# Community of Chewing Lice (Phthiraptera: Amblycera and Ischnocera) Parasites of Resident Birds at the Archipelago of São Pedro and São Paulo in Northeast Brazil

H. M. SILVA,  $^{1,2}$  M. P. VALIM,  $^3$  and R. A. GAMA $^1$ 

J. Med. Entomol. 51(5): 941–947 (2014); DOI: http://dx.doi.org/10.1603/ME14094

ABSTRACT The current study describes the chewing lice community associated with seabird populations resident at the São Pedro and São Paulo Archipelago in the Atlantic Ocean in Pernambuco State, Brazil. Adults of three species of seabirds were captured using hand-nets for the collection of biometric data and specimens of ectoparasites. In total, 320 birds were examined (120 Sula leucogaster (Boddaert), Brown Booby; 120 Anous stolidus (L.), - Brown Noddy; and 80 Anous minutus Boie, Black Noddy) of which 95% were infested with 8,625 chewing lice, representing eight species of the genera Actornithophilus, Austromenopon, Eidmanniella, Pectinopygus, Quadraceps, and Saemundssonia. On S. leucogaster, Pectinopygus garbei (Pessôa & Guimarães) was more prevalent and had a mean and median intensity of infestation significantly greater than those recorded for Eidmanniella albescens (Piaget). On the two Noddies, the species of Actornithophilus and Quadraceps were significantly more prevalent and abundant than Austromenopon atrofulvum (Piaget) and Saemundssonia remota Timmermann Most of the louse species had a highly aggregated distribution, with k exponent of the negative binomial distribution ranging from 0.04 to 3.06. A weak but significant correlation was found between the abundance of chewing lice and morphometric variables (body weight, wing, beak, tail, and tarsus lengths). It is possible that high rates of infestation have a negative effect on the morphological characteristics of the hosts, including the health of the plumage. All the lice species collected—except for P. garbei (ex S. leucogaster)—were reported for the first time from Brazilian populations of these seabird species.

KEY WORDS Sula leucogaster, Anous minutus, Anous stolidus, ectoparasite, chewing louse

Chewing lice (Phthiraptera: Amblycera and Ischnocera) are ectoparasites associated with an enormous diversity of bird species worldwide (Johnson and Clayton 2003, Arzua and Valim 2010). These lice may be found typically on either the skin (Amblycera) or feathers (Ischnocera) of their avian hosts, but may also exploit other microhabitats, and complete their whole life cycle on the same host (Johnson and Clayton 2003). These insects feed on fragments of skin and feathers, and the blood that seeps from the wounds they provoke on the skin of their hosts (Wilson 1933, Johnson and Clayton 2003). Heavy infestation may lead to irritation of the skin, causing intense itching, skin ulcers, plumage defects, modifications of the voice, and even the abandoning of nests (Duffy 1994, Love and Carrol 1998, Johnson and Clayton 2003).

In Brazil, a growing number of studies have focused on the chewing lice associated with birds, although the vast majority of them have focused on terrestrial hosts (Oniki 1990, 1999; Marini et al. 1996; Roda and Farias 1999; Lyra-Neves et al. 2000, 2005; Enout et al. 2009, 2012). Inventories of the chewing louse parasites of seabirds have been published for a number of oceanic islands around the world (Palma and Horning 2002, Palma and Jensen 2005), including the Atlantic (Hänel and Palma 2007), although few studies are available for Brazilian seabird populations (Guimarães 1945, Valim et al. 2006).

The dynamics of chewing lice populations have been studied in a number of seabirds, focusing either on individual host species (Fowler et al. 1984, Fowler and Price 1987, Fowler and Hodson 1988, Fowler and Shaw 1990) or species groups (Eveleigh and Threlfall 1976, Fowler and Miller 1984, Choe and Kim 1988), primarily procellariiforms.

The São Pedro and São Paulo Archipelago (SPeSPA) is a group of six islets located in the Atlantic Ocean off northeastern Brazil, 100 km north of the equator (00° 55′ N, 29° 20′ W). This archipelago has resident populations of three seabird species, although it is visited sporadically by many bird species (Both and Freitas 2004). The three resident species are the Brown Noddy, *Anous stolidus* (L.), the Black Noddy, *Anous minutus* Boie, and the Brown Booby, *Sula leu*-

<sup>&</sup>lt;sup>1</sup> Departamento de Microbiologia e Parasitologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte (UFRN), Campus central, n° 3000, Lagoa Nova 59072-970, Natal, RN, Brasil.

