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AN ALTERNATIVE HYPOTHESIS FOR HEAVIER PARASITE LOADS OF BRIGHTLY COLORED BIRDS: EXPOSURE AT THE NEST

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ABSTRACT.—Hamilton and Zuk (1982) proposed that bright plumage in birds evolved as an advertisement of parasite resistance in response to heavy parasite loads, and they predicted that sexual dichromatism should be strongly correlated with parasite loads across species. To test their hypothesis, we sampled 935 individuals of 19 species of passerine birds in Louisiana for the presence of blood parasites. Nest height, a variable generally not considered in most recent literature on the Hamilton-Zuk hypothesis, was as good or better a predictor of parasite prevalence as was sexual dichromatism or plumage brightness. Because certain ornithophilic vectors are most common in the canopy, the relationship between nest height and parasite prevalence may follow from the natural history of parasitism. Ecological conditions may influence blood-parasite loads in the species studied, suggesting that genetically based resistance is less important. If parasite vectors are more common in the canopy, then more colorful bird species will be more heavily parasitized, on average, than less colorful species, because bird species that live high in the trees tend to be more colorful than those that live closer to the ground. *Received 18 July 1994, accepted 14 August 1995.*

HAMILTON AND ZUK (1982) predicted that bird species with strong plumage dichromatism also will have the highest prevalence of parasitic infection. They indicated that species with heavy parasite burdens have undergone strong selection for ways to advertise relative healthiness, such as by evolution of bright plumage. They proposed that males of such species would experience strong sexual selection, generating strong sexual dimorphism in plumage. Hamilton and Zuk's specific prediction was that "those [species] with most evident sexual selection are most subject to attack by debilitating parasites." Their review of data on blood parasites in 109 species of North American passerines revealed that bright plumage was positively associated with prevalence of blood parasites, a finding consistent with predictions of their hypothesis. They concluded that although "alternative explanations for their results could be offered," their results suggested that genetic variation for disease resistance contributes to sexual selection and evolution of bright plumage.

The data available to Hamilton and Zuk (1982) did not allow them to assess several variables that could affect the prevalence of parasites, such as geographic and seasonal variation in parasite density and diversity (Bennett and Cameron 1974, Weatherhead et al. 1991). Furthermore, Hamilton and Zuk did not analyze migratory and sedentary species separately; certainly, those species that winter in the tropics are exposed to a different array of arthropod vectors (Manwell and Herman 1935). A further complication is that sexual dimorphism in plumage is not evenly distributed between migratory and sedentary bird groups, or among phylogenetic groups.

We tested the Hamilton-Zuk hypothesis by comparing levels of blood-parasite prevalence in 19 species of North American birds, while controlling for seasonal and geographic variation in parasite burden. We also examined another variable, nesting stratum, that has not been used in most other tests of the Hamilton-Zuk hypothesis, although its potential significance to parasite burdens of birds was suggested and tested more than 30 years ago by Bennett and Fallis (1960). Specifically, birds are thought to acquire infections of blood parasites primarily on their breeding grounds from blood-feeding insects (Janovy 1966). Nestlings of altricial birds, nearly defenseless due to their incomplete feathering and poorly developed

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motor control, are especially vulnerable to such insects (Scott and Edman 1991, and references therein). Consequently, Bennett and Fallis (1960) proposed that the prevalence of blood parasites in birds was influenced strongly by nest height. Because ornithophilic biting flies, including ceratopogonids, culicids, and simuliids, show vertical feeding stratification, with most vectors occurring in mid-canopy (Snow 1955, Bennett 1960, Anderson and DeFoliart 1961, Bennett and Coombs 1975, Henry and Adkins 1975), Bennett and Fallis (1960) reasoned that canopy-nesting bird species may be exposed to higher concentrations of potential vectors. Bennett and Fallis' data supported this hypothesis, with the highest incidence of infection found in species that nest in the canopy.

The outcome of the analysis of prevalence levels of blood parasites prompted us to expand our interspecific comparisons to two other groups of birds to explore the potential relationship between nesting and foraging strata and plumage brightness.

METHODS

We evaluated four potential correlates of parasite prevalence to test the Hamilton-Zuk hypothesis: migration, plumage brightness, sexual plumage dimorphism, and nesting stratum. Because monogamy is the primary mating system in 17 of the 19 bird species in our sample, we could not evaluate mating system as a correlate of parasite load (Read 1991).

The relatively small number of bird species examined limited quantitative analyses of other potentially confounding variables, such as phylogeny. Although elaborate methods have been developed for controlling for phylogeny in comparative analyses (Pagel and Harvey 1988, Harvey and Pagel 1991), many systematists have little confidence in the underlying phylogenies used. For example, use of the phylogenetic hypotheses produced by Sibley and Ahlquist (1990), the ones most frequently used in comparative analyses, may pose a serious problem (Gill and Sheldon 1992, Lanyon 1992, Mindell 1992, Peterson 1992, Harshman 1994) for such analyses. Many ecologists who attempt to control for phylogenetic effects in comparative analyses evidently do not realize that the bifurcating branching patterns in any phylogenetic hypothesis may not represent the true phylogeny. No well-corroborated phylogeny exists that would allow the among-subfamily/family comparisons made by a number of authors (e.g. Read 1991); this applies to the interfamilial relationships of the bird taxa in our sample as well. Therefore, our only means of controlling for phylogenetic effects was to compare the six pairs of congeners and, in the two cases with a third species in a family or subfamily with a pair of congeners (i.e. Turdinae, Icteridae). Our treatment of families and subfamilies reflects nomenclature that will appear in the forthcoming 7th edition of the *AOU Checklist*.

