

AN ANALYSIS OF PHYSICAL,
PHYSIOLOGICAL, AND
OPTICAL ASPECTS OF
AVIAN COLORATION WITH
EMPHASIS ON WOOD-WARBLEDERS

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To my parents
who continue to provide enthusiastic encouragement
and to
Charlotte and Charles Smith
who sparked my fascination in all things avian

TABLE OF CONTENTS

LIST OF FIGURES	vii
LIST OF APPENDICES	ix
LIST OF TABLES	ix
CHAPTER 1: STATEMENT OF THE PROBLEM	1
COLORS	1
PHYSICAL HYPOTHESES	1
VISUAL HYPOTHESES	2
OPTICAL HYPOTHESES	2
MEASUREMENT OF ADAPTIVE SIGNIFICANCE	2
COMPARATIVE METHOD	3
WHY WOOD-WARBLEDERS?	4
CHAPTER 2: COLORATION OF WOOD-WARBLEDERS	5
TOPOGRAPHY	5
COLORATION	5
Reflectance spectra of plumage colors	5
Frequency and distribution of plumage colors	8
Reflectance spectra of legs and bills	10
Frequency and distribution of color of legs and bills	11
COLOR VARIATION OF THE LEGS	14
CHAPTER 3: DURABILITY	17
HOW NATURAL IS EXPERIMENTAL ABRASION?	18
Methods	18
Comparison	18
EXPERIMENTAL ABRASION OF WOOD-WARBLEDER FEATHERS	18
Methods	20
Results	21
Discussion	21
ABRASION BY AIRBORNE PARTICLES	23
PREDICTIONS BASED ON VELOCITY OF PARTICLES	24
Dorsal color	24
Rectrix color	24
Remex color	25
PARTICULATE ABRASION OF PERCHED BIRDS	25
OBSERVED TOPOGRAPHY OF ABRASION-RESISTANT COLORS	26
PREDICTIONS BASED ON NUMBER AND SIZE OF PARTICLES	31
HABITAT DIFFERENCES IN THE NUMBER OF SPECIES WITH DIFFERENT PROPORTIONS OF MELANIC PLUMAGE	31
PREDICTIONS BASED ON RESISTANCE TO FRICTION	35
OBSERVED COLOR TOPOGRAPHY IN RESPONSE TO FRICTION	36
CONCLUSIONS REGARDING DURABILITY	36
CHAPTER 4: COLOR AND ENERGY BALANCE	38
ENERGY BALANCE: A GENERAL EQUATION	39

ENERGY BALANCE IN THE LEGS OF WOOD-WARBLERS	40
MEASUREMENT OF THERMODYNAMIC VARIABLES	41
Mean solar absorptivity	41
Incident sunlight	42
Thermal absorptivity	42
Equilibrium-temperature	43
Evaporative energy loss	45
Convective energy loss: postural changes	46
Convective energy loss: diameter of the legs	47
AIR TEMPERATURE AND DISTRIBUTION OF WOOD-WARBLERS	49
Migratory patterns	49
December distribution of North American Parulinae	51
CONFOUNDING VARIABLES	54
MANDIBULAR COLOR AND BEHAVIOR OF WOOD-WARBLERS	54
Absorbed energy	54
Energy loss	56
CHAPTER 5: REDUCED VISUAL INTERFERENCE	58
COLORATION TO REDUCE REFLECTANCE	58
Regions that reflect into the eyes	58
Reflectance of differently colored feathers	58
Observed facial coloration	59
BEHAVIOR TO REDUCE REFLECTANCE	60
CONCLUSIONS	62
CHAPTER 6: COLOR PATTERNS THAT INCREASE VISIBILITY	64
WINGBARS AND TAILSPOTS	64
REVEALING BEHAVIOR	65
Methods	65
Results	66
Discussion	69
DISPLAY BEHAVIOR	71
Circle flight	72
Glide	72
Moth flight	72
Hover	72
Song flight	72
Supplant	72
Chase	72
Wings-out	72
Tail-spread	72
CONCLUSIONS	74
CHAPTER 7: COLOR OF OPTICAL SIGNALS	75
CALCULATION OF CONTRAST	75
Irradiance	75
Surface reflection	75
Dominant frequency	77
Excitation purity	77

Relative luminance	79
Discriminability scaling of purity and luminance	79
Discriminability scaling of frequency	80
Color-space	81
CALCULATION OF A COLOR-SPACE FOR WOOD-WARBLEDERS	83
Ambient irradiance	83
Sample color-space	88
PREDICTED COLOR OF TAILSPOTS AND WINGBARS	88
OBSERVED COLOR OF TAILSPOTS AND WINGBARS	91
CONCLUSIONS REGARDING COLOR-CONTRAST	92
CHAPTER 8: AN INTEGRATIVE APPROACH	95
COLOR AND COLOR PATTERNS IN WOOD-WARBLEDERS: A SUMMARY	95
Unfeathered surfaces	95
Feathered surfaces	96
CONCLUDING REMARKS	97
ACKNOWLEDGMENTS	99
LITERATURE CITED	100
APPENDICES	110

LIST OF FIGURES

Figure 1. Topography of a wood-warbler	6
2. Reflectance spectra from feathers	7
3. The solar spectrum	11
4. Reflectance spectra of the legs of Ovenbirds and Magnolia Warblers	12
5. Munsell color values of the upper and lower mandibles of males	13
6. Munsell color values of the upper and lower mandibles of females	14
7. Undamaged and abraded Ovenbird feathers	19
8. The mean percentage of broken barbs in feathers of different colors	20
9. The percentage of area lost by differently colored feathers	22
10. Percentage of area lost during abrasion plotted as a function of the percentage of broken barbs	23
11. The frequency of feather colors among dorsal regions plotted as a function of abrasion resistance	26
12. The frequency of feather colors among ventral regions plotted as a function of abrasion resistance	27
13. The frequency of tail colors of 112 species	28
14. Right outermost rectrix of some eastern North American wood-warblers	29
15. The frequency of wing colors of 112 species	30
16. The proportion of oceanic or desert-dwelling species plotted as a function of the proportion of non-melanic plumage	32
17. The frequency of nape colors of 112 species	33
18. The frequency of collar colors of 112 species	34

