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LATITUDINAL GRADIENTS IN COLORS AND PATTERNS OF PASSERINE BIRDS

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Tropical landbirds are commonly believed to be more colorful than non-tropical landbirds. In this paper I use a latitudinal series of passerine avifaunas from Panama to Canada and Alaska to quantitatively test this belief.

Tropical birds can be stunningly colorful (Dunning 1970), some to an extent apparently unmatched by non-tropical species. That the most colorful landbirds are tropical could be due largely to the greater diversity of tropical landbirds because the species pool is much larger. In order to discover whether tropical landbirds are more colorful than non-tropical landbirds in general, one must quantify specific components of colorfulness and compare the entire pools of species (or of individuals!) from equivalent tropical and non-tropical regions. For example, one can count the number of bright spectral colors on the exterior of a typical breeding male of each passerine species of North and Middle America and compare the tropical species with the non-tropical species. Or one can compare the average number of bright colors or the proportion of the species in each region's avifauna having a certain number of bright colors. In this paper I make many such comparisons and attempt to discover whether the colors or color patterns of neotropical passerines differ from those of nearctic passerines in ways such that the former seem more colorful than the latter.

Willson and von Neumann (1972) made a pioneer study of this subject, using two characters for evaluating all diurnal landbirds. Using 14 characters and similar but more objective methods, I looked at passerines. Unfortunately, I limited my study to passerines before I was aware of Willson and von Neumann's work. Some of our conclusions can be directly compared, because their appendix allowed me to separate their results for passerines and for non-passerine landbirds, but our methodological differences obscure these comparisons.

METHODS

Full color illustrations of all species of North and Middle American landbirds are available in field guides. I characterized the colors and basic color pattern of each native breeding species of passerine bird from Alaska and Canada through Panama using the color illustrations and plumage descriptions in these guides. The breeding range of each species also was compiled from field guides. Palearctic species that breed marginally in arctic Alaska or Canada were excluded. I characterized a total of 784 species representing 34 families.

The primary field guides used were those of Peterson (1947, 1961), Robbins et al. (1966), Davis (1972), and Edwards (1972). Meyer de Schauensee (1970) was useful for species occurring into South America, and Blake (1953) and Land (1970) were used occasionally. My data were compiled before the publication of Peterson and Chalif (1973).

Middle and North America were divided into ten regions (Fig. 1) representing a roughly latitudinal series: (1) Panama, (2) Costa Rica, (3) Nicaragua, (4) Honduras, (5) southern Mexico through El Salvador (Mexico east of the Isthmus of Tehuantepec plus Guatemala, Belize, and El Salvador), (6) central Mexico (from the Isthmus of Tehuantepec to roughly the northern limits of Jalisco and Veracruz), (7) northern Mexico (Mexico north of region 6), (8) southern United States (south of the northern borders of North Carolina, Tennessee, Arkansas, Oklahoma, New Mexico, and Arizona and a line across southern Nevada and from Lake Tahoe to San Francisco), (9) northern and central United States (the remainder of the contiguous United States), (10) Canada and Alaska. The division of Mexico into southern, central, and northern portions follows Edwards (1968, 1972), and Mexican breeding ranges were obtained from his range summaries. The numbers of passerine species and families breeding in each region are indicated in Table 1. By using larger regions to the north I held the maximum difference in sample size (number of species) to a factor of two, despite the steep latitudinal gradient in numbers of species per unit area.

The plumages of each species were characterized by the use of 14 general characters of color and pattern. The first four characters deal with intraspecific plumage differences:

1. Presence or absence of pronounced sexual dichromatism. For example, the Bay-breasted Warbler (*Dendroica castanea*) was considered markedly dichromatic but the Prairie Warbler (*D. discolor*) was not.
2. If the species is markedly sexually dichromatic, is the male much brighter or more conspicuous than the female?
3. If the species is markedly sexually dichromatic, is the female also bright or contrastingly patterned?
4. Presence or absence in the adult male of a much duller, nonbreeding plumage (e.g., present in Bay-breasted Warbler, absent from Prairie Warbler).

The 10 remaining characters deal with the male in breeding plumage. I identified the specific state exhibited by each species for each of these general characters of color and pattern.

5. The number of quartiles of the body surface covered by bright colors. "Body surface" means all surfaces exposed while the bird is perched. "Quartiles" here refers to fourths of a sampling distribution (Michaelis 1963), with the sampling distribution being the body surface of the bird in this case. I have

added a zero category for birds without any bright colors as explained and exemplified below. States are 0 = at most very small area covered (e.g., Ruby-crowned Kinglet, *Regulus calendula*—crown patch usually concealed); 1 = small area to 25% of body (e.g., Golden-crowned Kinglet, *R. satrapa*); 2 = 26% to 50% (e.g., Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*); 3 = 51% to 75% (e.g., Scarlet Tanager, *Piranga olivacea*); 4 = 76% to 100% (e.g., Hepatic Tanager, *P. flava*). Except for bright chestnut, only spectral colors were considered "bright."