From March through June 1988, thin blood smears were collected in Louisiana from 935 individuals of 19 passerine species representing eight families and subfamilies (Appendix 1; see also Garvin 1989). The species sampled were chosen to span the range in plumage brightness, sexual dimorphism, and nest height available among local species for which reasonably large sample sizes could be obtained. By restricting analyses to those species for which we could obtain relatively large sample sizes, we avoided the bias caused by small sample sizes, as found by Read and Harvey (1989), Pruett-Jones et al. (1991), and Chandler and Cabana (1991). The range in sampling dates was less than 30 days for all except two species, Carolina Wren (*Thryothorus ludovicianus*) and Northern Cardinal (*Cardinalis cardinalis*), whose blood smears were collected over a period of 70 days. Therefore, potential problems with within-year temporal variation in parasite prevalence (Kirkpatrick et al. 1991; Weatherhead and Bennett 1991, 1992) were minimized. Approximately equal numbers of males and females were analyzed for all target species, and no hatching-year individuals were sampled. Therefore, we also minimized heterogeneity in parasite prevalence associated with differences among age-sex cohorts (Kirkpatrick et al. 1991; Weatherhead and Bennett 1991, 1992).

Birds were netted or shot, and a drop of blood taken from the brachial vein or from blood around the wounds. Blood films were air-dried and fixed in 100% methanol upon return to the laboratory. Slides were stained in Giemsa stain (Bennett 1970) and examined for parasites by scanning under high dry (40×) and oil (100×) objectives. A minimum of 100,000 blood cells was examined per smear for the presence of parasites. To minimize potential problems of relying on only one kind of parasite (Weatherhead et al. 1991), we scored each smear for the presence of five types of parasites: (1) *Plasmodium*, (2) *Haemoproteus*, and (3) *Leucocytozoon* (genera of sporozoans that parasitize blood cells, reticulo-endothelial cells, and other tissues); (4) *Trypanosoma* (flagellates found in blood plasma); and (5) microfilaria (larval filarioid nematodes, adults of which parasitize body cavity and tissues of host). Species identification was determined by host-family specificity and morphological characteristics of the gametocyte (see Garvin et al. 1993). Species were identified at the International Reference Center of Avian Haematozoa, Memorial University of Newfoundland, Canada (where all positive slides are deposited).

A weakness of our study is that we assume, without corroborating data, that these blood parasites reduce the fitness of their hosts. Until such data become

available, we have no alternative but to state the assumption, a reasonable one given that these parasites are vector borne (Ewald 1983, 1993). Studies so far (e.g. Bennett et al. 1988; Kirkpatrick et al.1991; Weatherhead and Bennett 1991, 1992) have not revealed any consistent association between haematozoan infection and body mass, used as an index of fitness. Nevertheless, laboratory studies of domesticated birds and anecdotal information on wild birds suggest that most haematozoa in our study are potentially pathogenic (Atkinson and van Riper 1991).

Bird species were grouped into four categories based on sexual plumage dimorphism and migratory tendency (Table 1). Bird species were ranked according to a subjective combination of brightness and showiness (Pruett-Jones et al. 1991) of male breeding plumage by six ornithologists who had no knowledge of the parasite data or of the rankings of one another; the mean rank was used for each species (Appendix 2). Rankings were restricted to plumage; none of the bird species in our sample has bright or contrasting irides, bills, facial skin, or legs that would affect overall scores. The mean range of the individual ranks for the 19 species was 4, with a maximum of 8 (for *Thryothorus ludovicianus*; some ornithologists ranked this species high because of its reddish brown back, orange-buff underparts, and conspicuous superciliary, whereas others regarded it as just a "brownish" bird) and a minimum of 1 (for Scarlet Tanager [*Piranga olivacea*]). Use of such plumage scores is an important issue. As emphasized by Endler and Lyles (1989), Endler (1990), and Weatherhead et al. (1991), whether brightness scores produced by humans reflect the perceptions by animals of other animals in their natural background is unknown. We used such plumage scores to make our analyses comparable to most other studies.

Each of the 19 bird species was assigned to a nest stratum based on its mean nest height (Appendix 2). Height categories follow Greiner et al. (1975) and conform to those used to describe vector distribution (Snow 1955, Anderson and DeFoliart 1961): 1 (0 to 0.3 m), 2 (>0.3 to 3.0 m), and 3 (>3.0 m).

