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Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera)

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Summary

1. Data are presented comprising the first quantitative survey of lice from Neotropical birds. The data were collected in the Andean foothills of south-eastern Peru using a novel scheme for quantitative sampling of ectoparasites from freshly killed hosts.

2. In total, 685 birds representing 127 species in 26 families were sampled for lice; 327 (47·7%) birds were parasitized, with a mean intensity of 6·6 lice per bird and a mean richness of 1·1 louse species per host species.

3. The bulk of variation in louse load was among host species nested within genera, although some variation occurred at higher taxonomic levels.

4. Lice were extremely host-specific; nearly all species were restricted to a single species of host (monoxenous).

5. Thirteen metapopulations of lice (10%) had significantly skewed sex ratios, of which four were skewed toward males, representing the first male-biased sex ratios reported for chewing lice. Thirty-four metapopulations (27%) had significantly skewed age ratios and showed an overall bias toward adults.

6. Results are discussed in relation to current life-history theory and are compared with the findings of a recent survey of lice from temperate-zone birds. Tropical lice are neither more speciose nor more abundant than temperate-zone lice, which is consistent with the view that the environment for chewing lice is delimited by the body of the host rather than by 'external' conditions.

7. Non-quantitative host–parasite records are reported for lice collected from an additional 75 birds representing 45 species in 20 families.

Key-words: birds, comparative, ecology, lice, tropical.

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Introduction

Host–parasite interactions are powerful arenas for ecological studies, particularly in the case of 'continuous' parasites that complete their entire life cycle on the host (Dogiel 1964). Because resources for continuous parasites are delimited chiefly by the host, factors governing their ecology may be easier to identify than factors governing the ecology of free-living organisms in more complicated environments (Price 1980). Comparative studies of continuous parasites can help to identify such factors (Holmes & Price 1986; Price 1990). Two general comparative approaches are possible: (i) comparison of similar parasites on different host taxa; and (ii) comparison of different parasites on the same host.

In this paper, we perform both kinds of comparisons using data on the relative abundance and life history of avian chewing lice (Insecta: Phthiraptera (formerly Mallophaga)). Firstly, we present original data comprising the first quantitative survey of lice from Neotropical birds. Second, we compare the richness, prevalence and intensity of lice recovered from a variety of host taxa. Third, we compare the host specificity, number, sex ratio and age distribution of the major suborders of chewing lice across all hosts. Finally, we compare our results with those of a recent quantitative survey of lice from temperate-zone birds (Wheeler & Threlfall 1986).

Chewing lice are continuous ectoparasites that rely on the warmth and humidity of the host's body for reproduction. They seldom leave the host except to transfer between parents and their offspring, or

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during other instances of direct contact. The life cycle requires 3–4 weeks and includes the egg (= nit), three nymphal instars and the adult stage (Marshall 1981a). Eggs are glued to the feathers with a glandular cement, often in positions protected from preening, the primary defence of the host against lice (Waage 1979; Clayton 1991).

Avian chewing lice are divided into the suborders Ischnocera and Amblycera. Ischnocera feed exclusively on feathers and dermal debris, which they metabolize in the presence of symbiotic bacteria (Eichler *et al.* 1972; Marshall 1981a). Ischnocera are morphologically specialized for locomotion on feathers and rarely if ever venture onto the skin of the host. In contrast, Amblycera are more agile and occur on the skin as well as the feathers and feed on both feathers and blood (Ash 1960; Marshall 1981a). Amblycera are capable of abandoning a dying host and so may be less dependent than Ischnocera on direct contact between hosts for transmission.

Members of both suborders have the potential to reduce host fitness. Feather damage by Ischnocera impairs the thermoregulatory ability and winter survival of wild hosts (Clayton 1989; Clayton, Booth & Block, unpublished) and reduces the ability of captive hosts to attract mates (Clayton 1990a). Amblycera promote dermatitis and scratching and are responsible for serious reductions in the egg production of poultry (DeVaney 1976; Nelson *et al.* 1977). Amblycera also serve as intermediate hosts for endoparasites (reviewed by Clayton 1990a).

Materials and methods

Data were collected between August and December 1985 at several localities in the Andean foothills of south-eastern Peru near Parque National del Manu (11°54′S, 71°18′W). Most of the collecting localities were situated in primary rain forest. Birds were collected by shooting or with mist nets; netted birds were killed humanely upon removal from the net. Freshly killed birds were placed in individual paper bags which were rolled shut to prevent ectoparasites from transferring between hosts. Each bird was later fumigated for at least 10 min in a plastic chamber containing cotton soaked in ethyl acetate, which kills ectoparasites rapidly. Following fumigation, birds were 'quantitatively' or 'qualitatively' sampled for lice, as described below. All sampling was done by a single person (D.H.C.).

Two methods of quantitative sampling were used: feather agitation and visual examination. Most species were sampled by feather agitation, as follows. The host was removed from the fumigation chamber and suspended over a sheet of 28 × 38 cm white paper. Its feathers were agitated vigorously for a period of 1 min, with attention directed to all regions of the body (see Fig. 14.5 in Clayton 1991). Lice falling onto the paper during agitation were located under a 2× jeweller's headset and transferred to a vial of 70% ethyl alcohol with a fine-tipped brush. This procedure was repeated for two additional 1-min bouts. If no lice were recovered during the three bouts, no further attempt was made to sample lice from the host. If lice were recovered, additional 1-min bouts were conducted until the number of lice collected during a single bout was less than 5·0% of the total number recovered during the first three bouts. Thus, the decision to stop sampling a given host was based on the recovery rate from that host. This approach presumably gives a more accurate estimate of louse load than when hosts are sampled for an arbitrary period of time.

A second method of quantitative sampling was used in the case of extremely small birds (<25 g) for which feather agitation was awkward. Members of the Trochilidae, *Pipra* spp., *Tangara* spp. and *Stelgidopteryx ruficollis* were sampled by carefully examining their plumage for at least several minutes under the headset with illumination from a headlamp. Lice were removed from the plumage with forceps and transferred to a vial of 70% ethyl alcohol.

Some species of hosts were less carefully examined for lice, with no attempt being made to examine all of their feathers. Lice from these 'qualitatively' sampled species were collected mainly for taxonomic purposes.