6. The number of distinctly different bright colors on the bird. For example, Ruby-crowned Kinglet lacks any; Indigo Bunting (*Passerina cyanea*) has 1; Lazuli Bunting (*P. amoena*) has 2; Painted Bunting (*P. ciris*) has 3; Bay-headed Tanager (*Tangara gyrola*) has 4.

7. The color that covers the greatest proportion of the body: black, gray, white, brown, red, orange, yellow, green, blue, pink or purple, and bright chestnut.

8. The dominant bright color, if any. Species lacking pronounced bright colors were not categorized under this character. States are red, orange, yellow, green, blue, pink or purple, and chestnut.

9. The dominant dull color if no bright color dominates the bird's appearance. For example, red is the dominant bright color of the Tricolored Blackbird (*Agelaius tricolor*), but black, a dull color, dominates its appearance. Thus, this species was categorized under both Characters 8 and 9, whereas Character 8 was inapplicable to the Common Raven (*Corvus corax*), and Character 9 was inapplicable to the Scarlet Tanager. States are black, gray, white, brown, blue, green, dull yellow-green, and very dull orange.

10. Subjective estimate of pattern contrast in perching position: 0 = no or very little contrast (e.g., Hepatic Tanager; Swainson's Thrush, *Catharus ustulatus*); 1 = moderately contrasting (e.g., Lazuli Bunting; White-crowned Sparrow, *Zonotrichia leucophrys*); 2 = strongly contrasting (e.g., Yellow-headed Blackbird; Black-and-white Warbler, *Mniotilta varia*). The effects of countershading were considered; thus, the pattern of the Hermit Warbler (*Dendroica occidentalis*) was judged strongly contrasting (2), but that of the more countershaded Yellow-throated Warbler (*Dendroica dominica*) was judged only moderately contrasting (1).

11. Dominant pattern type: Entire = entire body unicolor, blended, or blended bicolor (e.g., Hepatic Tanager, Swainson's Thrush); Solid Areas = solid areas of color, including patched, blotched, sharply bicolor or multicolor, non-repeating bars and stripes (e.g., Scarlet Tanager; Hermit Warbler; Tricolored Blackbird; Olive Warbler, *Peucedramus taeniatus*); Streaked = dominated by repeated longitudinal streaks or stripes (e.g., Black-and-white Warbler; Brown Thrasher, *Toxostoma rufum*); Barred = dominated by repeated transverse bars or rings (e.g., Barred Antshrike, *Thamnophilus doliatus*; Black-crowned Antpitta, *Pittasoma michleri*); Spotted = dominated by repeated rounded spots not arranged in clear lines (e.g., Ocellated Antbird, *Phaenostictus mcleannani*; Cactus Wren, *Campylorhynchus brunneicapillus*).

12. Presence or absence of bright colors or contrasting patterns on the dorsal surface (especially compared to the ventral surface).

13. Presence or absence of conspicuous iridescence. For example, the iridescence of the Brewer's Blackbird (*Euphagus cyanocephalus*) was judged con-

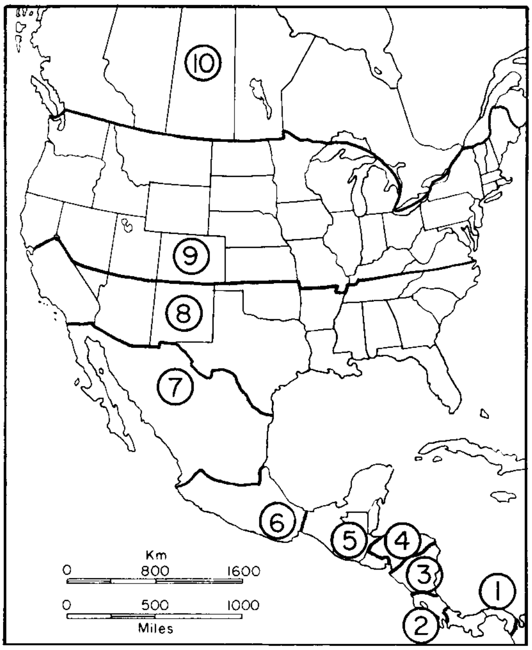

FIGURE 1. The ten sampling regions.

TABLE 1. Total numbers of species and families per region.

	Region	Ubiquitous families[1] No. species	Ubiquitous families[1] No. families	All families No. species	All families No. families
10	Canada and Alaska	156	12	178	20
9	Northern and Central U.S.	196	12	226	22
8	Southern United States	204	12	238	23
7	Northern Mexico	215	12	249	25
6	Central Mexico	237	12	291	27
5	Southern Mexico to El Salvador	212	12	273	24
4	Honduras	175	12	246	22
3	Nicaragua	168	12	236	21
2	Costa Rica	218	12	321	24
1	Panama	235	12	360	27

[1] Those 12 passerine families represented in all ten regions.

spicuous while that of the Rusty Blackbird (*E. carolinus*) was not.

14. Conspicuous colors or patterns on the bird's 'soft parts.' Such colors were recorded according to their location: bill, eyes, around eyes (this includes all types of eye-rings), elsewhere on bare face, and/or legs and feet.