To determine whether a correlation exists between nest height and plumage brightness within a single clade of birds, we analyzed the wood-warblers (Parulidae) of eastern North America (unfortunately, parasite data were not available for most species). This family is the only one in North America that has a sufficient number of species and a sufficient range of brightness and nest heights for such an analysis. Only those species that breed in forests (i.e. vs. early second-growth or bogs) were included. Each species was assigned to one of the three strata used by Greiner et al. (1975) based on its mean nest height, or if not available, the midpoint of the range of nest heights given by Harrison (1975). Each species also was assigned to one of three brightness categories based on the breeding plumage of the male: (1) *dull* = no bright spectral colors or strong, contrasting patterns, and general color dull shades of brown or greenish; (2) *intermediate* = no bright spectral colors, but substantial portion of plumage dominated by striking patterns of stripes or spots; and (3) *bright* = at least some portion of plumage contains at least one bright spectral color (Appendix 3).

TABLE 1. Migratory tendency and plumage dimorphism for 19 species studied for blood parasites.

Species	Mean brightness score	Nest stratum
Monomorphic nonmigratory		
Carolina Chickadee (*Parus carolinensis*)	10.0	2
Tufted Titmouse (*P. bicolor*)	3.2	3
Carolina Wren (*Thryothorus carolinensis*)	7.0	2
Monomorphic migratory		
Veery (*Catharus fuscescens*)	6.8	1
Swainson's Thrush (*C. ustulatus*)	4.2	2
Wood Thrush (*Hylocichla mustelina*)	10.0	2
Gray Catbird (*Dumetella carolinensis*)	1.8	2
Red-eyed Vireo (*Vireo olivaceus*)	3.0	3
Ovenbird (*Seiurus aurocapillus*)	5.3	1
Northern Waterthrush (*S. noveboracensis*)	5.1	1
Dimorphic migratory		
Summer Tanager (*Piranga rubra*)	16.0	3
Scarlet Tanager (*P. olivacea*)	18.3	3
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	14.8	3
Indigo Bunting (*Passerina cyanea*)	15.2	2
Painted Bunting (*P. ciris*)	18.3	2
Orchard Oriole (*Icterus spurius*)	10.3	3
Dimorphic nonmigratory		
Northern Cardinal (*Cardinalis cardinalis*)	16.3	2
Boat-tailed Grackle (*Quiscalus major*)	12.2	2
Common Grackle (*Q. quiscula*)	11.2	3

In addition, we performed a similar analysis on a complex tropical avifauna in Amazonian Peru (Terborgh et al. 1984). The 280 tropical species included only those species found in "high ground forest" or "transitional forest" (i.e. "Fh" and "Ft" in Terborgh et al. 1984), but did not include members of the Falconiformes, nocturnal species, and boreal and austral migrants. We also made two changes in the analysis. First, we added a fourth category of brightness, *gaudy*, for those species with a substantial portion of the plumage covered by two or more bright spectral colors (e.g. trogons [Trogonidae], certain macaws [*Ara*

spp.], and certain tanagers [e.g. *Tangara* spp.]). Second, because the nests are unknown for most species, we used the first foraging stratum given for each species by Terborgh et al. (1984). We recognize that some species that forage in one stratum may nest in another; however, in the absence of data on nest height, we were unable to devise an alternative approximation of nest height. Furthermore, it is not known for certain that parasites are acquired only or primarily at the nestling stage; we assume that foraging adults also are vulnerable to some extent. Nevertheless, our analysis of the tropical avifauna cannot be considered comparable to that of the Parulidae above. Additionally, we cannot find any analyses of vertical distribution of bird-biting vectors in tropical forests.

RESULTS

Migration.—Of the 13 migrant species sampled, the mean prevalence of infection, 34%, was virtually identical to the 33% found in the six resident species (see Appendix 1). For the six pairs of congeners, none contained species that differed in migratory tendency, thus prohibiting comparisons of within-family differences in prevalence with respect to migratory tendency, as done by Zuk (1991).

Sexual dimorphism and plumage brightness.—We found a positive relationship between plumage brightness and parasite prevalence (Fig. 1); the nine sexually dimorphic species had significantly higher levels of infection than the 10 monomorphic species (51 vs. 24%, respectively; Kruskal-Wallis chi-square approximation, $P = 0.016$, $n = 413$ and 522 individuals, respectively). In three of the six pairs of congeners, the species with the highest prevalence also had the highest brightness score and, in the other three, the converse was true (binomial test, $P = 0.50$); therefore, the hypothesis that the trend could be the result of phylogenetic biases cannot be rejected. Because the brightness scores of the third species in the two taxa (Turdinae, Icteridae) with a pair of congeners was intermediate and close to values of the two species of congeners, we believed that an analysis would be questionable.

Nesting stratum.—A highly significant relationship was also found between mean parasite prevalence and mean nest height (Spearman rank correlation, $r_s = 0.77$, $P < 0.001$, $n = 19$). The highest mean percentage of infected individuals, 63%, was found in species in the upper stratum, where vector potential likely is highest (Snow 1955, Anderson and DeFoliart 1961). In addition, we found a positive relationship between the mean (or midpoint) nest height and percent of infected individuals for all species combined (Fig. 2).

