

Influence of host ecology and morphology on the diversity of Neotropical bird lice

D. H. Clayton and B. A. Walther

Clayton, D. H. and Walther, B. A. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. – *Oikos* 94: 455–467.

Host-parasite systems can be powerful arenas in which to explore factors influencing community structure. We used a comparative approach to examine the influence of host ecology and morphology on the diversity of chewing lice (Insecta: Phthiraptera) among 52 species of Peruvian birds. For each host species we calculated two components of parasite diversity: 1) cumulative species richness, and 2) mean abundance. We tested for correlations between these parasite indices and 13 host ecological and morphological variables. Host ecological variables included geographic range size, local population density, and microhabitat use. Host morphological variables included body mass, plumage depth, and standard dimensions of bill, foot and toenail morphology, all of which could influence the efficiency of anti-parasite grooming. Data were analysed using statistical and comparative methods that control for sampling effort and host phylogeny. None of the independent host variables correlated with louse species richness when treated as a dependent variable. When richness was treated as an independent variable, however, it was positively correlated with mean louse abundance. Host body mass was also positively correlated with mean louse abundance. When louse richness and host body mass were held constant, mean louse abundance correlated *negatively* with the degree to which the upper mandible of the host's bill overhangs the lower mandible. This correlation suggests that birds with longer overhangs are better at controlling lice during preening. We propose a specific functional hypothesis in which preening damages lice by exerting a shearing force between the overhang and the tip of the lower mandible. This study is the first to suggest a parasite-control function of such a detailed component of bill morphology across species. Avian biologists have traditionally focused almost exclusively on bills as tools for feeding. We suggest that the adaptive radiation of bill morphology should be reinterpreted with both preening and feeding in mind.

D. H. Clayton, Dept of Biology, Univ. of Utah, Salt Lake City, UT 84112, USA (clayton@biology.utah.edu). – B. A. Walther, Dept of Zoology, Oxford Univ., Oxford, UK OX1 3PS (present address: Zoologisk Museum, Københavns Universitet, Universitetsparken 15, DK-2100 København Ø, Denmark).

The composition of vertebrate parasite communities is influenced by many variables including phylogenetic history, host specificity, parasite competition, and parameters of host biology such as population size, habitat, diet, migration and anti-parasite defences (Esch et al. 1990, Simberloff and Moore 1997, Poulin 1998). Unravelling the relative contributions and interactions of factors responsible for the organisation of parasite communities is a tall order. However, recent applica-

tions of the comparative method, with appropriate phylogenetic control, show considerable promise in identifying candidates for further study and experimental manipulation (Gregory 1997, Poulin 1998).

Parasites are often viewed as highly tractable in space and time, making them excellent candidates for ecological studies. This view can be oversimplified in the case of parasites with complex life cycles requiring one or more intermediate hosts (Sousa 1994). However,

Accepted 9 April 2001

Copyright © OIKOS 2001

ISSN 0030-1299

Printed in Ireland – all rights reserved

tractability remains a powerful feature of permanent ectoparasites, such as chewing lice (Insecta: Phthiraptera), which spend their entire life cycle on the body of a single host (Marshall 1981). In this study, we report the results of a comparative analysis of variables that may contribute to the diversity (species richness and mean abundance) of chewing lice on Neotropical birds.

Bird lice are obligate parasites that feed primarily on feathers and dermal debris, although some species feed on blood. Lice are so well adapted to the warm, humid microhabitat near the skin of the host that they are unable to survive off the host for more than a few hours or days (Tompkins and Clayton 1999). Louse eggs, which are glued to the feathers with a glandular cement, also depend on conditions near the skin for successful incubation and hatching (Nelson and Murray 1971). Transmission of lice between individual birds normally occurs during direct physical contact, such as that between parents and offspring in the nest (Clayton and Tompkins 1995). Birds keep most of their lice in check by killing or removing them during preening with the bill (Brown 1972, 1974) while they control lice on the head by scratching with their feet (Clayton 1991). It is critical for birds to keep their louse populations under control because high numbers of lice cause extensive feather damage, with a concomitant reduction in survival (Clayton et al. 1999) and mating success (Clayton 1990).

Most species of lice are restricted to a single species or genus of host (Marshall 1981). This host specificity is often indicative of a prolonged history of association that yields congruent bird-lice phylogenies (Paterson and Gray 1997). Congruence is a useful feature since it makes it possible to control simultaneously for both host and parasite phylogenies in comparative analyses (Harvey and Pagel 1991, Morand et al. 2000). When host-parasite phylogenies are not congruent, it is difficult to take the history of both parties into account in a single analysis. Although one cannot assume congruence a priori, the evidence to date suggests that cospeciation is common between birds and lice (Clayton et al. in press). Unfortunately, as for most parasites (Brooks and McLennan 1993), phylogenies are lacking for the majority of lice. However, preliminary phylogenetic information is available for most groups of birds (Sibley and Ahlquist 1990, Mindell 1997). We used this information to perform phylogenetically controlled comparisons of louse diversity in relation to components of host biology.

Most studies of parasite diversity have focused on species richness, with little or no information on abundance, which is harder to quantify for most parasites (Clayton and Moore 1997). Fortunately, because lice are so closely tied to the body of their host, it is relatively easy to quantify louse abundance accurately, even under field conditions (Clayton and Walther 1997,

Clayton and Drown in press). For this study, we analysed data on the species richness and mean abundance of lice from 52 species of Peruvian birds. We also gathered data on ecological and morphological parameters of hosts that might influence louse richness and abundance.

The ecological data, which were taken from the literature, included host geographic range size, population density and microhabitat use. For parasites, host range can be considered analogous to island size for free-living organisms, assuming widespread hosts "capture" new parasites through host transfer more often than do hosts with restricted distributions (Price et al. 1988, Simberloff and Moore 1997). Therefore, we predicted that hosts with large geographic ranges would have more parasite species. This prediction has been supported for parasite richness (Gregory 1990) and abundance (Tella et al. 1999). However, Poulin (1997) warned that the strength of the relationship between host range and parasite richness is reduced when analyses properly control for sampling effort and phylogeny.

At the level of host populations, parasite transmission increases with host density (Grenfell and Dobson 1995), meaning that host species with dense populations should have more parasites than those with sparse populations. Recent studies have confirmed host density as a significant predictor of parasite richness (Morand and Poulin 1998) and abundance (Arneberg et al. 1998, Tella et al. 1999).

Parasite transmission also can be influenced by host microhabitat use (Read 1991). For example, canopy birds have more blood parasites than ground birds, apparently because of the higher abundance of vectors, such as biting flies, in the canopy (Garvin and Remsen 1997). Conversely, ground birds have more ticks than canopy birds because ticks have an obligate free-living stage found in vegetation near the ground (Pruett-Jones and Pruett-Jones 1991). Since lice spend all of their time on the host and are not transmitted by vectors, we did not expect louse richness or abundance to covary with host microhabitat use. To test this prediction we used data on foraging stratum as an index of host microhabitat use.

Host morphology can also have an important influence on parasite diversity. Host body size may determine the resource base for parasites, as well as the number of parasite niches available. Several studies have shown a positive relationship between host body size and parasite species richness (reviewed in Poulin 1997) as well as parasite abundance (Poulin and Rohde 1997, Rózsa 1997a, b, Grutter and Poulin 1998, Morand et al. 1999). However, the strength of these relationships is often diminished after controlling for sampling effort and phylogeny (Poulin 1997). Correlations between host body size and parasite richness or abundance are not necessarily expected to be positive. As Gregory (1997) has argued, it is conceivable that

small-bodied species will have higher parasite abundance, since such species tend to have denser populations, which improves the efficiency of parasite transmission. We used host body mass as an index of body size to explore the relationship between body size and louse diversity. The quantity of plumage on a bird, corrected for body size, may further reflect the resource base for feather feeding lice (Rózsa 1997a, b). We therefore also collected data on relative plumage depth to examine its possible relationship to louse diversity.