<sup>&</sup>lt;sup>2</sup> Corresponding author, e-mail: honaramorgana@gmail.com.

 $<sup>^3\,\</sup>mathrm{Museu}$  de Zoologia, Universidade de São Paulo, Caixa Postal 42.494, 04218-970, São Paulo, SP, Brasil.

cogaster (Boddaert). These colonial species are found in large numbers on the archipelago, where they compete for the available nesting sites. Although the local avian fauna has been well-documented, virtually no data are available on their ectoparasites (Both and Freitas 2004).

Given the paucity of data on the ectoparasite fauna associated with Brazilian populations of seabirds, the current study provides data on the chewing lice species found in association with the resident seabird populations of the SPeSPA. Chewing lice community structure and population dynamics are discussed for the three host species.

### **Materials and Methods**

The SPeSPA is made up of a small group of rocky islets with a total surface area of  $17,000 \text{ m}^2$ , and a distance of 420 m between its outermost points. The climate is tropical oceanic, with negligible variation in temperature over the course of the year  $(26.0-28.7^{\circ}\text{C})$ . Data were collected every 6 mo between 2010 and 2012.

Only juvenile and adult seabirds not associated with nests were targeted for the current study. The birds were captured using hand-nets, and morphological data were collected using a spring balance and a set of calipers (Ecotone, Gdynia, Poland).

The study protocol was approved by the Brazilian Institute of Environment and Renewable Natural Resources, protocol 54628938 (07 January 2010). For the anesthesia and collection of parasites, the birds were placed individually in plastic bags (except for their heads) containing cotton wool soaked in ethyl acetate, using an approach adapted from Clayton and Walther (1997) and Arzua and Valim (2010). After 20 minutes, the feathers of the bird were ruffled manually to dislodge the ectoparasites, which were transferred to vials containing 70% ethanol for subsequent processing and identification. The breast feathers of each bird were marked with dye between the legs to ensure that they were not resampled during the same expedition.

In the laboratory, the lice were mounted on microscope slides following the protocol recommended by Palma (1978). The specimens were examined using a biological microscope, generic keys (Clay 1969, Price et al. 2003), and the literature available for the identification of species (Guimarães 1945; Timmermann 1952; Clay 1959, 1962; Ryan and Price 1969). The voucher specimens were deposited in the ectoparasite collection of the Zoology Museum of the University of São Paulo, and the remainder were deposited in the Adalberto Varela Freire entomological collection (under construction) at the Federal University of Rio Grande do Norte, Natal, Brazil.

The prevalence, mean, and median intensity of infestation (and their respective confidence intervals) were calculated for each species of chewing louse. The prevalence values were compared using chi-square, and differences between mean and median infestation intensities were compared using a bootstrap test and mood's median test, respectively (Reiczigel and Rósza

2005). The k exponent of negative binomial distribution was used to evaluate the frequency distribution of each chewing louse species in the community. Negative k values indicate a uniform distribution, whereas low positive values (k < 2) reflect a highly aggregated distribution, and values from 2 to 8 indicate moderate aggregation, and those >8 point to a random distribution of parasites in the community (Southwood 1978). Similar observed and expected frequencies—tested using chi-square—imply that the model is well-adjusted to the original data (Bush et al. 1997, Rózsa et al. 2000). All these analyses were run in the Quantitative Parasitology 3.0 software (Reiczigel and Rósza 2005). The sex ratio (males: females) and adult: immature ratio were also calculated (Marshall 1981).

The relationship between the morphological characteristics of the hosts (body weight, in grams; flat wing, beak, tail, and tarsus lengths, in millimeters) and the absolute abundance of the parasites was evaluated using Spearman or Pearson correlation coefficients, depending on the normality of the data. Initially, the relationship was tested for each species separately, and then for the community as a whole. Lastly, the coefficients were calculated for the two Noddy species together, with the objective of compensating for the possible underestimation of the infestation rates in S. leucogaster.

# Results

In total, 320 birds were examined: 120 S. leucogaster, 120 A. stolidus, and 80 A. minutus, of which 95% were infested with 8,625 chewing lice representing eight different species of the genera Actornithophilus, Austromenopon, and Eidmanniella (Amblycera, Menoponidae), and Pectinopygus, Quadraceps, and Saemundssonia (Ischnocera, Philopteridae). The Brown Boobies were infested by two species of lice—Eidmanniella albescens (Piaget) and Pectinopygus garbei (Pessôa and Guimarães)—represented by 1,805 individuals (Table 1).