The correlation between nesting height and parasite prevalence (0.77) exceeded that between plumage brightness and parasite prevalence ($r_s = 0.45$, $P = 0.06$, $n = 19$). Both nesting height and plumage brightness had a significant effect on parasite prevalence (ANOVA; nest height, $F = 29.7$, $P < 0.001$; brightness, $F = 30.4$, $P < 0.001$; nest height × brightness interaction, $F = 28.2$, $P \leq 0.001$). Consequently, we used partial correlation analysis (SAS Institute 1985) to examine the relative contribution of these two variables to variations in parasite load. When the effect of plumage brightness was removed, the correlation between nest height and parasite load was significant (Kendall's Tau = 0.58, $P \leq 0.001$); in contrast, when the effect of nest height was removed, the correlation between plumage brightness and parasite load was positive but not significant (Kendall's Tau = 0.30, $P \leq 0.08$). This indicates that nest height is a better predictor of variation in parasite load than is brightness. However, given the uncertainty of the applicability of parametric tests to these data, a more cautious conclusion is that nest height predicts parasite load "as well as" any other variable.

Of particular interest were two species, the Tufted Titmouse (*Parus bicolor*) and the Red-eyed Vireo (*Vireo olivaceus*), that are unique in our sample in that both are dull-colored, monomorphic species that nest in the mid-canopy. Both species were heavily infected (Fig. 1), contrary to the prediction of the Hamilton-Zuk hypothesis, but consistent with that of the Bennett-Fallis hypothesis. An alternative interpretation, however, is that the red iris of the vireo and the short crest of the titmouse are not considered in rankings such as ours that are restricted to plumage brightness (M. Zuk pers. comm.).

For five of the six pairs of congeners, the species with the highest parasite prevalence also had the higher nest height (binomial test, $P = 0.031$); in the only genus (*Seiurus*) in which the relationship did not hold, nest heights were virtually identical. Therefore, in contrast to the relationship between parasite loads and plumage brightness, the hypothesis that the relationship between parasite prevalence and nest height reflects phylogenetic effects can be rejected, at least at the within-genus level. At a higher level, if we average the data for conge-

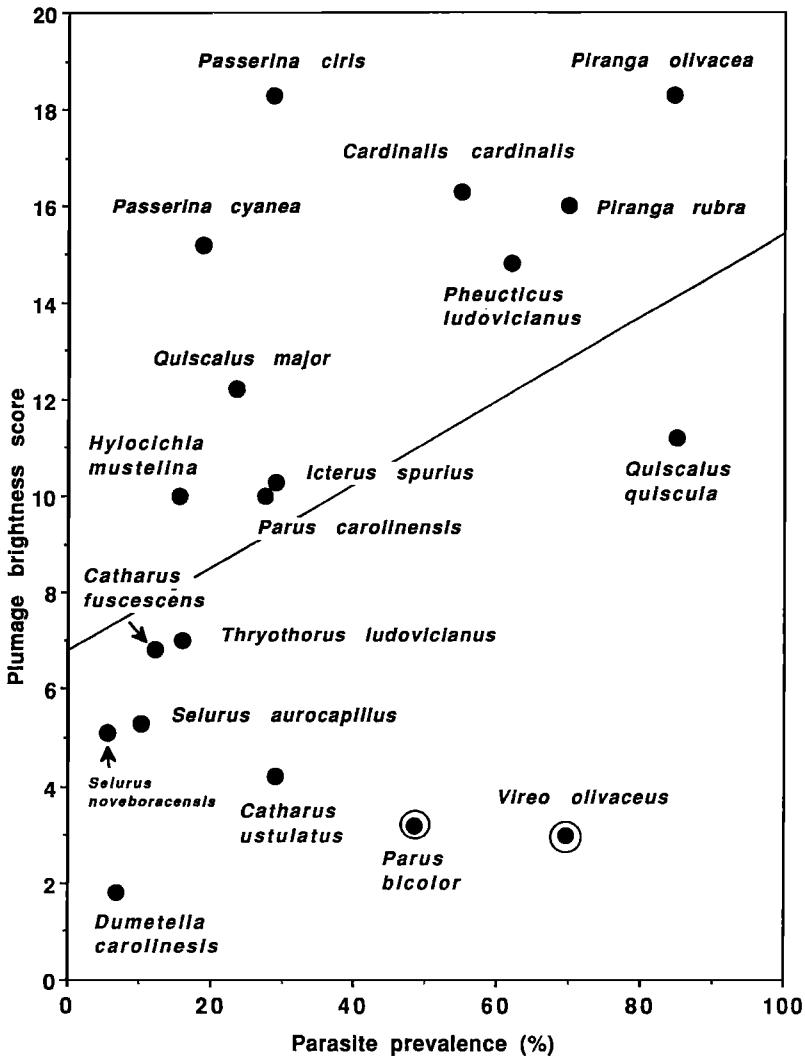

FIG. 1. Relationship ($r^2 = 0.18$, $r_s = 0.45$) between blood-parasite prevalence and brightness of male plumage in 19 passerine species. Points for two dull-plumaged species with relatively high parasite prevalence values are circled.