Host defence is yet another parameter that could influence parasite diversity. Immunocompetence may be one such factor (e.g. John 1995, Tella et al. 1999). Since most chewing lice feed on feathers and dermal debris (Marshall 1981), rather than blood, they do not come into direct contact with the host immune system. Immunity should therefore be of little importance in structuring bird louse communities. On the other hand, behavioural defences such as preening and scratching could well influence the diversity of lice among different species of hosts. For example, grooming time is correlated with louse species richness among different species of birds (Cotgreave and Clayton 1994). Consequently, the size and shape of a bird's bill may influence the composition of its ectoparasite community (Murray 1990), much as bill morphology influences what a bird can eat (Gosler 1987, Peterson 1993, Temeles 1996). To test for a possible relationship between morphological components of grooming (preening and scratching) and louse diversity, we measured various parameters of bill, foot and toenail morphology, as described below.

Materials and methods

Parasite data

A common criticism of the analyses of previous comparative parasite data sets is that sampling effort confounds estimates of species richness (Walther et al. 1995) and abundance (Poiani 1992). Therefore, we took particular care to avoid any confounding effects of sampling effort. Specifically, all birds were sampled by one person using a standardised method. Furthermore, the summary data for each species were generated by excluding species with small sample sizes and using statistical extrapolation methods, as explained below.

All lice were quantified by DHC in August–December, 1985 at several rainforest localities in the Andean foothills of south-eastern Peru near Parque Nacional del Manu (11°55' S, 71°18' W; see map in Walther 1997 for specific sites). The lice were collected from birds being prepared as specimens for the Field Museum, Chicago (accession numbers 320356–324105). The 52 species of birds sampled were all non-migratory residents, thereby eliminating migration as a potential complicating influence on estimates of parasite diversity (Zuk 1991).

Freshly killed birds were placed in individual paper bags that were rolled shut to prevent ectoparasites from infesting other hosts. Each bag was then placed for a minimum of 10 min in a plastic chamber containing cotton soaked in ethyl acetate, which kills ectoparasites rapidly (Fowler 1984). After fumigation birds were sampled for lice using one of the following two methods:

Post-mortem-ruffling

Most species were sampled by ruffling their feathers. Each bird was removed from the ethyl acetate chamber and suspended over a clean, white sheet of 28 × 38 cm paper. The bird's feathers were ruffled vigorously for a period of 1 min, with attention to all body regions. Lice falling onto the paper were located using 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% of the total recovered during the first three bouts combined. Thus, the decision to stop sampling a given host was based on the recovery rate from that host. This approach, which recovers 70% of "wing" lice and 42% of "body" lice, predicts abundance with a high degree of accuracy ($df = 24$, $r^2 = 0.98$, $P < 0.0001$) (Clayton and Drown in press).

Visual examination

This method was used on the 15 species of hummingbirds and three other small-bodied species for which feather ruffling would have been difficult (Table 1; two *Pipra* spp. and *Stelgidopteryx ruficollis*). Because such small-bodied birds have relatively few feathers (Wetmore 1936), it was feasible to examine all of their feathers for lice within a few 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.

All lice were later mounted on microscope slides and identified to the most specific taxon possible. The complete list of taxa is provided in Appendix 1 of Clayton et al. (1992a). Two components of parasite diversity were determined as follows:

Cumulative species richness

The cumulative number of louse species collected from all individuals of a given host species was tabulated from Appendix 1 of Clayton et al. (1992a). Unidentified lice were conservatively tallied as one additional species; e.g. if a host had one identified louse, as well as lice that could not be identified, it was given a richness score of 2.

Table 1. Cumulative species richness and mean abundance of lice on 52 species of Peruvian birds (n is the number of individuals sampled for lice). Body mass and length of the bill overhang were the two host variables significantly correlated with mean abundance (see text). Residual bill overhang values are the residuals of bill overhang regressed against body mass to control for variation in body size among bird species. Host names follow Sibley and Monroe (1990), and the sequence of host families follows Sibley and Ahlquist (1990).

Bird taxa	n	Louse species richness	Mean louse abundance	Body mass (g)	Bill overhang (mm)	Residual bill overhang
Piciformes						
Picidae (woodpeckers)						
<i>Celeus grammicus</i>	5	1	6.6	79.2	1.0	0.03
<i>Picumnus aurifrons</i>	4	1	2.5	9.1	0.9	0.46
<i>Picumnus rufiventris</i>	7	0	0.0	20.2	1.2	0.73
<i>Veniliornis affinis</i>	3	1	6.0	35.8	0.4	-0.19
Rhamphastidae (barbets/toucans)						
<i>Capito niger</i>	3	2	2.0	67.8	0.9	-0.03
<i>Eubucco richardsoni</i>	3	2	27.7	31.8	0.6	-0.06
<i>Eubucco versicolor</i>	3	0	0.0	35.9	0.6	-0.04
<i>Pteroglossus mariae</i>	5	1	0.8	139.8	4.0	2.58
<i>Selenidera reinwardtii</i>	13	2	18.0	169.8	2.0	0.35
Galbuliformes						
Galbulidae (jacamars)						
<i>Galbula cyanescens</i>	4	1	1.0	25.0	1.8	1.19
Bucconidae (puffbirds)						
<i>Malacoptila fulvogularis</i>	5	2	5.0	52.5	0.7	-0.07
<i>Malacoptila semicincta</i>	16	2	2.4	44.1	1.0	0.30
Coraciiformes						
Momotidae (motmots)						
<i>Baryphthengus martii</i>	6	2	46.8	147.2	2.0	0.52
Apodiformes						
Apodidae (swifts)						
<i>Chaetura cinereiventris</i>	9	1	1.7	18.7	0.3	-0.21
<i>Cypseloides rutilus</i>	3	2	3.3	22.8	0.6	0.11
<i>Streptoprocne zonaris</i>	3	1	4.3	110.8	0.6	-0.60
Trochiliformes						
Trochilidae (hummingbirds)						
<i>Adelomyia melanogenys</i>	11	0	0.0	3.3	0.0	-0.40
<i>Campylopterus largipennis</i>	8	0	0.0	8.5	0.0	-0.44
<i>Doryfera ludovicae</i>	19	1	0.1	5.3	0.0	-0.41
<i>Eutoxeres condamini</i>	17	0	0.0	9.6	0.0	-0.44
<i>Heliodoxa aurescens</i>	4	0	0.0	6.4	0.0	-0.42
<i>Heliodoxa branickii</i>	47	2	0.8	6.1	0.0	-0.42
<i>Heliodoxa leadbeateri</i>	6	0	0.0	6.8	0.0	-0.42
<i>Heliodoxa schreibersii</i>	7	1	0.6	8.9	0.0	-0.44
<i>Phaethornis guy</i>	17	2	0.4	5.2	0.0	-0.41
<i>Phaethornis koepckeae</i>	36	0	0.0	5.0	0.0	-0.41
<i>Phaethornis stuarti</i>	6	1	1.0	2.6	0.0	-0.39
<i>Phaethornis superciliosus</i>	7	0	0.0	5.2	0.0	-0.41
<i>Phlogophilus harteri</i>	6	0	0.0	2.7	0.0	-0.39
<i>Thalurania furcata</i>	17	3	0.3	4.2	0.0	-0.40
<i>Threnetes leucurus</i>	7	2	5.6	5.9	0.0	-0.42
Strigiformes						
Strigidae (owls)						
<i>Otus ingens</i>	3	2	15.3	181.2	3.6	1.87
Columbiformes						
Columbidae (pigeons/doves)						
<i>Columba plumbea</i>	3	3	23.0	207.0	1.3	-0.62
<i>Geotrygon montana</i>	16	3	9.4	115.8	1.5	0.26
Passeriformes						
Tyrannidae (flycatchers/allies)						
<i>Cephalopterus ornatus</i>	3	1	0.7	383.3	1.4	-1.85
<i>Lipaugus subalaris</i>	4	1	3.0	78.0	0.5	-0.46
<i>Pipra chloromeros</i>	8	2	1.9	17.9	0.8	0.29
<i>Pipra coerulescapilla</i>	6	1	0.8	9.9	0.4	0.00
<i>Tyrannus melancholicus</i>	15	3	5.9	48.5	1.5	0.76
Furnariidae (woodcreepers/ovenbirds)						
<i>Automolus ochrolaemus</i>	3	3	12.0	33.9	0.6	0.02

