrapopulations, as demonstrated by the value of the exponent of the negative binomial distribution,  $K = 0.2773$ ; by the discrepancy index,  $D = 0.656$  and by the variance/mean ratio, 12.44. The female/male sex ratios found in all infrapopulations were always greater than 1, showing a bias in favour of female abundance. This tendency was especially marked in infrapopulations containing fewer individuals. The sizes of infrapopulations ranged from 5 to 31 individuals. The mean sex ratio observed was  $2.69 \pm 3.28$  (median 1.83; range 0–11). In infrapopulations with 5–15 individuals, the sex ratios observed varied from 2.6 to 11, while in those with 17–31 individuals, the sex ratios were lower, ranging from 1.7 to 2.4. There was a negative correlation between the intensity of infection and the sex ratio of infrapopulations. Results are discussed in terms of possible factors influencing the processes that lead to niche restriction and biased sex ratios in parasite infrapopulations.

## Introduction

The family Capillaridae (Neveu-Lemaire 1936) includes a large group of trichurid nematodes, with approximately 300 species, which are widely distributed and parasites of all vertebrate groups (Moravec, 1982, 1987). In 1982,

Moravec proposed a new taxonomic arrangement for the Capillaridae, considering that the morphological characteristics of the species, habitat differences and heterogeneity of definitive hosts provide sufficient evidence to establish several genera. Various species formerly considered representatives of the *Capillaria* genus were redistributed in valid new genera. The *Baruscapillaria* Moravec, 1982 was one of these new

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genera, and the species *Baruscaphyllaria obsignata* (Madsen 1945) is a very common parasite in the Americas (Morgan, 1932). In Brazil, it has been reported in the states of Piauí, Pernambuco, Rio de Janeiro, Minas Gerais, São Paulo, Goiás, Mato Grosso do Sul, Paraná and Rio Grande do Sul (Costa & Freitas, 1970; Costa *et al.*, 1986; Pinto *et al.*, 2004). Other authors have reported the presence of *B. obsignata* in the small intestine of *Columba livia*, *Zenaidura carolinensis*, *Gallus gallus*, *Phasianus colchicus* and *Meleagris gallopavo* (Travassos, 1915; Morgan, 1932; Freitas & Lins de Almeida, 1935; Miller, 1937; Pinto *et al.*, 2004). There are scarce data in the literature on the population ecology of *B. obsignata*. Most studies focus only on hosts and locations where the parasites occur.

The main aim of the present study was to present evidence of niche restriction and biased sex ratios of *B. obsignata* in *C. livia* in favour of female worm abundance. Results are discussed in terms of possible factors influencing the processes that lead to niche restriction and biased sex ratios in parasite infrapopulations.

## Materials and methods

### Collection and examination of birds

Male and female individuals of *B. obsignata* were obtained from 27 birds of the *C. livia* species (18 females and 9 males) captured at two locations in the municipality of Juiz de Fora: at Mariano Procópio Museum and Jarbas de Lery Santos Square.

All organs of the digestive tract were removed and dissected apart in separate Petri dishes containing 0.85% sodium chloride solution. The intestine was removed, measured and divided into three sections: the anterior third, median third and posterior third. These portions were analysed separately. The mucosal surface of the intestine was scraped with the aid of microscope slides and the content was analysed.

Nematodes were fixed in alcohol/formalin/acetic acid (AFA) and preserved in 70% ethanol (Amato *et al.*, 1991). Nematodes were identified and then counted under a stereoscopic microscope. For morphometric analysis, 41 specimens (13 males and 28 females) were clarified in lactophenol, mounted on semi-permanent slides and measured with the aid of an ocular micrometer coupled to the objective lens of a photonic microscope. The results of the morphological analysis were compared to the description made by Madsen (1950) and to morphometrical data provided by other authors.

### Data analysis

The ecological terminology used in this study was that recommended by Bush *et al.* (1997). The sex ratio within each infrapopulation was calculated by dividing the number of females by the number of males (Roche & Patrzec, 1966). The spatial distribution pattern of the infected parasite infrapopulation in the host populations was obtained by calculating the variance/mean ratio and the discrepancy index (Poulin, 1993).