ners and consubfamilials, then the relationship between parasite prevalence and nest height is statistically significant (genera, $r_s = 0.70$, $P = 0.015$; subfamilies, $r_s = 0.90$, $P = 0.01$). Similarly, the relationship between plumage brightness and percentage of individuals infected (genera, $r_s = 0.53$, $P = 0.065$; subfamilies, $r_s = 0.60$, $P = 0.09$) suggests that phylogenetic effects are present, even though the probability levels are slightly higher than conventional criteria for statistical significance (i.e. $P = 0.05$). In general, congeners and confamilials in our sample were more similar to one another than to most other species in combinations of parasite prevalence, plumage brightness, or nesting stratum. Therefore, phylogenetic effects may have influenced the outcomes of our analyses, but proper measurement of this influence requires a larger sample of species and a well-corroborated phylogeny.

Our analysis of nest height and plumage brightness in the wood-warblers removes one level of phylogenetic effects by restricting the analysis to confamilials, or consubfamilials if wood-warblers are considered a subfamily (Parulinae) of the Emberizidae (e.g. AOU 1983). For wood-warblers from eastern North America, nest height and brightness of male plumage are

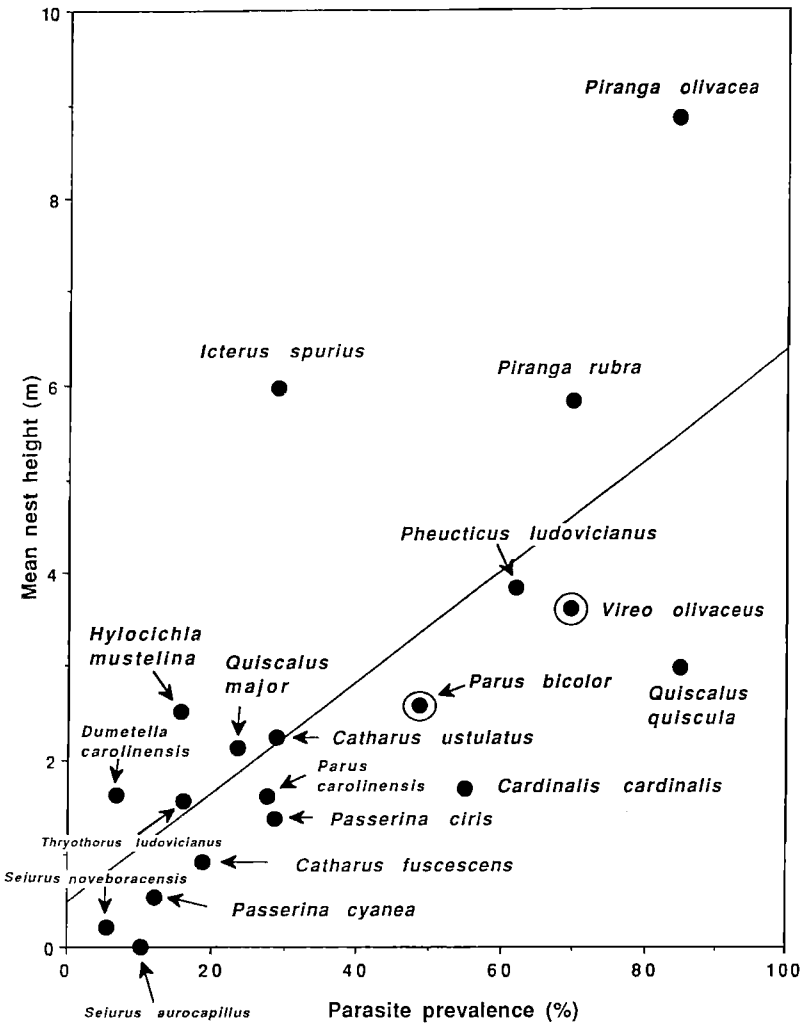

FIG. 2. Relationship ($r^2 = 0.50$, $r_s = 0.77$) between parasite prevalence and nest height in 19 passerine species. Points for two dull-plumaged species with relatively high parasite prevalence values are circled.

highly significantly associated ($\chi^2 = 18.7$, $P < 0.001$; Table 2). Switching the dullest species in the "bright" category (e.g. Pine Warbler [*Dendroica pinus*]) to the "intermediate" category does not affect the outcome of the analysis. Evaluations of color variation (Bailey 1978, Baker and Parker 1979, Burtt 1986) have not considered foraging or nest stratum among the factors potentially affecting plumage brightness, although Shutler and Weatherhead (1990) showed that ground-nesting wood-warblers were less sexually dichromatic than those nesting above the ground.

TABLE 2. Number of wood-warbler species with various combinations of male plumage brightness and nesting stratum.

