

Showiness of Neotropical birds in relation to ectoparasite abundance and foraging stratum

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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.

The evolution of bird coloration has inspired many hypotheses. We report the results of comparative tests involving the interacting effects of microhabitat use, sexual selection and parasite transmission on colour evolution. We used a data set of chewing lice (Insecta: Phthiraptera) sampled from 122 Neotropical bird species to test Hamilton and Zuk's prediction that species subjected to high parasite "pressure" evolve showy traits that enhance the ability of females to choose parasite free mates. We found no significant relationship between mean parasite abundance and showiness among the 122 species. However, for the 66 non-passerine species in the data set, we found a significant *negative* relationship between parasite abundance and showiness, contrary to the Hamilton and Zuk prediction. These results are discussed in light of recent work on parasite-mediated sexual selection. We also tested for a relationship between showiness and the microhabitat use of different species of rainforest birds. Like other authors, we found a significant positive relationship between showiness and foraging stratum among the 113 species analysed. While drab species occur in all forest strata, showy species occur mostly in the midstorey and canopy. We discuss variables which may influence the evolution of such a pattern among forest birds.

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The intriguing and beautiful colours of birds have inspired dozens of hypotheses explaining the adaptive significance of coloration. Savalli (1995) classified these hypotheses into several major categories, the two largest of which pertain to the role of coloration for signalling conspecifics and members of other species, such as predators. Showy traits such as colourful plumage and elaborate crests are thought to play a role in conspecific mate choice and be favoured by sexual selection (Andersson 1994). Showy coloration may also render birds more conspicuous or more cryptic to predators, depending on background coloration and other factors (Cott 1957, Endler 1990, Götmark 1999). Comparative studies can help to reveal the adap-

tive function of avian coloration. We report the results of a comparative study which investigates the possible roles of among- and between-species signalling on the evolution of showy coloration in Peruvian birds.

Hamilton and Zuk (1982) suggested that showy male coloration conveys information to females regarding male parasite load. According to their hypothesis, females choose low load males on the basis of showy traits whose full expression depends on health and vigour, such as brightly coloured plumage subject to fading in the presence of high parasite loads. Thus parasite load and showiness are predicted to be inversely correlated within species. Hamilton and Zuk further predicted that the negative correlation of para-

Accepted 27 January 1999

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ISSN 0030-1299

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site load and showiness *within* species will generate a positive correlation between these variables *among* species since selection for showiness should be most pronounced in species with the highest mean parasite loads. While Hamilton and Zuk found comparative evidence for the among-species hypothesis, further studies have produced equivocal results (reviewed in Andersson 1994, Hillgarth and Wingfield 1997).

Garvin and Remsen (1997) recently documented a positive relationship among species between showiness and blood parasite prevalence, in accordance with the Hamilton and Zuk hypothesis. However, they argued that the relationship is a spurious correlation generated by covariation of showiness and prevalence with differences in host microhabitat use. Since blood parasite vectors such as biting flies are more abundant in the forest canopy than in the understorey, host species which spend most of their time in the canopy have more blood parasites simply because of the greater vector abundance in the canopy.

Garvin and Remsen presented further results demonstrating that canopy birds are significantly showier than understorey birds, a relationship found by several other workers (Baker and Parker 1979, Shutler and Weatherhead 1990, Johnson 1991, Pruett-Jones et al. 1991). Explanations for this relationship usually involve third variables that covary with forest stratum, such as the abundance of predators and parasites (Shutler and Weatherhead 1990, Garvin and Remsen 1997). For example, greater abundance of predators near the ground may select for crypsis, and against showiness, in species of birds that spend more time near the ground (Shutler and Weatherhead 1990).

We report the results of a comparative study of showiness, parasite load and forest stratum for 122 species of Peruvian birds sampled for chewing lice by Clayton et al. (1992a). Chewing lice are obligate parasites that are confined to the body of the host, making it possible to obtain accurate estimates of louse abundance under field conditions (Clayton and Walther 1997). They are known to have a significant impact on mate choice and other components of host fitness (Clayton 1990, Spurrier et al. 1991, Booth et al. 1993, Brown et al. 1995). Chewing lice complete their entire life cycle on the body of the host; eggs are glued to the feathers with a glandular cement. Transmission of lice to new hosts requires direct contact between individuals such as that between parents and offspring in the nest (Marshall 1981).