19. The frequency of throat colors of 112 species	35
20. Absorption spectra of representative wood-warblers' legs	41
21. The temperature difference between dark and light legs plotted as a function of solar irradiance	43
22. The temperature difference between dark and light legs plotted as a function of ground temperature	44
23. The probability of drawing one or both legs into the ventral feath- ers plotted as a function of potential convective energy loss	47
24. Diameter of the legs plotted against their Munsell color value	48
25. Mean minimum air temperature on the mean earliest arrival date for each species of wood-warbler seen at Madison, Wisconsin, plotted as a function of the Munsell color value of its legs	50
26. Mean minimum air temperature on the mean earliest arrival date for each species of wood-warbler seen at Itasca, Minnesota, plotted as a function of the Munsell color value of its legs	51
27. Mean minimum air temperature on the mean latest departure date for each species of wood-warbler seen at Madison, Wisconsin, plotted as a function of the Munsell color value of its legs	52
28. Mean air temperature at the northern limit of the species' range (Audubon Christmas Bird Count) plotted as a function of the Munsell color value of its legs	53
29. The percentage of time spent in sunlight plotted against the Mun- sell color value of the upper mandibles	55
30. Probability of foraging in sunlight plotted against the Munsell color value of the upper mandible	61
31. Interval between consecutive flights plotted as a function of the mean length of continuous observation	67
32. Coloration of an optical signal as a product of ambient irradiance	76
33. Commission Internationale de l'Eclairage chromaticity diagram	78
34. The cubic color-space	82
35. The spectral composition of sunlight shown as a power-density function of spectral position	84
36. A comparison of spectral irradiances beneath the canopy in one- layered, two-layered, and young coniferous forests	85
37. A comparison of spectral irradiances beneath the canopy in one- layered, two-layered, and young broadleaf forests	87
38. A comparison of the spectral irradiances beneath the canopy in two-layered and young broadleaf forests in May 1974 and June 1973	88
39. C.I.E. chromaticity diagram with points representing the illumi- nation in six forested habitats and in direct sunlight	89
40. A sample color-space	90
41. Calculation of the silhouette area of a cylinder	117

LIST OF TABLES

Table 1.	Numerical equivalents of representative colors used to describe the plumage colors of wood-warblers	9
2.	Frequency of occurrence of colors on male wood-warblers in nuptial plumage	10
3.	Frequency of occurrence of colors on female wood-warblers in nuptial plumage	10
4.	Intraspecific comparison by sex and age of Munsell color values of legs	12
5.	Intraspecific comparison by season of Munsell color values of legs	15
6.	Probabilities that the difference in percentage of broken barbs between any two feather colors is due to chance	21
7.	Probabilities that the difference in percentage of surface area lost between any two feather colors is due to chance	22
8.	Size and density of airborne particles recorded in different habitats	31
9.	Mean absorptivity of sunlight by wood-warbler legs	42
10.	Comparison of the Munsell color value of the upper mandible with the legs in males of 115 species of wood-warblers	56
11.	Number of species in which males or females have eyebrow stripes, eye-rings, or eyelines of the indicated color	60
12.	Frequency of flight among wood-warblers located by song	66
13.	Flight duration of wood-warblers located by song	68
14.	Frequency of commutes among wood-warblers located by song ..	69
15.	Frequency of aerial hawking among wood-warblers located by song ..	70
16.	Frequency of sally-gleaning among wood-warblers located by song ..	71
17.	Frequency of flight among genera of wood-warblers	71
18.	Occurrence of aerial and non-aerial displays among wood-warblers ..	73
19.	Frequency of aerial displays among wood-warblers located by song ..	74
20.	Irradiance and illuminance of direct sunlight measured in a clearing and of transmitted and reflected sunlight measured in six different forest types at different times of year	86
21.	Contrast-distances	92
22.	Preferred habitat of species with differently colored tailspots and wingbars	93
23.	Preferred habitat of species with orange and yellow tailspots	93
24.	Evaluation of hypotheses	96

LIST OF APPENDICES

I.	Scientific and Common Names of Wood-warblers	110
II-1.	Relative Areas of Body Regions	113
II-2.	Proportions of Non-melanic Plumage	114
III.	Systemé Internationale (SI) Units Used in the Text and the Following Appendices	115
IV.	Details of Energy Balance in the Legs of Wood-warblers	116
V.	Correlations with Arrival, Departure, and December Distribution of Wood-warblers	122
V-1.	Spring Arrival Sequence at Madison, Wisconsin, 1971-1975	122
V-2.	Spring Arrival Sequence at Itasca, Minnesota, 1973, 1974	123
V-3.	Autumn Departure Sequence from Madison, Wisconsin, 1971-1974	124
V-4.	December Distribution in North America, 1947-1973	124
V-5.	Correlation of Weight and the Color of Wood-warblers' Legs	125
VI.	Correlation between Munsell Color Value of the Upper Mandible and Percent of Foraging Time Spent in Sunlight	126

CHAPTER 1

STATEMENT OF THE PROBLEM

COLORS

My skin is kind of sort of brownish
Pinkish yellowish white.
My eyes are greyish bluish green,
But I'm told they look orange in the night.
My hair is reddish blondish brown,
But it's silver when it's wet.
And all the colors I am inside
Have not been invented yet.

(Silverstein 1974:24)

Color is a characteristic of multicellular organisms, each of which has one or more colors distributed in a pattern that may be a single uniform color or a multicolored patchwork. Many evolutionary functions have been suggested for the effect of color on optical signalling (Thayer 1909; Cott 1957; Hailman 1977a; Rohwer et al. 1980; Rohwer 1982). More recently nonoptical functions of color have received limited attention (Burt 1979, 1984; Underwood 1979; Walsberg 1982, 1983) and an integrated approach to the evolutionary significance of color has begun to emerge (Burt 1979, 1981). By exploring a variety of evolutionary hypotheses relating color and color patterns of wood-warblers (Emberizidae: Parulinae) to the physical environment, this monograph further emphasizes the important insights that follow from an integrated approach to the evolutionary significance of color.