	Nesting stratum[a]		
Plumage brightness	1	2	3
Dull	3	1	0
Intermediate	4	0	0
Bright	1	6	11

[a] Nest height: 1 (0 to 0.3 m), 2 (>0.3 to 3.0 m), 3 (>3.0 m).

Similarly, for the tropical forest avifauna, foraging stratum and brightness of male plumage are highly significantly associated ($\chi^2 = 66.8$, $P < 0.001$; Table 3). This relationship also holds when Passeriformes ($\chi^2 = 42.6$, $n = 184$, $P < 0.001$) and non-Passeriformes ($\chi^2 = 44.0$, $n = 96$,

TABLE 3. Number of bird species in a Peruvian tropical forest with various combinations of male plumage brightness and foraging stratum. Data taken in part from (Terborgh et al. (1984).

Plumage brightness	Foraging stratum			
	Terrestrial	Undergrowth	Subcanopy	Canopy
Dull	12	26	20	11
Intermediate	20	31	30	28
Bright	2	7	14	41
Gaudy	0	2	9	27

$P < 0.001$) are analyzed separately. However, only one statistically significant relationship was found (for hummingbirds, Trochilidae; $\chi^2 = 13.8$, $n = 17$, $P = 0.03$) within seven smaller taxonomic units for which the number of species was large enough and the heterogeneity in color or foraging stratum sufficient to permit analysis (Piciformes; Formicariidae; Tyrannidae; Thraupidae; Dendrocolaptidae + Furnariidae; and Cotingidae + Pipridae excluding *Schiffornis, Pachyramphus,* and *Tityra*). Even within the Trochilidae, however, the relationship has a strong phylogenetic component, with all but one of the dull-colored and intermediate-colored species of the undergrowth belonging to one subfamily, Phaethorninae. Therefore, the overall relationship between brightness and foraging stratum is one that has a strong phylogenetic component: The brightest taxa tend to occur in the higher strata. However, all analyses for the smaller taxonomic groups show a positive association, albeit statistically nonsignificant, between brightness and foraging stratum, with probability values ranging from 0.06 (Piciformes) to 0.46 (Formicariidae). The probability that all seven subunits would show a positive relationship by chance alone is less than 0.012 (sign test). Therefore, larger sample sizes of species for each taxon would potentially reveal statistically significant associations within each clade.

DISCUSSION

Migration.—Although migratory species are exposed to a different array of insect vectors and other ecological factors than are sedentary species, we found no difference in parasite prevalence between the two groups. The similar prevalences found in our study perhaps can be explained in the phenology of the vector transmission. If infections are acquired primarily on the breeding grounds (Beaudoin et al. 1971), which are largely at temperate latitudes for both residents and migrants in our study, then no difference in prevalence levels would be predicted between the two groups, assuming relatively similar vector and parasite communities over the extensive range of temperate latitudes.

Sexual dimorphism and plumage brightness.—Our finding of a positive relationship between both plumage brightness and degree of sexual dimorphism with parasite prevalence is consistent with the interspecific analyses of birds by Hamilton and Zuk (1982), Read (1987), Pruett-Jones et al. (1990), and Zuk (1991; brightness only). However, as explained below, we propose that the cause of this relationship involves an underlying vertical stratification of parasite vectors and brightly colored birds, and not with an evolutionary interaction between parasites and bird coloration, as proposed by Hamilton and Zuk (1982).

Nesting stratum.—As predicted by Bennett and Fallis (1960), parasite loads were positively correlated with nest height. Our prevalence data are consistent with a hypothesis of greatest exposure to parasite vectors in the upper stratum, intermediate exposure in the middle stratum, and the least exposure near the ground. This hypothesis has a simple rationale based in the natural history of birds and their blood parasites; i.e. the bird species most heavily exposed to vectors that transmit blood parasites are those most heavily infected. In contrast to the Hamilton-Zuk hypothesis, the Bennett-Fallis hypothesis requires no complex, cyclic, coadaptational interactions among effects of parasites on hosts, genetically based resistance to parasites, and feedback from sexual selection. We think that the Bennett-Fallis hypothesis deserves attention from a research field that has ignored it almost completely. Read (1991) stated it is "well-known that the density of biting flies, the main vectors of avian hematozoa, is higher above ground level." However, Garvin (1989) was the first to integrate this into tests of the Hamilton-Zuk hypothesis, and Read's own previous inter-

specific analyses (e.g. Read 1987, Read and Harvey 1989) neither included nest height as a variable nor cited Bennett and Fallis (1960).

The Bennett-Fallis hypothesis applies exclusively to bird species that differ in nest height. Perhaps the positive correlations between parasite load and brightness in other taxa for which nest height is of little or no relevance (e.g. fishes, Ward 1988; waterfowl, Scott and Clutton-Brock 1990) might also be explained by similar hypotheses based on parasite exposure; in other words, perhaps the parasite-brightness correlation might explained by a brightness-exposure relationship. The potential importance of exposure was also shown by Bennett et al. (1992), who found that individuals of the same bird species differed in levels of parasite prevalence depending on nesting habitat.