A larger number of louse species were found on the two Noddies, which were very similar in terms of species richness and prevalence (Table 1). Overall, 112 of the 120 A. stolidus examined were infested by four louse species, Actornithophilus incisus Piaget, Quadraceps separatus (Kellogg & Kuwana), Austromenopon atrofulvum (Piaget), and Saemundssonia remota Timmermann. The latter two species also were found on A. minutus, in addition to Actornithophilus ceruleus (Timmermann) and Quadraceps hopkinsi (Timmermann) (Table 1).

In most cases, the sex ratio was close to one to one, except for the *Au. atrofuluum* specimens collected from *A. minutus* (2.75 males per female) and the *Sa. remota* collected from *A. stolidus* (0.32 males per female). The ratio between adults and immature of lice varied considerably from 1.07 adults per immature in the *Au. atrofuluum* specimens collected from *A. minutus* to18.5 adults per immature in the *Sa. remota* specimens collected from *A. stolidus* (Table 1).

Table 1.	Chewing lice associated with resident populations of $S$ . $leucogaster$ , $A$ . $minutus$ , and $A$ . $stolidus$ on the SPeSPA, Pernamb	ouco,
Brazil, exan	ned between July 2010 and July 2012	

Birds and their		Abundance		I	Ratio
chewing lice	Adults	Immature	Total	Male:female	Adult:immature
S. leucogaster					
E. albescens	345	182	527	0.92	1.90
P. garbei	795	483	1,278	1.17	1.65
A. minutus					
Ac. ceruleus	879	320	1,199	0.96	2.75
Au. atrofulvum	15	14	29	2.75	1.07
Q. hopkinsi	659	152	811	0.87	4.34
Sa. remota	6	2	8	1.00	3.00
A. stolidus					
Ac. incisus	2,210	724	2,934	1.14	3.05
Au. atrofulvum	134	48	182	0.72	2.79
Q. separatus	1,348	270	1,618	1.01	4.99
Sa. remota	37	2	39	0.32	18.50
Total	6,428	2,197	8,625	_	=

On S. leucogaster, the highest prevalence ( $\chi^2$  = 2.963; df = 1; P = 0.085) and intensity of infestation were recorded for P. garbei, although only mean (bootstrap test [t] = -4.895; P < 0.001) and median intensity (mood's median test [P] = 0.001) were significantly different in comparison with E. albescens (Table 2). On the Noddies, the highest prevalence  $(\chi^2 = 508.868; df = 7; P < 0.001)$  and intensity values (mood's median test [P] < 0.001; bootstrap test [P]<0.001) were recorded for species of the genera Actornithophilus and Quadraceps. The k parameter of the negative binomial distribution (Table 2) pointed a highly aggregated distribution for most chewing louse species among hosts (0 < k < 2), except for the two Actornithophilus species and Q. separatus, for which the k values between two and eight indicate a moderate degree of aggregation (Table 2; Fig. 1). The adjustment of the negative binomial distribution was statistically acceptable for all the species (Table 2).

In the correlation analysis, when each species was analyzed separately, morphological characteristics of the hosts (except tail length) presented some negative correlation with the abundance of chewing lice, and when all species were analyzed together was observed negative correlation with the five morphological mea-

surements (Table 3). When the *S. leucogaster* data were excluded from this analysis, however, a positive correlation between absolute abundance of chewing lice and all the morphological variables was found, except for tail length.

#### Discussion

The chewing lice species recovered from *S. leuco-gaster* had already been recorded for host populations from Florida, Panama, British West Indies, Java, Australia, and New Zealand (Ryan and Price 1969, Pilgrim and Palma 1982, Forrester et al. 1995, Murray et al. 2001). In Brazil, only *P. garbei* has been recorded parasitizing the Brown Booby in the southern states of São Paulo and Paraná (Guimarães 1945); with exception of *P. garbei*, all other chewing lice species were recorded on their respective hosts for the first time in Brazil.