## Results

The morphological and morphometric characteristics, host and habitat of the specimens studied during the present work are similar to those described for *B. obsignata* by Madsen (1950) and other authors (Travassos, 1915; Graybill, 1924; Morgan, 1932; Freitas & Lins de Almeida, 1935; Miller, 1937; Levine, 1980) (table 1). Of the 27 birds necropsied, 15 were infected by *B. obsignata*, corresponding to a prevalence of 55.6%, mean intensity of  $11.8 \pm 9.22$  (median 11.0; range 1–31) and mean abundance of 6.56. The total worm burden found was 177 helminths (46 males and 131 females). In the present study, an aggregated distribution pattern of infrapopulations was observed, as demonstrated by the

Table 1. Morphometrics of male and female *Baruscaphyllaria obsignata* from *Columba livia* (Aves, Columbidae).

	Travassos (1915)	Graybill (1924)	Morgan (1932)	Freitas & Lins de Almeida (1935)	Miller (1937)	Levine (1980)	Present work
Body (L) ♂	8.8–10.5	8.6–10	9.5–11.5	9.7–11.8	11.4	6.1–9.3	5.83–11.25 (9.29)
Body (L) ♀	14–18	10–12.3	10.5–14.5	12.5–14.7	14–19	10.2–40	11.8–18 (14.8)
Body (W) ♂	0.064	0.085	0.055	0.024–0.057	*	0.023–0.031	0.042–1.1 (0.059)
Body (W) ♀	0.085	0.079	0.08	0.016–0.098	*	0.041–0.05	0.065–0.092 (0.074)
Oesophagus (L) ♂	5–6	*	5.2	4.7–5.7	5.53	*	*
Oesophagus (L) ♀	5–6	4.6–5.6	4.5	4.2–6.1	*	*	4.6–6.3 (5.4)
R a/p ♂	11:14	*	*	1:1.4–1:2	*	*	*
R ♀	2:3	*	*	1:0.9–1:1.1	*	*	*
Dv-e ♀	*	*	0.06	0.060–0.172	*	0.046–0.076	0.05–0.2
Vagina (L) ♀	0.12–0.14	*	*	0.12–0.21	*	*	0.05–0.21 (0.13)
Egg (L) ♀	53–56	50–62	48–55	41–51	47–72	41–51	45.8–56.8 (51)
Egg (W) ♀	28–32	20–27	22–27	24–32	24–31	*	27–34.2 (29.5)
Spicule (L) ♂	1.50–1.57	1.2	1.08–1.43	1.20–1.56	1.4–1.56	1.16–1.53	1–4.2 (1.5)
Spicule (W) ♂	*	0.0082	*	0.005–0.012	*	*	0.0075–0.012 (0.009)
Spicular sheath (L) ♂	*	*	*	*	2.94	*	*
Spicular sheath(W) ♂	*	*	*	0.016–0.018	0.034	*	*

(L), Length; (W), width; R a/p, ratio between the anterior and posterior body region; R, ratio between the pre-vulvar and post-vulvar region; Dv-e, distance between the vulva and the oesophagus; ♀, female; ♂, male. All measures are given in millimetres, with the exception of egg length and width, which are given in micrometres. \* Unavailable information.

discrepancy index,  $D = 0.656$  and by the variance/mean ratio, 12.44. No infrapopulation was found occupying the entire length of the small intestine. Of the 15 infrapopulations observed, only three were found occupying more than one of the three intestinal regions (anterior and median third), 11 were found exclusively in the anterior third and one in the posterior third. Of the hosts examined, 51.9% had nematodes in the anterior third of the small intestine, in contrast to the lower prevalence in the median third, 11.1%, and posterior third, 3.7%. When the aggregation index and variance/mean ratios were calculated considering each intestinal segment separately, the smallest values were related to the anterior third ( $D = 0.6$ ; variance/mean ratio, 9.62), when compared to the median third ( $D = 0.89$ ; variance/mean ratio, 11.21) and posterior third ( $D = 0.92$ ; variance/mean ratio, 31). Thus, there is a more uniform distribution of nematodes in the anterior third because of the greater frequency of *B. obsignata*. The anterior third harboured the highest worm burden (128 helminths, corresponding to 72.31% of the total worm burden; sex ratio 0–11;  $n = 14$ ). The worm burden in the median (18; sex ratio: 0–1.4;  $n = 3$ ) and posterior third (31; sex ratio: 2.44;  $n = 1$ ) corresponded to 10.16% and 17.51% of the total worm burden, respectively.

