Composition and distribution patterns of chewing lice of two neotropical species of *Turdus*

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We analyzed the prevalence and intensity of chewing lice on two neotropical species of *Turdus* and identified morphological parameters of birds influencing louse population dynamics. The study was conducted in southernmost Rio Grande do Sul state (RS), Brazil, between July 2009 and June 2010. Chewing lice were collected by dust-ruffling. The prevalence of chewing lice on both species of *Turdus* was high. Chewing lice from both species of *Turdus* exhibit similar composition and distribution patterns. However, chewing lice were more abundant on *Turdus rufiventris*, whereas species richness was higher on *Turdus amaurochalinus*. *Myrsidea* and *Brueelia* were the most prevalent and abundant genera on both host species in all seasons of the year. A predominance of chewing louse females and adults was observed. Aggregated distributions were observed. Body length was the only morphological parameter correlated with louse abundance, suggesting that specimens with a larger body have a higher abundance of lice.

**Keywords:** Phthiraptera; Amblycera; Ischnocera; Ectoparasitism

**Introduction**

Parasite–host interactions are considered powerful arenas to ecological studies (Dogiel 1964) especially for permanent and obligatory parasites, such as chewing lice, which complete their entire life cycle on the host (Johnson and Clayton 2003).

On birds, two suborders of chewing lice, Amblycera and Ischnocera, have been described. Amblycera are more agile, live on the skin as well as between feathers, whereas many genera of Ischnocera show morphological specializations that suggest that they may be adapted to preferentially inhabit specific areas of the host’s body (Ash 1960; Marshall 1981), however positive evidence of this is rare, and many ischnoceran lice are perhaps better considered generalists, with no obvious specialization (Johnson et al. 2012).

Like all parasites, chewing lice affect the fitness of the host (Clayton et al. 1999) as they feed on skin debris, blood, and secretions or feather keratin (Price et al. 2003), damage feathers, affect flight (Barbosa et al. 2002) and thermoregulatory ability of
the host (Booth et al. 1993), making it more susceptible to predation (Anderson and May 1979).

Most studies examining the inter-relationship between parasites and their hosts are considered unidirectional as they evaluate only the effects of parasites on their hosts (Clayton and Moore 1997). However, the population dynamics of these parasites are influenced by several host characteristics, such as body mass (Clayton and Walther 2001), body size (Tryjanowski et al. 2007), bill size and shape (Clayton 1991), and immunological condition (Clayton 1990). Also, the distribution patterns of ectoparasites on the body of the host may be affected by male and female behavioural differences (Matthee et al. 2010).

The genus *Turdus* Linnaeus, 1758 has a cosmopolitan distribution, being found in the Americas, Asia, Europe, Africa, and Oceania (IUCN 2011). Information on the diet (Bartuszevige and Gorchov 2006; Gutián and Bermejo 2006; Baldwin et al. 2008) and reproductive aspects (Sim et al. 2007; Halupka and Greeney 2009; Najmanová and Adamík 2009) of some species are relatively well known, but few studies have examined their ectoparasites.

Recent studies have revealed high levels of prevalence and infestation intensity (Enout et al. 2009; Brooke 2010), and aggregation patterns (Lindell et al. 2002) of species of chewing lice on thrushes. However, patterns of sex ratio and age structure are still poorly known, as are the morphological parameters of the host species that could influence the population dynamics of chewing lice. Therefore, we analyzed the distribution patterns of prevalence and intensity of chewing lice collected from two neotropical hosts – *Turdus amaurochalinus* Cabanis, 1850 and *Turdus rufiventris* Vieillot, 1818 – and examined whether these data correlated with morphology of the hosts.

**Materials and methods**

Both host species have a broad geographical distribution and are frequently found at forest edges (Sick 1997). They are omnivores with a preference for fruits, although they also feed on insects captured while scratching the ground (Belton 1994).