Table 1. (Continued)

Bird taxa	<i>n</i>	Louse species richness	Mean louse abundance	Body mass (g)	Bill overhang (mm)	Residual bill overhang
<i>Campylorhampus trochilirostris</i>	7	1	31.1	36.1	0.0	-0.64
<i>Dendrocincla fuliginosa</i>	7	1	6.6	31.0	0.4	-0.21
<i>Glyphorhynchus spirurus</i>	69	3	9.9	14.4	0.0	-0.48
<i>Premnoplex brunnescens</i>	22	3	2.6	14.6	1.2	0.77
<i>Sclerurus albigularis</i>	3	1	0.3	41.9	0.8	0.06
<i>Sittasomus griseicapillus</i>	3	1	21.3	15.4	0.6	0.09
<i>Thripadectes melanorhynchus</i>	4	2	41.2	45.7	0.4	-0.27
<i>Xiphorhynchus ocellatus</i>	44	2	4.1	32.3	0.9	0.23
<i>Xiphorhynchus triangularis</i>	18	2	8.4	42.8	1.2	0.51
Conopophagidae (gnateaters)						
<i>Conopophaga ardesiaca</i>	28	3	4.3	26.8	1.0	0.48
<i>Conopophaga peruviana</i>	5	1	4.0	23.9	1.2	0.65
Hirundinidae (swallows)						
<i>Stelgidopteryx ruficollis</i>	3	1	1.7	15.0	0.2	-0.29

Mean abundance

Mean louse abundance was calculated by dividing the total number of individual lice collected from a host species (pooling species and age classes) by the number of individuals of the host species sampled, including uninfected host individuals (Bush et al. 1997). We did not analyse louse prevalence (proportion of hosts infested) because prevalence is not an informative parameter for macroparasites such as lice; rather, prevalence is more relevant when estimating the abundance of fast reproducing parasites such as haematozoa (Clayton et al. 1992b).

Host data

Many host variables have the potential to influence parasite communities. Unfortunately, the ecology of many of the bird species we sampled for lice is poorly known (Stotz et al. 1996). We restricted our analyses to those few ecological variables that are known for all of the host species we studied (see below). Other ecological parameters, for which some data exist, were investigated by Walther (1997), and the relationship of host "showiness" to parasite diversity was investigated by Walther et al. (1999). These earlier studies treated a larger data set containing 122 host species. The current paper focuses on a conservative subset of these data restricted to the 52 species for which at least three individual birds were sampled for lice. None of the additional parameters examined by Walther (1997) or Walther et al. (1999) were significantly correlated with parasite richness or abundance in the restricted data set (Walther 1997).

Ecological parameters

Parameters 1–3 were entered as continuous variables.

1) Geographic range: Estimated by enlarging range maps (Dunning 1982, 1987) and using a grid to tally

the number of 10 000 km² squares filled on each map. Sibley and Monroe (1990) was used to estimate the ranges of a few species not shown in Dunning (1982, 1987).

- 2) Local population density: (1) rare, (2) uncommon, (3) fairly common, (4) common (Parker III et al. 1996).
- 3) Microhabitat use (foraging stratum): (1) terrestrial, (2) terrestrial and understorey, (3) understorey, (4) understorey and midstorey, (5) midstorey, (6) midstorey and canopy, (7) canopy, (8) aerial (Parker III et al. 1996).

Morphological parameters

Morphological measurements were taken from specimens at the Field Museum of Natural History, Chicago. Parameters 4–9 and 12–13 were entered as continuous variables. Unless noted, each measurement is the mean of one male and one female specimen. Categorical scores (parameters 10–11) were identical for males and females.

- 4) Body mass (gr): mean of five males and five females weighed in the field. Smaller samples had to be used in a few cases owing to lack of specimens.
- 5) Plumage depth (mm): distance from skin to the tip of the longest feather in a clump pinched between thumb and forefinger near centre of the bird's breast.
- 6) Bill length (mm): distance from point at which upper mandible meets forehead to distal tip of the mandible.
- 7) Bill width (mm): horizontal distance between sides of the upper mandible at its base.
- 8) Bill depth (mm): vertical distance between top of upper and bottom of lower mandible at deepest part of the bill.
- 9) Bill overhang (mm): length of overhang of upper mandible beyond tip of lower mandible.

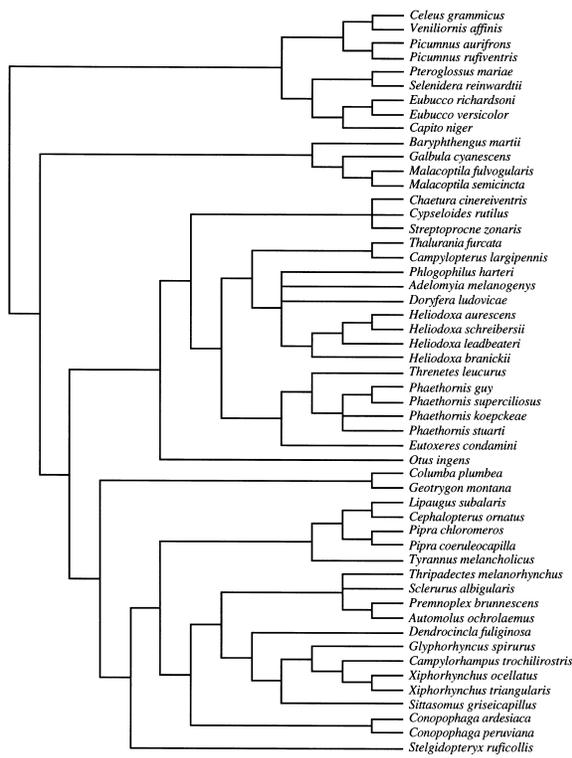


Fig. 1. Phylogeny of the 52 bird species from which lice were sampled. See Materials and methods for sources of phylogenetic information.

- 10) Bill curvature: (1) straight, (2) slightly curved, (3) curved, (4) greatly curved.
- 11) Bill occlusion: (1) fully occluded, (2) finely toothed, (3) coarsely serrate.
- 12) "Foot" length (mm): distance from proximal end of tarsometatarsus to tip of nail on longest front toe.
- 13) Toenail flange (mm): width of widest part of solid or serrate flange on middle toenail.

