

How do seasonality and host traits influence the distribution patterns of parasites on juveniles and adults of *Columba livia*?



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ABSTRACT

Parasites may influence host fitness and consequently exert a selective pressure on distinct phenotypes of the host population. This pressure can result in an evolutionary response, maintaining only individuals with certain traits in the population. The present study was aimed at identifying the morphological characteristics of juveniles and adults of *Columba livia* that may influence the distribution patterns of lice, *Pseudolynchia canariensis* and *Haemoproteus columbae* and how the populations of these parasites vary throughout the seasons of the year. Between July 2012 and July 2014, 377 specimens of *C. livia* were captured. We observed a significant increase in the mean intensities of infestation by pigeon flies and lice, as well as in species richness of ectoparasites during the warmest seasons, suggesting a reproductive synchrony between ectoparasites and host species. Bill length, body mass, and body length did not affect the infestation levels of ectoparasites on adults and juveniles of *C. livia* with three distinct plumage colors. In juveniles, plumage color affected only the mean intensity of infestation by lice, with Spread individuals as the most infested. This indicates that melanin in feathers was not an effective barrier against ectoparasites.

1. Introduction

Parasitism, similar to predation and competition, is an important selective force on populations, as it reduces the energy available to physiological processes of their hosts (Loye and Carrol, 1995; Sorci et al., 1996). In birds, feathers form a complex environment that allow the occurrence of many groups of arthropod ectoparasites (Janovy, 1997). Ectoparasitism on birds is determined by different factors, including biological aspects, such as susceptibility, and ecological components that include social, reproductive, and foraging behaviors (Begon et al., 1990; Marini et al., 1996; Heeb et al., 2000).

Parasites, in general, affect the fitness (reproductive capacity) (Clayton, 1990) and survival (Clayton et al., 1999) of their hosts. Parasitism levels in animal populations involve a delicate relationship between host immunity and life history traits (Dawson and Bortolotti, 2000; Sol et al., 2003). They are influenced by the abundance and transmission efficiency of vectors (Bennet and Cameron, 1974; Dufva,

1996), as well as by the susceptibility and physiology of the host species (Applegate, 1970; Bennet and Cameron, 1974) and may vary in time in the host population (Atkinson, 1988; Weatherhead and Bennett, 1991) and geographically (Tella et al., 1999; Moyer et al., 2002). Within a host population (;), parasitism levels may also vary causing in some cases, a decrease in the survival rates of individuals of a certain age (Bennet and Cameron, 1974; Merino and Potti, 1995; Waldenström et al., 2002; Sol et al., 2003). Thus, parasites may exert a selective pressure on distinct phenotypes of the host population that in turn can respond in an attempt to control parasite populations (Haldane, 1949).

Host morphological traits may also influence parasite diversity. For instance, host body size may determine how much resources can be exploited by ectoparasites, as well as the number of available niches. Studies have demonstrated a positive relationship between host body size and parasite richness (Poulin, 1997), as well as parasite abundance (Poulin and Rohde, 1997).

Some studies have reported that many parasite groups synchronize

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their reproduction with that of their host species (Marshall, 1981). According to Foster (1969), this synchronization is the result of a close coevolutionary relationship that favors the colonization of new hosts. For some groups with limited mobility, such as mites (Acari) (Jovani et al., 2001) and lice (Insecta: Phthiraptera) (Johnson and Clayton, 2003), this reproductive synchronization is very important, since dispersion and consequently colonization of new habitats occurs only by direct contact among hosts (Marshall, 1981) or in some cases, by phoresy (Jovani et al., 2001). Because of this synchronization between the reproduction of ectoparasites and hosts, spring and summer are expected to be the periods with the highest infestation rates by lice and Pigeon fly *Pseudolynchia canariensis* Macquart, 1840 (Diptera: Hippoboscidae). Also, juveniles hosts are expected to have higher infestation levels by *P. canariensis* due to their close proximity with pupae and low efficiency in the control of ectoparasites when compared to adults.