In Characters 7, 8, and 9, the colors orange, yellow, and green were difficult to classify because they included a continuum of intermediates. For this reason, I made rather fine distinctions between colors in this range, and treated each hue both by itself and combined with the spectrally adjacent hues. For example, greenish yellow (gY) was treated separately as well as combined alternately with yellowish green (yG) to form total yellow-green (Tyg) and with all other yellows as total yellow (TY). This was done so that real latitudinal trends in some of these colors would not be masked by an unfortunate classification which grouped together hues with dissimilar geographic patterns.

The data for all the species were grouped by region so that the avifauna of each region could be considered as a whole. The percentage of species in each region exhibiting each character state was calculated. For each character state, the 10 percentages (one for each region) were ranked from lowest to highest; a two-tailed Hotelling and Pabst Rank-Order Correlation Test (Bradley 1968:91–96, 314) was performed using these ranks and the latitudinal ranks of the 10 regions in order to detect significant latitudinal gradients in color or pattern frequencies. 'Significance levels' are reported for $\alpha \leqslant .05$. I used Hotelling and Pabst's Test instead of other distribution-free tests because, as the rank differences are squared, large discrepancies between the ranked variables are weighted much more heavily than small ones (Bradley 1968:95). This is clearly desirable for this study. Ties were resolved by assigning ranks among the tied values in the least correlated manner so as to use the most conservative test.

I also followed the same procedure using only the 599 species belonging to the 12 families represented in all 10 regions. This part of the analysis, detecting the pooled trends for these *ubiquitous* families, eliminates the compounding effect of the presence or absence of various families in different parts of the latitudinal series of regions.

Similarly, I excluded non-passerines in order to avoid the compounding effects of the many lesser and non-ubiquitous orders that do not share as similar an evolutionary heritage as the passerines. In effect this represented examining the effects of a treatment (change in latitude) on the characteristics of a relatively uniform and ubiquitous set of subjects (the order Passeriformes) without compounding from less similar and/or non-ubiquitous sets of subjects (non-passerine orders). My separate examination of the ubiquitous families alone was a further attempt toward this end.

My conclusions concerning trends were based on frequencies of characters states (percentages of avifaunas), not absolute numbers of species.

In addition to the rank-order correlations, I performed log likelihood ratio tests (G Tests) on the complete 10×5 (region $\times$ character state) tables for Characters 5 and 6 in order to test the null hypothesis of independence of region and character state against alternatives not restricted to the form of latitudinal gradients.

Willson and von Neumann (1972) also categorized from field guides but used only the categories 'colorful' and 'not so.' "If the plumage [sic—they included soft part colors] of a species was described as having fairly large patches of bright yellow, orange, red, blue, purple or green [i.e., bright spectral colors], or any combination thereof, it was called 'colorful'" (Willson and von Neumann 1972:141). Pattern contrast was excluded. All diurnal terrestrial species of North America, Europe, and South America were categorized on the basis of descriptions and pictures. South American species were divided into 'lowland tropical' and 'non-tropical' groups with the latter including wide-ranging and highland (1,400 m +) species. I believe that this system is less informative, objective, and repeatable than my own, but it can be valid if carefully standardized and applied consistently. Comparison of the three field guides that Willson and von Neumann used suggests that they could not maintain the rigorous standards necessary for such a categorization. They referred to one guide for each continent; thus, they had no control against differences in descriptions, illustrations, and printing. Many of these differences are pronounced. The plates of the European (Peterson et al. 1966) and South American (Meyer de Schauensee 1970) field guides underrepresent plumage brightness. Furthermore, only a minority of the species are illustrated in the South American guide, and many of those illustrations are black-and-white or incomplete. Thus Willson and von Neumann were forced to rely primarily on very brief descriptions in their categorization of South American species. These descriptions often emphasize differences in colors and any sexual dichromatism rather than overall coloration.

My use of many field guides and of full color illustrations and standard poses for every species was important in minimizing bias. Since I used many discrete and fairly objectively determinable characters, I believe that another worker, following my system, would duplicate the patterns of my results with no more than minor differences. Variations in viewers' standards should not create or mask geographical trends if the standards are applied consistently and systematic bias is minimized. The observed latitudinal gradients *cannot* be mere artifacts of my use of different sets of field guides for northern and southern regions; for most character states, the same latitudinal trend found over the entire transect is observed over those segments of the transect for which I used the same sets of field guides. Within a segment the trend could not be affected by differences between field guides.

RESULTS

Table 2 summarizes my results, illustrating the latitudinal pattern of each character state. The more detailed results and the initial classification of species cannot be presented for reasons of space.

For most character states, the geographic patterns in ubiquitous families and in all families are similar, differing only in details such as the absolute percentage represented in each region (Table 2). In some instances a statistically significant latitudinal trend in ubiquitous families is paralleled by a weaker, not statistically significant, trend in all families, or vice versa. Often this occurs if the trend is strong at one end of the latitudinal transect and weak or absent elsewhere. The geographic patterns of only three character states differ markedly between ubiquitous families and all families. More than half of the character states show latitudinal gradients that are statistically significant at $\alpha \leqslant .05$. Many of these trends are highly significant and/or represent a large change in the frequency of the character state over the latitudinal transect.