Statistical analyses

Comparative studies of parasite communities across host taxa are more robust when controlled for sampling effort and phylogenetic history (Poulin 1998). We controlled for the influence of both sampling effort and host phylogeny on louse species richness and mean abundance. To explore the effect of sampling effort on estimates of species richness and mean abundance, we analysed increasingly restrictive data sets containing host species with at least 3, 5 and 7 individuals sampled for lice. These data sets included 52, 34 and 25 species, respectively.

We further controlled for effects of sampling effort on estimates of cumulative species richness with two non-parametric estimation methods (first-order jack-knife and Chao2 estimation). Among nine estimation methods applied to real and simulated parasite data sets, these

two methods provided the most accurate estimates of parasite species richness (Walther and Morand 1998). Prerequisites for using these estimation methods were met by only 13 of the host species in our study (see Table 6.2 in Walther 1997 for further details). For these 13 species, we averaged the estimates provided by the two estimation methods and then tested for relationships between louse species richness and each of the 13 host variables outlined above.

To control for effects of host phylogeny, we calculated phylogenetically independent contrasts using comparative methods developed by Felsenstein (1985, 1988), Harvey and Pagel (1991) and Pagel (1992). We used the program CAIC, Version 2.0 (Purvis and Rambaut 1995), which generates independent contrasts for the variables being analysed at each node within a phylogeny. Variables were subjected to Box-Cox transformation (Krebs 1989) before CAIC calculations. For the comparative analyses we used standardised contrasts that conform to the assumptions of linear regression (Harvey and Pagel 1991, Garland et al. 1992). Adequate standardisation of each variable was tested by plotting the absolute values of the standardised contrasts against (1) their standard deviations and (2) the ages of the corresponding nodes (Garland et al. 1992, Purvis and Rambaut 1994). For a more detailed description of the use of standardised contrasts, see Garland et al. (1992) and Purvis and Rambaut (1994).

The phylogeny used for our analyses (Fig. 1) was derived from Sibley and Ahlquist (1990) and more detailed phylogenies of the Dendrocolaptinae (Raikow 1994), Picinae (Swierczewski and Raikow 1981), Trochilidae (Bleiweiss et al. 1994) and the hummingbird genera *Phaethornis* (Gill and Gerwin 1989) and *Heliodoxa* (Gerwin and Zink 1989). Branch lengths were logarithmically transformed to standardise the independent contrasts (Garland et al. 1992).

We tested for association between host variables and parasite load using multiple regression fitted through the origin (Grafen 1989, Garland et al. 1992). The regression model was generated by subjecting an initial regression to a backward elimination procedure that omitted non-significant variables ($P > 0.05$; Sokal and Rohlf 1995). All P -values are two-tailed.

Purvis and Rambaut (1994) recommend subdividing and reanalysing large data sets to check for consistency of results among major clades. Therefore, after analysing our entire data set of 52 species, we conducted separate analyses of the 34 non-passerine species and 18 passerine species (Table 1).

Results

Data set

The parasite data analysed in this study were collected from 581 individual birds representing 52 species in 13

families. These 52 species, chosen from a larger data set published by Clayton et al. (1992a), include only those with at least three individual birds sampled for lice (see Materials and methods). Table 1 lists the host species sampled, together with data on louse species richness and mean abundance, as well as the values for host variables that were significantly correlated with mean abundance (see below).

Determinants of cumulative species richness

Louse species richness varied from 0 to 3 across the 52 host species (Table 1; mean \pm 1 SE = 1.4 ± 0.1 ; median = 1). Richness was not significantly correlated with any of the 13 host variables in the overall analysis, nor when the analysis was restricted to data subsets containing species with at least 5 or 7 individuals sampled for lice. Similarly, none of the host variables correlated significantly with louse species richness when passerines and non-passerines were analysed separately. Unidentified lice, which were tallied as one additional species (see Materials and methods), were present for 9 of the 18 passerine species (50%), but only four of the 34 non-passerine species (12%), which is a significant difference (Fisher Exact $P = 0.03$). Despite this fact, the parasite species richness of passerines did not differ significantly from that of non-passerines (Mann-Whitney $P > 0.05$). Furthermore, the nine passerine species with unidentified lice did not differ significantly in louse species richness from the nine species without unidentified lice (Mann-Whitney $P > 0.05$).

Using species richness estimators to further control for sampling effort, we repeated the analysis for the 13 applicable species (see Materials and methods). Again, none of the host variables correlated significantly with louse species richness.

Determinants of mean abundance

All host species

Cumulative species richness and mean abundance are positively correlated in many communities (e.g. Southwood et al. 1982, Stork 1991, Siemann et al. 1996). A bird species infested by only one louse species can be expected to have a lower overall louse abundance than a bird species colonised by two louse species, given that lice are adapted to exploit different microhabitats on the body of the host (see Discussion). We controlled for the effect of species richness on mean abundance by entering louse species richness as an independent variable in our model, allowing us to assess the effect of other variables, e.g. body size, independent of the effect of the number of louse species colonising a host species.

Mean louse abundance varied from 0–46.8 across the 52 host species (Table 1; mean \pm 1 SE = 6.6 ± 1.5 ; me-

dian = 2.4). Mean abundance was positively correlated with louse species richness ($n = 46$, $r^2 = 0.30$, $P < 0.0001$) and host body mass ($n = 46$, $r^2 = 0.14$, $P = 0.02$) entered separately. After controlling for louse species richness, host body mass was still positively correlated with mean abundance (partial P -value = 0.04, see Table 2a). Furthermore, louse species richness and host body mass were positively correlated with mean abundance at higher levels of sampling effort (Table 2a, Fig. 2a, b). A third variable, length of the bill overhang, was *negatively* correlated with mean abundance in two of the three analyses (Table 2a, Fig. 2c). None of the eight remaining morphological variables, nor any of the three ecological variables, correlated significantly with mean louse abundance.

Small-bodied species omitted

We repeated the analyses after omitting the 18 species sampled by visual examination rather than feather ruffling. For the remaining 34 species, r -values increased and P -values remained essentially the same, indicating that the overall relationships were not altered by excluding birds sampled by visual examination.

Non-passerine species

Louse species richness was positively correlated with mean abundance at all levels of sampling effort when the analysis was restricted to non-passerines (Table 2b). Host body mass was also positively correlated with mean abundance, except when the analysis was restricted to species with at least seven individuals sampled. Length of the bill overhang among non-passerines was not correlated with mean louse abundance at any level of sampling effort (Table 2b). None of the other host variables correlated significantly with mean abundance among non-passerines.

Passerine species

A different picture emerged when the analysis was restricted to passerines. Louse species richness was not correlated with mean abundance at any level of analysis, whereas host body mass was positively correlated with abundance at all levels (Table 2c). In addition, length of the bill overhang was negatively correlated with mean abundance at all levels of sampling effort. None of the other host variables correlated significantly with mean abundance among passerines.