Recent studies have demonstrated that the health condition of some bird species may be assessed based on the color of feathers. Bird coloration is a result of the physical structure of feathers or the pigments in them (Gill, 1995). This pigmentation has several functions, such as camouflage, thermoregulation, and inter and intraspecific communication (Savalli, 1995). In the last decade, the first studies on the effect of plumage colors of birds on ectoparasites were conducted. Kose et al. (1999) reported that *Machaerilaemus malleus* Burmeister, 1838 (Amblycera: Menoponidae), a louse that parasites *Hirundo rustica* Linnaeus, 1758 (Aves: Hirundinidae), remained significantly longer on white feathers of their hosts than black ones. A few years earlier, Møller (1991) found that the quantity of lesions on white feathers on this host bird caused by the same species of louse was higher than on black feathers. These results support the hypothesis that the melanin present in the feathers of birds may be considered a protection against lice, by making feathers more resistant. Ducrest et al. (2008) demonstrated that some of the genes that express melanin pigmentation have pleiotropic effects on the expression of other physiological processes in several taxa, in particular immunological functions. This suggests that the amount of melanin present in hair or feathers of animals may be an adaptation directly associated to environmental variables (Roulin, 2004), including parasitism (Gasparini et al., 2011).

The wide range of coloration in *Columba livia* Gmelin, 1789 (Aves: Columbidae) resulted from the artificial selection of domestic stocks makes this species an ideal model for studies on the influence of plumage colors on ectoparasites. This species has a gradient of melanin-based colors (Johnston and Janiga, 1995), which can be easily distinguished by the human eye. These various types of plumage colors are genetically determined (Johnston and Janiga, 1995; Jacquin et al., 2013) but are also associated with variables such as behavior, reproductive rate, and resistance to parasites (Johnson and Johnston, 1989; Jacquin et al., 2011). Interestingly, previous studies have shown a relationship between urbanization level and frequency of melanic morphotypes, with darker individuals as the most abundant (Johnston and Janiga, 1995; Obukhova, 2011). Thus, we hypothesize that these individuals have higher immune response (Jacquin et al., 2011) and lower parasite load when compared to individuals with other plumage colors.

Based on this information, this study was aimed at examining the seasonal variation of the richness and abundance of lice, *P. canariensis* and *Haemoproteus columbae* Kruze, 1890 in juvenile and adult specimens of *C. livia* of three distinct plumage colors.

2. Material and methods

Specimens of *C. livia* were classified into three distinct types of plumage colors according to Johnston and Janiga, (1995): (1) “Wild-type” – gray-bluish specimens with two dark blue stripes on wings; (2) “Checker” – individuals with several triangular-shaped dark spots, and (3) “Spread” – black or almost entirely black specimens (Fig. 1). These plumage colors do not differ between sexes and can be identified from the sixth week of life of birds (Johnston and Janiga, 1995).

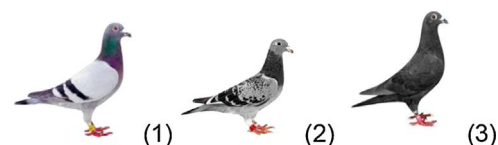


Fig. 1. Wild-type (1), Checker (2), and Spread (3) plumage colors in juvenile and adult specimens of *Columba livia* captured between July 2012 and July 2014 in the municipality of Pelotas, RS, Brazil. *Columba livia* figures:.

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2.1. Study site

Specimens of *C. livia* were collected between July 2012 and July 2014 in three distinct sites in the municipality of Pelotas, in southernmost Rio Grande do Sul – storage sheds in the Port of Pelotas (31°46'55"S; 52°20'01"O), the facade of the Grande Hotel (31°46'55"S; 52°20'01"O), and inside the old building of the Finance Department of the city of Pelotas (31°46'13"S; 52°20'31"O). The city is located in the Coastal Plain, a geomorphological region located at the banks of the São Gonçalo Channel, a navigable waterway linking the Patos and Mirim Lagoons, the largest lagoons in Brazil. Its population is approximately 330,000 inhabitants, with an area of 1609 km² (Instituto Brasileiro de Geografia e Estatística-IBGE, 2010). The city is inserted in the Pampas Biome, in the Pioneiras Formation (vegetation associated with fluvial and/or lacustrine environments) and receives the influence of the semideciduous seasonal forest to the west (Instituto Brasileiro de Geografia e Estatística-IBGE, 1986).

The climate of southern Rio Grande do Sul is moist temperate, according to the classification proposed by Maluf (2000). The mean annual temperature in the urban area of Pelotas is 17.5 °C and the average annual rainfall is 1405 mm, evenly distributed throughout the year (Maluf, 2000).