Both louse species presented high infestation rates, but those of *P. garbei* were considerably higher than those recorded for *E. albescens*, although this may be at least partly related to the collection procedure, which may have favored the dislodging of the lice normally found on the feathers in comparison with

Table 2. Parasitological characteristics of the chewing louse community associated with the populations of three seabird species resident on the SPeSPA, Pernambuco, Brazil, examined between July 2010 and July 2012

Birds and their chewing lice	Prev	CI	MnT	Bootstrap CI	MdI	CI	k	$\chi^2$ (P)
S. leucogaster $(n = 120)$								
Eidmaniella albescens	86.7	79-92	5.03	4.25 - 6.12	4	3–5	1.21	0.23
Pectinopygus garbei	93.3	87-97	11.2	9.36-14.1	6	5-8	0.96	0.26
A. minutus $(n = 80)$								
Ac. ceruleus	100	95-100	15.0	12.9-17.4	13	10-15	2.62	0.61
Au. atrofulvum	15	8-25	2.42	1.42 - 4.17	1	1-4	0.11	0.80
Q. hopkinsi	95	88-99	10.7	8.79-13.2	9	6-10	1.35	0.89
Sa. remota	5	1-12	2.00	1.00 - 3.00	1	_	0.04	_
A. stolidus $(n = 120)$								
Ac. incisus	100	97-100	24.4	22.2 - 27.2	23	20-26	3.07	0.78
Au. atrofulvum	59.2	50-68	2.56	2.15 - 3.25	2	1-2	0.86	0.96
Q. separatus	99.2	95-100	13.6	11.9-15.3	12	11-15	2.09	0.58
Sa. remota	20.8	14-29	1.56	1.24-2.00	1	1-2	0.38	0.98

n, sample size (hosts); Prev, prevalence; MnI, mean intensity of infestation; MdI, median intensity of infestation; k, exponent of binomial distribution;  $\chi^2$  (P), adjustment of the data to a binomial distribution. CIs belong to the 95% probability.

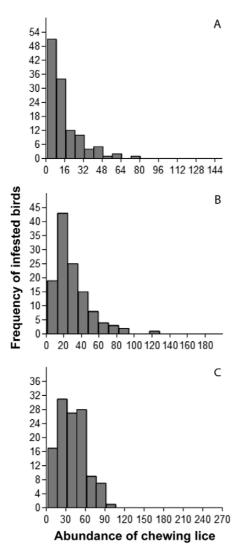


Fig. 1. Frequency of occurrence of chewing lice associated with the resident populations of three seabird species on the SPeSPA, Pernambuco, Brazil, examined between July 2010 and July 2012. (A) S. leucogaster (n=120), (B) A. minutus (n=80), and (C) A. stolidus (n=120). The x-axis represents the abundance of chewing lice per bird, and the y-axis represents the frequency of infested seabirds with this number of lice.

those, such as *E. albescens*, which are more typically found on the skin (Clayton and Walther 1997, Johnson and Clayton 2003).

Most S. leucogaster individuals were infested by both species (*P. garbei* and *E. albescens*), which represent the two different suborders (Amblycera and Ischnocera) of chewing lice. The prevalence of these two species did not vary significantly, although the mean and median intensity of infestation were significantly higher for *P. garbei*. However, the prevalence of 86.7% recorded for E. albescens was exceptionally high in comparison with available data on the infestation of seabirds by amblyceran lice, i.e., rates of 0.8-13.6% (Choe and Kim 1987, 1988; Fowler and Shaw 1990), except for the Common Guillemot, Uria aalge (Pontoppidan) (Charadriiformes, Alcidae), for which prevalence values of 72.4-91.6% have been recorded (Ballard and Ring 1979; Choe and Kim 1987, 1988). The mean intensity values recorded for E. albescens in the current study were also relatively high (Ballard and Ring 1979, Fowler and Miller 1984, Fowler and Shaw 1990), except for the studies of Choe and Kim (1987), who recorded a mean intensity of 5.5 for Austromenopon uriae Timmermann on U. aalge.

The prevalence of *P. garbei* recorded in the current study (93.3%) was nevertheless comparable with the values recorded for other ischnocerans, which generally have a prevalence of >75% (Ballard and Ring 1979; Choe and Kim 1987, 1988; Fowler and Miller 1984; Fowler et al. 1984; Fowler and Shaw 1990).

The marked similarities of the chewing lice fauna recorded on the two Noddy species is probably related to the morphological similarities of these sternids. In the SPeSPA, pairs of these two species generally build their nests on distinct islets, except in São Paulo, where they may compete for nesting sites, which possibly leads to the exchange of ectoparasites in SPeSPA (Both and Freitas 2004).