Hypotheses that account for the evolution of a particular color or color pattern fall into four major categories: (1) physical hypotheses that depend on the molecular properties (e.g., radiation absorption spectra, strength and type of chemical bonds) of the chemicals that create color, (2) visual hypotheses in which color or its pattern affects the organism's own vision, (3) optical hypotheses in which color or its pattern affects the organism's visibility to other animals, and (4) identity hypotheses in which an individual's color or pattern depends on the color and pattern of competitors. Hypotheses from the last category are not considered in this monograph, but see Rohwer (1975, 1982) and Rohwer et al. (1980).

PHYSICAL HYPOTHESES

Biological colors are created by biochromes, schemochromes, or some combination of both (Fox 1953; Needham 1974). Biochromes are molecules that create color by the differential absorption and reflection of visible light within their molecular structures. Schemochromes are structures that create color by macromolecular, optical principles (e.g., diffraction, refraction, interference). Biochromes and schemochromes have many characteristics unrelated to color, for example solubility, polarity, or photosensitivity. Selection may favor a particular biochrome or schemochrome for one or more of its nonoptical characteristics that

supply only physiological or structural needs of the organism. Thus, color *per se* is selected indirectly and may not be adaptive.

Dark hair is mechanically stronger than light hair (Laxer and Whewell 1955) and dark feathers resist abrasion better than light feathers (Chapman 1912:87; Van Tyne and Berger 1976:163). The effect of different biochromes on the abrasion-resistance of feathers is evaluated experimentally in Chapter 3. I expand a previous model of abrasion by airborne particles (Burt 1979, 1981) and discuss how differential abrasion-resistance may affect the color and pattern of color.

Chapter 3 includes material discussed elsewhere (Burt 1979, 1981) so that the reader will gain an appreciation for the diversity of interacting hypotheses without having to consult previous publications. The chapter also contains new material that may answer questions raised by the earlier publications and the physical model of abrasive damage is revised, thereby extending its ecological applicability.

Several studies (Norris 1967; Porter and Gates 1969; Porter et al. 1973) have suggested that coloration of reptiles evolved to optimize energy exchange between the organism and its environment. Among birds the color of feathers appears less important to energy exchange than ptiloerection and behavior (Walsberg et al. 1978; Walsberg 1982, 1983). Nevertheless, color of uninsulated surfaces may be important to the energy balance of birds. In Chapter 4 that hypothesis is developed quantitatively and tested with comparative data on migration and winter range of wood-warblers.

VISUAL HYPOTHESES

Although this is a distinct functional category, few hypotheses have been proposed or evaluated. Most of Chapter 5 is devoted to developing and evaluating the hypothesis that coloration of surfaces near the eye may be an adaptation to reduce reflectance that interferes with vision. Previously suggested hypotheses (Ficken and Wilmot 1968; Ficken et al. 1971) are briefly discussed.

OPTICAL HYPOTHESES

Displays often evolve from noncommunicative behavior by a process known as ritualization. Tinbergen (1952) suggested that during ritualization conspicuous morphological structures or patterns of color evolve to accentuate the ritualized behavior. Chapter 6 evaluates the correlation between wingbars and tailspots of wood-warblers and the frequency of noncommunicative behavior accentuated by these patterns. The chapter then examines the association of wingbars and tailspots with ritualized displays.

Conspicuousness and inconspicuousness are not understood quantitatively. Conspicuousness appears to consist of three components, (1) contrast, (2) pattern, and (3) movement. Although unable to deal quantitatively with all three, I devote Chapter 7 to developing a method for the quantification of contrast and applying that method to the color of tailspots and wingbars of wood-warblers, patterns shown to be conspicuous optical signals and therefore requiring high color contrast.

MEASUREMENT OF ADAPTIVE SIGNIFICANCE

Behavioral and morphological characters that are adaptive persist in a population because they contribute to the reproductive potential of the organism. Three

methods are available for the study of selective pressures that maintain a behavioral or morphological character in a population (based on Tinbergen 1963; Klopfer and Hailman 1967).

1. Direct measurement of selective pressures is possible where the character varies within the population. Because intraspecific variation in color and pattern of wood-warblers is slight (see Chap. 2), direct measurement was not possible.

2. Selective pressures can be studied experimentally by creating variation where none exists and measuring selection against such variation or by manipulation that creates variation similar to that seen naturally and assuming that the manipulation approximates natural selection. The latter experimental method was used when natural abrasion of feathers was simulated by sand blasting which led to formulation of a model for abrasion by airborne particles. The experimental method was also used in the abstract to develop and test engineering models that were presumed to describe selective pressures. Engineering analysis (Tracy's evolutiono-engineering approach, 1979a) assumes that an optimal solution to one adaptive problem has little effect on other adaptations. Clearly, adaptations exist in concert and much of the variation seen in subsequent chapters results from the interaction of adaptations and the multiple effects of a single adaptive solution. Despite the interdependence of adaptations, engineering analysis offers a rigorous, quantitative approach to the study of adaptation (Lewontin 1978), thus all subsequent models assume that adaptive problems can be isolated. Tests were based on interspecific variation which introduces the third method.

3. Selective pressures that maintain a character in a population may be inferred from comparative study of phylogenetically or ecologically related species. The traditional cornerstone of this method is the prediction made from a comparison of two or more species and the subsequent confirmation or rejection of that prediction in previously unstudied species. Comparative study is used to evaluate the adaptive significance of color and its pattern. My approach differs from a straightforward application of the comparative method because I often start with a physical model (see above). Predictions of the behavior associated with differently colored species are deduced from these models and tested using the comparative method. Because survival and reproduction are not measured directly, my observations can reject hypotheses, can suggest which hypotheses merit further exploration, but cannot confirm hypotheses concerning the selective pressures acting on color and its pattern. Predictions generated by comparative study of wood-warblers must be extended to and confirmed in other untested taxa.

COMPARATIVE METHOD

Ideally the taxa chosen for comparative study should include phylogenetically related and unrelated taxa as well as those with similar and dissimilar ecologies (Hailman 1976). If the character is similar among phylogenetically related species and different among species with similar ecologies, then the similarity is of phylogenetic origin. If ecologically similar species share a character that is not shared by phylogenetically related species, then the comparison suggests an adaptive function for the character. The comparative method leads to testable hypotheses concerning adaptive function and phylogenetic relationship. These hypotheses predict the behavior or morphology of unstudied species. Thus the comparative

method allows function to be examined in situations where direct measurement of selective pressures is impossible.