Once sampled, hosts were prepared as museum specimens and deposited in the bird collection of the Field Museum of Natural History in Chicago (accession numbers 320356-324105). Lice were mounted on microslides, identified to the most specific taxon possible, sexed, aged and deposited in the insect collection of the Field Museum (accession card Z-17-561). No attempt was made to distinguish among unidentified lice. Host names follow Sibley & Monroe (1990) and the sequence of hosts follows Sibley & Ahlquist (1990).

In this paper, 'load' is used in a generic sense encompassing three explicit measures of the abundance of lice among the members of a given host taxon. 'Richness' is the number of species of lice on a host taxon (unidentified lice were counted as an additional species, e.g. if a host had one identified species, as well as lice that could not be identified, it was given a richness score of 2). 'Prevalence' is the proportion of the members of a taxon infested with lice. 'Intensity' is the *mean* number of lice among the members of a host taxon, including uninfested individuals (analogous to 'relative abundance' of Margolis *et al.* (1982)).

Host specificity — the range of host taxa infested by a given louse taxon — was scored on the basis of categories in Marshall (1981a): 1, infesting a single host species (monoxenous); 2, infesting two or more congeneric host species (oligoxenous); 3, infesting two or more confamilial host genera (pleioxenous); or 4, infesting two or more host families (polyxenous). The lower the rank, the more specific the louse.

'Population' refers to conspecific lice living on a single host individual. 'Metapopulation' refers to conspecific lice living among the individuals of a host population. For the purposes of this paper, lice identified only to genus were considered to represent different metapopulations if collected from different host taxa. Although congeners from different host taxa may eventually prove to be conspecific, they can be viewed as distinct metapopulations because direct contact between hosts, upon which lice depend for transmission, rarely occurs between different host taxa.

Results

A total of 685 birds representing 127 species in 26 families was sampled quantitatively for a total of 4544 lice (see Appendix 1). Of these, 93% (4208), representing 125 metapopulations, were identified at least to genus for a total of 36 genera. The mean host specificity score for these genera was 2·3 (range = 1–4). Forty-two metapopulations of lice could be identified to species for a total of 41 species. The mean host specificity for these species was 1·0 (range = 1–2). The mean richness was 1·1 species of louse per species of host (range = 0–6). Of the individual birds sampled, 327 (47·7%) were parasitized, with an average intensity of 6·6 lice per bird.

The overall sex ratio of lice from quantitatively sampled hosts was female-biased (1124 males: 1350 females; df = 1, $\chi^2 = 20{\cdot}65$, $P < 0{\cdot}0001$). The sex ratios of 13 of the 125 metapopulations (10%) were significantly skewed, of which nine (69%) were female-biased and four (31%) were male-biased (Appendix 1).

The overall age ratio of lice from quantitatively sampled hosts was adult-biased (2474 adults: 1662 immatures; df = 1, $\chi^2 = 159{\cdot}42$, $P < 0{\cdot}0001$). The age ratios of 34 metapopulations were significantly skewed, of which 27 (79%) were adult-biased and 7 (21%) were biased in favour of immatures (Appendix 1) ($\chi^2 = 11{\cdot}76$, $P < 0{\cdot}0006$).

A total of 75 birds representing 45 species in 20 families was sampled qualitatively for lice (Appendix 2). The analyses which follow are based solely on data from Appendix 1.

Comparisons among host taxa

Most of the variation in louse load (richness, prevalence and intensity) among host taxa was accounted for at the level of species nested within genera (Table 1). None of the variation was explained at the level of genera nested within families. Families nested within orders accounted for the next greatest amount of variation and orders within Aves accounted for the least.

Comparisons between louse suborders

Sixty-two metapopulations of lice (in 19 genera) were Ischnocera; 63 metapopulations (in 17 genera) were Amblycera. Nineteen of the former and 22 of the latter were identified to species (Appendix 1). The host specificity scores of the suborders were similar, whether calculated at the level of genus or species (Table 2).

Ischnocera and Amblycera were similar in richness (Table 2); however, the average prevalence of Ischnocera was marginally higher than that of Amblycera, and the average intensity of the former was much higher than that of the latter.

Ischnocera and Amblycera had similar sex ratios (Table 2), but of the 13 metapopulations with significantly skewed ratios (Appendix 1), ischnocerans tended to be female-biased (7 of 8 cases), whereas amblycerans tended to be male-biased (3 of 4 cases). Ischnocera and Amblycera also had similar age ratios (Table 2). Of the 34 metapopulations with significantly skewed ratios (Appendix 1), 22 were Ischnocera and 12 were Amblycera, a non-significant difference (df = 1, $\chi^2 = 2{\cdot}94$, $P = 0{\cdot}09$).

Discussion

Although several broad, quantitative surveys of bird lice have been conducted (Geist 1935; Ash 1960; Keirans 1967; McClure & Ratanaworabhan

Table 1. Distribution of variance in louse load among bird taxa. Tabulated values are percentages of total variance accounted for at successive taxonomic levels, estimated from nested ANOVAS performed on louse richness, prevalence and intensity scores for 127 species of birds (Appendix 1). This approach partitioned the total variation in louse load into components representing the taxonomic levels: species within genera, genera within families, families within orders, and orders within the class Aves (after Harvey & Pagel 1991)

Among: Within:	Species Genera	Genera Families	Families Orders	Orders Class
Variance component:	σ^2 s(g)	σ^2 g(f)	σ^2 f(o)	σ^2 o(c)
Richness*	78	0	14	8
Prevalence†	76	0	15	9
Intensity*	65	0	27	8

Data were * logarithmically $(x+1)$ or † square-root transformed prior to analysis.

Table 2. Comparisons between louse suborders

Variable	Suborder	N	Mean	$z^{\dagger}$	P
Specificity of genera	Ischnocera	19	2·3		
	Amblycera	17	2·2	−0·10	0·92
Specificity of species	Ischnocera	19	1·0		
	Amblycera	22	1·0	−0·79	0·43
Richness	Ischnocera	54*	1·1		
	Amblycera	51*	1·2	−0·69	0·49
Prevalence	Ischnocera	62‡	74·4		
	Amblycera	63‡	61·7	−1·94	0·05
Intensity	Ischnocera	62‡	17·5		
	Amblycera	63‡	6·3	−4·11	<0·0001
Percentage males	Ischnocera	62‡	41·4		
	Amblycera	63‡	40·9	−0·41	0·68
Percentage immatures	Ischnocera	62‡	34·5		
	Amblycera	63‡	36·8	−0·05	0·96

† Mann-Whitney *U*.
* Number of infested host species.
‡ Number of metapopulations.