Only two other analyses of the interspecific predictions of the Hamilton-Zuk hypothesis for birds included a variable that might be related to parasite exposure. Pruett-Jones et al. (1991) found a strong correlation between foraging strata and parasite prevalence. Read (1991) found that monogamous species have higher prevalence levels than polygynous species and that monogamous species have higher nests; however, when restricting comparisons to sister taxa, he found no tendency for monogamous species with the higher nests to have the higher prevalence. In general, results from the interspecific approach have not provided much support for the Hamilton-Zuk hypothesis (e.g. Møller 1990, Chandler and Cabana 1991, Lefcort and Blaustein 1991), and predictions of the hypothesis are controversial (Clayton et al. 1992).

Although we found strong positive relationships between brightness and nesting or foraging strata, we recognize that many problems plague such interspecific analyses (Pagel and Harvey 1988, Read and Harvey 1989). Additionally, our perception of brightness may not be comparable to that of the bird species involved (Endler and Lyles 1989, Weatherhead et al. 1991). We predict, however, that more sophisticated analyses with a much larger number of species would show that, throughout the world, brightly colored bird species form a higher proportion of the canopy avifauna than of the near-ground avifauna. With some exceptions (e.g. Pittidae, Momotidae, and many members of the Phasianinae), taxa renowned for species with brilliant coloration are those generally associated with upper or middle vegetation strata (e.g. Capitoninae, Cotingidae, Irenidae, Musophagidae, Nectariniidae, Oriolidae, Psittaciformes, Ramphastinae, Thraupidae, Trochilidae, Trogonidae). For bird species in a tropical forest in New Guinea, Pruett-Jones et al. (1991) found a strongly significant correlation between foraging strata and male plumage showiness. Whether the distribution of ornithophilic vectors in tropical forests is similar to that known for temperate forests is critical to interpretations of these data. Currently, the degree of similarity is unknown.

Why would bird taxa that nest in the canopy tend to be more brightly colored than those nesting near the ground? Proponents of the Hamilton-Zuk hypothesis might argue that high nesters are more brightly colored because they are more heavily parasitized. However, factors other than parasite loads that might influence vertical distribution of bright coloration include predator avoidance, uneven vertical distribution of avian mating systems, and constraints on signal visibility. Shutler and Weatherhead (1990), for example, proposed that few wood-warbler species with brightly colored males nest on the ground because conspicuous males might signal the presence of the nest to predators. The resolution of this cause-and-effect problem awaits more detailed, comparative studies.

We found that few gaudy or bright species of tropical forest birds are found in the undergrowth or on the ground, whereas many dull species are found in the canopy. This suggests that, if there is an adaptive explanation for the trend observed, it is most likely to be a constraint on bright coloration near the ground. Predator avoidance might serve as such a constraint in the following way. Morphological limitations probably reduce the number of arboreal predators relative to terrestrial ones. Perhaps terrestrial and near-ground bird species, therefore, are exposed to a greater variety of visually oriented, diurnal predators, thereby selecting against bright coloration. (However, do most such near-ground predators have the color vision that would make bright birds conspicuous to them?) Alternatively, bright coloration might be obscured in the more evenly lit but darker undergrowth relative to the more complex background but bright light of the canopy. For this reason, it also is unclear whether the signal value of bright coloration is greater in the

undergrowth or the canopy (Endler 1990). Following the reasoning of Endler and Lyles (1989), Endler (1990), and Weatherhead et al. (1991), how do we know whether a strongly marked species without bright colors is less conspicuous in the undergrowth to other birds or predators than is a brilliantly colored species in its canopy environment? Therefore, conclusions that depend on human judgment of plumage brightness must be regarded as tentative (Bennett et al. 1994). Our analyses depend on the assumption that even if bird and human perceptions of coloration are not equivalent, at least they are correlated.

We propose that the relationship between nesting stratum and parasite burden in birds is one of cause and effect (brighter birds are found in higher strata, where bird-biting vectors are more common), whereas the association of parasite burden with bright coloration may be merely correlational at the interspecific level.

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APPENDIX 1. Prevalence of hematozoa in samples of 19 passerine species from Louisiana. Migratory status: R (resident), M (migrant).