The Actornithophilus and Quadraceps species associated with the two Noddy species have been recorded previously for Anous (Hopkins and Clay 1952;

Table 3. Spearman  $(\rho)$  and Pearson (r) correlation coefficients for the relationship between the total abundance of chewing lice and morphological variables (weight, flat length of the left wing, beak, tail, and tarsus lengths) of *S. leucogaster* (n=120), *A. stolidus* (n=120), and *A. minutus* (n=80) on the SPeSPA, Pernambuco, Brazil, examined between July 2010 and July 2012

Correlation Coefficients Spearman $(\rho)$ and Pearson $(r)$	Weight	Wing length	Beak length	Tail length	Tarsus length
S. leucogaster					
ρ	-0.34	-0.12	-0.26	-0.01	-0.41
P	0.00	0.24	0.01	0.96	0.00
A. minutus					
ρ	-0.17	-0.25	-0.16	-0.16	-0.24
P	0.14	0.03	0.17	0.18	0.04
A. stolidus					
ρ	-0.32	0.19	-0.14	0.08	-0.10
P	0.00	0.07	0.18	0.45	0.32
Community					
r	-0.49	-0.39	-0.37	-0.15	-0.44
P	0.00	0.00	0.00	0.01	0.00
Anous spp.					
r	0.21	0.37	0.29	-0.00	0.21
P	0.00	0.00	0.00	0.96	0.00

P, probability level (significant in bold type).

Clay 1953, 1962; Price et al. 2003; Palma and Peck 2013). Au. atrofulvum has been recorded in A. minutus and Anous stolidus galapagensis Sharpe by Pilgrim and Palma (1982) and Palma and Peck (2013), who also recorded Sa. remota.

In both *Anous* species, the chewing lice communities consisted of two amblyceran (*Actornithophilus* and *Austromenopon*) and two ischnoceran (*Quadraceps* and *Saemundssonia*) species. As both amblycerans probably share the same skin-dwelling niche, a clear predominance of *Actornithophilus* over *Austromenopon* was recorded in the current study, and a similar relationship was observed between *Quadraceps* and *Saemundssonia*, although these latter two live on distinct body feathers on the host body.

The data available on prevalence in *Austromenopon* vary enormously, with values ranging from 1.25 to 91.6% (Eveleigh and Threlfall 1976; Ballard and Ring 1979; Choe and Kim 1987, 1988; Fowler and Shaw 1990; Fowler and Miller 1984). With the exception of the study of Fowler and Shaw (1990), however, the *Austromenopon* species was the only amblyceran in the community, coexisting with at least two ischnocerans.

A predominance of adults is a typical pattern in chewing louse populations, especially when the sampling procedure does not target nestling hosts, as in the current study. Lee and Clayton (1995) recorded a predominance of immature lice in the transmission between adults and nestlings, while in the juvenile birds, the louse populations generally undergo rapid expansion and results in the infestation of the adult birds with larger numbers of adults (Clayton et al. 1992). In general, then, there is a tendency for the proportion of adult lice to be higher in juveniles and adult birds in comparison with nestlings, although the reproductive seasonality of the lice also may be a factor. Previous studies have recorded adult: immature ratios of 0.90 for amblycerans and 0.56-0.75 for ischnocerans (Choe and Kim 1987, 1988), less than half the values recorded in the current study, i.e., 1.07-3.05 for amblycerans and 1.65-4.99 for ischnocerans (except Saemundssonia remota).

While exceptions have been recorded in some genera of chewing lice, a sex ratio of approximately one to one is typical in most ectoparasite populations. In the current study, a balanced sex ratio was recorded for the species with the largest samples (E. albescens, P. garbei, Actornithophilus spp., and Quadraceps spp.). Some studies (e.g., Marshall 1981) have found a predominance of females owing to the shorter life cycle and greater mobility of the males, which increases the probability of becoming detached from the host, although the results of the current study are only partially consistent with this. In S. leucogaster, more female amblycerans were collected than males, whereas male ischnocerans predominated. In contrast, a completely different situation was observed in the two Anous species. In A. stolidus, the sex ratio of the two dominant chewing louse species (Ac. incisus and Q. separatus) was biased toward males, whereas females prevailed in the nondominant species (Au. atrofulvum and Sa. remota).

Like other macroparasites, chewing lice form aggregated populations, with most hosts being infested with only small number of lice, whereas a minority of hosts present extremely high infestation rates (Rózsa et al. 1996, Clayton et al. 1999). The intensity of this distribution pattern may, nevertheless, be reduced in colonial hosts, where horizontal transmission is more common (Rózsa et al. 1996). In the current study, a highly aggregated distribution was found in most species, with a tendency for a negative binomial distribution, found in other studies of chewing lice associated with birds (Fowler and Miller 1984, Fowler and Price 1987, Fowler and Shaw 1990). The reasons for this pattern may be related to a number of factors, such as the seasonal variation in infestation rates, the nonrandom distribution of hosts in the environment, the possible development of resistance to infestation in infected hosts, in addition to the many nonrandom differences in the behavior and physiology of the different host species, including age-related variation (Fowler and Price 1987).