1972; Wheeler & Threlfall 1986), this study is the first such survey of lice from Neotropical birds. Only one other study, the Wheeler & Threlfall (1986) survey of lice on 17 species of Newfoundland passerines, provides sufficiently detailed results for comparison with our own. To make such comparisons we have calculated indices of specificity and abundance (see Methods) using the data presented in Wheeler & Threlfall (Table 3).

The average richness, prevalence and intensity of lice in the Wheeler & Threlfall survey were similar to our respective values (Table 3), suggesting that lice on tropical birds are neither more speciose nor more abundant than lice on temperate birds. This result is consistent with the view that the environment for chewing lice is delimited by the body of the host rather than by 'external' conditions. This view, in turn, suggests that the high diversity of tropical lice is chiefly due to the high diversity of tropical hosts (Dobzhansky 1950).

The lice in our survey were more host-specific than those in the Wheeler & Threlfall survey both at the level of genus and species (Table 3). The greater host specificity of lice in our study is probably an artefact of the poor state of Neotropical louse taxonomy. Modern taxonomic revisions reveal excessive 'splitting' of chewing lice by early taxonomists, who tended to rely on the assumption that specimens collected from different species of hosts must themselves be different. Fewer tropical than temperate lice have been the subject of modern taxonomic study, partly due to an acute shortage of specimens. It is likely that future revisions will reveal that many Neotropical taxa are less host-specific than is implied by their current taxonomy (e.g. see Price & Clayton, in press). It is interesting to note, in this regard, that *Strigiphilus crucigerus*, the only species collected by us from more than one species of host (Appendix 1), is a member of one of the only recently revised genera of lice represented in this survey (Clayton 1990b).

The overall proportion of male lice in our survey was similar to that reported by Wheeler & Threlfall (Table 3), who noted: 'Among adult lice females were more numerous than males in almost all species.' Unfortunately, the authors did not report

Table 3. Comparisons between tropical and temperate lice

Variable	Peru (n)	Newfoundland*(n)
Mean specificity of genera	2·3 (36)	3·5 (6)
Mean specificity of species	1·0 (41)	2·2 (6)
Mean richness	1·1 (127)†	1·2 (17)†
Overall prevalence	47·7 (685)‡	41·0 (144)‡
Mean intensity	6·6 (685)‡	6·9 (144)‡
Percentage males	45·4 (2474)§	33·7 (584)§
Percentage immatures	40·0 (4136)#	41·5 (998)#

* Wheeler & Threlfall (1986).
† Number of host species.
‡ Number of host individuals.
§ Number of adult lice.
\# Number of aged lice.

how many of their species had *significantly* skewed sex ratios. Marshall (1981b) reported significantly skewed ratios in 17 of 30 species (57%) for which he could locate data on at least 100 adult specimens. Of the three metapopulations in our study meeting this criterion (Appendix 1), two (67%) had skewed sex ratios. However, of the 12 metapopulations with at least 50 adults, only three (25%) had skewed ratios. This result suggests that relatively large samples of lice may be required to estimate the frequency of skewed sex ratios with accuracy. The small proportion of total metapopulations with skewed sex ratios (13 of 125 (10%)) is to some extent an artefact of the large number of metapopulations for which too few lice were collected to reveal potential skew (66 of 125 (53%) were represented by ≤5 adult lice).

None of the sex ratios reported by Marshall (1981b) were significantly male-biased, whereas four of 13 biased ratios in our study were skewed toward males (Appendix 1). To our knowledge, these are the first significantly biased male sex ratios reported for chewing lice. Two cases involved *Myrsidea*, the only genus found to contain more males than females in the Wheeler & Threlfall survey. Sex ratios are discussed in more detail below.

The overall proportion of immature lice in our study was similar to that reported in the Wheeler & Threlfall study (Table 3), which provided no additional data on age structure. Thirty-four (27%) of the 125 metapopulations of lice in our study had skewed age ratios (Appendix 1), with a significant tendency toward an adult bias. Marshall (1981a) suggests: '. . . age structure will depend upon whether the population is increasing, when there will be relatively fewer adults, is stable, or decreasing, when there will be relatively more adults.' To test Marshall's suggestion, which refers to the relative number of adults over time, requires longitudinal sampling of a metapopulation's age structure. Because we did not perform longitudinal sampling, we are unable to draw firm conclusions about metapopulation dynamics from our data on age structure.

Comparisons among host taxa

The greatest variance in all three measures of louse load occurred among host species nested within genera (Table 1), indicating that many congeneric hosts harboured loads as variable as those of hosts from different genera, families and orders (Appendix 1). This result contrasts with the results of some other studies of the distribution of variance among taxonomic levels. For example, Read & Harvey (1989) showed that the greatest variance in life-history traits of placental mammals, such as body weight, gestation length and fecundity, occurs among higher taxonomic levels, particularly among orders nested within Mammalia.

Of the variation in louse load present at higher taxonomic levels in our study, the most pronounced was among host families nested within orders, especially in the case of louse intensity. For example, Trochilidae (hummingbirds) harboured an average intensity of 0·22 lice per bird, whereas Ramphastidae (toucans/barbets) harboured an average intensity of 17·7, Fringillidae (finches and allies) 28·8 and Formicariidae (ground antbirds) 49·0 lice per bird. Reasons for among-host variation in louse intensity or other measures of load are poorly understood. We have examined such variation in detail elsewhere (R.D. Gregory & D.H. Clayton, unpublished), including parameters of host morphology, ecology and behaviour that may govern louse load.