The method has three requirements. The species studied must (1) be related to varying degrees, (2) have ecologies with varying degrees of similarity, and (3) an abundance of species must be available for comparison. If the phylogenetic and ecological relationships among species are not varied, or if only a few species are studied, no valid conclusion can be drawn.

WHY WOOD-WARBLERS?

The New World wood-warblers (Parulinae) offer many advantages, particularly with respect to use of the comparative method. The subfamily's 115 species and 27 genera provide substantial phylogenetic diversity (Mengel 1964; Barrowclough and Corbin 1978; Avise et al. 1980). Ecological variation is also substantial. Some species inhabit tropical rainforest, whereas others frequent mangrove swamps, temperate deserts, or boreal forest. Some species migrate; others are sedentary. Even diet varies from the partially frugivorous Yellow-rumped Warbler to the entirely insectivorous Blackburnian Warbler (Bent 1953). Phylogenetically related and unrelated species exist, as do ecologically similar and dissimilar species.

Despite a variety of colors and patterns, the size and proportions of wood-warblers are similar throughout the Parulinae, with the sole exception of the Yellow-breasted Chat. The chat's behavior and morphology suggest that it may not be a wood-warbler (Eisenmann 1962; Ficken and Ficken 1962a; Avise et al. 1980; but see Sibley and Ahlquist 1982). Therefore, I have excluded the chat and consider body size and physiology to be similar throughout the subfamily.

Wood-warblers are often abundant, and a variety of species can usually be found in an area of a few square kilometers making comparative study possible. Where personal observation was impossible, comparative data were often available from the large literature on wood-warblers. Finally, specimens for morphological study are plentiful in museum collections. Classification, scientific names (Lowery and Monroe 1968), and common names (Skutch 1954; Griscom and Sprunt 1957; Meyer de Schauensee 1970; A.O.U. 1983) of wood-warblers used in this study are given in Appendix I.

CHAPTER 2

COLORATION OF WOOD-WARBLERS

“What limitless possibilities there are in a flock of Warblers!”

(Chapman 1912:430)

Before proceeding to an analysis of the functional significance of colors and color patterns, I present a standardized set of topographical terms for use throughout the monograph. I introduce the Munsell color system to standardize color names and broadly equate its color categories with the spectral reflectance of differently colored feathers. Finally, I describe the color patterns of wood-warblers and examine the limits to variability within the subfamily Parulinae.

TOPOGRAPHY

I divided the wood-warbler's body into 22 regions (Fig. 1). Occasionally, some of the smaller regions may be grouped under one collective term. The eyebrow stripe, eye-ring, eyeline, and whisker are referred to collectively as the *face*. The nape, collars, and throat comprise the *neck*. The *dorsum* is formed by the back, rump, and upper tail coverts, and the *venter* is formed by the breast, belly, and under tail coverts (*crissum*).

The regions identified in Figure 1 approximate the natural limits of contrastingly colored patches of feathers.

COLORATION

The colors of wood-warblers can be described quantitatively by their reflectance spectra. However, measurement of all differently colored patches on males and females of 115 species of wood-warblers would be difficult. Therefore similar spectra were grouped into color categories and these categories equated with color swatches in the Munsell color system. The Munsell system was then used to categorize the colors of wood-warblers.

Reflectance spectra of plumage colors.—The Beckman DK-2A spectrophotometer determines reflectance of a sample by comparing the reflection from that sample to the reflection from a reference. A light beam originates at a tungsten filament (near infrared and visible) or hydrogen arc (ultraviolet) source, passes through a monochromator, and shines on a reference or sample port. The beam switches between ports by means of a mirror that oscillates about 15 times per sec. On its way to the mirror the light beam passes through a slit formed by movable blades. These blades automatically maintain a constant beam energy for any wavelength by letting more or less light through.

After reflection from the mirror the light beam enters a spherical chamber, the inside of which is coated with ultra-pure BaSO₄ which diffusely reflects more than 99% of the incident energy. The beam reflected from the sample or reference ports is reflected by the chamber to a photomultiplier (UV and visible) or lead sulfide (near infrared) detector at the top of the chamber.

To measure reflectance the reference port is covered with a white (BaSO₄) blank.

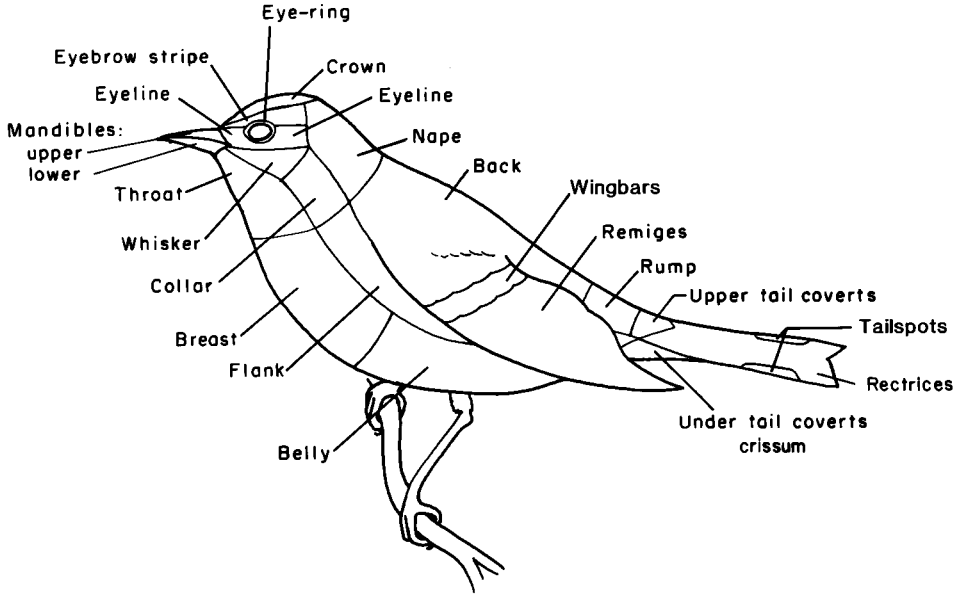


FIGURE 1. Topography of a wood-warbler.