At a population level, negative relationships between morphological variables and the abundance of chewing lice may be accounted for by the debilitation of the individuals with a high parasite load (Johnson and Clayton 2003). Among other things, these individuals may present lower body weight and less healthy plumage in comparison with those with a lower parasite load. Observed variation in the parasite load may be related to a range of factors, including the body size of the host and its antiparasite preening behavior (Rózsa 1997, Clayton and Walther 2001, Hughes and Page 2007). In general, larger hosts provide a larger resource base and are longer-lived, resulting in a longer time period for infestation, while the antiparasite preening of birds with smaller beaks and tarsi may be more efficient (Rózsa 1997, Hughes and Page 2007). In the current study, the larger host the Brown Booby—not only presented a lower species richness of louse parasites, but also a reduced abundance of chewing lice. When this species was excluded from the community-level analysis, a significant positive relationship was found between all the morphometric variables (except for beak length) and the abundance of lice (Table 3). One possibility here is that the relatively large size of S. leucogaster, which complicated the handling of the specimens, may have reduced the effectiveness of the parasite sampling procedure.

A single bird may host as many as 20 species of chewing lice (Johnson and Clayton 2003). Once again, factors such as body size, morphological features related to preening, and host behavior, such as the formation of colonies, have been implicated in the variation found in species richness among hosts. However, there is no conclusive evidence on the influence of any of these factors on parasite species richness (see Clayton and Walther 2001, Hughes and Page 2007). In the current study, parasite community structure was similar in the two Noddy (*Anous*) species. The large number of individuals examined and the sampling procedures proved adequate for the analysis of ecto-

parasite community structure and the discussion of the factors that determine the assemblage rules in seabirds.

# Acknowledgments

We thank Mauro Pichorim for help in the identification of bird species; Liêvin Virgínio, Ivana Nicácio, and Luara Musse for their essential support in field work during collection. We also thank CNPq (557163/2009-9) and Marinha do Brasil for the technical and financial support. This study was also partially supported by the FAPESP-São Paulo Research Foundation (MPV: 2011/11420-5; 2012/06951-4).

## References Cited

- Arzua, M., and M. P. Valim. 2010. Bases para o estudo qualitativo e quantitativo de ectoparasitos em aves. pp 347–366. In S. Von Matter, F. Straube, Jr. J. F. Candido, V. Piacentini, I. Accordi (eds.), Ornitologia e conservação: ciência aplicada, técnicas de pesquisa e levantamento, Technical Books, Rio de Janeiro, RJ.
- Ballard, J. T., and R. A. Ring. 1979. The ectoparasites of some marine birds from Bamfield Marine Station, British Columbia with particular reference to the common murre, *Uria aalge* (Pont.). Can. J. Zool. 57: 1980–1984.
- Both, R., and T.O.R. Freitas. 2004. Aves marinhas no arquipélago de São Pedro e São Paulo. pp 193–212. *In J. O.* Branco (ed.), Aves marinhas e insulares brasileiras: bioecologia e conservação, Editora da Univali, Itajaí.
- 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. J. Parasitol. 83: 575–583.
- Choe, J. C., and K. C. Kim. 1987. Community structure of arthropod ectoparasites on Alaskan seabirds. Can. J. Zool. 65: 2998–3005
- Choe, J. C., and K. C. Kim. 1988. Microhabitat preference and coexistence of ectoparasitic arthropods on Alaskan seabirds. Can. J. Zool. 66: 987–997.
- Clay, T. 1953. Systematic notes on the Piaget collections of Mallophaga. - Part IV. Ann. Mag. Nat. Hist. 6: 641–657.
- Clay, T. 1959. A key to the species of Austromenopon Bedford (Mallophaga) parasitic on the Charadriiformes. Proc. R. Soc. Lond. B. Biol. Sci. 28: 157–168.
- Clay, T. 1962. A key to the species of *Actornithophilus* Ferris with notes and descriptions of new species. Bull. Br. Mus. (Nat. His.) Entomol. 11: 191–244.
- Clay, T. 1969. A key to the genera of the Menoponidae (Amblycera: Mallophaga: Insecta). Bull. Br. Mus. (Nat. His.) Entomol. 24: 3–26.
- Clayton, D. H., and B. A. Walther. 1997. Collection and quantification of arthropod parasites of birds. pp 419–440. In D. H. Clayton and J. Moore (eds.), Host-parasite evolution: general principles and avian models, Oxford University Press, Oxford, United Kingdom.
- Clayton, D. H., and B. A. Walther. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. Oikos 94: 455–467.
- Clayton, D. H., R. D. Gregory, and R. D. Price. 1992. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). J. Anim. Ecol. 61: 781–795.
- Clayton, D. H., P.L.M. Lee, D. M. Tompkins, and E. D. Brodie III. 1999. Reciprocal natural selection on hostparasite phenotypes. Am. Nat. 154: 261–270.
- Duffy, D. C. 1994. The guano islands of Peru: the once and future management of a renewable resource. pp 68-76. *In*