Therefore, chewing lice provide a unique opportunity to circumvent covariation of showiness and parasite load with foraging stratum, as in the case of Garvin and Remsen's study. We predict that louse abundance should be unrelated to foraging stratum as there is little or no opportunity for host microhabitat use to influence the probability of louse transmission. We should thus be able to exclude the possibility that any correla-

tion between louse abundance and showiness is due to covariation with stratum.

Furthermore, chewing lice are generally not exposed to the host's immune system because most taxa feed solely on feathers and dermal debris. Rather, the main defence of birds against chewing lice is to remove them by grooming. Experimental work has shown that male birds with lower louse loads are more attractive to females and obtain significantly more mates than males with higher louse loads (Clayton 1990, Spurrier et al. 1991). The cues used by females to assess parasite load range from ornamental traits altered by the lice (Spurrier et al. 1991) to reduced rates of male display (Clayton 1990) as a result of the thermoregulatory costs of high louse loads (Booth et al. 1993). Females choosing to mate with low-load males might obtain several benefits, including "good genes" for grooming ability (Hamilton and Zuk 1982) or the avoidance of direct transmission of lice to themselves or their offspring (Able 1996). Species in which louse-mediated mate choice is strong should have more elaborate louse-indicative traits, all else being equal. Therefore, it is reasonable to predict a correlation between louse load and showiness among species of birds (Clayton et al. 1992b), in line with the original Hamilton and Zuk prediction. Our study is the first comparative test of parasite-mediated sexual selection using data for chewing lice.

Materials and methods

Parasite data

A total of 685 birds representing 127 species in 26 families was sampled in south-eastern Peru for chewing lice (Insecta: Phthiraptera). Birds were sampled for lice by DHC prior to being prepared as museum specimens. Each freshly killed bird was placed in a fumigation chamber to kill its ectoparasites, which were then removed from the plumage with repeated bouts of feather ruffling. See Clayton et al. (1992a) for full details including a list of host and parasite taxa, numbers of hosts sampled and raw parasite abundance data.

The negative impact of chewing lice on an individual host is proportional to the population size of lice on that host (Booth et al. 1993). It is thus reasonable to assume that, all else being equal, lice have the greatest impact on host species with the largest mean louse population sizes. Mean population size, or "mean abundance" (Bush et al. 1997), was the parasite parameter used for all our analyses. To calculate mean abundance, we averaged the total number of lice (pooling all louse species) from all individuals of a given bird species, including louse-free individuals.

Five bird species were excluded a priori from the original Clayton et al. (1992a) data set for the following

reasons: Two orders (Gruiformes and Trogoniformes) were each represented by parasite samples from only a single individual bird. The species *Opisthocomus hoazin* was omitted because it has twice the body mass of the next largest species in the data set, and body mass is known to be a significant correlate of chewing louse abundance (see Results). Finally, the species *Conopophaga peruviana* and *Phlogophilus harteri* had to be excluded because no illustration could be found to use in scoring showiness. Our final host data set thus totalled 122 species. On average, 5.4 ± 0.9 (mean \pm S.E.) individuals of each species were sampled.

Host data

Showiness scores

Ideally, to measure showiness one should measure colour under relevant light conditions in relation to the background coloration and the perceptual visual system of the receiver (Endler 1990, 1992, Bennett et al. 1994). Although this is practical for limited numbers of bird species (Théry 1990, Endler and Théry 1996), it is not feasible for a data set containing 122 species of rain-forest birds. Instead, like many previous workers, we asked human volunteers to score showiness from photographs or paintings (e.g. Baker and Parker 1979, Hamilton and Zuk 1982, Read 1987, Read and Harvey 1989, Pruett-Jones et al. 1990, Shutler and Weatherhead 1990, Johnson 1991, Pruett-Jones et al. 1991, Weatherhead et al. 1991, Zuk 1991, John 1995, Garvin and Remsen 1997). Of course, human vision is not a substitute for avian vision (Bennett et al. 1994). Unlike humans, birds have (1) oil droplets in their retinas which may change their colour perception, (2) four or five cone types which may result in a four- or even five-dimensional colour system, and (3) receptors that perceive ultraviolet radiation. Nevertheless, human scores are unlikely to correlate spuriously with parasite abundance or foraging stratum. Therefore, analyses relying on human scores are unlikely to generate a Type 1 error (rejection of a true null hypothesis). In contrast, analyses using human scores could well generate a Type 2 error (acceptance of a false null hypothesis). Thus we caution readers against drawing firm conclusions from an apparent lack of relationship between human showiness scores and other variables.