Analysis of Character 1 demonstrates that pronounced sexual dichromatism is more common at higher latitudes, especially within the ubiquitous families. Character 2 virtually repeats Character 1: in relatively few strongly dichromatic species are females almost as bright as males. Nearly all such cases are suboscines, primarily Formicariidae. Females of dichromatic species are brightly colored or contrastingly patterned (Character 3) more frequently in the temperate zone than in the tropics; this trend is not statistically significant for all families because they show no increase until the higher latitudes are reached. Character 4 indicates that a much greater proportion of temperate species molt to a much duller nonbreeding plumage in comparison to tropical species.

My two most important measures of colorfulness are Character 5, the number of quartiles of the body covered by bright colors, and Character 6, the number of different bright colors present on the bird in sizeable area. None of the states of Character 5 shows a significant latitudinal gradient (Fig. 2a, Table 2). The distribution of species with respect to the number of quartiles of bright color is very similar in all regions. No dependence of the number of quartiles on latitudinal region could be detected by the G Test in either ubiquitous families or all families. The mean number of quartiles per species shows no significant gradient (Table 3), but it is slightly greater in the mid-latitude regions. Over 50% of the species in each of the regions lacks any significant bright color. This group is largest in Costa Rica, representing over 60% of the passerine species.

The state 'zero bright colors' of Character 6 is identical to Character 5's state 'zero quartiles of bright color' just discussed. Thus, a latitudinal gradient is likewise absent, the majority of species in all passerine faunas lacking significant bright colors. One bright color (BC) accounts for 31 to 41% of the species and similarly lacks a latitudinal trend (Fig. 2b, Table 2). Combining the character states 0 and 1 bright color does not produce any trend. The frequency of two bright colors increases northward, up to 8.4% in Canada and Alaska. The frequency of three bright colors, conversely, increases southward, reaching a maximum of less than 3%. Only two species, both tropical, have four bright colors. Combining character states 3 and 4 bright colors improves the statistical significance of their increase southward. The latitudinal gradients in frequencies of particular character states were detected by the Hotelling and Pabst Test, which is specifically sensitive to monotonic trends. The G Test is sensitive to many additional forms of dependence. I detected no form of dependence of the number of bright colors on latitudinal region by the G Test in either ubiquitous families or all families. The G Test can detect, but not identify, gradients of the form observed, but the observed magnitudes are insufficient for such a general test. As was the case with quartiles of color, the mean number of bright colors per species shows no significant gradient but is slightly greater in the mid-latitude regions (Table 3). The overall mean is slightly more than one-half bright color per species.

The only colors that commonly occupy a greater area than any other color are brown, black, gray, and green plus yellowish green (G +yG) (Table 2). Of such dominant colors, black is most frequent in the tropics. Brown is most frequent to the north. This trend is strong and highly significant in ubiquitous families, but when all families are considered, the trend is not significant and is absent except at higher latitudes due to the addition of many brown tropical suboscines, especially species of Furnariidae and Dendrocolaptidae. Gray increases significantly to the north and is most common in the three regions containing extensive deserts. Green plus yellowish green (and therefore total yellow-green plus green, Tyg + G) are much more common to the south. Results for the less common colors are also in Table 2.

Pure yellow (Y) is the most common dominant bright color (Character 8), with greenish yellow (gY), red, blue, and orange plus yellowish orange (O + yO) somewhat less frequent. All colors of this character show the same direction or lack of latitudinal gradation as they do under Character 7, with the following exceptions: greenish yellow, fairly common as the dominant bright color, is much more common to the south; total yellow-orange plus orange (Tyo + O) is more com-

TABLE 2. Summary of results for all characters, to illustrate the presence or absence, magnitude, and statistical significance of latitudinal gradients. The approximate frequency of each character state at each end of the latitudinal series of regions, indication of any consistent frequency difference at mid-latitudes, and the significance level of observed gradients are given.