The female/male sex ratios found in all infrapopulations were always greater than 1, showing a bias in favour of female abundance. This tendency was particularly marked in infrapopulations containing fewer individuals. The mean sex ratio observed was  $2.69 \pm 3.28$  (median 1.83; range 0–11). The sizes of infrapopulations ranged from 5 to 31 individuals. In infrapopulations with 5–15 individuals, the sex ratios observed varied from 2.6 to 11, while in those with 17–31 individuals, the sex ratios were lower, ranging from 1.7 to 2.4. Four infrapopulations with the lowest worm burdens observed (1, 3, 3 and 4, respectively), consisted only of females. There was a negative correlation between the intensity of infection and the sex ratio of infrapopulations (Spearman correlation rank,  $P < 0.05$ ; correlation coefficient:  $-0.709$ ; significance: 0.022), confirming the tendency of bias in favour of female abundance at low intensities.

## Discussion

Silva (1990) and Carneiro *et al.* (1975) reported the occurrence of *Capillaria columbae* (= *Baruscapillaria obsignata*) in *C. livia* in Rio de Janeiro, with a prevalence of 25.7% and mean intensity of 6.8; and in Goiânia, with a prevalence of 8.3%. Pinto *et al.* (2004) recorded for the first time the occurrence of *B. obsignata* in *Phasianus colchicus* Linnaeus, 1758 (Phasianidae), in Rio de Janeiro, finding a prevalence of 2%, mean intensity of 1.0 and mean abundance of 0.02.

The results of the present study indicate that *B. obsignata* has a restricted niche within the host. The ecological niche of a parasite species can be defined as a multi-dimensional hyperspace determined by a large number of physical and biotic variables, including the microhabitat (Rohde, 1994). The specific site in the host may often represent a first approximation of its niche, and, thus, the restriction of the microhabitat may reflect the restriction

of that species' niche (Rohde, 1979, 1994; Combes & Théron, 2000).

It is possible that the aggregation of the parasites at the host population level and microhabitat level in the host, observed in the present study, represents a strategy to enhance the probability of mating and genetic exchange. However, in order to reveal the cause of the aggregation and the consequent microhabitat restriction observed in infrapopulations of *B. obsignata*, an investigation of the role of the coexistence between *B. obsignata* and other helminth species, their nutritional needs and the occurrence of specializations aimed at satisfying such needs is required, as well as of the importance of aggregation in a restricted microhabitat on reproductive performance.

Various authors have discussed the possible factors that influence the processes that lead to niche restriction in helminth species, and have proposed hypotheses regarding the adaptive value of this restriction. Rohde (1994) reported competition, probability of finding mates, reinforcement of reproductive barriers and adaptation to environmental complexity as selective pressures causing niche restriction. Holmes (1990) discussed the importance of specialization, competition and mating.

The probability of finding mates is regarded as a factor that might promote niche restriction in helminth species. According to this hypothesis, aggregating in a restricted microhabitat increases mating success, genetic exchange and, hence, the genetic diversity of the parasites. There is experimental evidence that this aggregation might be mediated by pheromones (Salm & Fried, 1973; Bone *et al.*, 1977, 1978; Bone & Shorey, 1977a, b; Bone, 1982; Eveland *et al.*, 1982, 1983; Schirazian & Schiller, 1982; Bone & Bottjer, 1985). The microhabitat restriction, combined with the chemical mediation of the aggregation and the search for mates, could also have the advantage of encouraging stronger reproductive barriers to gene flow between proximate species, avoiding hybridization (Holmes, 1990; Rohde, 1994; Combes & Théron, 2000).

According to Rohde (1979), niche restriction can be explained by the advantages provided by the enhanced mating probability and consequent genetic diversity. Combes & Théron (2000) suggested that specialization causes the aggregation of individuals at three levels: in a small number of host species (host specificity), in a relatively small number of individuals of the host population (overdispersion) and in only a few microhabitats among those available in the host (site specificity or niche restriction). According to Combes & Théron (2000), specialization promotes aggregation, which in turn increases genetic diversity, favouring specialization in response to the characteristic heterogeneity of the living environment represented by the host.

Another key factor in niche restriction processes is intra- and inter-specific competition (Holmes, 1990; Sukhdeo & Sukhdeo, 1994; Dezfuli *et al.*, 2002). Various types of space-temporal heterogeneity models have been used to explain the coexistence of species, e.g. the aggregation model of coexistence, according to which species coexistence can be favoured by less intensive competition through the aggregate use of fragmented resources (e.g. hosts) (Šimková *et al.*, 2000). Aggregation in response to competition can occur both at the

microhabitat level within the host and at the level of parasite distribution in the host population. Theoretically, this process promotes stable communities, minimizing the frequency of inter-specific interactions and making intra-specific mechanisms predominant in regulating the population size (Von Zuben, 1997).