Comparisons between louse suborders

Although ischnocerans are generally regarded as more host-specific than amblycerans (Marshall 1981a), we found no significant difference in the specificity of members of the two suborders at the level of either genus or species (Table 2). As suggested earlier, this result may be an artefact of the paucity of taxonomic work on Neotropical lice. Modern taxonomic revisions indicate that early taxonomists described relatively more synonymous species of Amblycera than Ischnocera, thus exaggerating the host specificity of the former. For example, Nelson & Price (1965) recognized only four of 36 former species of the amblyceran genus *Laemobothrion*, and Price (1975) synonymized 36 names in a redescription of the single amblyceran species *Menacanthus eurysternus*. In contrast, Price & Clayton (1983) recognized 11 of 12 species of the ischnoceran genus *Psittaconirmus*, and Clayton & Price (1984) recognized 21 of 28 former members of the ischnoceran genus *Strigiphilus*. Future revisions may reveal that Neotropical Amblycera are less host-specific than our results would suggest.

Ischnocera and Amblycera did not differ in richness, but the prevalences and intensities of the two suborders were different (Table 2). The significant difference in intensity occurred both when intensity was calculated across all individuals sampled for lice, as well as when it was calculated across infested individuals only (analogous to 'mean intensity' of Margolis *et al.* 1982). This second approach eliminates the possibility that some hosts have low intensities merely because they have not been exposed to lice. By controlling for exposure, this approach is more likely to reveal parameters of the host itself which are responsible for the subordinal difference in intensity.

The different prevalences and intensities of Ischnocera and Amblycera were related to the uneven distribution of the two suborders with respect to host body size. Species of hosts parasitized exclusively by Ischnocera ($n = 29$) were large in size, compared to species parasitized exclusively by

Amblycera ($n = 27$; Mann-Whitney U, $z = -2{\cdot}96$, $P = 0{\cdot}003$). Furthermore, the significant difference in the intensities of the two suborders was removed when the analysis was restricted to species of hosts infested with *both* suborders ($n = 25$; $z = -1{\cdot}65$, $P = 0{\cdot}10$). Hence, the subordinal difference in intensity can be attributed to the fact that 'Amblycera-only' taxa tended to be small-bodied, whereas 'Ischnocera-only' taxa tended to be large-bodied. We address the issue of host body size and louse load in more detail elselwhere (R.D. Gregory & D.H. Clayton, unpublished).

Ischnocera had more female-biased sex ratios (seven of eight cases), whereas Amblycera had more male-biased ratios (three of four cases). Female-biased ratios should evolve in isolated populations subject to inbreeding and local mate competition, which arises when relatively few males are required to fertilize all of the females in a population (Hamilton 1967; Charnov 1982). Under such conditions, the production of females is selectively favoured because eggs are more limited than sperm. Recent studies show that populations of Ischnocera on different host individuals are genetically isolated (Nadler & Hafner 1989, 1990). Thus, ischnoceran populations appear to be excellent candidates for the evolution of female-biased sex ratios.

Female-biased ratios are not expected in populations where mating occurs more or less at random. Fisher (1930) argued that in such cases parents should invest equally in male and female offspring, with the result that sex ratios will be skewed in favour of the sex which is least expensive to produce. Most species of chewing lice have males which are only two-thirds are large as females, suggesting that the former may cost less to produce than the latter. If this assumption is correct, it would accord with the existence of male-biased sex ratios in more or less randomly mating populations of chewing lice. Random mating is more likely to be the case for Amblycera than Ischnocera, given the ability of the former to disperse more easily than the latter (see Introduction). This is a possible explanation for the male-biased metapopulations in our study, most of which were members of the Amblycera.

Additional quantitative data are required before the above hypothesis, and others, can be tested. Large samples of lice are needed to facilitate accurate estimation of life-history parameters. Smaller samples of lice from a wide variety of hosts are also required to enable taxonomists to conduct sorely needed revisions. Ecological studies of chewing lice are particularly sensitive to the mistakes of past taxonomists, who tended to classify lice on the basis of host classification, rather than on the basis of the lice themselves (Hafner & Nadler 1990). Only through the concerted efforts of ecologists and taxonomists are we likely to achieve a better understanding of the population biology of chewing lice.

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Appendix 1

Lice from quantitatively sampled birds

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Piciformes						
Picidae (woodpeckers)						
Campephilus rubricollis (Boddaert 1783) (1)	0	–	–	–	–	–
Celeus grammicus (Natterer and Malherbe 1845) (5)	100	*Picicola* sp.[†]	9	3	21	0
Colaptes punctigula (Boddaert 1783) (1)	0	–	–	–	–	–
Melanerpes cruentatus (Boddaert 1783) (2)	50	*Myrsidea* sp.*	0	0	1	0
Piculus leucolaemus (Natterer and Malherbe 1845) (1)	100	*Penenirmus* sp.[†]	0	1	0	0
Piculus rubiginosus (Swainson 1820) (2)	100	*Menacanthus* sp.*	0	1	0	0
		Penenirmus auritus (Scolopi 1763)[†‡]	4	13	13	0
		Picicola sp.[†]	2	2	2	0
Picumnus aurifrons Pelzeln 1870 (4)	75	*Penenirmus* sp.[†]	4	3	3	0
Picumnus rufiventris (Bonaparte 1838) (7)	0	–	–	–	–	–
Picumnus subtilis (Stager 1968) (1)	0	–	–	–	–	–
Veniliornis affinis (Swainson 1821) (3)	100	*Penenirmus* sp.[†]	5	7	6	0
Veniliornis passerinus (Linnaeus 1766) (1)	0	–	–	–	–	–
Ramphastidae (toucans/barbets)						
Aulacorhynchus derbianus Gould 1835 (2)	100	*Austrophilopterus microgaster* Carriker 1950[†§]	35	42	132	0
Aulacorhynchus prasinus (Gould 1834) (1)	0	–	–	–	–	–
Capito niger (Muller 1776) (3)	67	*Myrsidea* sp.*	0	0	1	0
		Penenirmus sp.[†]	2	2	1	0
Eubucco richardsoni (Gray 1846) (3)	100	*Menacanthus eurysternus* (Burmeister 1838)*[‡,§]	5	21	49	0
		Penenirmus sp.[†]	0	4	4	0
Eubucco versicolor (Muller 1776) (3)	0	–	–	–	–	–
Pteroglossus beauharnaesii Wagler 1832 (2)	100	*Austrophilopterus* sp.[†]	2	2	4	0
		Myrsidea sp.*	2	0	1	0
Pteroglossus castanotis Gould 1854 (1)	100	*Myrsidea* sp.*	0	1	0	0
Pteroglossus mariae Gould 1854 (5)	60	*Myrsidea dorotheae* Eichler 1953*	0	0	4	0
Selenidera reinwardtii (Wagler 1827) (13)	100	*Austrophilopterus* sp.[†]	19	21	45	60
		Unidentified	0	0	0	89
Galbuliformes						
Galbulidae (jacamars)						
Galbula cyanescens Deville 1849 (4)	50	*Picicola* sp.[†]	1	2	1	0
Bucconidae (puffbirds)						
Bucco macrodactylus (Spix 1824) (2)	50	*Picicola* sp.[†§]	1	7	1	0
Malacoptila fulvogularis Sclater 1854 (5)	40	*Penenirmus* sp.[†]	0	0	1	0
		Picicola sp.[†‡§]	4	14	6	0