Discussion

Comparative studies of parasite community ecology are often hampered by uneven data sets cobbled together from a number of smaller studies by investigators using inconsistent methods. We used consistent methodology

Table 2. Multiple regression of mean louse abundance on louse species richness, host body mass and length of the bill overhang for a) all bird species, b) non-passerine species and c) passerine species. The first column gives the sample size required for inclusion of a species in the analysis (number of species meeting this criterion given in brackets). Percent variation and partial P -values are given for each independent variable. Percent variation is the amount by which the overall r^2 increased when the variable was added to the regression model. In cases of significant correlations, species richness and host body mass were positively and bill overhang was negatively correlated with mean abundance.

a		Mean abundance vs			
host individuals (species)	df	louse species richness	host body mass	bill overhang	overall model
$n \geq 3$ (52)	3,43	30% <0.0001	4% 0.04	2% 0.24	36% 0.0002
$n \geq 5$ (34)	3,27	26% 0.0008	18% 0.0005	10% 0.02	54% <0.0001
$n \geq 7$ (25)	3,20	26% 0.0005	23% 0.0004	12% 0.02	61% 0.0002
b		Mean abundance vs			
host individuals (species)	df	louse species richness	host body mass	bill overhang	overall model
$n \geq 3$ (34)	3,26	49% <0.0001	6% 0.05	1% 0.38	56% <0.0001
$n \geq 5$ (23)	3,16	44% 0.002	11% 0.03	4% 0.24	59% 0.002
$n \geq 7$ (16)	3,11	47% 0.006	17% 0.17	0% 0.95	64% 0.009
c		Mean abundance vs			
host individuals (species)	df	louse species richness	host body mass	bill overhang	overall model
$n \geq 3$ (18)	3,13	2% 0.27	40% 0.005	13% 0.04	55% 0.02
$n \geq 5$ (11)	3,7	4% 0.28	37% 0.002	36% 0.01	77% 0.01
$n \geq 7$ (9)	3,5	10% 0.18	36% 0.01	36% 0.01	82% 0.03

to compare parasite richness and abundance across a diverse set of birds (Table 1) sampled in a single geographic region over a relatively short time interval. Sampling a diverse set of species is desirable because it increases the range of variation in host parameters which, in turn, increases the inferential power of the comparative study. Peru is home the most diverse assemblage of birds on the planet (Parker et al. 1982), making it an excellent location for the present study. We controlled for the effects of sampling effort by using increasingly restrictive data sets and species richness estimation methods (Walther and Morand 1998). Finally, the data were analysed using comparative methods that control for host phylogeny, which is known to influence estimates of parasite richness and abundance (Poulin 1998).

Cumulative species richness of lice

Previous workers have demonstrated significant correlations between parasite species richness and host body size, local population density, and geographic range size (see Introduction). In this study, however, we found no

correlation between louse species richness and any of the 13 host variables examined, including host body size, density and geographic range, regardless of which data set we analysed. Two factors may have contributed to the lack of any correlation between louse species richness and host variables. First, Poulin (1997) demonstrated that correlations between parasite richness and host variables can be considerably diminished after controlling for sampling effort and host phylogeny. An across-species correlation between louse species richness and body weight is significant for our overall data set (unpublished results), but we lose significance once we control for sampling effort and phylogeny. Second, louse species richness did not show much variation, ranging only from 0–3 species (Table 1). All else being equal, it is more difficult to detect correlations involving variables that show little variation.

In the only other comparative study of louse species richness, Walther (1997) used a data set in which richness varied from 0–12 species. He found a significant correlation between louse species richness and body mass, even after controlling for sampling effort and phylogeny. Thus, host morphology can influence the species richness of louse communities.

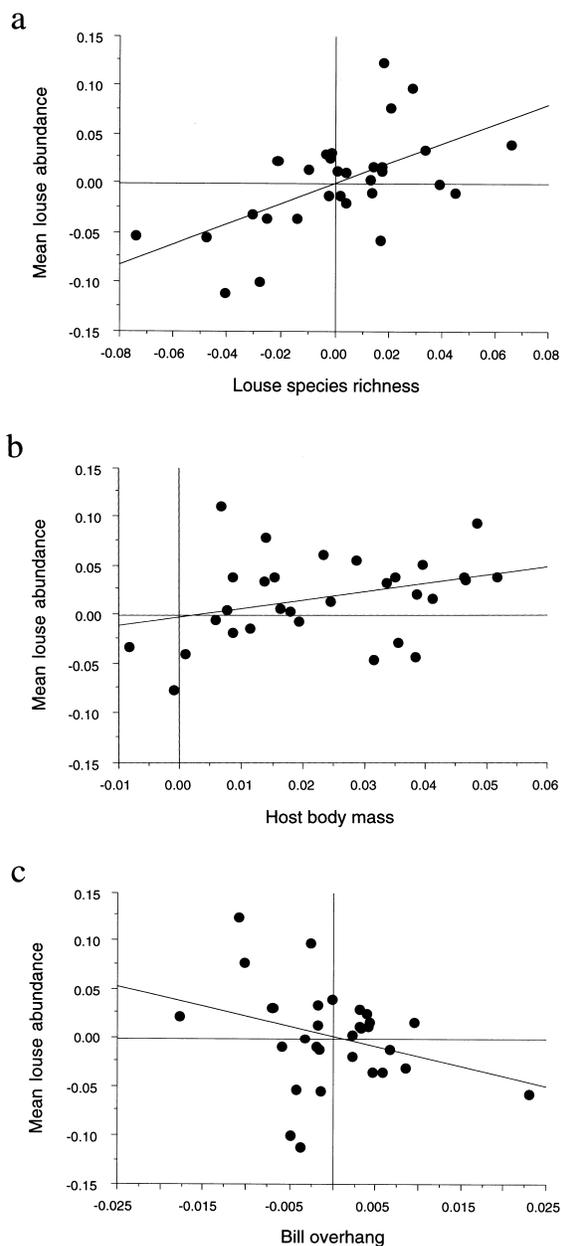


Fig. 2. Relationship between residual contrasts in louse abundance and residual contrasts in a) louse species richness, b) host body mass, and c) length of the bill overhang. Residual contrasts in a and c are residuals of the independent contrasts of the x and y variables regressed against the independent contrasts of body mass. Residual contrasts in b are the residuals of the contrasts of the x and y variables regressed against the contrasts of louse species richness. Data in all three panels are for the 34 host species with a minimum of five individuals sampled for lice (Table 2a).

Mean abundance of lice

Although louse richness was not correlated with any of the host variables we examined, it was highly correlated

with mean louse abundance, explaining $> 25\%$ of the variation in abundance (Table 2a, Fig. 2a). We believe the explanation for this relationship is straightforward. Many species of lice show morphological and behavioural specialisations for particular microhabitats on the body of the host, such as the wings or the head (Nelson and Murray 1971, Marshall 1981, Clayton 1991). Microhabitat specialisation should result in the overall abundance of lice on a bird infested by two species of lice being greater than that on a bird infested by only one species. This prediction could conceivably be tested by monitoring the overall abundance of lice on birds experimentally infested with different combinations of species.

Unlike richness, louse abundance was correlated with some of the host variables we measured. The strongest relationship was a positive correlation between host body size and abundance, explaining up to 23% of the variation in abundance (Table 2a, Fig. 2b). Although several earlier studies showed a similar correlation between host body size and parasite abundance (see Introduction), Poulin cautioned that the strength of the correlation is diminished after controlling for sampling effort and phylogeny. The relationship of host body size to louse abundance remained strong even though we controlled for both of these parameters.

Both the correlation between mean abundance and richness, and that between mean abundance and host body mass, were significant for our overall data set (Table 2a). Separation of the data into passerine vs non-passerine hosts yielded dissimilar results. Louse species richness was the strongest correlate of louse abundance on non-passerines (Table 2b), whereas host body mass was the strongest correlate of louse abundance on passerines (Table 2c). This difference may have been due partly to the fact that variation in louse richness was greater on non-passerines ($CV = 0.81$) than on passerines ($CV = 0.49$), whereas the opposite trend held for variation in the body mass of non-passerines ($CV = 1.30$) versus passerines ($CV = 1.70$).