The study was carried out in three areas of Atlantic Forest in the rural area of the municipality of Pelotas, Rio Grande do Sul state: Estação Experimental Cascata–Embrapa Clima Temperado (31°37' S; 52°31' W), Hotel Bachini (31°31' S; 52°28' W), and Sítio Araçá (31°39' S; 52°31' W). From July 2009 to June 2010, birds were captured during four field trips per area, one in each season. Once a month, from 06:00–07:00 until 17:30–18:30 hours, four mist nets (12 m × 2.5 m) were set up in forest edges, totalling 144 h/net of sampling. Dust-ruffling (Walther and Clayton 1997) with a pyrethroid consisting of 0.25 g permethrin and 2.5 g precipitated sulfur (Piolhaves® – ProvetS Simões Laboratório Ltda.) was used to collect chewing lice from *T. amaurochalinus* and *T. rufiventris*. Permethrin and precipitated sulfur are commonly used for ectoparasites control (Kidd and James 1991; Tomlin 2006). Samples were considered independent, as each captured bird was sampled once. After chewing lice were collected, birds were fitted with metal rings (provided by CEMAVE/IBAMA), measured for body mass, body length, and bill length, and later released near the capture site.

Chewing lice of each captured bird were conserved in containers filled with ethanol 70% and the identification was carried out in the Laboratory of Insect
Biology, at the Institute of Biology of the Pelotas Federal University (UFPel). Chewing lice were mounted in permanent preparations according to Palma (1978) and identified following Price (1975), Castro and Cicchino (1978), Cicchino (1986; 1987) and Price et al. (2003).

Age structure (nymphs and adults) and sexual ratio were analyzed for the infra-populations of *Myrsidea* sp. and *Brueelia persimilis* Cicchino, 1987 on *T. amaurochalinus*, and of *Myrsidea* sp. and *Brueelia addoloratoi* Cicchino, 1986 on *T. rufiventris*. We calculated the prevalence and mean infestation intensity of chewing lice on each host species following Bush et al. (1997), and the terms mean abundance, infracommunity, infrapopulation and component community were used as proposed by the same authors.

For both species of *Turdus*, the mean richness of chewing lice per host was calculated and compared using the *t*-test. The mean abundance of chewing lice was compared using the Mann–Whitney test.

The aggregation of chewing lice on host species was analyzed based on the parameter *k* of the negative binomial distribution.

The effect of seasonality on the average intensity of infestation of chewing lice on both species of *Turdus* was examined using generalized linear models (GLM) with Poisson or Quasi-Poisson distribution to correct for overdispersion (Crawley 2007).

The influence of morphological parameters of hosts (body mass, total body length, and bill length) on the intensity of chewing lice was evaluated by GLM with Quasi-Poisson distribution. The similarity between the models constructed was tested by chi-square (χ²) as suggested by Crawley (2007).

The tests were conducted with the statistical software R (R Development Team 2009), Past 2.09 and Quantitative Parasitology 3.0 (Reiczigel and Rózsa 2005). All tests were considered significant at a *P < 0.05* after Bonferroni correction for the number of tests (Rice 1989).

**Results**

**Prevalence and mean intensity of infestation**

Altogether, we captured 36 specimens of *T. amaurochalinus* and 53 specimens of *T. rufiventris*. Four genera of chewing lice were observed, with *Philopterus* Nitzsch, 1818 being associated solely with *T. amaurochalinus*. *Menacanthus eurysternus* Burmeister, 1838 was the only species observed on both species of *Turdus*.