We asked six volunteers unaware of the details of this study to rank "plumage showiness" and "overall showiness" for each of the 122 bird species using illustrations or photographs of male birds in breeding plumage (as illustrations of females were not available for many species). The volunteers were not allowed to communicate with one another. In addition to the illustrations of the birds, we provided them with written instructions defining plumage showiness as "showiness of plumage coloration" and overall showiness as "showiness of

overall appearance, including plumage showiness, skin colour, ornamentation, and any other visual cues that might be used by females when choosing males". Scorers were asked to rank birds on an interval scale from 1 (drab) to 6 (showy), disregarding any knowledge of non-anatomical traits such as behaviour or song. Scores were significantly correlated among the six scorers for both plumage showiness and overall showiness (Table 1).

For analyses involving showiness scores we used the mean of the six scores for each species. Mean plumage showiness and overall showiness were highly correlated across the 122 species ($r = 0.96$, $P < 0.0001$), and the results of all analyses using the two types of scores were quite similar. Therefore, "showiness" hereafter refers to analyses of overall showiness. For analyses restricted to plumage showiness, see Walther (1997).

Foraging stratum

We used foraging stratum to estimate and compare the amount of time birds spend in different strata of the forest. Parker et al. (1996) assign each bird species to one of the following foraging strata: (1) terrestrial, (2) terrestrial and understorey, (3) understorey, (4) understorey and midstorey, (5) midstorey, (6) midstorey and canopy, (7) canopy and (8) aerial. We omitted the four aerial species (swallows and swifts) a priori because the ecology and behaviour of these species are very different from those of forest habitats. We also omitted the five predatory bird species (falcons, hawks and owls) because selective pressures on predators may be very different from those of potential prey species.

Comparative analyses

We used Model 1 regression and multiple regression to test for correlations between continuous variables, including independent contrasts (see below). We used nonparametric regression to test for correlations involving foraging stratum, which is a categorical variable. All continuous variables were Box-Cox transformed prior to regression analysis (Krebs 1989). All P -values are two-tailed.

Table 1. Scorer correlations for plumage showiness and overall showiness (upper-right and lower-left triangle, respectively). Numbers are Spearman rank correlations corrected for ties ($P < 0.0001$ in all cases). The average correlation was 0.78 for both plumage showiness and overall showiness.

Scorer	1	2	3	4	5	6
1	—	0.85	0.74	0.78	0.80	0.76
2	0.81	—	0.78	0.74	0.79	0.74
3	0.73	0.79	—	0.73	0.83	0.73
4	0.79	0.75	0.77	—	0.80	0.75
5	0.83	0.83	0.82	0.78	—	0.81
6	0.82	0.76	0.71	0.75	0.83	—

Species are not statistically independent data points because of their shared evolutionary history. Therefore, we calculated phylogenetically independent contrasts using comparative methods developed by Felsenstein (1985, 1988), Burt (1989), Harvey and Pagel (1991) and Pagel (1992). We used the program CAIC (Purvis and Rambaut 1995), which generates independent contrasts for the variables being analysed at each node within a phylogeny. If adequately standardised, these contrasts conform to the assumptions of standard regression procedures (Harvey and Pagel 1991, Garland et al. 1992). All phylogenetically controlled regression equations were fitted through the origin (Grafen 1989, Garland et al. 1992).

We used Sibley and Ahlquist (1990) for phylogenetic information, combined with more detailed phylogenies of the Dendrocolapinae (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). Taxa not resolved by the above sources were entered in the analysis as polytomies. Branch lengths were logarithmically transformed to standardise contrasts (Garland et al. 1992). Purvis and Rambaut (1994) recommend subdividing and re-analysing large data sets to check for consistency of results among major clades. Therefore, after analysing the entire data set of 122 species, we conducted separate analyses of non-passerine species ($n = 66$) and passerine species ($n = 56$), in keeping with earlier authors (Pruett-Jones and Pruett-Jones 1991, Garvin and Remsen 1997).