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Bucconidae (*cont'd*)						
Malacoptila semicincta Todd 1925 (16)	44	*Picicola* sp.†‡§	7	23	5	0
		Unidentified	0	0	0	3
Monasa morphoeus (Hahn and Kuster 1823) (2)	0	–	–	–	–	–
Monasa nigrifrons (Spix 1824) (2)	50	Unidentified	0	0	0	11
Trogoniformes						
Trogonidae (trogons)						
Pharomacrus pavoninus (Spix 1824) (1)	0	–	–	–	–	–
Coraciiformes						
Momotidae (motmots)						
Baryphthengus martii (Spix 1824) (6)	83	*Brueelia humphreyi* Oniki and Emerson 1982†‡§	83	117	30	0
		Philopterus barypthenga (Carriker 1963)†§	19	30	2	0
Electron platyrhynchum (Leadbeater 1829) (1)	100	*Philopterus* sp.†	1	1	6	0
Momotus momota (Linnaeus 1766) (1)	100	*Philopterus prionitis* (Denny 1841)†	0	2	2	0
Cerylidae (kingfishers)						
Chloroceryle amazona (Latham 1790) (1)	100	*Alcedoffula* sp.†	0	4	0	0
Chloroceryle americana (Gmelin 1788) (1)	0	–	–	–	–	–
Cuculiformes						
Opisthocomidae (hoatzin)						
Opisthocomus hoazin (Muller 1766) (1)	100	*Cuculiphilus megaspinus* (Carriker 1940)*	2	0	2	0
		Hoazineus armiferus (Kellogg 1910)*	5	1	14	0
		Laemobothrion opisthocomi Cummings 1913*	3	1	1	0
		Osculotes curta (Burmeister 1838)†§	51	39	37	0
		Osculotes macropoda (Guimaraes 1940)†	46	32	71	0
		Wilsoniella absita (Kellogg 1910)†	5	4	11	0
Crotophagidae (anis)						
Crotophaga ani (Linnaeus 1758) (2)	100	*Osborniella crotophagae* (Stafford 1943)*§	0	0	9	10
		Vernoniella guimaraesi Thompson 1948†	2	0	4	0
Psittaciformes						
Psittacidae (parrots)						
Brotogeris sanctithomae (Muller 1766) (1)	100	*Psittacobrosus* sp.*	0	1	0	0
Pyrrhura picta (Muller 1766) (1)	100	*Heteromenopon pictae* Price and Beer 1967*	3	1	2	0
		Paragoniocotes sp.†	1	4	3	0
		Psittacobrosus pyrrhurae Price and Beer 1968*	1	2	0	0
Pyrrhura rupicola (Tschudi 1844) (1)	100	*Heteromenopon* sp.*	2	4	3	0
		Paragoniocotes sp.†	3	3	2	0
		Psittacobrosus sp.*	0	1	0	0

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Apodiformes						
Apodidae (swifts)						
Chaetura cinereiventris Sclater 1862 (9)	33	*Dennyus* sp.*§	2	0	13	0
Cypseloides rutilus (Vieillot 1817) (3)	100	*Dennyus brunneitorques* Carriker 1954*	1	0	3	0
		*Eureum yepezi**§	4	2	0	0
Streptoprocne zonaris (Shaw 1796) (3)	67	*Dennyus rotundocapitis* Carriker 1954*‡	7	0	6	0
Trochiliformes						
Trochilidae (hummingbirds)						
Adelomyia melanogenys (Fraser 1840) (11)	0	–	–	–	–	–
Aglaiocerus kingi (Lesson 1832) (1)	0	–	–	–	–	–
Campylopterus largipennis (Boddaert 1783) (8)	0	–	–	–	–	–
Coeligena coeligena (Lesson 1833) (2)	0	–	–	–	–	–
Colibri coruscans (Gould 1846) (2)	0	–	–	–	–	–
Colibri delphinae (Lesson 1839) (1)	0	–	–	–	–	–
Doryfera ludovicae (Bourcier and Mulsant) 1847 (19)	5	*Trochiliphagus* sp.*	0	1	0	0
Eutoxeres condamini (Bourcier 1851) (17)	0	–	–	–	–	–
Heliodoxa aurescens (Gould 1846) (4)	0	–	–	–	–	–
Heliodoxa branickii (Taczanowski 1874) (47)	19	*Trochiliphagus* sp.*§	1	6	0	0
		Trochiloecetes sp.*§	8	13	7	4
Heliodoxa leadbeateri (Bourcier 1843) (6)	0	–	–	–	–	–
Heliodoxa schreibersii (Bourcier 1847) (7)	43	*Trochiliphagus* sp.*	2	1	0	1
Klais guimeti (Bourcier 1843) (2)	50	*Trochiliphagus* sp.*	0	0	1	0
Phaethornis guy (Lesson 1833) (17)	18	*Trochiloecetes grandior* Carriker 1960*	2	2	2	0
		Unidentified	0	0	0	1
Phaethornis hispidus (Gould 1846) (2)	50	*Trochiloecetes* sp.*	0	0	1	0
Phaethornis koepckeae (Weske and Terborgh 1977) (36)	0	–	–	–	–	–
Phaethornis stuarti (Hartert 1897) (6)	33	*Trochiloecetes* sp.*	1	1	3	1
Phaethornis superciliosus (Linnaeus 1766) (7)	0	–	–	–	–	–
Phlogophilus harteri Berlepsch and Stolzmann 1901 (6)	0	–	–	–	–	–
Thalurania furcata (Gmelin 1788) (17)	18	*Trochiliphagus* sp.*	0	1	1	0
		Trochiloecetes emeliae Paine and Mann 1913*	0	2	0	0
		Unidentified	0	0	0	1
Threnetes leucurus (Linnaeus 1766) (7)	29	*Trochiliphagus* sp.*	1	1	0	0
		Trochiloecetes mandibularis Carriker 1960*§	4	6	27	0
Strigiformes						
Strigidae (owls)						
Otus atricapillus (Temminck 1822) (2)	100	*Colpocephalum cholibae* Price and Beer 1963*	2	3	0	0
		Strigiphilus crucigerus Carriker 1966†	1	2	2	0