Character	Ubiquitous families				All families			
	Temp.[1]		Trop.[1]	Signif.[2]	Temp.		Trop.	Signif.
1. Significant sexual dichromatism present	40		20	****	35		27	**
2. ♂ significantly brighter	40		19	****	35		22	****
3. If dichromatic, ♀ also bright	8		1.5	**	7		4	N.S.
4. Molt to much duller plumage present	15		1.3	*	13.5		1	**
5. No. of quartiles of bright color:								
0 quartiles	53	L[3]	53	N.S.	57	L	60	N.S.
1 quartile	19	L	17	N.S.	18	L	15	N.S.
2 quartiles	16		20	N.S.	14		16	N.S.
3 quartiles	7.5	H[4]	5	N.S.	6	H	4	N.S.
4 quartiles	4	H	4	N.S.	3.5	H	4	N.S.
Quartiles/species	0.9	H	0.9	N.S.	0.8	H	0.8	N.S.
6. No. of significant bright colors:								
0 BCs	53	L	53	N.S.	57	L	60	N.S.
1 BC	40		40	N.S.	35		33	N.S.
2 BCs	8		2.5	**	8		4	*
3 BCs	0		2.5	*	0		2	*
4 BCs	0		0.9	*	0		0.6	*
0 or 1 BC	92.5		94	N.S.	92.5		93	N.S.
3 or 4 BCs	0		3.4	**	0		2.7	**
BCs/species	0.55	H	0.56	N.S.	0.50	H	0.50	N.S.
7. Color dominant by area:								
White	2		1	N.S.	2		2	N.S.
Black	15.5		20	*	13.5		20.5	***
Gray	11	H	10.5	*	16	H	11.5	*
Brown	41.5		25.5	****	43		33.5	N.S.
Green + yG	11.5		33.5	***	10		24	***
gY	1.4	L	1.8	N.S.	1.2	L	1.6	N.S.
Total yg + Green	13		35	***	11		26	***
oY	0		0.9	*	0		1.1	**
Orange + yO	1.3	H	0.4	N.S.	1.1	H	0.3	N.S.
Total yo + Orange	1.3	H	1.3	N.S.	1.1	H	1.4	N.S.
Pure yellow	3.2		1.3	**	2.8		0.8	**
Total yellow	4.5	L	4.0	N.S.	3.9	L	3.9	N.S.
Blue	6.3	H	2.6	N.S.	5.5	H	3.1	N.S.
Pink or purple	2.5		0	**	2.3		0	**
Red	1.9	H	1.3	N.S.	1.7	H	0.8	*
8. Dominant bright color:								
Green + yG	0		3	***	0		2.8	***
gY	2		12	****	2		11	****
Total yg + Green	2		15	****	2		13.5	****
oY	0.6		3.8	**	0.5		3.4	****
Orange + yO	5		5	N.S.	4.6		3.4	*
Total yo + Orange	5.8		8.9	*	5.1		6.9	*
Pure yellow	19		14	*	18		10	***
Total yellow	21		31	N.S.	20		24	N.S.
Blue	4.5	H	3	N.S.	3.9	H	4.7	N.S.
Pink or purple	4.5		0.4	****	3.9		0.6	****
Red	3.9	H	4.6	N.S.	3.4	H	3.6	N.S.
Chestnut	7		1.7	***	6.2		1.1	****
9. Dominant color, if dull:								
White	3.9		2.2	N.S.	3.9		3.6	N.S.
Black	11		10.3	N.S.	9.7		11.9	N.S.
Gray	11	HL	9	*	16	HL	11	*
Brown	38		23	***	39		31	N.S.
Green + yG	7		22	**	6		15	**
gY	0	H	0.9	N.S.	0	H	0.6	N.S.

Table 2. *Continued.*

	Ubiquitous families			All families		
	Temp.[1]	Trop.[1]	Signif.[2]	Temp.	Trop.	Signif.
Total yg + Green	7	23	**	6	16	**
yO		no species			one species	
Blue	0.6	0	*	0.5	0	**
10. Pattern contrast:						
0 = Little or no contrast	51	58	N.S.	51	61.7	**
1 = Some contrast	30	28	N.S.	31	27	N.S.
2 = Strong contrast	18	14	*	15.7	11	**
11. Dominant pattern:						
Entire	43.5	53	*	41.5	52.5	N.S.
Solid areas	41.7	42.5	N.S.	42.7	38	***
Streaked	14	2	**	14.5	5	N.S.
Spotted	0.6 H	0.4	*	0.6	1.6	N.S.
Barred	0	1.5	*	0	2.6	**
12. Bright colors or contrasting patterns dorsally	28	19	**	25.5	20	*
13. Strong iridescence	4.5	7.5	**	4	5	*
14. Conspicuous colors or patterns on soft parts:						
Bill	9.4	9.4	N.S.	8.2	6.6	*
Eyes	3.2	7.5	***	3.9	7.9	N.S.
Around eyes	18	7	***	16	7	**
Legs and feet	0.6	2.5	*	0.5	3	*
Bare face	0	0.8	**	0	0.8	**

[1] Temp. = approximate frequency at the temperate-zone end of the series of regions. Trop. = approximate frequency at the tropical end of the series. These approximations are from regions 10 and 1, respectively, unless the trend is irregular near its ends, in which case weighted averages for the terminal 2 or 3 regions are presented.
[2] Signif. = significance level of trend by Hotelling and Pabst Test. * = $P < .05$; ** = $P < .01$; *** = $P < .001$; **** = $P < .0001$; N.S. = not significant = $P > .05$.
[3] L = frequency generally lower at mid-latitudes than at higher or lower latitudes.
[4] H = frequency generally higher at mid-latitudes.

mon to the south despite a significant trend in the opposite direction by orange and yellowish orange if all families are included; and bright chestnut is much more common to the north.

Brown is the most common dominant dull color in the absence of a dominant bright color (Character 9). Green plus yellowish green, gray, and black are also common as dominant dull colors. The latitudinal frequency pattern of each color of Character 9 is similar to its pattern in Character 7, except for black, which has no trend, and blue, which is very rare as the dominant dull color.