Results

Showiness versus mean parasite abundance

Across-species plots showed no significant correlation between showiness and mean louse abundance among the 122 species ($r = 0.10$, $P = 0.25$), nor among the 56 passerine species ($r = 0.03$, $P = 0.85$) or 66 non-passerine species ($r = 0.12$, $P = 0.34$). Likewise, phylogenetically controlled analyses revealed no significant relationship between showiness and mean louse abundance among all species ($n = 84$ contrasts, $r = -0.07$, $P = 0.52$), or the passerine species ($n = 32$ contrasts, $r = 0.16$, $P = 0.37$). However, showiness and mean louse abundance were significantly negatively correlated among the non-passerine species (Fig. 1).

Although phylogenetically controlled, the initial analyses did not take into account the possible confounding effect of host body mass, which is known to correlate with parasite load (e.g. Poiani 1992, Gregory et al. 1996, Gregory 1997). Clayton and Walther (unpubl.) reported significant effects of host body mass on mean louse abundance for this same data set. When we included body mass as an independent variable in a

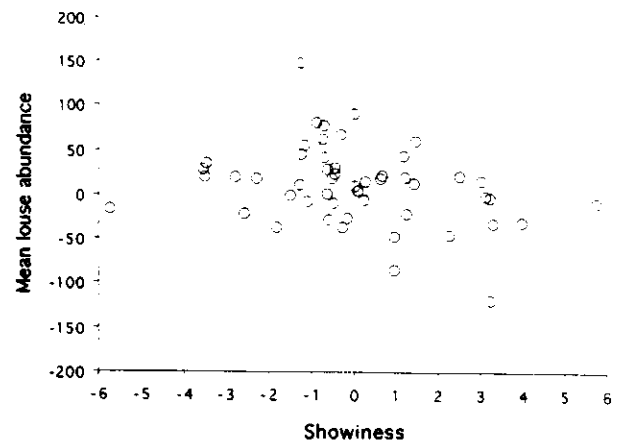


Fig. 1. Independent contrasts of showiness and mean louse abundance for 66 species of non-passerine Neotropical birds ($n = 51$ contrasts, $r = -0.28$, $P = 0.04$).

multiple regression analysis there was again no significant relationship between showiness and mean louse abundance among passerines; however, among non-passerines the significant negative correlation was still present (Table 2). As before, among all 122 species there was no significant relationship between showiness and mean louse abundance (Table 2).

Foraging stratum versus mean parasite abundance

Across-species plots showed no significant correlation between foraging stratum and mean louse abundance for the 122 species ($r_s = 0.08$, $P = 0.35$), nor among the 56 passerine species ($r_s = -0.04$, $P = 0.75$) or the 66 non-passerine species ($r_s = 0.26$, $P = 0.07$). Likewise, phylogenetically controlled analyses revealed no significant relationship between foraging stratum and mean louse abundance among all species ($n = 84$ contrasts, $r = -0.12$, $P = 0.28$), nor among the passerine species ($n = 32$ contrasts, $r = -0.27$, $P = 0.13$), or non-passerine species ($n = 51$ contrasts, $r = -0.003$, $P = 0.98$).

Showiness versus foraging stratum

An across-species plot revealed a significant correlation between showiness and foraging stratum among 113 species (Fig. 2). The relationship between these variables remained significant when the data were split into passerines ($n = 55$ species, $r_s = 0.27$, $P = 0.04$) and non-passerines ($n = 58$ species, $r_s = 0.32$, $P = 0.01$). It was also apparent at the level of family (Fig. 3), as well as in a phylogenetically controlled analysis of the 113 species ($n = 76$ contrasts, $r = 0.22$, $P = 0.04$). However, the relationship between showiness and foraging stratum was not significant in phylogenetically controlled analyses restricted to the passerines ($n = 31$ contrasts,

Table 2. Multiple regression of mean louse abundance on host body mass and showiness. Regressions were performed on independent contrasts data to control for host phylogeny. "% variation" is the amount by which overall r^2 increases when the respective variable is included in the regression model. Standard partial regression coefficients (std. coeff.) provide a measure of the strength and direction of a partial regression. Overall P -values for each regression analysis were $P = 0.09$ (all species), $P = 0.42$ (passerines) and $P = 0.02$ (non-passerines).