In a recent study that also controlled for sampling effort and phylogeny, Rózsa (1997a) showed a correlation between host body mass and the mean abundance of lice among 36 species of temperate birds. He hypothesised that the correlation could be explained by 1) more resources on larger hosts, 2) more refugia from preening on larger hosts, or 3) greater longevity of larger hosts, which would provide a larger window of opportunity for infestation by lice. Our data are insufficient to evaluate the relative merits of these three hypotheses. Further comparative and experimental studies should try to disentangle these possible explanations.

Another factor that might contribute to the positive correlation between host body size and louse abundance is grooming time. Hart et al. (1992) showed that small-bodied antelope species groom significantly more than large-bodied species. They interpreted this correla-

tion to be a result of selection for increased grooming in smaller species, which may be more vulnerable to damage by blood-sucking ticks because of their higher surface:volume ratio. However, in a comparative analysis of birds, Cotgreave and Clayton (1994) found no significant relationship between body mass and grooming time. Walther (1997) found a significant *positive* correlation between body mass and grooming time, suggesting that, if anything, grooming should diminish the positive correlation between body mass and louse abundance in birds.

We found no correlation between louse abundance and host geographic range or foraging stratum. Geographic range might be expected to correlate with parasite species richness, but not abundance (see Introduction). Foraging stratum is not expected to correlate either with louse richness, nor abundance. Lice spend their entire life cycle on the body of the host and therefore have little opportunity to be influenced by these components of host ecology. Our data on foraging stratum are a subset of a larger data set analysed by Walther et al. (1999), who similarly found no relationship between foraging stratum and mean louse abundance.

Local host population density could conceivably be correlated with louse abundance since transmission rates are known to increase with increasing host density (Clayton 1991). The fact that we found no significant relationship between host density and louse abundance could be a result of the rather crude index of host population density, which nevertheless remains the best data available (Parker III et al. 1996).

Host defence is another potential determinant of parasite abundance. Behavioural defences such as preening and scratching might well influence louse diversity. For this reason we examined the relationship of bill, foot and toe morphology to the species richness and mean abundance of lice. After controlling for sampling effort, host phylogeny, louse species richness and host body mass, a significant *negative* relationship between length of the bill overhang and mean louse abundance was apparent for the overall data set (Table 2a, Fig. 2c). Separation of the data set into passerine vs non-passerine hosts revealed no correlation between the overhang and louse abundance in non-passerines, but a relatively strong negative correlation between these variables in passerines, explaining up to 36% of the variation in mean louse abundance. Additional data, discussed below, confirm that the overhang is important for controlling lice.

Role of the bill overhang in host defence

“This is how I see the near future of parasite evolutionary ecology – comparative studies based on robust phylogenies used to identify associations between variables, and to

generate hypotheses that can then be tested with extant taxa under experimental conditions” (Poulin 1998)

Our study identifies a novel morphological component of host defence that appears to play a role in structuring louse communities. The relationship between bill overhang and mean louse abundance nicely illustrates the power of comparative approaches for identifying variables worthy of subsequent study (Losos 1996, Poulin 1998). This correlation directly motivated a recent test of the importance of the bill overhang for preening by captive feral pigeons (*Columba livia*). Experimental removal of the 1–2 mm overhang triggered a dramatic increase in louse abundance (Moyer and Clayton in press), with accompanying feather damage sufficient to reduce host survival (Clayton et al. 1999). This experiment differed from published experiments in which preening was impaired through the removal of 5–10 mm from the upper mandible (reviewed in Clayton 1991). Removal of this much tissue makes the bill tips asymmetrical, precluding the forceps action required for efficient preening. In contrast, removal of just the tiny overhang increases symmetry of the bill, simulating the morphology of species lacking a bill overhang (Table 1). The results of this experiment clearly demonstrate that the bill overhang is critical for louse control in feral pigeons, which are non-passerines.

The importance of the bill overhang for controlling parasites in passerines is reinforced by a “natural” experiment involving geographically distinct populations of the western scrub jay (*Aphelocoma californica*). Scrub jays living in oak woodland have a pronounced bill overhang, whereas those living in pinyon–juniper woodland have a much reduced overhang. Jays in oak feed mainly on acorns, whereas those in pinyon–juniper feed mainly on pine seeds. Peterson (1993) showed that jays in pinyon–juniper have a reduced overhang because it interferes with the forceps action of the bill used in extracting pine seeds from between the scales of pine cones (Bardwell et al. in press). A recent comparison of the diversity of lice on the jays in these two habitats revealed that individuals with a reduced overhang have significantly more lice than those with a pronounced overhang (Moyer et al. unpubl.). This finding is consistent with the results of the feral pigeon experiment showing that the overhang plays a role in louse control.

The parasite-control function of the overhang is thus suggested by three lines of evidence: 1) comparisons among species (current study); 2) comparisons among populations within a host species (jays); and 3) results of a controlled experiment (pigeons). Although the important role of preening in controlling ectoparasites has long been recognised (Rothschild and Clay 1952), this study is the first to suggest a parasite-control function for such a detailed component of bill morphology among species. Rather than enhancing perfor-

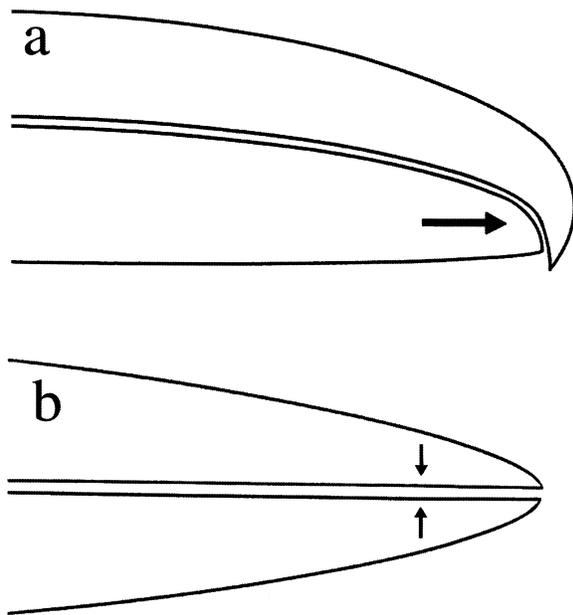


Fig. 3. Functional hypothesis for the role of the bill overhang in preening. (a) The bill overhang generates a shearing force sufficient to damage lice as the lower mandible moves forward slightly during preening; (b) straight mandibles can only exert a relatively weak vertical force, by comparison.

mance, symmetry of the bill actually impairs preening for louse control.

We suggest a functional hypothesis for how the overhang may work (Fig. 3). Chewing lice are dorsoventrally flattened and extremely resistant to damage (Marshall 1981). Preening birds disable lice by crushing or otherwise damaging them (DHC pers. obs.). Birds with straight mandibles (Fig. 3b) may have trouble damaging lice because the vertical force that can be exerted between the tips of straight mandibles is relatively weak (Bock 1966). Birds with an overhang (Fig. 3a), however, could generate a shearing force sufficient to damage lice. This model assumes that the lower mandible moves forward during preening. Slow-motion video of preening by captive feral pigeons shows that the lower mandible does, in fact, move forward slightly, consistent with this functional hypothesis (unpubl.; see <http://darwin.biology.utah.edu/preen.html>).

Birds may incur a parasite-related cost if their foraging ecology has selected for loss of the bill overhang, which may be compensated by other mechanisms of parasite defence (Moyer and Clayton in press). Our results suggest that bill morphology is influenced by the need for efficient preening, in addition to the more generally recognised need for efficient foraging. Preening and foraging are both selective forces shaping the evolution of bill morphology. Avian biologists have focused almost exclusively on bills as tools for feeding. We suggest that the adaptive radiation of bill morphol-

ogy should be reinterpreted with both preening and feeding in mind.