The other port is covered with a sample, such as feathers. Both sample and reference ports are located normal to the incident beam so that specular reflection from the quartz disc covering the sample port is directed back along the beam's path and not toward the detector.

Reflectance from wood-warbler feathers was measured by covering the sample port with a museum skin oriented so that the port was filled with a uniformly colored, feathered surface. A visual survey of wood-warblers suggested nine color categories. Within categories specimens were measured that represented the full range of variation. All specimens were from the zoological museum at the University of Wisconsin-Madison, were recently collected, and in perfect condition. Blue was measured from the backs of the Black-throated Blue Warbler (6 specimens), Cerulean Warbler (3), and Northern Parula (5). Yellow-green was measured from the backs of the Blue-winged Warbler (5), Common Yellowthroat (10), and Mourning Warbler (3). Yellow was measured from the breasts of the Blue-winged Warbler (5) and Nashville Warbler (7). Brown was measured from the backs of the Ovenbird (10) and Northern Waterthrush (6). Chestnut was measured from the flank of the Bay-breasted Warbler (5), orange from the throat of the Blackburnian Warbler (4), and black from the back of the American Redstart (10). White was measured from the throat of the Cerulean Warbler (3) and the breast of the Chestnut-sided Warbler (10). Gray was measured from the backs of the Golden-winged Warbler (5) and Canada Warbler (4). Red is rare among wood-warblers and no specimen was available for measurement.

Because coloration of feathers is discussed primarily in terms of its communicatory function (Chap. 6 and 7), Figure 2 shows only the visible spectrum. Reflectance spectra from wood-warbler feathers fall into nine, distinct patterns (Fig. 2) that correspond well with the color categories named above. Differences

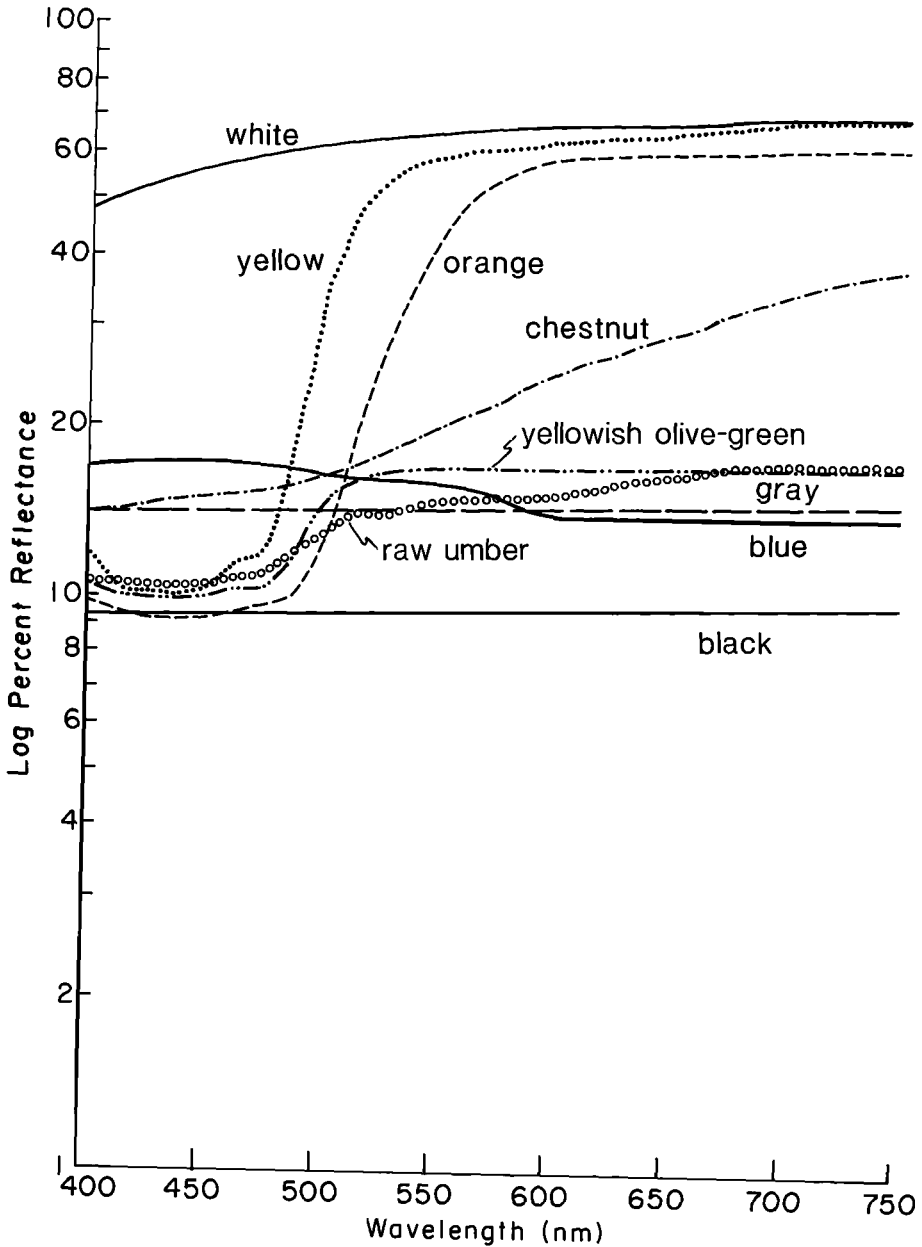


FIGURE 2. Reflectance spectra from the feathers of the following species with color names from Smithe (1975) and abbreviations as used throughout the monograph: American Redstart (jet black; Bk), Golden-winged Warbler (light neutral gray, Gy), Cerulean Warbler (white, W; cerulean blue, Bu), Northern Waterthrush (raw umber, Br), Blue-winged Warbler (yellowish olive-green, Gr; spectrum yellow, Y), Bay-breasted Warbler (chestnut, Ch), and Blackburnian Warbler (spectrum orange, O).

were slight among conspecific specimens and among colors within categories, thus only one spectral curve is shown for each color.

Natural colors usually reflect a wide range of frequencies. When all reflected frequencies have approximately equal physical intensity, the color is achromatic.