Taxon	Migratory status	*n*	% infected	No. of individuals infected				
				Haemoproteus	*Plasmodium*	*Leucocytozoon*	*Trypanosoma*	Microfilaria
Paridae								
Parus carolinensis	R	40	27.5	0	0	0	9	2
P. bicolor	R	35	48.6	0	8	1	7	5
Troglodytidae								
Thryothorus carolinensis	R	25	16.0	0	0	0	1	3
Muscicapidae, Turdinae								
Catharus fuscescens	M	41	12.2	3	0	1	2	1
C. ustulatus	M	76	28.9	15	0	7	2	0
Hylocichla mustelina	M	64	15.6	0	3	2	6	0
Mimidae								
Dumetella carlinensis	M	59	6.8	0	4	0	0	0
Vireonidae								
Vireo olivaceus	M	59	69.5	39	2	0	8	3
Parulidae								
Seiurus aurocapillus	M	68	10.3	6	0	0	0	1
S. noveboracensis	M	55	5.5	1	0	0	1	0
Thraupidae								
Piranga rubra	M	33	69.7	20	1	1	4	0
P. olivacea	M	32	84.4	25	1	0	3	2
Cardinalidae								
Cardinalis cardinalis	R	51	54.9	27	0	0	5	3
Pheucticus ludovicianus	M	50	62.0	30	0	1	1	0
Passerina cyanea	M	64	8.8	0	8	0	4	0
P. ciris	M	35	28.6	0	5	0	6	0
Icteridae								
Quiscalus major	R	64	23.4	12	0	0	0	1
Q. quiscula	R	46	84.8	27	0	0	4	28
Icterus spurius	M	38	8.9	9	0	0	2	0
Total		935	34.2	213 (22.8%)	32 (3.4%)	12 (1.3%)	65 (6.9%)	47 (5.0%)

APPENDIX 2. Nest heights (from Cornell Laboratory of Ornithology nest records) and brightness rankings for 19 bird species used in analysis. "Original rankings" are those given independently to each species by six ornithologists unaware of results of analysis of blood parasite loads.

Species	Mean nest height (m)	Mean brightness (range)	Original rankings
Gray Catbird	1.63	1.8 (1–4)	4, 1, 1, 1, 1, 3
Red-eyed Vireo	3.60	3.0 (1–5)	5, 2, 3, 3, 4, 1
Tufted Titmouse	2.57	3.2 (1–7)	1, 3, 7, 2, 2, 4
Swainson's Thrush	2.24	4.2 (2–7)	2, 4, 2, 7, 3, 7
Northern Waterthrush	0.21	5.1 (4–6)	6, 5, 5, 4, 6, 5
Ovenbird	0.004	5.3 (4–6)	6, 5, 5, 4, 6, 6
Veery	0.52	6.8 (3–9)	3, 7, 8, 6, 9, 8
Carolina Wren	1.57	7.0 (2–10)	10, 8, 4, 10, 8, 2
Wood Thrush	2.51	10.0 (9–12)	9, 12, 11, 9, 10, 9
Carolina Chickadee	1.62	10.0 (5–13)	8, 11, 12, 13, 5, 11
Orchard Oriole	5.97	10.3 (8–13)	11, 9, 13, 8, 11, 10
Common Grackle	2.98	11.2 (9–13)	12, 10, 9, 11, 13, 12
Boat-tailed Grackle	2.13	12.2 (10–13)	13, 13, 10, 12, 12, 13
Rose-breasted Grosbeak	3.83	14.8 (14–17)	17, 14, 14, 15, 14, 17
Indigo Bunting	0.91	15.2 (14–16)	16, 15, 15, 14, 15, 14
Summer Tanager	5.82	16.0 (15–17)	15, 16, 17, 16, 17, 15
Northern Cardinal	1.70	16.3 (14–18)	14, 17, 18, 17, 16, 16
Painted Bunting	1.38	18.3 (18–19)	18, 19, 16, 19, 19, 19
Scarlet Tanager	8.85	18.3 (18–19)	19, 18, 19, 18, 18, 18

APPENDIX 3. Wood-warbler species of some eastern North American forests, with values for nesting strata (1 to 3) and plumage scores in parentheses.

Bachman's Warbler (*Vermivora bachmanii*, 2, bright); Tennessee Warbler (*V. peregrina*, 1, dull); Orange-crowned Warbler (*V. celata*, 1, dull); Nashville Warbler (*V. ruficapilla*, 1, bright); Northern Parula (*Parula americana*, 3, bright); Magnolia Warbler (*Dendroica magnolia*, 2, bright); Cape May Warbler (*D. tigrina* 3, bright); Black-throated Blue Warbler (*D. caerulescens*, 2, bright); Yellow-rumped Warbler (*D. coronata*, 3, bright); Black-throated Green Warbler (*D. virens*, 3, bright); Blackburnian Warbler (*D. fusca*, 3, bright); Yellow-throated Warbler (*D. dominica*, 3, bright); Pine Warbler (*D. pinus*, 3, bright); Bay-breasted Warbler (*D. castanea*, 3, bright); Cerulean Warbler (*D. cerulea*, 3, bright); Black-and-white Warbler (*Mniotilta varia*, 1, intermediate); American Redstart (*Setophaga ruticilla*, 3, bright); Prothonotary Warbler (*Protonotaria citrea*, 2, bright); Worm-eating Warbler (*Helmitheros vermivorus*, 1, dull); Swainson's Warbler (*Limnothlypis swainsonii*, 1, dull); Ovenbird (*Seiurus aurocapillus*, 1, intermediate); Northern Waterthrush (*S. noveboracensis*, 1, intermediate); Louisiana Waterthrush (*S. motacilla*, 1, intermediate); Kentucky Warbler (*Oporornis formosus*, 1, bright); Hooded Warbler (*Wilsonia citrina*, 2, bright); Canada Warbler (*W. canadensis*, 2, bright).