In conclusion, our study shows that hosts with more species of lice have more individual lice. Our study further shows that larger-bodied hosts have more lice, even when species richness is held constant. Finally, our study reveals a morphological component of host defence: birds with longer bill overhangs have fewer lice. As such, this is one of the first comparative studies to demonstrate an impact of host defence on parasite abundance.

Acknowledgements – We are grateful to J. Fitzpatrick, D. Stotz, and D. Willard for making the fieldwork possible. We also thank the following individuals for assistance at various stages in the project: P. Bühler, C. Clarebrough, K. Clayton, P. Ewald, A. Gosler, R. Gregory, P. Iseemann, K. Johnson, R. McCall, D. Milson, S. Morand, B. Moyer, M. Pagel, T. Peterson, R. Poulin, R. Price, A. Purvis, A. Rambaut, A. Read, D. Schemske, D. Tompkins, and G. Wragg. We are grateful to R. Gregory and J. Howe for calculating geographic range sizes, and to K. Johnson and S. Al-Tamimi for preparing Figs 1 and 3, respectively. DHC was supported by NSF CAREER award DEB-9703003. BAW was supported by an Evan Carroll Commager Fellowship and a John Woodruff Simpson Fellowship, both from Amherst College. Funding for fieldwork was provided by the Field Museum of Natural History, Chicago and NSF grant BSR-8508361 to J. Fitzpatrick for Peruvian faunal inventory work.

References

- Arneberg, P., Skorping, A., Grenfell, B. and Read, A. F. 1998. Host densities as determinants of abundance in parasite communities. – *Proc. R. Soc. Lond. B* 265: 1283–1289.
- Bardwell, E., Benkman, C. W. and Gould, W. R. In press. Adaptive geographic variation in Western scrub-jays. – *Ecology*.
- Bleiweiss, R., Kirsch, J. A. W. and Matheus, J. C. 1994. DNA-DNA hybridization evidence for subfamily structure among hummingbirds. – *Auk* 111: 8–19.
- Bock, W. J. 1966. An approach to the functional analysis of bill shape. – *Auk* 83: 10–51.
- Brooks, D. R. and McLennan, D. A. 1993. *Parascript: parasites and the language of evolution*. – Smithsonian Inst. Press.
- Brown, N. S. 1972. The effect of host beak condition on the size of *Menacanthus stramineus* populations of domestic chickens. – *Poultry Sci.* 51: 162–164.
- Brown, N. S. 1974. The effect of louse infestation, wet feathers, and relative humidity on the grooming behavior of the domestic chicken. – *Poultry Sci.* 53: 1717–1719.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. – *J. Parasitol.* 83: 575–583.
- Clayton, D. H. 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. – *Am. Zool.* 30: 251–262.
- Clayton, D. H. 1991. Coevolution of avian grooming and ectoparasite avoidance. – In: Loye, J. E. and Zuk, M. (eds), *Bird-parasite interactions: ecology, evolution, and behaviour*. Oxford Univ. Press, pp. 258–289.
- Clayton, D. H. and Tompkins, D. M. 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). – *Parasitology* 110: 195–206.
- Clayton, D. H. and Moore, J. 1997. *Host-parasite evolution: general principles and avian models*. – Oxford Univ. Press.

- Clayton, D. H. and Walther, B. A. 1997. Collection and quantification of arthropod parasites of birds. – In: Clayton, D. H. and Moore, J. (eds), *Host-parasite evolution: general principles and avian models*. Oxford Univ. Press, pp. 419–440.
- Clayton, D. H. and Drown, D. M. In press. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). – *J. Parasitol.*
- Clayton, D. H., Gregory, R. D. and Price, R. D. 1992a. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). – *J. Anim. Ecol.* 61: 781–795.
- Clayton, D. H., Pruett-Jones, S. G. and Lande, R. 1992b. Reappraisal of the interspecific prediction of parasite-mediated sexual selection: opportunity knocks. – *J. Theor. Biol.* 157: 95–108.
- Clayton, D. H., Lee, P. L. M., Tompkins, D. M. and Brodie III, E. D. 1999. Reciprocal natural selection on host-parasite phenotypes. – *Am. Nat.* 154: 261–270.
- Clayton, D. H., Al-Tamimi, S. and Johnson, K. P. In press. The ecological basis of coevolutionary history. – In: Page, R. D. M. (ed.), *Tangled trees: phylogenies, cospeciation and coevolution*. Univ. of Chicago Press.
- Cotgreave, P. and Clayton, D. H. 1994. Comparative analysis of time spent grooming by birds in relation to parasite load. – *Behaviour* 131: 171–187.
- Dunning, J. S. 1982. *South American birds: a photographic aid to identification*. – Harrowood Books.
- Dunning, J. S. 1987. *South American birds: a photographic guide to identification*. – Harrowood Books.
- Esch, G. W., Bush, A. O. and Aho, J. M. 1990. *Parasite communities: patterns and processes*. – Chapman & Hall.
- Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.
- Felsenstein, J. 1988. Phylogenies and quantitative methods. – *Annu. Rev. Ecol. Syst.* 19: 445–471.
- Fowler, J. A. 1984. A safer anaesthetic for delousing live birds. – *Ringer's Bull.* 6: 69.
- Garland, T., Harvey, P. H. and Ives, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. – *Syst. Biol.* 41: 18–32.
- Garvin, M. C. and Remsen, J. V. 1997. An alternative hypothesis for heavier parasite loads of brightly colored birds: exposure at the nest. – *Auk* 114: 179–191.
- Gerwin, J. A. and Zink, R. M. 1989. Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymic perspective. – *Wilson Bull.* 101: 525–544.
- Gill, F. B. and Gerwin, J. A. 1989. Protein relationships among hermit hummingbirds. – *Proc. Acad. Nat. Sci. Phila.* 141: 409–421.
- Gosler, A. G. 1987. Pattern and process in the bill morphology of the great tit *Parus major*. – *Ibis* 129: 451–476.
- Grafen, A. 1989. The phylogenetic regression. – *Philos. Trans. R. Soc. Lond. B* 326: 119–156.
- Gregory, R. D. 1990. Parasites and host geographic range as illustrated by waterfowl. – *Funct. Ecol.* 4: 645–654.
- Gregory, R. D. 1997. Comparative studies of host-parasite communities. – In: Clayton, D. H. and Moore, J. (eds), *Host-parasite evolution: general principles and avian models*. Oxford Univ. Press, pp. 198–211.
- Grenfell, B. T. and Dobson, A. P. 1995. *Ecology of infectious diseases in natural populations*. – Cambridge Univ. Press.
- Grutter, A. S. and Poulin, R. 1998. Intraspecific and interspecific relationships between host size and the abundance of parasitic larval gnathiid isopods on coral reef fishes. – *Mar. Ecol. Prog. Ser.* 164: 263–271.
- Hart, B. L., Hart, L. A., Mooring, M. S. and Olubayo, R. 1992. Biological basis of grooming behaviour in antelope; the body size, vigilance and habitat principles. – *Anim. Behav.* 44: 615–631.
- Harvey, P. H. and Pagel, M. D. 1991. *The comparative method in evolutionary biology*. – Oxford Univ. Press.
- John, J. L. 1995. Parasites and the avian spleen: helminths. – *Biol. J. Linn. Soc.* 54: 87–106.
- Krebs, C. J. 1989. *Ecological methodology*. – Harper & Row.
- Losos, J. B. 1996. Phylogenies and comparative biology, stage II: testing causal hypotheses derived with data from extant taxa. – *Syst. Biol.* 45: 259–260.
- Marshall, A. G. 1981. *The ecology of ectoparasitic insects*. – Academic Press.
- Mindell, D. P. 1997. *Avian molecular evolution and systematics*. – Academic Press.
- Morand, S. and Poulin, R. 1998. Density, body mass and parasite species richness of terrestrial mammals. – *Evol. Ecol.* 12: 717–727.
- Morand, S., Poulin, R., Rhode, K. and Hayward, C. 1999. Aggregation and species coexistence of ectoparasites of marine fishes. – *Int. J. Parasitol.* 29: 663–672.
- Morand, S., Hafner, M. S., Page, R. D. M. and Reed, D. L. 2000. Comparative body size relationships in pocket gophers and their chewing lice. – *Biol. J. Linn. Soc.* 70: 239–249.
- Moyer, B. R. and Clayton, D. H. In press. Avian defenses against ectoparasites. – In: van Emden, H. F. and Rothschild, M. (eds), *Insect and bird interactions*. Intercept.
- Murray, M. D. 1990. Influence of host behaviour on some ectoparasites of birds and mammals. – In: Barnard, C. J. and Behnke, J. M. (eds), *Parasitism and host behaviour*. Taylor and Francis, pp. 290–315.
- Nelson, B. C. and Murray, M. D. 1971. The distribution of Mallophaga on the domestic pigeon *Columba livia*. – *Int. J. Parasitol.* 1: 21–29.
- Pagel, M. D. 1992. A method for the analysis of comparative data. – *J. Theor. Biol.* 156: 431–442.
- Parker III, T. A., Stotz, D. F. and Fitzpatrick, J. W. 1996. Ecological and distributional databases for Neotropical birds. – In: Stotz, D. F., Fitzpatrick, J. W., Parker III, T. A. and Moskovits, D. K. (eds), *Neotropical birds: ecology and conservation*. Univ. of Chicago Press, pp. 131–436.
- Parker, T. A. I., Parker, S. A. and Plenge, M. A. 1982. An annotated checklist of Peruvian birds. – Buteo Books.
- Paterson, A. M. and Gray, R. D. 1997. Host-parasite cospeciation, host switching and missing the boat. – In: Clayton, D. H. and Moore, J. (eds), *Host-parasite evolution: general principles and avian models*. Oxford Univ. Press, pp. 236–250.
- Peterson, A. T. 1993. Adaptive geographical variation in bill shape of scrub jays (*Aphelocoma coerulescens*). – *Am. Nat.* 142: 508–527.
- Poiani, A. 1992. Ectoparasitism as a possible cost of social life: a comparative analysis using Australian passerines (Passeriformes). – *Oecologia* 92: 429–441.
- Poulin, R. 1997. Species richness of parasite assemblages: evolution and patterns. – *Annu. Rev. Ecol. Syst.* 28: 341–358.
- Poulin, R. 1998. *Evolutionary ecology of parasites: from individuals to communities*. – Chapman & Hall.
- Poulin, R. and Rohde, K. 1997. Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. – *Oecologia* 110: 278–283.
- Price, P. W., Westoby, M. and Rice, B. 1988. Parasite-mediated competition: some predictions and tests. – *Am. Nat.* 131: 544–555.
- Pruett-Jones, M. and Pruett-Jones, S. 1991. Analysis and ecological correlates of tick burdens in a New Guinea avifauna. – In: Loye, J. E. and Zuk, M. (eds), *Bird-parasite interactions: ecology, evolution, and behaviour*. Oxford Univ. Press, pp. 154–176.
- Purvis, A. and Rambaut, A. 1994. *Comparative analysis by independent contrasts (C.A.I.C.): user's guide*. – Oxford Univ., Oxford.

- Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. – *Comput. Appl. Biosci.* 11: 247–251.
- Raikow, R. J. 1994. A phylogeny of the woodcreepers (Dendrocolaptinae). – *Auk* 111: 104–115.
- Read, A. F. 1991. Passerine polygyny: a role for parasites? – *Am. Nat.* 138: 434–459.
- Rothschild, M. and Clay, T. 1952. Fleas, flukes and cuckoos. – Collins.
- Rózsa, L. 1997a. Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). – *J. Avian Biol.* 28: 249–254.
- Rózsa, L. 1997b. Wing-feather mite (Acari: Proctophylloidae) abundance correlates with body mass of passerine hosts: a comparative study. – *Can. J. Zool.* 75: 1535–1539.
- Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds: a study in molecular evolution. – Yale Univ. Press.
- Sibley, C. G. and Monroe, B. L. 1990. Distribution and taxonomy of birds of the world. – Yale Univ. Press.
- Siemann, E., Tilman, D. and Haarstad, J. 1996. Insect species diversity, abundance and body size relationships. – *Nature* 380: 704–706.
- Simberloff, D. and Moore, J. 1997. Community ecology of parasites and free-living animals. – In: Clayton, D. H. and Moore, J. (eds), *Host-parasite evolution: general principles and avian models*. Oxford Univ. Press, pp. 174–197.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry: the principles and practice of statistics in biological research*. – Freeman.
- Sousa, W. P. 1994. Patterns and processes in communities of helminth parasites. – *Trends Ecol. Evol.* 9: 52–57.
- Southwood, T. R. E., Moran, V. C. and Kennedy, C. E. J. 1982. The richness, abundance and biomass of the arthropod communities on trees. – *J. Anim. Ecol.* 51: 635–649.
- Stork, N. E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. – *J. Trop. Ecol.* 7: 161–180.
- Stotz, D. F., Fitzpatrick, J. W., Parker III, T. A. and Moskovits, D. K. 1996. *Neotropical birds: ecology and conservation*. – Univ. of Chicago Press.
- Swierczewski, E. V. and Raikow, R. J. 1981. Hind limb morphology, phylogeny, and classification of the Piciformes. – *Auk* 98: 466–480.
- Tella, J. L., Blanco, G., Forero, M. G. et al. 1999. Habitat, world geographic range, and embryonic development of hosts explain the prevalence of avian hematozoa at small and phylogenetic scales. – *Proc. Natl. Acad. Sci. USA* 96: 1785–1789.
- Temeles, E. J. 1996. A new dimension to hummingbird-flower relationships. – *Oecologia* 105: 517–523.
- Tompkins, D. M. and Clayton, D. H. 1999. Host-resources govern the specificity of swiftlet lice: size matters. – *J. Anim. Ecol.* 68: 489–500.
- Walther, B. A. 1997. *Comparative studies of ectoparasite communities of birds*. – PhD, Oxford Univ., Oxford.
- Walther, B. A. and Morand, S. 1998. Comparative performance of species richness estimation methods. – *Parasitology* 116: 395–405.
- Walther, B. A., Cotgreave, P., Gregory, R. D. et al. 1995. Sampling effort and parasite species richness. – *Parasitol. Today* 11: 306–310.
- Walther, B. A., Clayton, D. H. and Gregory, R. D. 1999. Showiness of Neotropical birds in relation to ectoparasite abundance and foraging stratum. – *Oikos* 87: 157–165.
- Wetmore, A. 1936. The number of contour feathers in passeriform and related birds. – *Auk* 53: 159–169.
- Zuk, M. 1991. Parasites and bright birds: new data and a new prediction. – In: Loye, J. E. and Zuk, M. (eds), *Bird-parasite interactions: ecology, evolution, and behaviour*. Oxford Univ. Press, pp. 317–327.