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Strigidae (*cont'd*)						
Otus ingens (Salvin 1897) (3)	100	*Kurodaia* sp.*§	3	4	0	0
		Strigiphilus crucigerus Carriker 1966†§	18	11	10	0
Caprimuligidae (nightjars)						
Hydropsalis climacocerca (Tschudi 1844) (2)	100	*Mulcticola* sp.†	6	9	10	0
Columbiformes						
Columbidae (pigeons/doves)						
Columba plumbea Vieillot 1818 (3)	100	*Columbicola* sp.†	17	9	21	10
		Hohorstiella sp.*	0	1	0	0
		Physconelloides wolfdietrichi Kaddou 1973†	3	2	6	0
Geotrygon montana (Linnaeus 1758) (16)	100	*Columbicola macrourae* (Wilson 1941)†	18	15	39	0
		Hohorstiella corpulenta Carriker 1963*	1	0	1	0
		Physconelloides montana Carriker 1961†§	35	22	19	0
Gruiformes						
Euripygidae (sun-bittern)						
Eurypyga helias (Pallas 1781) (1)	0	–	–	–	–	–
Ciconiformes						
Accipitridae (hawks)						
Accipiter striatus Vieillot 1807 (1)	0	–	–	–	–	–
Falconidae (falcons)						
Micrastur gilvicollis (Vieillot 1817) (1)	100	*Colpocephalum* sp.*	0	0	1	0
Micrastur ruficollis (Vieillot 1817) (1)	100	*Colpocephalum holzenthali* Clayton and Price 1989*§	11	11	5	0
		Craspedorrhynchus sp.†§	6	8	1	0
Passeriformes						
Tyrannidae (flycatchers & allies)						
Cephalopterus ornatus Geoffroy Saint-Hilaire 1809 (3)	67	Unidentified	0	0	0	2
Laniisoma elegans (Thurnberg 1823) (2)	50	*Philopterus* sp.†‡	2	10	6	0
Laniocera hypopyrra (Vieillot 1817) (1)	0	–	–	–	–	–
Lipaugus subalaris Sclater 1861 (4)	75	Unidentified	3	7	2	0
Pipra chloromeros Tschudi 1844 (8)	63	*Myrsidea* sp.*	1	4	1	0
		Ricinus pessimalis Eichler 1956*	0	5	4	0
Pipra coeruleocapilla Tschudi 1844 (6)	33	*Ricinus* sp.*	0	5	0	0
Pipreola frontalis (Sclater 1858) (1)	100	*Myrsidea* sp.*	5	4	2	0
		Philopterus sp.†	0	3	1	0
Querula purpurata (Muller 1776) (2)	50	Unidentified	2	8	2	0
Rupicola peruviana (Latham 1790) (1)	100	*Cotingacola rupicolae* Carriker 1956†‡,§	27	14	75	0
Tyrannus melancholicus Vieillot 1819 (15)	80	*Menacanthus tyranni* Price 1977*	0	4	3	0
		Myrsidea sp.*	21	19	29	0
		Ricinus arcuatus (Kellogg and Mann 1912)*	1	1	10	0

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Thamnophilidae (typical antbirds)						
Cercomacra serva (Sclater 1858) (1)	0	–	–	–	–	–
Cymbilaimus sanctaemariae (Gyldenstolpe 1941) (1)	0	–	–	–	–	–
Frederickena unduligera (Pelzeln 1868) (1)	0	–	–	–	–	–
Hylophalyx naevia (Gmelin 1789) (2)	50	Unidentified	0	0	0	1
Myrmoborus myotherinus (Spix 1825) (1)	0	–	–	–	–	–
Myrmotherula haematonota (Sclater 1875) (1)	0	–	–	–	–	–
Neoctantes niger (Pelzeln 1859) (1)	0	–	–	–	–	–
Percnostola leucostigma Pelzeln 1868 (1)	0	–	–	–	–	–
Rhegmatorhina melanosticta (Sclater and Salvin 1880) (2)	50	Unidentified	0	0	0	1
Furnariidae (ovenbirds/woodcreepers)						
Ancistrops strigilatus (Spix 1825) (1)	100	*Myrsidea* sp.*	0	2	7	0
Automolus ochrolaemus (Tschudi 1844) (3)	100	*Myrsidea* sp.*	7	5	9	0
		Rallicola sp.†	0	1	0	0
		Unidentified	0	0	0	14
Campylorhampus trochilirostris (Lichtenstein 1820) (10)	100	*Rallicola* sp.†‡	69	99	146	1
Deconychura longicauda (Pelzeln 1868) (2)	50	*Rallicola* sp.†	4	2	1	0
Dendrocincla fuliginosa (Vieillot 1818) (7)	43	*Rallicola fuliginosa* (Carriker 1963)†§	17	15	14	0
Dendrocolaptes certhia (Boddaert 1783) (1)	0	–	–	–	–	–
Dendrocolaptes picumnus Lichtenstein 1820 (2)	100	*Myrsidea* sp.*	1	0	0	0
		Rallicola sp.†§	5	6	0	0
Dendrexetastes rufigula (Lesson 1844) (1)	0	–	–	–	–	–
Glyphorhyncus spirurus (Vieillot 1819) (69)	84	*Kaysius emersoni* Price and Clayton 1989*§	19	23	3	2
		Rallicola cephalosa (Carriker 1944)†§	148	176	227	7
		Unidentified	0	0	0	78
Hyloctistes subulatus (Spix 1824) (2)	100	*Myrsidea* sp.*	1	0	1	0
		Rallicola sp.†	5	4	5	0
		Unidentified	0	0	0	1
Metopothrix auranticus Sclater and Salvin 1866 (1)	0	–	–	–	–	–
Philydor erythrocercus (Pelzeln 1859) (1)	100	*Myrsidea* sp.*	1	0	0	0
		Rallicola sp.†	3	0	0	0
Premnoplex brunnescens (Sclater 1856) (22)	50	*Myrsidea* sp.*	1	2	0	0
		Rallicola sp.†§	22	18	5	0
		Unidentified	0	0	0	9
Sclerurus albigularis Sclater and Salvin 1869 (3)	33	Unidentified	0	0	0	1
Sclerurus caudacutus (Vieillot 1816) (1)	100	*Rallicola* sp.†	1	2	9	0
Sclerurus mexicanus Sclater 1857 (2)	100	*Myrsidea* sp.*	4	6	7	0
		Rallicola sp.†§	3	3	0	0
Sittasomus griseicapillus (Vieillot 1818) (3)	67	*Rallicola* sp.†‡	11	23	30	0
Syndactyla rufosuperciliata (Lafresnaye 1832) (1)	100	*Myrsidea* sp.*	0	2	2	0
		Rallicola sp.†	1	4	2	0