2.2. Data collection

In the three study sites, a three-day field trip was carried out per season, with sampling activities starting at 08:00 and ending at 18:00. Adult individuals of *C. livia* were captured with the aid of mist nets, while juveniles individuals were captured by hand, since they were located on or near the nests (Permit SISBIO # 38447-1).

Each captured bird was individually placed in cotton bags until the collection of ectoparasites. First, *P. canariensis* specimens were collected manually by inspecting the feathers of each host bird. With the aid of forceps, flies were individually placed in Eppendorf microtubes with 70% alcohol, and later identified with the aid of a stereo-microscope, according to Bequaert (1955) and Gracioli and Carvalho (2003).

After the collection of hippoboscids, lice were collected by dust-ruffling (Walther and Clayton, 1997). A pyrethroid composed of 0.25 g of permethrin, 2.5 g of precipitated sulfur, and excipient q. s. P. 100.0 g (Piolhaves – ProvetS Simões Laboratory Ltda.) was applied in between the feathers of each bird. Lice of each bird were placed in plastic containers with 70% alcohol, mounted in permanent preparations, following Palma (1978), and identified according to Price et al. (2003) and Adams et al. (2005).

To avoid the contamination of samples, the materials used to remove and collect ectoparasites, such as brushes and tweezers, were washed in running water after each use. The surface used to collect lice, consisted of a 50 cm x 30 cm tissue paper sheet, placed under each captured specimen was discarded after use. Each captured specimen of *C. livia* was tagged with colored rings to maintain the independence of ectoparasite samples.

Subsequent to the collection of lice, a small blood sample was taken from the bird's brachial vein using a glass capillary and insulin syringe for the detection of hematozoa. Three blood smears were prepared in the filed, air dried for 5–10 s, and fixed with absolute methanol for 10 min. In the Laboratory of Parasite and Vector Ecology (Laboratório de Ecologia de Parasitos e Vetores – LEPAV), the slides were stained for 30 min with 3% Giemsa solution and then examined under an Olympus microscope (model CX21FS1) with 1000 x magnification for hematozoa, following Valkiūnas (2005). Each blood sample was examined for 30 min and for the quantification of parasites, approximately 10,000 erythrocytes were analyzed. Only fields with a minimum of 50 erythrocytes were included (Gibb et al., 2005).

Following the collection of ectoparasites, each *C. livia* specimen was classified based on plumage color, body mass, bill length, and body length. Birds were then released near the capture site.

2.3. Data analysis

The prevalence and mean intensity of infestation by Pigeon fly and by species of lice on *C. livia* were calculated according to Bush et al. (1997)

Within matrices, generalized linear models (GLM) were used with Poisson or Quasipoisson distribution when there was over-dispersion, followed by residue analysis to verify the adequacy of the distribution of errors and adjustment of models, considering the response variables mean intensity of infestation by lice, mean intensity of infestation by Pigeon fly, and ectoparasite richness in function of bill length, body mass, body length, plumage color of the host. The simplest models were obtained by extracting non-significant terms ($P < 0.05$) from the complete model comprised of all variables and their interactions, as suggested by Crawley (2007). Each deletion of a term was followed by ANOVA with a Chi-square test (Chi) to recalculate the deviation explained by remaining terms.

If the model was not significant or if the only significant variable in the model was plumage color or season, or both, the Kruskal-Wallis test was used followed by the Wilcox test for pairwise comparison along with the Bonferroni correction.

All statistical analyses were carried out with significance level set at $P < 0.05$ in the statistical program R (R Development Core Team, 2013).

3. Results

A total of 377 specimens of *C. livia* was captured, of which 130 (juveniles = 67 and adults = 63) were Checker individuals, 122 (juveniles = 68 and adults = 54) were Spread, and 125 (juveniles = 46 and adults = 79) were Wild-type.

Five distinct species of lice, totaling 23,307 specimens, were collected: *Columbicola columbae* Linnaeus, 1758 ($n = 15,096$), *Colpocephalum turbinatum* Denny, 1842 ($n = 5432$), *Campanulotes compar* Burmeister, 1838 ($n = 2178$) (Ischnocera: Philopteridae), *Hohorstiella lata* Piaget, 1880 ($n = 439$), and *Bonomiella columbae* Emerson, 1957 ($n = 162$) (Amblycera: Menoponidae). On adults specimens of *C. livia*, 14,071 lice were found, while in juveniles, 9236 specimens were collected. Among the captured juveniles, Spread individuals were the most infested by lice ($n = 4059$), while on adults, the Wild-type ($n = 5237$). *Columbicola columbae* was the most prevalent species on *C. livia* juveniles and adults of the three different plumage colors (Table 1).