In all seasons *Myrsidea* sp. was the most prevalent and abundant parasite on *T. amaurochalinus* and *T. rufiventris* (Table 1). *Philopterus* sp. and *B. persimilis* were found only on *T. amaurochalinus* and were less abundant in the winter, spring, and autumn. *B. addoloratoi* also occurred in these seasons, but exclusively on *T. rufiventris* and was more prevalent in the spring. *M. eurysternus* was less common in the winter and autumn on *T. amaurochalinus*, and in the spring on *T. rufiventris* (Table 1). Although variations were observed in the levels of average intensity of infestation of all species of chewing lice on both species of *Turdus*, these differences were not significant throughout the seasons (X² = 2139.6; df= 3;80; *P < 0.3*). Of the 3319 chewing lice collected, 91.4% were observed on *T. rufiventris* and 8.6% on *T. amaurochalinus* (*T* = 142, *P* = 0.0001).
Table 1. General pattern of the distribution of chewing lice (Phthiraptera: Amblycera and Ischnocera) observed on *Turdus amaurochalinus* (*n* = 36) and *Turdus rufiventris* (*n* = 53), in three areas of Atlantic Forest, southern Brazil, between July 2009 and June 2010.

| Host/lice species | Season    | Prevalence %  | Mean intensity of infestation | Female/male ratio | Adult/nymph ratio |
|-------------------|-----------|---------------|-------------------------------|-------------------|------------------|
|                   |           | (number of hosts infected) | (confidence interval)         |                   |                  |
| **Host: T. amaurochalinus** |           |               |                               |                   |                  |
| *Myrsidea* sp.    | Winter    | 31.3% (*n* = 5) | 3.2 (1.8–4.6) | 1:1               | 1.5:1            |
| *Brueelia persimilis* | Winter    | 6.2% (*n* = 1)  | 2 (0)              | 1:1               | 2:0              |
| *Philopterus* sp. | Winter    | 12.5% (*n* = 2) | 1 (0)               | 1:0               | 1:1              |
| *Myrsidea* sp.    | Spring    | 60.0% (*n* = 6) | 8.8 (0–18.6)        | 1.3:1             | 2.5:1            |
| *M. eurysternus*  | Spring    | 20.0% (*n* = 2) | 7 (6–8)             | 1:1.3             | 2:1              |
| *Brueelia persimilis* | Winter    | 10.0% (*n* = 1) | 11 (0)              | 7:1               | 2.7:1            |
| *Philopterus* sp. | Autumn    | 20.0% (*n* = 2) | 2.5 (0.5–4.5)       | 1:2               | 1.5:1            |
| *Myrsidea* sp.    | Autumn    | 40.0% (*n* = 4) | 32 (0–88.1)         | 1.5:1             | 2.2:1            |
| *Brueelia persimilis* | Winter    | 20.0% (*n* = 2) | 4.5 (1.1–7.9)       | 1.25:1            | 9:0              |
| *Philopterus* sp. | Autumn    | 20.0% (*n* = 2) | 4 (2.4–5.6)         | 1:1               | 3:1              |
| **Host: T. rufiventris** |           |               |                               |                   |                  |
| *Myrsidea* sp.    | Winter    | 84.6% (*n* = 11) | 51 (24.1–77.9)      | 1.6:1             | 1.13:1           |
| *M. eurysternus*  | Winter    | 7.7% (*n* = 1)  | 8 (0)               | 7:1               | 8:0              |
| *B. addoloratoi*  | Winter    | 53.8% (*n* = 6) | 32 (5.4–58.6)       | 2.3:1             | 2.7:1            |
| *Myrsidea* sp.    | Spring    | 100.0% (*n* = 15) | 53.6 (30.7–76.5) | 1.41:1            | 1.72:1           |
| *B. addoloratoi*  | Spring    | 66.7% (*n* = 10) | 20.4 (1.1–39.7)     | 1.9:1             | 2.5:1            |
| *Myrsidea* sp.    | Summer    | 100.0% (*n* = 1) | 23 (0)             | 1:1.5             | 1:3.6            |
| *Myrsidea* sp.    | Autumn    | 95.6% (*n* = 22) | 37.8 (26–49.6)      | 1.15:1            | 1.4:1            |
| *M. eurysternus*  | Autumn    | 4.3% (*n* = 1)  | 2 (0)               | 2:0               | 2:0              |
| *B. addoloratoi*  | Autumn    | 47.8% (*n* = 11) | 35.4 (0–85.8)      | 2.2:1             | 3.9:1            |
Species richness

On *T. amaurochalinus*, the mean richness of species was significantly lower (mean = 1.1 ± 0.1 SE) compared with that of *T. rufiventris* (mean = 1.5 ± 0.07 SE) (*t* = –2.992, df = 1;72, *P* = 0.004). On *T. amaurochalinus*, 64% of birds had at least one species of chewing lice compared with 96% in *T. rufiventris*.