Jet black reflects the least light and has a flat, achromatic reflectance spectrum. Light neutral gray is equally achromatic, but reflects more light than black. White reflects strongly across the entire visible spectrum, although reflectance is slightly greater among longer wavelengths.

A surface that has an identifiable spectral color reflects some frequencies more intensely than others. Surfaces that reflect a narrow range of frequencies are said to be saturated. Surfaces with a broad reflectance spectrum, even approaching achromaticity, are said to be poorly saturated or desaturated. More blue than red is reflected by cerulean blue feathers, but the reflectance curve of blue is quite flat indicating poor saturation. Raw umber (brown) reflects somewhat more red than blue indicating that it is a poorly saturated red. Chestnut, like brown, is an unsaturated red, but the greater slope of the reflectance curve indicates more reddish saturation than brown, and the greater reflectance across the spectrum indicates a brighter color than brown. Yellowish olive-green (yellow-green) reflects relatively little light, but shows a very slight peak in the middle of the spectrum, the green region. The reflectance of spectrum orange rises sharply in the green to yellow regions of the spectrum and remains high in the red region of the spectrum. The reflectance of spectrum yellow increases rapidly in the blue-green region of the spectrum and continues to increase slightly through the yellow, orange, and red spectral regions. None of the colors is monochromatic. Brown and especially blue approach achromaticity.

From the reflectance spectra I calculated (see Smithe 1981) three numbers known as tristimulus values (X, Y, and Z) from which were calculated two additional numbers, the chromaticity coordinates (x, y). The chromaticity coordinates quantitatively describe colors within the color system of the Commission Internationale d'Eclairage (CIE) (see Chap. 7, Fig. 3 for further explanation). Visualization of the CIE system is accomplished by the Munsell color system (Smithe 1975) which specifies a color by its dominant frequency called hue, its brightness called value, and its saturation called chroma. Red (R), yellow-red (YR), yellow (Y), yellow-green (GY), green (G), blue-green (BG), blue (B), purple-blue (PB), purple (P), and red-purple (RP) are the major hues of the Munsell system. The value of each hue grades from black to white with 0/ indicating absolute blackness and 10/ indicating absolute whiteness. The chroma of each hue ranges from desaturated, /1, to highly saturated, /16. Within the Munsell system colors are specified by a colored swatch and a series of numbers and letters in the sequence hue value/chroma (Table 1). Because reflectance spectra could be grouped into nine distinct color categories, tristimulus values were used to equate the spectra with swatches in the Munsell color system (Table 1) and the Munsell system was used to describe the color of all differently colored patches on males and females of 115 species of wood-warblers.

Frequency and distribution of plumage colors.—The color of each body region (Fig. 1) of male and female wood-warblers in adult, nuptial plumage was determined by using the color categories described above (Fig. 2) and equated with the Munsell color system. Specimens and Munsell color swatches were compared in direct sunlight. Where subspecies were similarly colored, colors of the most geographically widespread subspecies were described. If subspecies differed markedly in color, each subspecies was described and treated as a separate data point when the color difference was relevant to the analysis.

TABLE 1
 NUMERICAL EQUIVALENTS OF REPRESENTATIVE COLORS USED TO DESCRIBE THE
 PLUMAGE COLORS OF WOOD-WARBLEDERS

Color	Percent reflectance from wood-warbler feathers	Tristimulus values			Chromaticity coordinates		Munsell notations		
		X	Y	Z	x	y	Hue	Value	Chroma
Jet black	9.6	1.89	1.95	2.65	0.29	0.30	0.9 PB	1.46/	0.6
Light neutral gray	14.5	29.40	30.18	34.55	0.31	0.32	N ¹	6.01/	
White	62.0				0.33	0.33			
Cerulean blue	15.3	15.66	18.31	48.93	0.19	0.22	8.3 PB	4.84/	9.3
Yellowish									
olive-green	14.8	14.92	16.37	3.90	0.42	0.46	8.2 Y	4.60/	6.2
Spectrum yellow	44.7	62.14	66.26	8.78	0.45	0.48	5.7 Y	8.34/	12.4
Spectrum orange	37.1	47.07	36.27	2.74	0.55	0.42	5.0 YR	6.51/	15.5
Chestnut	21.8	10.29	8.02	4.48	0.45	0.35	1.1 YR	3.31/	5.0
Raw umber	14.1	12.40	11.10	5.81	0.42	0.38	7.1 YR	3.86/	4.0

¹ N = neutral.

If the chroma of the color was less than 2, the color was neutral, white if its value was 8 or above, black if its value was 2 or below, and gray if its value was between 2 and 8.

The hypothesis that different colors are equally frequent was tested with the chi-square Goodness of Fit statistic (Sokal and Rohlf 1969) for those colors occurring at least once among wood-warblers. The hypothesis that colors are randomly distributed on a wood-warbler's body was tested by assuming that colors occurred on each body region in proportion to their frequencies throughout the subfamily Parulinae. Hypothetical and observed distributions were compared with the chi-square Test for Independence (Sokal and Rohlf 1969), as were frequencies of different colors in males and females.

Colors on male wood-warblers in nuptial plumage are not equally frequent ($\chi^2 = 861.6$, d.f. = 9, $P < 0.005$), nor are colors distributed randomly ($\chi^2 = 1832.2$, d.f. = 81, $P < 0.005$) over the body (Table 2). As with males, colors on females in spring plumage are not equally frequent ($\chi^2 = 1228.0$, d.f. = 9, $P < 0.005$), nor are they distributed randomly ($\chi^2 = 1909.2$, d.f. = 81, $P < 0.005$) over the body (Table 3). While not surprising, the nonrandom occurrence and distribution of color in both male and female wood-warblers emphasizes the existence of non-random selection operating on color and its pattern.