Of the total number of lice collected, 7688 were males, 7586 were females, and 8033 were nymphs. Male lice were more abundant on adults specimens of *C. livia* of three distinct plumage colors. However, female lice were more abundant on juveniles of *C. livia* of three distinct plumage colors (Table 2).

Of the 1381 specimens of *P. canariensis* collected, 60% ($n = 822$) were found in juveniles and 40% ($n = 559$), on adults. Of the total

Table 1
Prevalence (%) of species of lice and of *Pseudolynchia canariensis* collected on *Columba livia* juveniles and adults with the plumage colors Checker, Spread, and Wild, between July 2012 and July 2014, in the municipality of Pelotas, RS, Brazil. (n) number of infested hosts.







plumage color	Parasites	Adults		Juveniles	
		n	%	n	%
Checker 	<i>Columbicola columbae</i>	63	100	62	92.5
	<i>Campanulotes compar</i>	45	71.4	31	46.3
	<i>Colpocephalum turbinatum</i>	32	51	21	31.3
	<i>Hohorstiella lata</i>	23	36.5	16	24
	<i>Bonomiella columbae</i>	15	24	9	13.4
Spread 	<i>Pseudolynchia canariensis</i>	43	68.2	54	80.1
	<i>Columbicola columbae</i>	54	100	65	95.6
	<i>Campanulotes compar</i>	40	74	39	57.3
	<i>Colpocephalum turbinatum</i>	34	63	25	37
	<i>Hohorstiella lata</i>	21	39	15	22
Wild-type 	<i>Bonomiella columbae</i>	6	11	12	18
	<i>Pseudolynchia canariensis</i>	41	76	58	85.3
	<i>Columbicola columbae</i>	77	97.5	46	100
	<i>Campanulotes compar</i>	49	62	29	63
	<i>Colpocephalum turbinatum</i>	44	55.7	22	47.8
	<i>Hohorstiella lata</i>	26	33	9	19.6
	<i>Bonomiella columbae</i>	7	8.9	6	13
	<i>Pseudolynchia canariensis</i>	46	58.2	42	91.3




Table 2
Number of males, females, and nymphs of lice collected on juveniles and adults of *Columba livia* with Checker, Spread, and Wild-type plumages, from July 2012 to July 2014, in the city of Pelotas, Brazil.

Plumage color	Host age	Number of male lice	Number of female lice	Number of nymphs	Total
Checker 	Juvenile	614	677	898	2,189
	Adult	1,470	1,411	1,222	4,103
Spread 	Juvenile	1,155	1,246	1,658	4,059
	Adult	1,682	1,595	1,454	4,731
Wild-type 	Juvenile	808	903	1,277	2,988
	Adult	1,959	1,754	1,524	5,237
	Total	7,688	7,586	8,033	23,307

hippoboscids collected, 30% ($n = 414$) were observed on Checker individuals, 40.2% ($n = 558$), on Spread individuals, and 29.8% ($n = 409$) on Wild-type individuals. Females of *P. canariensis* were more abundant than males. In the three distinct plumage colors, *P. canariensis* males were more abundant on adults of *C. livia*, while females were more abundant on juveniles of *C. livia* (Table 3).

Although mean intensity of infestation by lice was not influenced by host age (KW = 0.47; GL = 2; $P = 0.49$), juvenile and adult specimens have different body mass ($F_{1,15} = 203.63$; $P < 0.001$) and bill length ($F_{1,15} = 5.60$; $P = 0.02$). Therefore, the general matrix of data was divided between juveniles and adults for all response variables tested: mean intensity of infestation by lice (MII Lice), ectoparasite richness (S

Table 3
Number of males and females of *Pseudolynchia canariensis* collected on juveniles and adults of *Columba livia* with Checker, Spread, and Wild-type plumages, between July 2012 and July 2014, in the city of Pelotas, Brazil.