Variables Mean abundance vs	df	r	% variation	std. coeff.	partial P -values
for 122 species:					
host body mass	2.82	0.24	5	0.15	0.04
showiness			1	-0.10	0.36
for 56 passerine species:					
host body mass	2.30	0.24	4	0.12	0.33
showiness			2	0.14	0.45
for 66 non-passerine species:					
host body mass	2.49	0.38	5	0.18	0.04
showiness			9	-0.31	0.03

$r = 0.23$, $P = 0.20$) or non-passerines ($n = 44$ contrasts, $r = 0.22$, $P = 0.16$).

Discussion

Showiness versus mean parasite abundance

We found no significant relationship between showiness and louse abundance among the 122 species of birds analysed. However, for the analysis restricted to the 66 non-passerine species, we found a significant *negative* relationship between showiness and louse abundance after controlling for host phylogeny (Fig. 1). The negative correlation remained significant after controlling for host body mass (Table 2), which is known to be a significant determinant of louse abundance (Poianni 1992, Clayton and Walther unpubl.). It is important to control for body mass because large birds can presumably withstand more ectoparasites than small birds.

Our results indicate that showier species have fewer lice among non-passerines but not among passerines. It is difficult to know how to interpret this difference, particularly because so little is known about the biology of most of the species in our data set (Stotz et al. 1996). In any case, a phylogenetically controlled comparison of the two groups would be difficult since there is only one independent contrast possible between passerines (assuming they are monophyletic) and non-passerines (Nee et al. 1996).

The Hamilton and Zuk (1982) model assumes that choice of males with few parasites is indirectly beneficial to females through the inheritance of parasite resistance genes by their offspring. However, parasite-mediated sexual selection could be driven by more direct fitness benefits. In their "parasite avoidance" model, Borgia and Collis (1989) suggested that females choose parasite-free males to avoid direct transmission of contact-transmitted parasites. As a necessary condition of this model, but without further explanation,

they predicted no correlation between parasite load and elaboration of the male trait within species (Borgia and Collis 1990). Clayton (1990, 1991) took the opposite view that the adaptive value of parasite transmission avoidance could result in a negative correlation between parasite load and elaboration of male traits within species. Able (1996) recently provided a meta-analysis of 15 within-species studies that provides strong support for the transmission avoidance model, which Able called the "contagion indicator hypothesis".

Although our negative correlation of showiness and parasite abundance contradicts the original Hamilton and Zuk prediction, it may be consistent with the transmission avoidance model. Considerable work over the past decade indicates that, within species, females prefer showy males (Andersson 1994), and that showiness is inversely correlated with parasite abundance, including lice (reviewed in Clayton 1991). Assuming

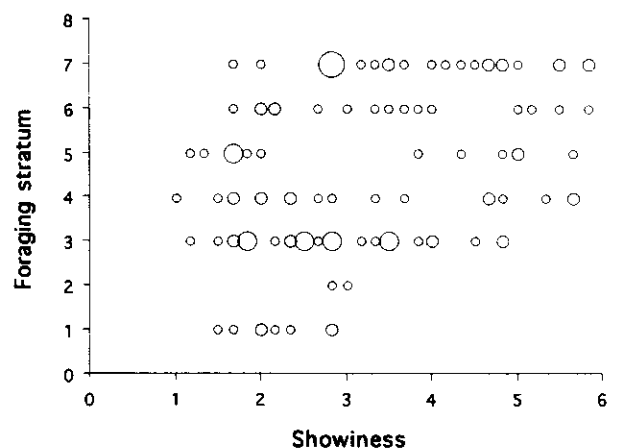


Fig. 2. Plot of showiness versus foraging stratum for 113 species of Neotropical birds (Spearman-Rank correlation, $r_s = 0.39$, $P < 0.0001$). Diameter of circles is proportional to the number of species (1-4). Species in the understorey are mostly drab, whereas those in the canopy are a mix of drab and showy.