Distribution patterns

An analysis of all species combined (*k* = 0.41), as well as those of *Myrsidea* Waterston, 1915 and *Brueelia* Kéler, 1936 analyzed separately, revealed an aggregated distribution pattern of lice on both host species (Figures 1, 2, and 3). The level of aggregation was *k* = 0.14 for *Myrsidea* sp. and *k* = 0.09 for *Philopterus* sp. on *T. amaurochalinus*, and *k* = 0.97 for *Myrsidea* sp. and *k* = 0.15 for *B. addoloratoi* on *T. rufiventris*. Because of the small sample size, the *k* parameter of distribution for *M. eurysternus* from both species of *Turdus* and *B. persimilis* on *T. amaurochalinus* could not be calculated. In both host species, most infrapopulations of *Myrsidea* and *Brueelia* consisted of up to 15 specimens, whereas on *T. rufiventris* the number of infrapopulations was higher and in different intervals of abundance (Figures 2 and 3).

Sex and age ratio

Of the 3319 chewing lice collected, 38% (*n* = 1274) were females, 37% (*n* = 1223) nymphs, and 25% (*n* = 822) males. In all seasons and on both host species chewing

![Figure 1](image-url)  
**Figure 1.** Infrapopulation size of all species of chewing lice and their corresponding distribution on *Turdus amaurochalinus* (*n* = 36) and *Turdus rufiventris* (*n* = 53), in three areas of Atlantic Forest, in southern Brazil, between July 2009 and June 2010.
Figure 2. Infrapopulation size of *Myrsidea* sp. on *Turdus amaurochalinus* \((n = 36)\) and *Turdus rufiventris* \((n = 53)\), in three areas of Atlantic Forest, in southern Brazil, between July 2009 and June 2010.

Figure 3. Infrapopulation size of *Brueelia persimilis* on *Turdus amaurochalinus* \((n = 36)\) and *Brueelia addoloratoi* on *Turdus rufiventris* \((n = 53)\), in three areas of Atlantic Forest, in southern Brazil, between July 2009 and June 2010.
lice female were more abundant than males, as well as the adults compared with nymphs (Table 1).

In the present study the specimens of *T. amaurochalinus* had a mean body mass of 64 g (± 0.87 SE), mean body length of 22.5 cm (± 1.1 SE), and mean bill length of 1.85 cm (± 0.02 SE), whereas the specimens of *T. rufiventris* had a mean body mass of 71.5 g (± 0.75 SE), mean body length of 23.8 cm (± 0.97 SE), and mean bill length of 1.94 cm (± 0.02 SE).

The abundance of chewing lice does not vary with body mass (Chi = 5315.4, df = 1; 86, \( P = 0.1526 \)) or bill length (Chi = 5332.4, df = 1; 86, \( P = 0.1534 \)) of *Turdus* species. On the other hand, body length variation influences chewing lice abundance variation, with higher abundance in *T. rufiventris* than *T. amaurochalinus* (Chi = 5438.3, df = 1; 86, \( P < 0.001 \), Figure 4).

**Discussion**

Our findings revealed a pattern of high prevalence of chewing lice on both *Turdus* species. *Myrsidea* was the most abundant genus of louse found on the examined host species, as was the case in the studies by Lindell et al. (2002) and Enout et al. (2009). The high prevalence and abundance of *Myrsidea* might be due to the high level of specificity of these parasites to their hosts, as they have had a long history with their hosts (Bueter et al. 2009) and may also strongly correlated with the transmission rate among hosts (Arneberg et al. 1998).