In all *B. obsignata* infrapopulations in this study, females were more abundant than males, a fact also reported by Graybill (1924). The bias toward female abundance and the correlation between sex ratio and intensity of infection in infrapopulations of *B. obsignata* are consistent with the observations of Roche & Patrzec (1966), Tingley & Anderson (1986), Stien *et al.* (1996), Poulin (1997) and Dezfuli *et al.* (2002).

Several authors have demonstrated, or at least hypothesized, the existence of a relationship between density-dependent ecological parameters and reproduction aspects, such as sex ratio, genetic exchange and diversity within parasite populations (Roche & Patrzec, 1966; Tingley & Anderson, 1986; Holmes, 1990; May & Woolhouse, 1993; Rohde, 1994; Stien *et al.*, 1996; Poulin, 1997; Combes & Théron, 2000; Dezfuli *et al.*, 2002). The primary sex ratio of nematode populations is usually 1:1, since, except for the oxuriids, the sexual chromosomes act as the genetic mechanism for determining the sex of these helminths (Tingley & Anderson, 1986; Stien *et al.*, 1996). Nevertheless, biased sex ratios in favour of females were observed in various nematode species (Roche & Patrzec, 1966; Tingley & Anderson, 1986; Guyatt & Bundy, 1993; Poulin, 1997). Aspects of the species' biology and ecology, such as longevity and differential development rate of males and females, intra- and inter-specific competition and the spatial and genetic structure of the populations were considered important factors in the promotion of deviations from a 1:1 sex ratio (Roche & Patrzec, 1966; May & Woolhouse, 1993; Stien *et al.*, 1996; Poulin, 1997).

Poulin (1997) examined the relation between sex ratio and prevalence or intensity of infection in nematode species. The sex ratios tended to be biased for females. In experimental populations of nematodes, the intensity of infection was negatively correlated with the sex ratio. In other words, the sex ratio was slightly skewed toward females at high population densities. Roche & Patrzec (1966) showed that the intensity of infection and female/male sex ratio were significantly correlated in infrapopulations of *Ancylostoma caninum*, obtained experimentally. These authors found higher sex ratio values in infrapopulations with fewer individuals. They also observed that the sex ratio was positively correlated with the infection time. In other words, the more recent the infection, the nearer the sex ratio was to 1, implying that some males were lost during the course of the infection. They concluded that the patterns observed were due to the different longevities of males and females.

The density and distribution patterns of parasite infrapopulations may favour the emergence of biased sex ratios when the probability of mating is affected by the abundance of parasites (May & Woolhouse, 1993; Poulin, 1997). In parasite populations with a polygamous mating system, sex ratios biased toward females can be favoured when the intensity of infection is low and, thus, the probability of mating is reduced. In such systems, when parasites are less abundant, the greater number of

females in the infrapopulation may enhance mating success.

The decline in the number of females in populations with high densities can also be the result of intra-specific competition for nutrients (Stien *et al.*, 1996) or environmental sex determination (Tingley & Anderson, 1986). The variations in the male–female ratio may regulate the population size (Tingley & Anderson, 1986; Stien *et al.*, 1996; Poulin, 1997). Regulation of reproductive success can occur due to changes in the sex ratio, so that as the infrapopulation density increases, limiting the amount of available resources, the proportion of females decreases. Thus, mating frequency is reduced, hampering population growth (Tingley & Anderson, 1986). Besides the effects of intra-specific competition, one must consider the impact of inter-specific competition on the mortality or fecundity of the helminths, and, finally, on the sex ratios observed in infrapopulations of a given species.

In the present work it has not been possible to determine the causes of the biased sex ratios for females in infrapopulations of *B. obsignata* with lower intensity of infection. However, we assume the hypothesis that the competition for nutrients among females, associated with the polygamous mating system, makes a sex ratio biased toward females an optimal strategy in infrapopulations with low intensities. We also suggest that the exclusion by competition among females, reflected in the lower sex ratio values in infrapopulations with high intensities, acts as a regulating process of the infrapopulation size, favouring an optimal size for individuals' reproductive success.

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