Plumage color	Host age	Number of male hippoboscids	Number of female hippoboscids	Total
Checker 	Juvenile	103	138	241
	Adult	87	86	173
Spread 	Juvenile	171	186	357
	Adult	108	93	201
Wild-type 	Juvenile	109	115	224
	Adult	102	83	185
	Total	680	701	1,381

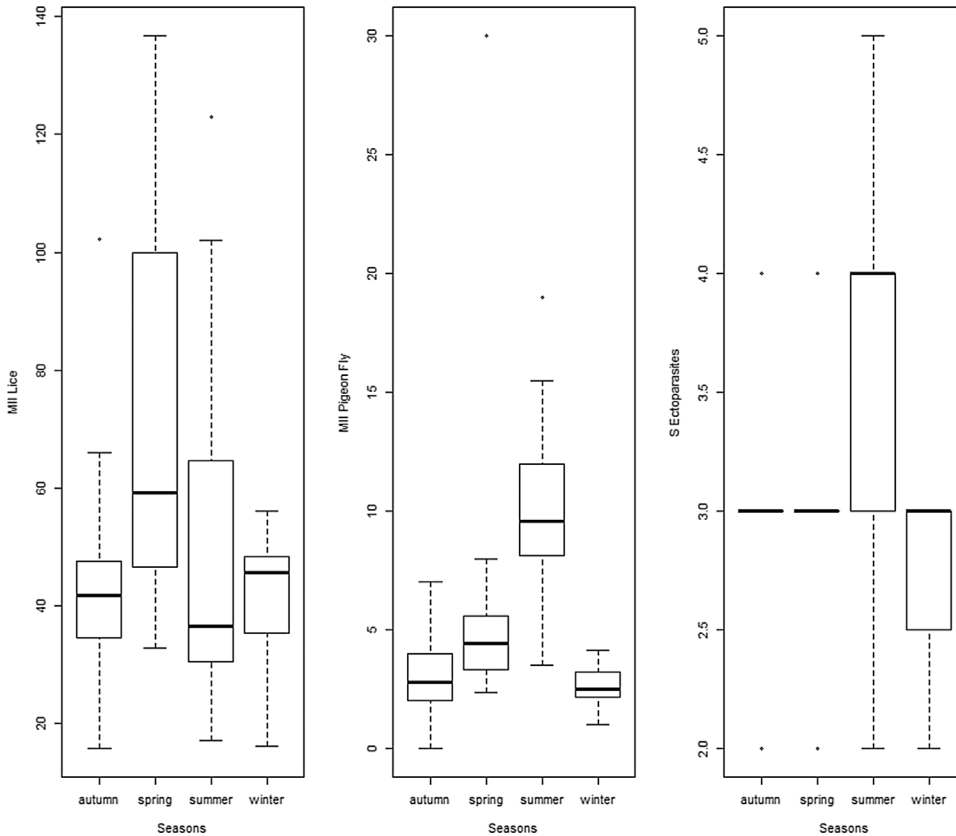


Fig. 2. Mean (dark bar), standard error (rectangle), and variation (dashed line) of mean intensity of infestation by lice (MII Lice), mean intensity of infestation by pigeon fly (MII PigeonFly), and ectoparasite richness (S Ectoparasites), in juveniles specimens of *Columba livia* with Checker, Spread, and Wild-type plumages, between July 2012 and July 2014, in the municipality of Pelotas, RS, Brazil.

Ectoparasites), mean intensity of infestation by pigeon fly (MII PigeonFly), and parasitemia.

For the data matrix of juveniles, there was no interference of bill length, body mass, and body length in the variation of mean intensity of infestation by lice, mean intensity of infestation by pigeon fly, ectoparasite richness and parasitemia ($P > 0.05$). The season of the year influenced ectoparasite richness (KW = 8.59, df = 3, $P = 0.03$) and mean intensity of infestation by pigeon fly (KW = 17.67, df = 3, $P < 0.001$). Fig. 2 presents the mean, standard errors, and variation, with higher ectoparasite richness and mean intensity of infestation by pigeon fly in summer than in other seasons ($P < 0.05$). In juveniles, plumage color influenced only mean intensity of infestation by lice (KW = 7.63, df = 2, $P = 0.02$). Fig. 3 shows means, standard errors, and data variation, with higher values of these variables for Spread juveniles than those for Blue-Checker individuals ($P < 0.05$), with no differences between Spread and Wild-type ($P > 0.05$) and between Checker and Wild-type plumages ($P > 0.05$).

For the data matrix of adults, no interference of bill length, body mass, and body length was found in mean intensity of infestation by lice, mean intensity of infestation by pigeon fly, ectoparasite richness, and parasitemia ($P > 0.05$).