The frequency of different colors in males and females is significantly different ($\chi^2 = 132.2$, d.f. = 9, $P < 0.005$). Colored patches of males are more often black and less often yellow-green or brown than colored patches of females. Surprisingly, white, yellow, orange, red, and chestnut are equally frequent in both sexes. However, the yellow, orange, red, and chestnut colors on female wood-warblers are less saturated than the same colors among males. The comparison confirms our intuitive grasp of the difference between male and female wood-warblers. Dark colors are blacker and light colors brighter among males than among females. Males have saturated colors and heightened contrast (see Chap. 7), whereas fe-

TABLE 2
 FREQUENCY OF OCCURRENCE OF COLORS¹ ON MALE WOOD-WARBLERS² IN
 NUPTIAL PLUMAGE

Feathered region	W	Y	O	R	Ch	Gr	G	Br	Bu	Bk
Crown	2	9	3	3	15	11	25	2	7	34
Face ³	71	90	6	8	14	28	74	14	10	131
Neck ³	31	60	7	8	7	58	89	16	14	46
Dorsum ³	4	8	0	1	6	148	97	24	27	22
Tail	0	0	0	0	0	29	11	39	0	33
Tailspots	48	1	2	0	0	28	6	20	0	6
Venter ³	123	144	6	15	11	1	18	4	0	14
Flank	17	19	1	2	5	30	26	5	2	5
Remiges	0	0	0	0	0	21	9	67	0	15
Wingbars	23	9	1	0	0	21	8	42	0	8
Total frequency	319	340	26	37	58	375	363	233	60	314

¹ W = white, Y = yellow, O = orange, R = red, Ch = chestnut, Gr = yellow-green, G = gray, Br = brown, Bu = blue, Bk = black.

² One specimen for each of 112 species.

³ Collective term for several smaller feathered regions; see page 5 for explanation.

males, although they possess similar color patterns, have less saturated colors that produce less optical contrast.

In addition to sexual differences, the patterns and colors of wood-warblers vary with age and season (Stewart 1952; Mayfield 1960; Foster 1967a, b; Nolan 1978; Rohwer et al. 1983). Such differences are undoubtedly important (Hamilton 1961; Hamilton and Barth 1962; Rohwer et al. 1980); however, when discussing patterns and colors of plumage I consider only nuptial plumage of adult wood-warblers.

Reflectance spectra of legs and bills.—The reflectance spectra of legs was measured for wood-warblers killed at local television towers during September 1973 using a Beckman DK-2A spectrophotometer as described above. The toes were removed and the tarsometatarsi aligned to make a light tight surface 1 cm². Reflectance was measured within 24 h of death. Construction of the tarsometatarsi sample required the legs of six to nine wood-warblers. Seven species were killed in large enough numbers to meet both the time and number limitations. The bill

TABLE 3
 FREQUENCY OF OCCURRENCE OF COLORS¹ ON FEMALE WOOD-WARBLERS² IN
 NUPTIAL PLUMAGE

Feathered region	W	Y	O	R	Ch	Gr	G	Br	Bu	Bk
Crown	1	6	2	3	13	28	23	7	5	18
Face	67	78	6	8	11	61	114	36	3	39
Neck	34	61	5	8	5	69	85	27	7	13
Dorsum	3	7	0	1	6	169	81	34	10	7
Tail	0	0	0	0	0	29	9	55	0	13
Tailspots	45	2	1	0	0	27	5	24	0	2
Venter	119	136	5	11	9	2	19	10	0	4
Flank	13	17	0	2	4	34	34	5	0	1
Remiges	0	0	0	0	0	22	4	71	0	9
Wingbars	30	1	0	0	0	21	4	45	0	6
Total frequency	312	308	19	33	48	462	378	314	25	112

¹ Color names as in Table 2.

² One specimen for each of 106 species.

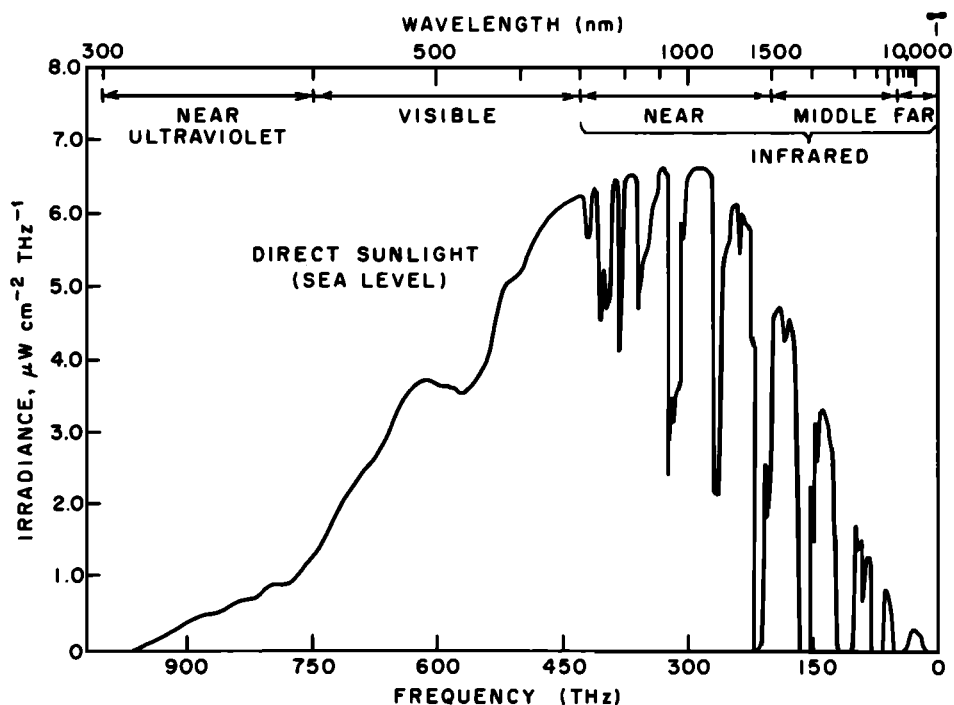


FIGURE 3. The solar spectrum measured at solar noon at sea level on the equator (adapted from Gates 1965b).

was too small to measure singly, and its elongate-conical shape prevented construction of a larger surface. Because melanin is the primary biochrome in both the legs and bills of wood-warblers, I assumed that bills and legs with the same Munsell color value had similar reflectance spectra (but see Schwalm et al. 1977; Bakken et al. 1978).