We did not observe a significant increase or decrease in the average intensity of infestation of chewing lice on both host species throughout the seasons. Although the environmental temperature did not affect the prevalence of chewing lice in the present...
Mean species richness of chewing lice was higher on *T. rufiventris* compared with that of *T. amaurochalinus*. These results are very similar to those found by Lindell et al. (2002), Wheeler and Threlfall (1986), and Clayton et al. (1992) in other species of *Turdus*. Mean and variance of richness (infracommunities) were lowest on both species of hosts when compared with total richness in our study area (component community), suggesting a size limit of infracommunities that would be saturated in relation to the component communities of chewing lice. In *T. rufiventris*, the component community included three species, whereas in *T. amaurochalinus* the component community included four species. Poulin (2007a) suggests that the influence of rare species is a significant factor in the interpretation of the saturation process, as the sampling effort may create the pattern and the process explaining it, despite the qualitative analysis revealing this pattern of chewing lice in the neotropics, as reported by Lindell et al. (2002) and Clayton et al. (1992).

For both species of *Turdus*, the mean intensity of infestation of *Myrsidea* and *Brueelia* was highly variable, which resulted in an aggregated distribution, as reported in other studies of *Turdus* species (Wheller and Threlfall 1986; Lindell et al. 2002; Amaral, Bergmann, Santos, et al. 2013). Aggregated distributions have been observed in studies of parasites from vertebrates (Shaw and Dobson 1995; Poulin 2007b; Amaral, Bergmann, Silveira, et al. 2013), characterized by a pattern in which many hosts have a low parasite intensity and few with a high intensity of parasites.

The aggregate distribution of the most common species of lice also influenced the distribution of individuals between the sexes. In the present study, females were predominant as in other studies (Clayton et al. 1992; Rózsa et al. 1996; Lindell et al. 2002; Brooke 2010; Wheller and Threlfall 1986). According to Fisher (1930), the predominance of females is not expected in populations where mating is random, where we would rather expect an equal investment in males and females. According to Marshall (1981) the predominance of males is not expected, as they are smaller than females and are generally shorter-lived than females. On the other hand, the predominance of females may not be observed, due to their larger body size, which facilitates their capture by the host (Kim 1985).

We observed a higher number of nymphs compared with adults in only one infrapopulation of *Myrsidea* sp. from *T. rufiventris*. However, Saxena et al. (2007) observed a predominance of nymphs in nine of ten populations of chewing lice collected from four species of Passeriformes. The age structure of an ectoparasite population varies with the reproductive cycle of the ectoparasite (Marshall 1981): larger numbers of nymphs over adults would indicate an active reproduction period, while a reduced number or absence of nymphs would indicate a period of lower reproduction. Moreover, these differences observed in the patterns of sex ratio and age ratio of louse species may be correlated with the length of the breeding seasons of the host species (Forster 1969). In the present study both thrush species have the same reproductive period (September to January) (Sick 1997). Chewing lice might increase in abundance during host reproduction and moult because during these costly annual events, hosts might have less energy to devote to defensive physiology or preening behaviours (Møller and Rózsa 2005).

The intensity of chewing lice was correlated with *T. rufiventris* body length. Several studies have shown a relationship between host body parameter and the
intensity of parasites (Clayton 1991; Poulin and Rohde 1997; Rozsa 1997; Morand et al. 1999). Moreover, ecological factors or even physiological parameters could affect the abundance and richness of parasites in each host species (Lindell et al. 2002). Another factor that may explain the observed results concerns the great abundance of *T. rufiventris*, as registered by Gasperin and Pizo (2009) and Fontana (2004) in two distinct localities in the state of Rio Grande do Sul. Some studies investigating directly transmitted parasites have confirmed host density as significant predictor of parasite richness and abundance (Arneberg et al. 1998; Morand and Poulin 1998).