The season of the year influenced ectoparasite richness (KW = 20.96, df = 3, $P < 0.001$), mean intensity of infestation by lice (KW = 10.29, df = 3, $P = 0.01$), and mean intensity of infestation by pigeon fly (KW = 21.57, df = 3, $P < 0.001$). Fig. 4 shows the means, standard errors, and variation of data. In summer, ectoparasite richness and mean intensity of infestation by pigeon fly were higher than in other seasons ($P < 0.05$).

Ectoparasite richness was higher in summer and spring than in fall and winter, as well as mean intensity of infestation by pigeon fly ($P < 0.05$). Mean intensity of infestation by lice was higher in spring than summer, fall, and winter ($P < 0.05$). Plumage color of adults of *C. livia* did not influence any of the variables evaluated ($P < 0.05$).

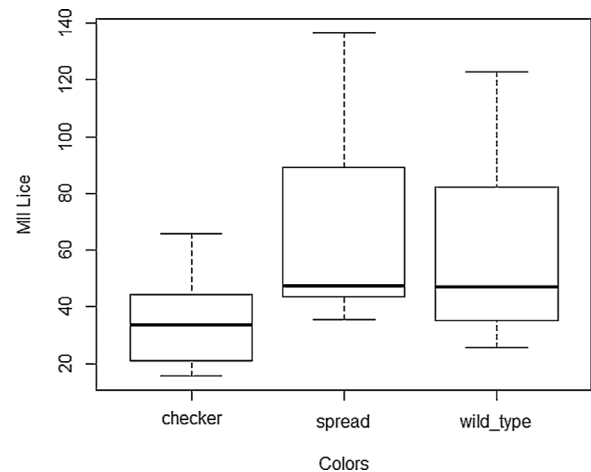


Fig. 3. Mean (dark bar), standard error (rectangle), and variation (dashed line) of mean intensity of infestation by lice (MII Lice), in juveniles specimens of *Columba livia* with Checker, Spread, and Wild-type plumages, between July 2012 and July 2014, in the municipality of Pelotas, RS, Brazil.

4. Discussion

In the present study, *C. columbae* was the most prevalent and abundant species of lice on specimens of *C. livia*, as also reported by Dranzoa et al. (1999), Radfar et al. (2012). This pattern may be due to the high level of specificity to *C. livia*, as well as its ability to colonize new hosts (Harbison et al., 2009).

Mean intensity of infestation by lice and ectoparasite richness significantly increased in the warmest seasons, since temperature and humidity can affect the structure of ectoparasite communities, as observed by Moyer et al. (2002). Seasonal alterations in prevalence and