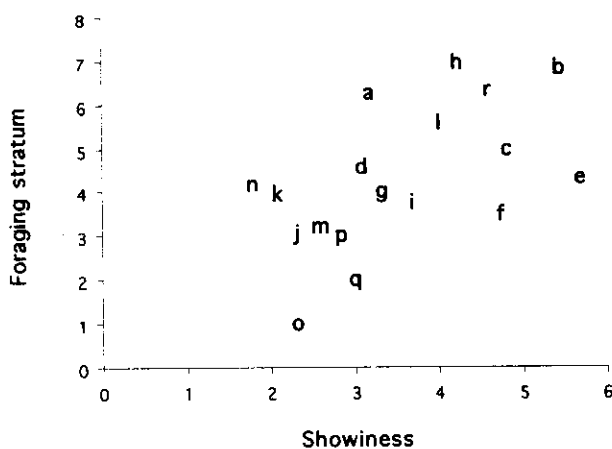


Fig. 3. Plot of family means for showiness versus foraging stratum for 18 families of Neotropical birds ($r_s = 0.59$, $P = 0.02$). Letters correspond to the following families (n = number of species sampled) listed in phylogenetic sequence (Sibley and Ahlquist 1990): a. Picidae (woodpeckers, $n = 11$); b. Ramphastidae (toucans/barbets, $n = 9$); c. Galbulidae (jacamars, $n = 1$); d. Bucconidae (puffbirds, $n = 5$); e. Momotidae (motmots, $n = 3$); f. Cerylidae (kingfishers, $n = 2$); g. Crotophagidae (anis, $n = 1$); h. Psittacidae (parrots, $n = 3$); i. Trochilidae (hummingbirds, $n = 20$); j. Caprimulgidae (nightjars, $n = 1$); k. Columbidae (pigeons/doves, $n = 2$); l. Tyrannidae (flycatchers and allies, $n = 10$); m. Thamnophilidae (typical antbirds, $n = 9$); n. Furnariidae (ovenbirds/woodcreepers, $n = 24$); o. Formicariidae (ground antbirds, $n = 4$); p. Conophegidae (gnateaters, $n = 1$); q. Certhiidae (wrens/creepers, $n = 1$); r. Fringillidae (finches and allies, $n = 6$).

that drab males do not acquire mates, few or none of their lice will be transmitted to females. Therefore, mean louse abundance should decrease in species where females select against louse-infested males. Species without such selection against louse-infested males may, in comparison, retain relatively high louse abundances. Such differential female-driven selection may lead to a negative correlation between louse abundance and showiness among species.

A drawback of this model is that any decrease in louse abundance implies a reduction in parasite pressure and thus reduced selection for showy traits (assuming they are costly; see Andersson 1994). However, if parasites other than lice, or factors other than parasites, are involved in sexual selection, showy traits might not be lost. The negative correlation of louse abundance and showiness could simply be due to sexual selection mediated by factors other than lice.

Correlational data cannot establish causation, much less the direction of causality between variables (Read 1990, Poulin 1998). For example, showy plumage could directly dictate ectoparasite abundance. Showy feathers may contain substances that reduce the palatability of feathers causing showier species to have fewer lice. Yet another possibility is that the negative correlation is the spurious result of covariation with some third variable such as host microhabitat use.

Foraging stratum versus mean parasite abundance

We found, however, no correlation between foraging stratum and louse abundance among all species in the data set, or when the analysis was restricted to the passerines or non-passerines. This result is not surprising because lice complete their entire life cycle on the host's body and are only transmitted via direct host contact (see Introduction). Therefore, host microhabitat use should not influence the probability of louse transmission.

In contrast, the influence of host microhabitat use on the transmission dynamics of other parasites is well illustrated. For example, canopy bird species have higher blood parasite prevalences because of a greater abundance of blood parasite vectors in the canopy (Garvin and Remsen 1997). In contrast, ticks are significantly more abundant on understorey bird species because ticks have an obligate free-living stage which is mainly found in vegetation near the ground (Pruett-Jones and Pruett-Jones 1991). Differential transmission dynamics of parasite taxa (blood parasites, ticks and lice, respectively) can thus lead to a positive, negative or no correlation between parasite load and foraging stratum. For our study at least, we can exclude the possibility that the negative correlation between louse abundance and showiness among non-passerines is due to covariation with foraging stratum.

Showiness versus foraging stratum

We found a positive correlation between showiness and foraging stratum among all species, in agreement with other studies (Baker and Parker 1979, Pruett-Jones et al. 1991, Garvin and Remsen 1997). Closer examination of Fig. 2, however, shows that drab species occur in all strata, while showy species occur mostly in the midstorey and canopy. Garvin and Remsen (1997) found a similar pattern in their Neotropical data set. The reasons for this pattern are unclear.