General patterns of chewing lice distribution and composition were analyzed, and differences were observed between the two *Turdus* species: the composition and community structure of the lice were similar on both host species, but not their infestation rates, which were higher in *T. rufiventris*. On this host species the importance of body length was also observed, suggesting that birds with longer body have a higher abundance of lice.

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**References**

Amaral HLC, Bergmann FB, Santos PRS, Krüger RF, Graciolli G. 2013. Community of arthropod ectoparasites of two species of *Turdus* Linnaeus, 1758 (Passeriformes: Turdidae) in southern Rio Grande do Sul, Brazil. Parasitol Res. 112:621–628. doi:10.1007/s00436-012-3174-5

Amaral HLC, Bergmann FB, Silveira T, Santos PRS, Krüger RF. 2013. *Pseudolynchia canariensis* (Diptera: Hippoboscidae): distribution pattern and phoretic association with skin mites and chewing lice of *Columba livia* (Aves: Columbidae). J Nat Hist. 47:2927–2936. doi:10.1080/00222933.2013.791939

Anderson RM, May RM. 1979. Population biology of infectious diseases: part I. Nature. 280:361–367. doi:10.1038/280361a0

Arneberg P, Skorping A, Grenfell B, Read AF. 1998. Host densities as determinants of abundance in parasite communities. Proc Royal Soc B Biol Sci. 265:1283–1289. doi:10.1098/rspb.1998.0431

Ash JS. 1960. A study of the Mallophaga of birds with particular reference to their ecology. Ibis. 102:93–110. doi:10.1111/j.1474-919X.1960.tb05095.x

Baldwin MJ, Barrow Jr WC, Jeske C, Rohwer FC. 2008. Metabolizable energy in chinese tallow fruit for yellow-rumped warblers, northern cardinals, and american robins. Wilson J Ornithol. 120:525–530. doi:10.1676/06-084.1

Barbosa A, Merino S, de Lope F, Moller AP. 2002. Effects of feather lice on flight behavior of male barn swallows (*Hirundo Rustica*). Auk. 119:213–216. doi:10.1642/0004-8038(2002)119[0213:EOFLOF]2.0.CO;2
Bartuszevige AM, Gorchov DL. 2006. Avian seed dispersal of an invasive shrub. Biol Invasions. 8:1013–1022. doi:10.1007/s10530-005-3634-2

Belton W. 1994. Aves do Rio Grande do Sul, distribuição e biologia. Porto Alegre (RS): Fundação Zoobotânica do Rio Grande do Sul.

Booth DT, Clayton DH, Block BA. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. Proc R Soc B: Biol Sci. 253:125–129. doi:10.1098/rspb.1993.0091

Brooke MDeL. 2010. Vertical transmission of feather lice between adult blackbirds Turdus merula and their nestlings: a lousy perspective. J Parasitol. 96:1076–1080. doi:10.1645/GE-2513.1

Bueter C, Weckstein J, Johnson KP, Bates JM, Gordon CE. 2009. Comparative phylogenetic histories of two louse genera found on Catharus thrushes and other birds. J Parasitol. 95:295–307. doi:10.1645/GE-1642.1

Bush AO, Lafferty KD, Lotz JM, Shostak AW. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol. 83:575–583. doi:10.2307/3284227

Castro DC, Cicchino AC. 1978. Contribucian al conocimiento de los malofagos argentinos III. Sobre algunos Menoponidae de la avifauna bonaerense: Menacanthus eurysternus (Burmeister) y Menacanthus pici (Denny) (Insecta: Mallophaga). Rev Soc Entomol Argent. 37:77–83.

Cicchino AC. 1986. Contribucio al conocimiento de los malofagos argentinos XIX. Cuatro nuevas especies del genero Brueelia Keler 1936 (Philopteridae) parasitas de especies de Turdus Linne 1758 (Aves, Passeriformes, Muscicapidae, Turdinae. Rev Soc Entomol Argent. 44:91–102.