The proportion of the passerine faunas whose patterns were rated as strongly contrasting increases with latitude (Fig. 2c, Table 2). Species with little or no pattern contrast are in the majority everywhere, becoming somewhat more frequent in the tropics. However, this trend is statistically significant only for all families.

Most species have patterns that were classed as "Entire" or as "Solid Areas of Color." Though spots and bars are common, patterns that are really dominated by these markings are rare. This Character 11 differs between ubiquitous families and all families more than any other character (Fig. 2d, Table 2). "Entire" decreases sharply into the temperate latitudes, but this trend is not quite statistically significant for all families ($.05 < P < .06$), being weak or absent elsewhere. Conversely, "Streaked" is much more common at higher latitudes, but the trend is significant only in ubiquitous families. "Solid Areas of Color" and "Spotted" show small and mixed trends though some are significant (Fig. 2d, Table 2). "Barred" appears increasingly to the south.

Bright colors or contrasting patterns on the dorsal surface are more frequent to the north (Character 12), whereas strong iridescence seems to be more common in the tropics (Character 13).

Colorful bills are slightly more common with latitude, a trend absent if ubiquitous families are examined alone. Conspicuously colored eyes are about twice as frequent in the tropics as in the temperate zone, but strong eye-rings are more than twice as frequent in the temperate zone as in the tropics. Conspicuously colored legs and feet are most common in the tropics, and brightly colored bare faces are absent north of Mexico.

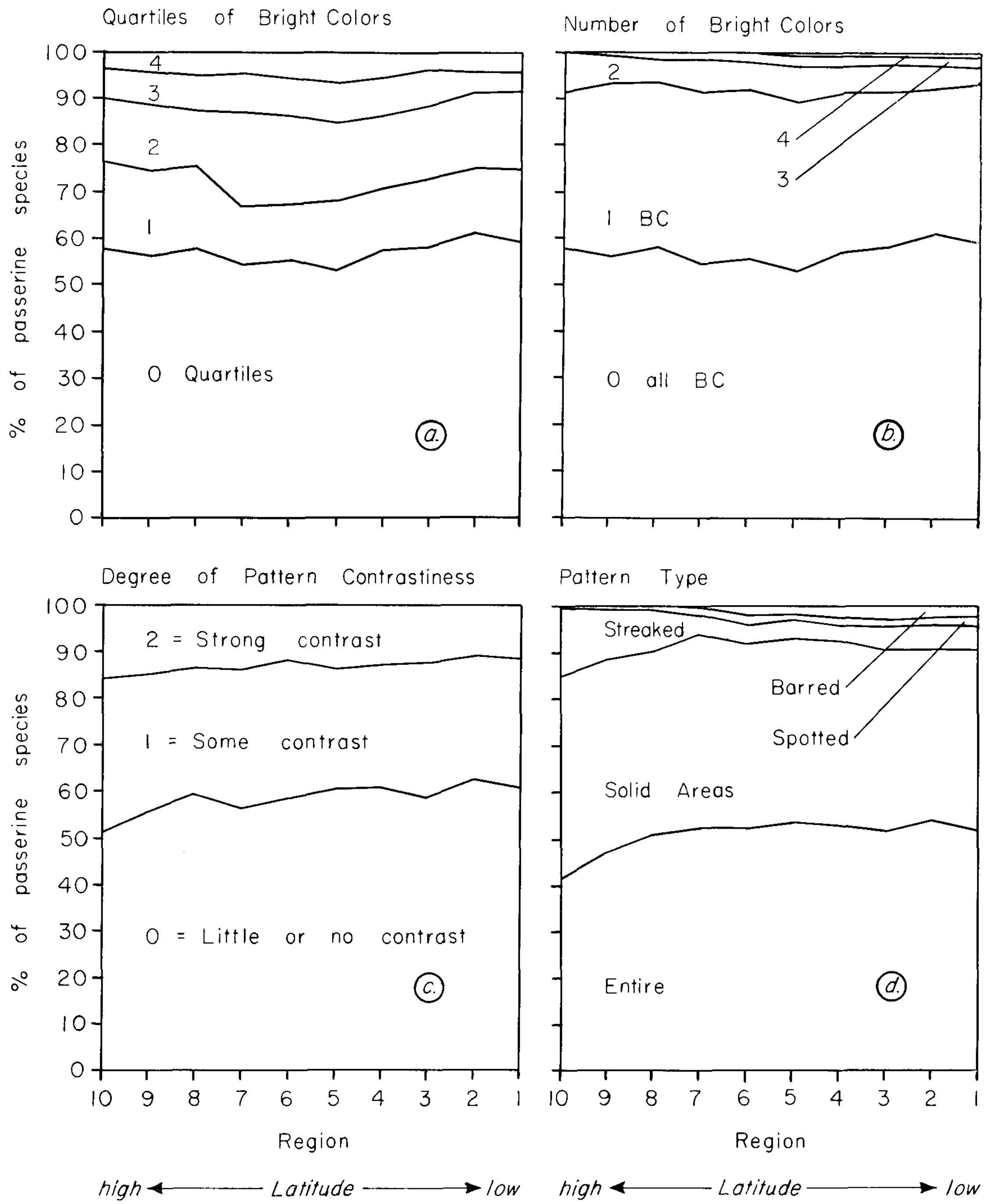

FIGURE 2. Regional frequencies of character states for Characters 5, 6, 10, and 11. Data from all families.