Different selection pressures may cause bird species to become cryptic or conspicuous (Savalli 1995, Götmark 1999). For a bird to be cryptic, its colour pattern must appear to be a random sample of the background (Edmunds 1974, Hailman 1977, Endler 1978, 1984, 1990). Therefore, most drab birds are probably cryptic when seen against the predominantly greenish background of a tropical rainforest habitat. On the other hand, showy birds may be cryptic when seen against a showy canopy background (e.g. parrots in a fruiting tree), or they may appear conspicuous (e.g. red tanagers in front of a green canopy). Regardless of the degree of crypsis, we may ask what factors make showiness more beneficial or less costly in the canopy. Several variables which may influence colour evolution covary with forest stratum: predator pressure (Shutler

and Weatherhead 1990), parasite abundance (Pruett-Jones and Pruett-Jones 1991, Garvin and Remsen 1997), ambient light and background colours (Endler 1978, 1990, 1993), e.g. the presence of flowers and fruits which may also influence the evolution of mating systems and territoriality (Orenstein 1973). These or yet other variables may explain this intriguing and, as Garvin and Remsen suggested, world-wide pattern among permanent forest birds. This pattern calls for a combination of experimental and further comparative work to be carried out.

Marchetti (1993) showed that warbler species living in low light environments compensate by displaying larger or more conspicuous colour patches when signalling conspecifics. The result is a negative correlation between light level and conspicuousness, opposite to the overall trend found in this and other studies (see above). However, all warbler species were much less conspicuous when not signalling. This example illustrates that some body regions may have evolved to maximise conspicuousness (to signal conspecifics) while others minimise conspicuousness (to avoid predators). Different body regions may evolve for different communicative purposes: most bird species are probably adorned with a "multi-purpose" plumage (Hailman 1977, Baker and Parker 1979, Johnson 1991, John 1995, Savalli 1995, Endler and Théry 1996). Future studies should try to distinguish which colour patterns are actually used for the specific communicative purposes being investigated.

The relationship between showiness and foraging stratum has a strong phylogenetic component, as our analysis of family means reveals (note that the letters a-i are all found in the top right of Fig. 3). Comparative studies that do not control for this phylogenetic component run the risk of spurious correlations generated by the shared evolutionary histories of related taxa (Harvey and Pagel 1991, Harvey et al. 1995a, b, Nee et al. 1996, Harvey and Rambaut 1998). Therefore, unlike other studies, we also performed phylogenetically controlled analyses between showiness and foraging stratum. These analyses suggest that an avian lineage which moved to a different foraging stratum in evolutionary time also evolved different body coloration, e.g. because of predation pressures. A predator, however, does not care about phylogeny. Rather, a predator sees the distribution of species across rainforest strata in ecological time, as depicted in Fig. 2. Therefore, if one wishes to test for relationships between showiness and stratum as they might appear to a predator, there is no need to reconstruct trait evolution (Westoby et al. 1995).

In conclusion, our study found that avian showiness is correlated with parasite abundance in non-passerines, and with forest stratum across all birds in our data set. Our results are relevant to hypotheses involving the interacting role of showiness, colour signalling, sexual selection, and parasite transmission.

Acknowledgements - Fieldwork was carried out with the assistance of John Fitzpatrick, Douglas Stotz and David Willard. Funding was provided by the Field Museum of Natural History, the Latin American Studies Center of the University of Chicago and NSF grant BSR-8508361 to J. Fitzpatrick for Peruvian faunal inventory work. For discussion, comments and other assistance we thank Fred Adler, Linda Birch, Richard Bradbury, Catherine Clarebrough, Peter Cotgreave, John Endler, Matthew Evans, Andy Gosler, Frank Götmark, Tim Guilford, Julian Howe, Kevin Johnson, Russ Lande, Thais Martins, Robert McCall, David McDonald, David Milson, Serge Morand, Ken Norris, Mark Pagel, Andy Purvis, Andy Rambaut, Andrew Read, John Reynolds, Marc Théry, Dan Tompkins, Hans Winkler and Graham Wragg. BAW was supported by an Evan Carroll Commager Fellowship and a John Woodruff Simpson Fellowship granted by Amherst College, USA. DHC was supported by a NATO Postdoctoral Fellowship. RDG was supported by a Junior Research Fellowship from St. Cross College, Oxford.

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