Bird species (*n*)	Prevalence	Louse species	♂	♀	Imm	?
Furnariidae (*cont'd*)						
Thripadectes melanorhynchus (Tschudi 1844) (4)	100	*Myrsidea* sp.*‡	32	15	40	0
		Rallicola sp.†§	23	29	26	0
Xenops rutilans Temminck 1821 (2)	0	–	–	–	–	–
Xiphorhynchus ocellatus (Spix 1824) (44)	48	*Rallicola chunchotambo* (Carriker 1944)†§	37	55	39	0
		Unidentified	0	0	0	51
Xiphorhynchus triangularis (Lafresnaye 1842) (18)	94	*Rallicola* sp.†§	32	49	23	0
		Unidentified	0	0	0	48
Xiphorhynchus guttatus (Lichtenstein 1820) (1)	0	–	–	–	–	–
Xiphorhynchus spixii (Lesson 1830) (1)	0	–	–	–	–	–
Formicariidae (ground antbirds)						
Chamaeza campanisona (Lichtenstein 1823) (1)	100	*Formicaricola willisi* Oniki and Emerson 1982†§	17	18	116	0
Formicarius analis (d'Orbigny and Lafresnaye 1837) (1)	100	*Formicaricola* sp.†	0	0	2	0
		Myrsidea sp.*	2	2	3	0
Formicarius rufipectus Salvin 1866 (2)	50	*Myrsidea* sp.*	1	0	0	0
		Formicaricola sp.†	3	4	1	0
Myrmothera campanisona (Hermann 1783) (2)	100	*Formicaphagus* sp.†§	21	24	18	0
Conophagidae (gnateaters)						
Conopophaga ardesiaca d'Orbigny and Lafresnaye 1837 (28)	21	*Formicaphagus* sp.†‡,§	17	73	29	0
		Philopterus sp.†	0	1	0	0
		Unidentified	0	0	0	1
Conopophaga peruviana Des Murs 1856 (5)	60	*Formicaphagus* sp.†	5	7	8	0
Certhiidae (wrens/creepers)						
Cyphorhinus thoracicus Tschudi 1844 (2)	100	*Myrsidea* sp.*	6	1	3	0
Hirundinidae (swallows)						
Stelgidopteryx ruficollis (Vieillot 1817) (3)	67	*Philopterus tropicalis* Carriker 1956†	3	1	1	0
Fringillidae (finches & allies)						
Cacicus cela (Linnaeus 1758) (1)	100	*Myrsidea picta* Carriker 1955*‡	20	9	36	0
Cacicus solitarius Vieillot 1816 (1)	100	*Myrsidea* sp.*§	33	21	28	0
Tangara arthus Lesson 1832 (1)	100	*Myrsidea* sp.*	1	6	5	0
Tangara chilensis Vigors 1832 (1)	100	*Myrsidea* sp.*§	2	7	1	0
Tangara punctata (Linnaeus 1766) (1)	0	–	–	–	–	–
Tangara ruficervix (Prevost and Des Murs 1846) (1)	100	*Myrsidea* sp.*	1	2	1	0

* Amblycera.
† Ischnocera.
‡ Biased sex ratio.
§ Biased age ratio
}($\chi 2$ test if ≥10 lice; two-tailed binomial test if <9 lice; $P < 0{\cdot}05$ level of significance in either case).