Cicchino AC. 1987. Una nueva especie del género Brueelia Keller 1936 (Phthiraptera: Philopteridae) parásita de Turdus amaurochalinus Cabanis (Passeriformes: Muscicapidae. Spheniscus. 5:35–36.

Clayton DH. 1990. Mate choice in experimentally parasited rock doves: Louse males lose. Am Zool. 30:251–262.

Clayton DH. 1991. Coevolution of avian grooming and ectoparasite avoidance. In: Loy JE, Zuk M, editors. Bird-parasite interactions: ecology, evolution and behaviour. Oxford: Oxford University Press; p. 258–289.

Clayton DH, Gregory RD, Price RD. 1992. Comparative ecology of neotropical bird lice (Insecta: Phthiraptera). J Anim Ecol. 61:781–795. doi:10.2307/5631

Clayton DH, Lee PLM, Tompkins DM, Brodie ED. 1999. Reciprocal natural selection on host-parasite phenotypes. Amer Nat. 154:261–270.

Clayton DH, Moore J. 1997. Host-parasite evolution: general principles and avian models. New York (NY): Oxford University Press.

Clayton DH, Walther BA. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. Oikos. 94:455–467. doi:10.1034/j.1600-0706.2001.940308.x

Crawley MJ. 2007. The R book. Chichester: Wiley.

Dogiel VA. 1964. General parasitology. Edinburgh (TX): Oliver & Boyd.

Enout AMJ, Lobato DN, Azevedo CS, Antonini Y. 2009. Parasitismo por malófagos (Insecta) e ácaros (Acari) em Turdus leucomelas (Aves) nas estações reprodutivas e de muda de penas no Parque Estadual do Rio Preto, Minas Gerais, Brasil. Zoologia (Curitiba). 26:534–540. doi:10.1590/S1984-46702009000300017

Fisher RA. 1930. The genetical theory of natural selection. Oxford: Clarendon Press.

Fontana CS. 2004. Estrutura de uma comunidade urbana de aves: um experimento em Porto Alegre, Rio Grande do Sul [Ph.D. thesis]. Porto Alegre (RS): Universidade Federal do Rio Grande do Sul.

Forster MS. 1969. Synchronized life cycles in the orange-crowned warbler and its mallophagan parasites. Ecology. 50:315–323. doi:10.2307/1934858
Gasperin G, Pizo MA. 2009. Frugivory and habitat use by thrushes (Turdus spp.) in a suburban area in south Brazil. Urban Ecosyst. 12:425–436.

Gutián J, Bermejo T. 2006. Dynamics of plant-frugivore interactions: a long-term perspective on holly-redwing relationships in northern Spain. Acta Oecol. 30:151–160.

Halupka K, Greeney HF. 2009. Breeding biology of Pale-eyed thrushes (Turdus leucops) in the cloud forest of northeastern Ecuador. Ornitol Neotrop. 20:381–389.

IUCN. 2011. IUCN Red List of Threatened Species [Internet]. [cited 2011 Oct 12]. Available from: http://www.iucnredlist.org

Johnson KP, Clayton DH. 2003. The biology, ecology and evolution of chewing lice. In: Price RD, Hellenthal RA, Palma RL, Johnson K, Clayton DH, editors. The chewing lice: word checklist and biological overview. Champaign (IL): Illinois Natural History Survey Special Publication; p. 1–25.

Johnson KP, Shreve SM, Smith VS. 2012. Repeated adaptive divergence of microhabitat specialization in avian feather lice. BMC Biol. 10:52. doi:10.1186/1741-7007-10-52

Kidd H, James DR. 1991. The agrochemicals handbook. Cambridge: Royal Society of Chemistry Information Services.

Kim KC. 1985. Evolutionary relationships of parasitic arthropods and mammals. In: Kim KC, editor. Coevolution of parasitic arthropods and mammals. New York (NY): Wiley-Interscience Publications; p. 3–82.

Lindell CA, Gavin TA, Price RD, Sanders AL. 2002. Chewing louse distributions on two neotropical thrush species. Comp Parasitol. 69:212–217.