- D. N. Nettleship, J. Burger, and M. Goechfeld (eds.), Seabirds on Islands, Threats, case studies and action plans.
- Enout, A.M.J., D. N. Lobato, C. S. Azevedo, and Y. Antonini. 2009. Parasitismo por malófagos (Insecta) e ácaros (Acari) em *Turdus leucomelas* (Aves) nas estações reprodutiva e de muda de penas no Parque Estadual do Rio Preto, Minas Gerais, Brasil. Zool. (Curitiba, Impresso) 26: 534–540.
- Enout, A.M.J., D. N. Lobato, F. C. Diniz, and Y. Antonine. 2012. Chewing lice (Insecta, Phthiraptera) and feather mites (Acari, Astigmata) associated with birds of the Cerrado in Central Brazil. Parasitol. Res. 111: 1731–1742.
- Eveleigh, E. S., and W. Threlfall. 1976. Population dynamics of lice (Mallophaga) on auks (Alcidae) from Newfoundland. Can. J. Zool. 54: 1694–1711.
- Forrester, D. J., H. W. Kale II, R. D. Price, K. C. Emerson, and G. W. Foster. 1995. Chewing lice (Mallophage) from birds in Florida: a listing by host. Bull. Fla. Mus. Nat. His. 39: 1–44.
- Fowler, J. A., and C. J. Miller. 1984. Non-haematophagous ectoparasite populations of Procellariiform birds in Shetland, Scotland. Seabird 7: 23–30.
- Fowler, J. A., C. J. Miller, and S. Cohen. 1984. Ectoparasite populations from breeding and wandering Storm Petrels. Bird Study 31: 126–130.
- Fowler, J. A., and R. A. Price. 1987. A comparative study of the Ischnoceran Mallophaga of the Wilson's Petrel *Oce*anites oceanicus and British Storm Petrel *Hydrobates pe*lagicus. Seabird 10: 43–49.
- Fowler, J. A., and D. Hodson. 1988. The Mallophaga of Leach's Petrels *Oceanodroma leucorhoa* from North Rona, Scotland. Seabird 11: 47–49.
- Fowler, J. A., and G. J. Shaw. 1990. The Mallophaga of Manx Shearwaters *Puffinus p. puffinus* from Ynys Enlli, Wales. Seabird 12: 14–19.
- Guimarães, L. R. 1945. Sobre alguns ectoparasitos de aves e mamíferos do litoral Paranaense. Arq. Mus. Parana. 4: 179–190.
- Hänel, C., and R. L. Palma. 2007. The lice of the Tristan da Cunha Archipelago. Beitr. Entomol. 57: 105–133.
- Hopkins, G.H.E., and T. Clay. 1952. A checklist of the genera and species of Mallophaga. Trustees of the British Museum, London, p. 447.
- Hughes, J., and R.D.M. Page. 2007. Comparative tests of ectoparasite species richness in seabirds. BMC Evol. Biol. 7: 227.
- Johnson, K. P., and D. H. Clayton. 2003. The biology, ecology, and evolution of chewing lice. pp 449–476. In R. D. Price, R. A. Hellenthal, and R. L. Palma, K. P. Johnson, D. H. Clayton (eds.), The chewing lice: world checklist and biological overview. Illinois Natural History Survey Special Publication, IL.
- Lee, P.L.M., and D. H. Clayton. 1995. Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. Ecol. Entomol. 20: 43–50.
- Loye, J. E., and S. P. Carrol. 1998. Ectoparasite behavior and its effects on avian nest site selection. Ann. Entomol. Soc. Am. 91: 159–163.
- Lyra-Neves, R. M., A.M.I. Farias, W.R.T. Júnior, M.C.N. Botelho, and M.C.A. Lima. 2000. Ectoparasitismo em aves silvestres (Passeriformes- Emberizidae) de Mata Atlântica, Igarassu, Pernambuco. Melopsittacus 3: 64–71.
- Lyra-Neves, R. M., A.M.I. Farias, and W.R.T. Júnior. 2005. Interações entre Phthiraptera (Insecta) e aves (Emberizidae) de Mata Atlântica, Pernambuco, Brasil. Ornithol. 1: 43–47.