DISCUSSION

For some of the gradients revealed by my data, causal hypotheses seem readily available. Most species that are strongly sexually dichromatic in the breeding season but whose males molt to a duller female-like plumage for the nonbreeding season are long-distance migrants. Hamilton (1961) proposed that strong seasonal dichromatism facilitates the rapid establishment of territories and pair bonds at the beginning of each brief northern breeding season. The dull coloration of these migrant species may help intraspecific flocking (Hamilton and Barth 1962) and make them "inoffensive" to the generally dominant resident tropical species with whom the migrants

TABLE 3. Mean number of quartiles of bright color per species and mean number of bright colors per species. Data from all families.

Region	Quartiles/ sp.	Rank	Bright colors/sp.	Rank
10	0.787	3	0.506	4
9	0.845	6	0.509	5
8	0.836	5	0.496	2
7	0.960	8	0.554	9
6	0.962	9	0.546	8
5	1.004	10	0.604	10
4	0.907	7	0.545	7
3	0.835	4	0.525	6
2	0.760	1	0.489	1
1	0.781	2	0.503	3

flock during the winter. Tropical species, whether colorful or not, are more typically monochromatic. Most are residents or short-distance migrants, and many pair for life.

Several of the gradients seem to be related to concealing coloration. The prevalence of green and yellow-green to the south appears to be related to the greater permanence and prevalence of green foliage, moss, etc. in many tropical habitats as compared to their temperate counterparts. Conversely, the shift to brown and gray at higher latitudes seems to reflect the increase of these colors alternating with green as dominant colors of terrestrial habitats. Pale gray and grayish brown are much more frequent in the deserts and semideserts of northern Mexico and the southwestern United States than in other areas. Other color trends are not as easily explained. For example, a few species of the snowy far north are predominantly white, but so are some tropical species, and no significant gradients in the frequency of white are observed.

The greater degree of pattern contrast and the greater frequency of contrasting patterns and bright colors on the dorsal surface in non-tropical avifaunas might represent a trend toward disruptive coloration in habitats that are visible from above. Alternatively, these patterns may be especially effective for some social functions in particular habitats. These two possibilities are not mutually exclusive.

The decrease in "Entire" at higher latitudes is closely related to a complementary 300–700% increase in the frequency of "Streaked" (Fig. 2d), which appears to serve predominantly as camouflage. That "Solid Areas of Color" shows no trend in ubiquitous families and only a slight increase with latitude in all families is of interest because this pattern type seems to be the most effective for conspicuously displaying bright and contrasting colors.

Two characteristics of iridescence may help to explain its commonness in the tropics. (1) Iridescent colors reflect light only at relatively small angles; a proper angle is needed in order to see them, especially in dim light. (2) Even if most of a bird's plumage is iridescent, only a portion of its body will appear iridescent to a viewer at any instant. By misrepresenting the bird's size and shape, this could act as disruptive coloration. Thus iridescent colors may provide a more directional signal for display than other plumage colors. Iridescence may be suited to the light conditions of tropical evergreen forests. Shade and extensive foliage should reduce the likelihood and range of accidental display of iridescence. Iridescence may be less suitable in deciduous forests, grasslands, and other habitats that are at least seasonally open. In such places a flash of iridescence might attract a predator from a distance. At temperate latitudes the low-angle winter sun may make iridescence visible to far-off predators. The tropical sun is low in the sky only briefly. In a tropical forest the combination of an unobstructed view, sufficient illumination, and a proper light angle may be rare; detection of iridescent prey by stationary predators would be difficult. Some iridescent birds such as grackles (*Quiscalus*) may escape predation through social organization and size.

"Entire" (Character 11) and "Little or No Pattern Contrast" (Character 12) are not the same, as they may seem. The species representing the "Entire" pattern type generally constitute a subset of the group representing "Little or No Contrast," with the latter containing 20% more species. Moreover, although these character states are positively correlated ($P < .05$, Hotelling and Pabst Test), they show different latitudinal gradients in both ubiquitous families and all families. The gradient of contrast is greater in all families, whereas the gradient of "Entire" is significant only in the ubiquitous families.

Among the many statistically significant latitudinal gradients demonstrated by this study, no major trend favors the supposed greater colorfulness of tropical birds. In terms of the proportion of a bird's surface covered by bright color and the number of different bright colors, the passerine faunas of all 10 regions are remarkably similar, and "dull" species predominate everywhere. The tropics do have more species of colorful birds, but they also have more species of each of the duller categories, and the relative proportions of the passerine fauna change very little with latitude. Even in Panama, less than 3% of the passerine species have three or four bright colors. The trend toward iridescence in the tropics probably favors tropical colorfulness, for the colors are often intense and/or multihued, but this trend also involves only a few passerine species. Furthermore, the increase in pattern contrast with latitude would seem to favor temperate "colorfulness."