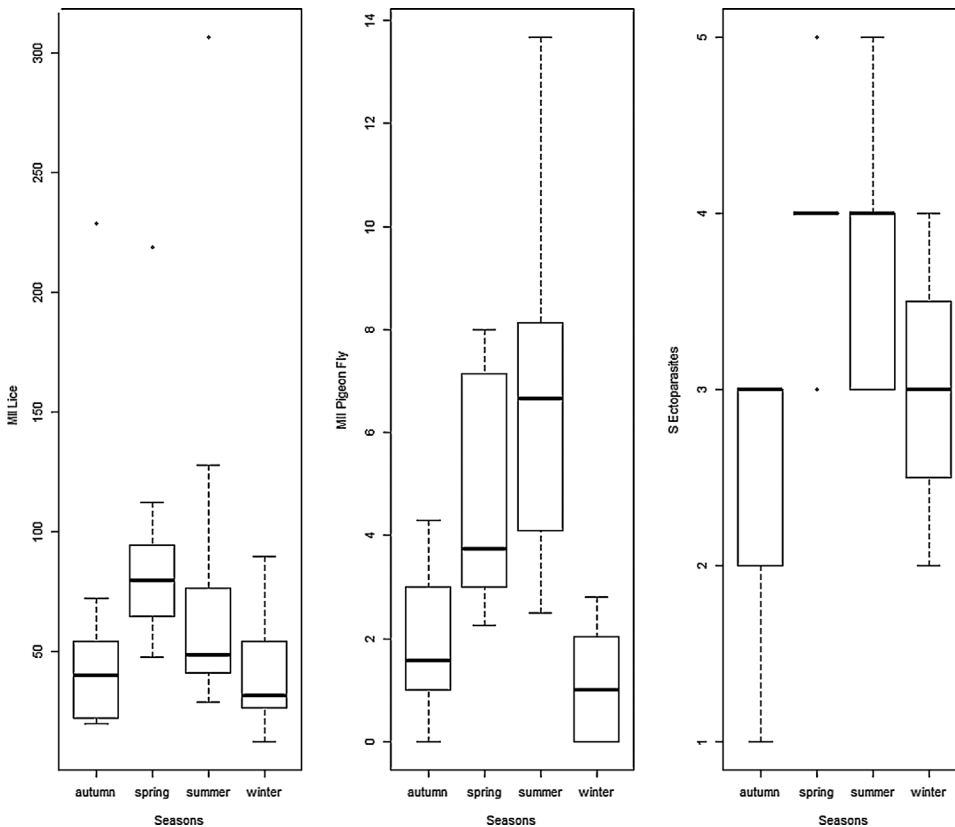


Fig. 4. Mean (dark bar), standard error (rectangle), and variation (dashed line) of mean intensity of infestation by lice (MII Lice), mean intensity of infestation by pigeon fly (MII PigeonFly), and of ectoparasite richness (S Ectoparasites), on *Columba livia* adults with Checker, Spread, and Wild-type plumages, between July 2012 and July 2014, in the municipality of Pelotas, RS, Brazil.

abundance can occur due to reproductive synchronization of some parasites with their hosts (Foster, 1969; Marshall, 1981; Blanco and Frías, 2001; Altizer et al., 2004; Dietsch, 2005), as well as seasonal changes in host immunological defenses (Stearns, 1989; Møller, 1993, 1994).

If melanin plays a defensive role against lice, then, hosts with large amounts of melanin in their feathers, such as Spread individuals, would be expected to be less infested than hosts with less melanin in the feathers, such as Checker and Wild-type specimens. However, contrary to our hypothesis and that of Bush et al. (2006), lice infestation on juvenile's hosts with black feathers was higher when compared with the other plumage color, suggesting that melanin does not play a defensive role against these ectoparasites. Different parasite pressures, associated with environmental characteristics, such as urbanization levels, and morphological traits may play an important role in the regulation of plumage color in *C. livia* (Jacquin et al., 2012). Therefore, further studies are needed to test this hypothesis and if these factors are associated with conditions for local adaptation that promote the maintenance of diversity of plumage colors.

Mean intensity of intensity by lice in *C. livia* was highly variable, resulting in an aggregated distribution pattern, as reported in other studies (Wheeler and Threlfall, 1986; Lindell et al., 2002; Amaral et al., 2013). This pattern is characterized by high infestation on a small portion of the hosts, while the majority of hosts has a low infestation.

The high prevalence of *P. canariensis* on *C. livia* observed in this study, as also reported by Dranzoa et al. (1999) and Marques et al. (2007), reveals a close relationship between this hippoboscid fly and its host species. Despite the high prevalence of *P. canariensis* on *C. livia* adults observed here and reported by Radfar et al. (2012), in both studies juveniles hosts were the most infested. Juveniles tend to have higher infestation rates due to their proximity to pupae, which are often found around the nests (Bequaert, 1953). On the other hand, the low infestation rates of adult hosts was expected due to their increased immunity compared to that of juveniles (Merilä et al., 1995). Adult

birds also spend more time in preening their feathers, which results in greater control of infestation of this and other ectoparasites (Clayton et al., 2010; Waite et al., 2012). Furthermore, the importance of bill length in the control of ectoparasites has been demonstrated by Waite et al. (2012) that found that hosts with larger bill were less infested by *P. canariensis*.

The highest infestation levels of *P. canariensis* on hosts occurred in the warm seasons. Species of Hippoboscidae are not permanent ectoparasites of mammals and birds, as free-living pupae are deposited in the nests of birds or burrows of mammals. The emergence of pupae usually coincides with the breeding season of the host species (Bequaert, 1953). The population of this hippoboscid fly tends to increase rapidly during spring and part of summer, reducing at the end of summer and fall, until reaching its lower density in winter (Bequaert, 1953).

Based on our findings, plumage color influenced only lice infestation patterns of Spread juveniles of *C. livia*. No significant changes in infestation levels by *P. canariensis* were observed in both juveniles and adults of *C. livia* with the three distinct plumage colors. However, in warm seasons, infestation levels by *P. canariensis* were higher as well as ectoparasite richness in juveniles. On the other hand, on *C. livia* adults, higher infestation rates by lice and *P. canariensis* and higher ectoparasite richness was observed in warm seasons.

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