- Marini, M. A., B. L. Reinert, M. R. Bornschein, J. C. Pinto, and M. A. Pichorim. 1996. Ecological correlates of ectoparasitism on Atlantic Forest birds, Brazil. Ararajuba 4: 93–102.
- Marshall, A. G. 1981. The ecology of ectoparasitic insects. Academic, London, United Kingdom, p. 459.
- Murray, M. D., R. L. Palma, R. L. C Pilgrim, and M. Shaw. 2001. Appendix 1: Ectoparasites of Australian, New Zealand & Antarctic birds. pp. 1261–1263. *In S. Marchant and P. J. Higgins (eds.)*, Handbook of Australian, New Zealand & Antarctic Birds, CSIRO, Melbourne VIC, Australia.
- Oniki, Y. 1990. Survey of lice (Mallophaga) and some remarks on their life cycles on birds at Balbina, Amazonas, Brasil. Rev. Bras. Biol. 50: 615–617.
- Oniki, Y. 1999. Avian parasites and notes on habits of lice from Mato Grosso, Brazil. Iheringia. Ser. Zool. 86: 183– 190
- Palma, R. L. 1978. Slide-mounting of Lice: a detailed description of the Canada Balsan technique. N. Z. Entomol. 6: 432–436.
- Palma, R. L., and D. S. Horning. 2002. The lice (Insecta: Phthiraptera) from Macquarie Island. ANARE Res. Notes 105: 1–27.
- Palma, R. L., and J. Jensen. 2005. Lice (Insecta: Phthiraptera) and their host associations in the Faroe Islands. Steenstrupia 29: 49-73.
- Palma, R. L., and S. B. Peck. 2013. An annotated checklist of parasitic lice (Insecta: Phthiraptera) from the Galápagos Islands. Zootaxa 3627: 1–87.
- Pilgrim, R.L.C., and R. L. Palma. 1982. A list of the chewing lice (Insecta: Mallophaga) from birds in New Zealand National Museum of New Zealand (Miscellaneous Series), Wellington J. 6: 1–32.

- Price, R. D., R. A. Hellenthal, R. L. Palma, K. P. Johnson, and D. H. Clayton. 2003. The chewing lice: world checklist and biological overview. Ill. Nat. His. Surv. 24: 1–501.
- Reiczigel, J., and L. Rózsa. 2005. Quantitative Parasitology 3.0. Budapest.
- Roda, S. A., and Â.M.I. Farias. 1999. Aves silvestres infestadas por Phthiraptera (Insecta) na Zona da Mata Norte de Pernambuco, Brasil. Rev. Bras. Zool. 16: 871–878.
- Rózsa, L. 1997. Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). J. Avian Biol. 28: 249–254.
- Rózsa, L., J. Rékási, and J. Reiczigel. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). J. Anim. Ecol. 65: 242–248.
- Rózsa, L., J. Reiczigel, and G. Majoros. 2000. Quantifying parasites in samples of hosts. J. Parasitol. 86: 228–232.
- Ryan, S. O., and R. D. Price. 1969. A review of the genus Eidmanniella (Mallophaga: Menoponidae) from the Pelecaniformes. Ann. Entomol. Soc. Am. 62: 815–823.
- Southwood, R. 1978. Ecological Methods. Wiley, New York, NY, p. 575.
- Timmermann, G. 1952. Revision der bei Seeschwalben schmarotzenden Kletterfederlinge der Gattung Quadraceps (Clay u. Meinertzhagen). Zool. Anz. 148: 71–87.
- Valim, M. P., M. A. Raposo, and N. M. Serra-Freire. 2006. Associations between chewing lice (Insecta: Phthiraptera) and albatroses and petrels (Aves, Procellarii-formes) collected in Brazil. Rev. Bras. Zool. 23: 1111–1116
- Wilson, F. H. 1933. A louse feeding on the blood of its host. Science 77: 490.

Received 27 May 2014; accepted 27 June 2014.