Willson and von Neumann concluded that tropical birds are more colorful than temperate ones. They found the following percentages of birds to be colorful (indicated differences significant at $P < .05$ by χ^2 tests): South American tropics (32%) > South American non-tropics (27%) = North America (25%) > Europe (10%). As these results include many non-passerines, I calculated separate percentages for non-passerines and passerines from their tables and found no difference between the North American temperate (26.12% 'colorful') and South American tropical (26.38%) passerine faunas. South American non-tropical and European passerines trail at 16.6% and 13.1%, respectively. For non-passerines their tables show the following: South American non-tropics (49.8%) South American tropics (43.3%), North America (22.3%), and Europe (3.5%). For the methodological reasons discussed earlier, I consider these figures suspect, at least for the intercontinental comparisons. Thus my finding that North American temperate and South American tropical passerines do not differ by Willson and von Neumann's analysis only weakly confirms my own results.

Willson and von Neumann concluded that sexual dichromatism is as frequent in the South American tropics as in North America (39%). Using a different method of scoring dichromatism, however, I found that many tropical species are only slightly dichromatic. My data indicate that the frequency of *significant* dichromatism increases with latitude.

There are several possible reasons for an illusion that tropical birds are more colorful than their temperate counterparts. Travelers may be misled by the romantic mystique and novelty of the tropics, the few very colorful species, and the diversity of the tropical avifaunas. It is likely that the many dull species are more easily forgotten than the fewer extremely colorful ones. As the most colorful birds in the world are unique to the tropics, some may think them representative and typical of tropical avifaunas as a whole. The diversity of tropical birds is impressive, and the multitude of different forms may distract the observer from considering each species individually. This effect of diversity may be accentuated by the great regional differentiation of tropical avifaunas from the local to the global scale; between-points diversity is also very high in the tropics.

Other factors not assessed in this study may cause tropical birds to be more colorful on the average than other birds. Non-passerines may include proportionally more of the very colorful tropical species than do the passerines, and tropical non-passerines may tend to be more colorful than temperate non-passerines, as suggested by Willson and von Neumann's (1972) data. Certainly, some of the most colorful birds are non-passerines, for example some hummingbirds, toucans, parrots, and trogons.

Color intensity and plumage texture may vary latitudinally, but these characters must be studied by using actual feathers, not field guides.

My study did not include a truly equatorial avifauna; thus it could not compare colorfulness between equatorial birds and those elsewhere. However, I doubt that a major difference could exist without some evidence of it appearing north to Panama and Costa Rica.

Seasonal changes in temperate zone birdlife probably have complex effects on latitudinal levels of colorfulness. Many of the more colorful temperate zone species migrate to the tropics for the winter, but most of them molt into a duller plumage beforehand. These two phenomena together probably cause both temperate and tropical avifaunas to be duller in the winter than in the temperate breeding season.

Many of the most colorful tropical birds are associated with brightly colored flowers, fruits, or even insects. Their colorfulness may be cryptic due to background matching (Willson and von Neumann 1972, Ned K. Johnson, pers. comm.). These birds should seem less colorful when observed in their normal microhabitats than when isolated as study skins or in portraits.

The tremendous diversity of tropical birds includes some extremely colorful species. Nevertheless, my study indicates that tropical passerines in general are no more colorful than temperate zone passerines in general, with respect to number and area of bright colors.

SUMMARY

This study examines whether tropical birds in general are more colorful than their non-

tropical relatives, using all 784 native passerine species of North and Middle America. I compared the entire membership of major taxa in tropical and non-tropical regions using objectively quantifiable components of colorfulness.

Each species was characterized from plates and descriptions in eight field guides by the use of 14 general characters of color and pattern. The breeding passerine faunas of ten regions in a roughly latitudinal series from Panama to Alaska and Canada were compared. Latitudinal gradients in colorfulness, colors, and pattern types were detected by means of rank-order correlation tests. A separate and parallel analysis was conducted using only the 599 species belonging to the 12 ubiquitous families, but results were in most cases similar to those from all families.

Many statistically significant latitudinal gradients were found, but none of them offers much support for the concept of tropical colorfulness. In terms of both the proportion of the bird's surface covered by bright color and the number of different bright colors, the passerine faunas of all the regions are remarkably similar. "Dull" species predominate everywhere.

Significant sexual dichromatism and the presence of a molt to a duller non-breeding plumage both become more common with latitude. Pattern contrast, bright colors or strongly contrasting patterns on the dorsal surface, and patterns dominated by streaks also become more common to the north. Strong latitudinal trends in some colors, especially green, brown, and gray, seem related to background-matching. Strong iridescence is more frequent in the tropics, and an explanation is offered.

I believe that the differences between my findings and those of Willson and von Neumann (1972) may be due to artifacts in their methods and our use of different methods.

I briefly discuss some factors not assessed in this study that may favor the supposed greater colorfulness of tropical birds.

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