Appendix 2

Lice from qualitatively sampled birds

Bird species (*n*)	Louse species
Tinamiformes	
Tinamidae (tinamous)	
Crypturellus atrocapillus (Tschudi 1844) (2)	*Discocorpus cephalosus* Carriker 1936†
	Heptapsogaster chinirii Carriker 1936†
	Heptapsogaster garleppi Carriker 1944†
	Kelloggia romainei Carriker 1962†
	Megapeostus parvigenitalis Carriker 1936†
	Pectenosoma angusta Carriker 1936†
	Physconella genitalis Carriker 1936†
	Pseudolipeurus garleppi Carriker 1944†
	Pseudophilopterus sp.†
	Strongylocotes interruptus Carriker 1936†
Crypturellus soui (Hermann 1783) (2)	*Kelloggia* sp.†
	Megapeostus platycephalus (Carriker 1936)†
	Pectenosoma meserythra Carriker 1944†
	Physconella kelloggi (Paine 1913)†
	Rhopaloceras rudimentarius Carriker 1936†
	Strongylocotes subconiceps Carriker 1936†
Crypturellus undulatus (Temminck 1815) (1)	*Heptapsogaster temporalis* Carriker 1936†
	Megaginus sp.†
	Megapeostus asymmetricus Carriker 1936†
	Pectenosoma yapurae Carriker 1944†
	Pseudolipeurus macrogenitalis Carriker 1953†
	Strongylocotes limai Guimaraes 1936†
Craciformes	
Cracidae (guans/chachalacas)	
Mitu mitu (Linnaeus 1766) (1)	*Amyrsidea mituensis* (Carriker 1954)*
	Menacanthus mituensis Carriker 1946*
Ortalis motmot (Linnaeus 1766) (1)	*Amyrsidea* sp.*
	Goniodes sp.†
	Menacanthus sp.*
	Oxylipeurus sp.†
Penelope jacquacu Spix 1825 (3)	*Goniodes* sp.†
	Menacanthus chaparensis Carriker 1946*
Psittaciformes	
Psittacidae (parrots)	
Amazona ochrocephala (Gmelin 1788) (1)	*Paragoniocotes grandis* Guimaraes 1947†
	Psittacobrosus amazonicus Carriker 1963*
Aratinga weddelli (Deville 1851) (1)	*Paragoniocotes* sp.†
	Psittacobrosus sp.*
Pionus menstruus (Linnaeus 1766) (1)	*Paragoniocotes* sp.†
	Psittacobrosus amazonicus Carriker 1963*
Trochiliformes	
Trochilidae (hummingbirds)	
Florisuga mellivora (Linnaeus 1758) (1)	*Trochiliphagus mellivorus* Carriker 1960*
Strigiformes	
Strigidae (owls)	
Otus watsonii (Cassin 1848) (1)	*Strigiphilus crucigerus* Carriker 1966†
Caprimulgidae (nightjars)	
Nyctidromus albicollis (Gmelin 1789) (1)	*Mulcticola* sp.†
Columbiformes	
Columbidae (pigeons/doves)	
Columba subvinacea (Lawrence 1868) (1)	*Columbicola macrourae* (Wilson 1941)†
Gruiformes	
Psophiidae (trumpeters)	
Psophia leucoptera Spix 1825 (1)	*Laemobothrion gracile* Giebel 1874*
	Rallicola foedus (Nitzsch 1866)†

Appendix 2 (cont'd)

Bird species (*n*)	Louse species
Rallidae (gallinules)	
Porphyrio martinica (Linnaeus 1766) (1)	*Rallicola elliotti* Emerson 1955†
Ciconiiformes	
Scolopacidae (sandpipers)	
Tringa solitaria Wilson 1813 (1)	*Quadraceps waterstoni* Hopkins and Timmermann 1954†
Accipitridae (hawks)	
Harpagus bidentatus (Latham 1790) (1)	*Degeeriella* sp.†
Ictinea plumbea (Gmelin 1788) (1)	*Craspedorrhynchus* sp.†
Ciconiidae (New World vultures)	
Cathartes aura (Linnaeus 1758) (1)	*Colpocephalum kellogi* Osborn 1902*
	Falcolipeurus marginalis (Osborn 1902)†
Passeriformes	
Tyrannidae (flycatchers & allies)	
Ampelioides tschudii (Gray 1846) (3)	*Myrsidea* sp.*
Corythopis torquata Tschudi 1844 (1)	*Philopterus* sp.†
Pipra fasciicauda Hellmayr 1906 (1)	*Myrsidea* sp.*
	Philopterus sp.†
	Ricinus sp.*
Mionectes olivaceus Lawrence 1868 (1)	*Myrsidea* sp.*
Muscisaxicola fluviatilis Sclater and Salvin 1866 (1)	*Philopterus* sp.†
Tolmomyias flaviventris (Wied 1831) (1)	*Myrsidea* sp.*
Tyrannus tyrannus (Linnaeus 1758) (2)	*Philopterus* sp.†
Thamnophilidae (typical antbirds)	
Pyriglena leuconota (Spix 1824) (1)	*Rallicola* sp.†
Furnariidae (ovenbirds/woodcreepers)	
Furnarius leucopus Swainson 1837 (1)	*Formicaricola* sp.†
Lochmias nematura (Lichtenstein 1823) (1)	*Myrsidea strobilisternata* Eichler 1956*
Simoxenops ucayalae (Chapman 1928) (3)	*Myrsidea* sp.*
Xenops minutus (Sparrman 1788) (3)	*Rallicola* sp.†
Corvidae (jays)	
Cyanocorax cyanomelas (Vieillot 1818) (1)	*Myrsidea fallax* Keler 1938*
Cyanocorax violaceus Du Bus de Gisignies 1847 (1)	*Brueelia violacea* Carriker 1963†
	Myrsidea sp.*
Muscicapidae (solitaires/thrushes)	
Entomodestes leucotis (Tschudi 1844) (1)	*Brueelia busharae* Ansari 1955†
	Myrsidea sp.*
Turdus nigriceps Cabanis 1874 (8)	*Brueelia similis* Cicchino 1986†
	Myrsidea sp.*
	Sturnidoecus rehanae Ansari 1955†
Certhiidae (wrens/creepers)	
Donacobius atricapillus (Linnaeus 1766) (1)	*Myrsidea* sp.*
Hirundinidae (swallows)	
Neochelidon tibialis (Cassin 1853) (1)	*Myrsidea* sp.*
Notiochelidon cyanoleuca (Vieillot 1817) (1)	*Myrsidea* sp.*
Fringillidae (finches & allies)	
Atlapetes brunneinucha (Lafresnaye 1839) (1)	*Brueelia brunneinucha* Cicchino 1983†
	Myrsidea sp.*
Gymnostinops bifasciatus (Spix 1824) (1)	*Myrsidea* sp.*
	Sturnidoecus sp.†
Psarocolius angustifrons (Spix 1824) (4)	*Myrsidea tropicalis* Clay 1968*
	Sturnidoecus sp.†
Psarocolius decumanus (Pallas 1769) (9)	*Myrsidea downsi* Clay 1968*
	Sturnidoecus sp.†
Psarocolius oseryi (Deville 1849) (1)	*Brueelia* sp.†
	Myrsidea sp.*
Scaphidura oryzivora (Gmelin 1788) (2)	*Brueelia mirabile* Carriker 1963†
	Myrsidea psittaci Carriker 1955*
	Philopterus sp.†
Tersina viridis (Illiger 1811) (1)	*Myrsidea* sp.*

* Amblycera.
† Ischnocera.