Marshall AG. 1981. The ecology of ectoparasitic insects. London: Academic Press.

Matthee S, McGeoch MA, Krasnov BR. 2010. Parasite-specific variation and the extent of male-biased parasitism: an example with a South African rodent and ectoparasitic arthropods. Parasitology. 137:651–660. doi:10.1017/S003118200991338

Møller AP, Rózsa L. 2005. Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. Oecologia. 142:169–176. doi:10.1007/s00442-004-1735-8

Morand S, Poulin R. 1998. Density, body mass and parasite species richness of terrestrial mammals. Evol Ecol. 12:717–727.

Morand S, Poulin R, Rohde K, Hayward C. 1999. Aggregation and species coexistence of ectoparasites of marine fishes. Int J Parasitol. 29:663–672. doi:10.1016/S0020-7519(99)00029-6

Moyer BR, Drown DM, Clayton DH. 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. Oikos. 97:223–228. doi:10.1034/j.1600-0706.2002.970208.x

Najmanová L, Adamík P. 2009. Effect of climatic change on the duration of the breeding season in three European thrushes. Bird Study. 56:349–356. doi:10.1080/00063650902937305

Palma RL. 1978. Slide-mounting of lice: a detailed description of the Canada Balsam technique. N Zeal Entomol. 6:432–436. doi:10.1080/00779962.1978.9722313

Poulin R. 2007a. Evolutionary ecology of parasites. Princeton (NJ): Princeton University Press.

Poulin R. 2007b. Are there general laws in parasite ecology? Parasitology. 134:763–776. doi:10.1017/S0031182006001210

Price RD, Hellenthal RA, Palma RL, Johnson KP, Clayton DH. 2003. The chewing lice: world checklist and biological overview. Champaign (IL): Illinois Natural History Survey.

R Development Team. 2009. R: a language and Environment for Statistical Computing. 2.8.1 edition. Vienna: R Foundation for Statistical Computing.
Reiczigel J, Rózsa L. 2005. Quantitative Parasitology 3.0 [Internet]. [cited 2012 Oct 07]. Available from: http://www.zoologia.hu/qp/qp.html

Rice WR. 1989. Analyzing tables of statistical tests. Evolution. 43:223–225. doi:10.2307/2409177

Rózsa L. 1997. Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). J. Avian Biol. 28:249–254. doi:10.2307/3676976

Rózsa L, Rékási J, Reiczigel J. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). J Anim Ecol. 65:242–248.

Saxena AK, Kumar S, Gupta N, Mitra JD, Ali SA, Srivastava R. 2007. Distribution pattern of phthirapterans infesting certain common Indian birds. J Parasitol. 93:957–958. doi:10.1645/GE-978R1.1

Shaw DJ, Dobson AP. 1995. Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology. 111:SS111–SS133. doi:10.1017/S0031182000075855

Sick H. 1997. Ornitologia Brasileira. Rio de Janeiro: Nova Fronteira.

Sim IMW, Burfield IJ, Grant MC, Pearce-Higgins JW, Brooke ML. 2007. The role of habitat composition in determining breeding site occupancy in a declining Ring Ouzel Turdus torquatus population. Ibis. 149:374–385. doi:10.1111/j.1474-919X.2007.00655.x

Tomlin CDS. 2006. The pesticide manual: a world compendium. Surry: British Crop Protection Council.

Tryjanowski P, Szczykutowicz A, Adamski Z. 2007. Size variation in chewing lice Docophorus coarctatus: how host size and louse population density vary together. Evol Ecol. 21:739–749. doi:10.1007/s10682-006-9148-2

Walther BA, Clayton DH. 1997. Dust-ruffling: a simple method for quantifying ectoparasite loads of live birds. J Field Ornithol. 68:509–518.

Wheeler TA, Threlfall W. 1986. Observations on the ectoparasites of some Newfoundland passerines (Aves: Passeriformes). Can J Zool. 64:630–636. doi:10.1139/z86-093