Because coloration of the legs is discussed in terms of absorption of solar energy, reflectance is expressed as a percent of the incident solar radiation at sea level on the equator (Fig. 3). The legs of Ovenbirds reflect more energy in the visible and near infrared regions of the spectrum than the legs of Magnolia Warblers (Fig. 4). Because the energy of the solar spectrum is concentrated in the same region (Gates 1966, 1980; Monteith 1973), the difference in reflectance of visible and near infrared radiation is not greatly reduced by increased reflectance of longer wavelengths from Magnolia Warbler legs (Fig. 4). The legs of Magnolia Warblers and Ovenbirds have similar solar reflectances from 1900 nm (about 160 TeraHertz [THz]) to the termination of the solar spectrum. Reflectance of thermal radiation (wavelengths in excess of 4000 nm, frequencies below 75 THz) is close to zero for all biological tissues (Gates 1980).

Frequency and distribution of color of legs and bills. — Reflectance spectra could be measured for only seven species, too few for comparative purposes. Thus I used museum specimens and the Munsell color value as a qualitative approximation of reflectance. Low color values indicate little reflectance (i.e., darkly colored legs) whereas high numbers indicate greater reflectance (i.e., lightly colored

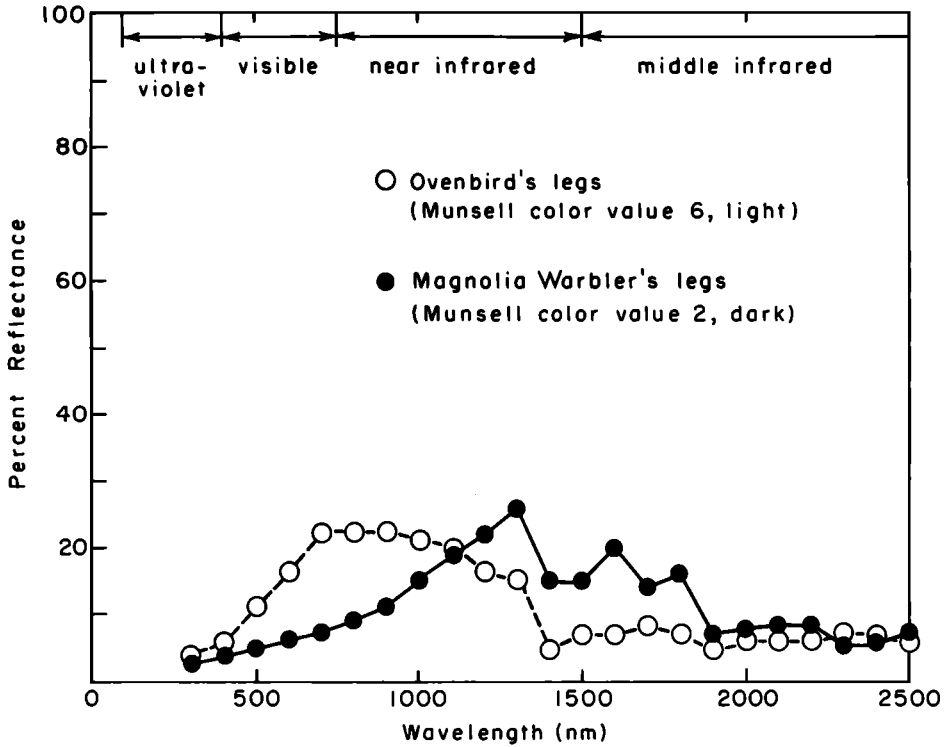


FIGURE 4. Reflectance spectra of the legs of Ovenbirds (light-legged) and Magnolia Warblers (dark-legged).

TABLE 4
INTRASPECIFIC COMPARISON BY SEX AND AGE OF MUNSELL COLOR VALUES OF
LEGS BASED ON THE KOLMOGOROV-SMIRNOV STATISTIC¹

Leg color	Season ²	Male vs female	Adult vs juvenile			
Dark	Spring	0/39	1/2			
			Black-and-white	2, 6		
	Summer	0/31	5/32			
			Black-and-white	2, 2		
			Blue-winged	2, 6		
			Orange-crowned	2, 4		
Grace's	1, 2					
Olive	1, 2					
Autumn	0/18	0/16				
		Winter	0/4			
Light	Spring	0/30	0/4			
			Summer	0/29	1/24	
	Yellow	4, 4				
	Autumn	0/23			1/10	
	Blackpoll	4, 4				
	Winter	0/18	0/4			

¹ The numerator is the number of species with a significant difference in coloration of the legs between indicated groups. The denominator is the total number of species compared. Listed below the numerical comparison are the species, if any, in which leg color differed significantly and the modal color values of the age groups compared. Color values are given in the order of the column heading. Smaller color values indicate darker legs.

² Spring; 21 March–20 June: summer; 21 June–20 September: autumn; 21 September–20 December: winter; 21 December–20 March.



FIGURE 5. Munsell color values of the upper and lower mandibles of males of 115 species of wood-warblers.

legs). To learn how drying affected the color of the legs I measured tarsometatarsi of Chestnut-sided Warblers, a species with dark legs (Munsell color value 2), and Ovenbirds, a species with light legs (Munsell color value 6) within 24 h of death, placed the samples in a desiccating chamber for one week, and measured the absorption spectra again. Legs of Chestnut-sided Warblers absorbed 89 percent of the incident solar radiation when measured within 24 h of death and 88 percent of the incident radiation one week later. Legs of the Ovenbird absorbed 66 percent of the incident radiation when measured within 24 h of death, and 69 percent one week later. In both cases the modal color value was unaffected by drying. These results suggest that the color value of wood-warbler legs is not seriously distorted by drying, probably because their color is based on melanins that resist fading. To a limited extent dark legs became lighter and light legs became darker, suggesting that any differences seen among museum specimens would be greater among living birds. I characterized the color value of the legs of approximately 13,000 individual study skins belonging to 115 species of Parulinae. Munsell color values are ordinal, so the mode was used to measure central tendency.

The legs of wood-warblers tend to be dark. Fifty-eight species of wood-warblers have legs with a Munsell color value of 2 (dark, e.g., Magnolia Warbler), 15 species have legs with a Munsell color value of 4 (light), 26 species have legs with a Munsell color value of 6 (lighter, e.g., Ovenbird), and 16 species have legs with

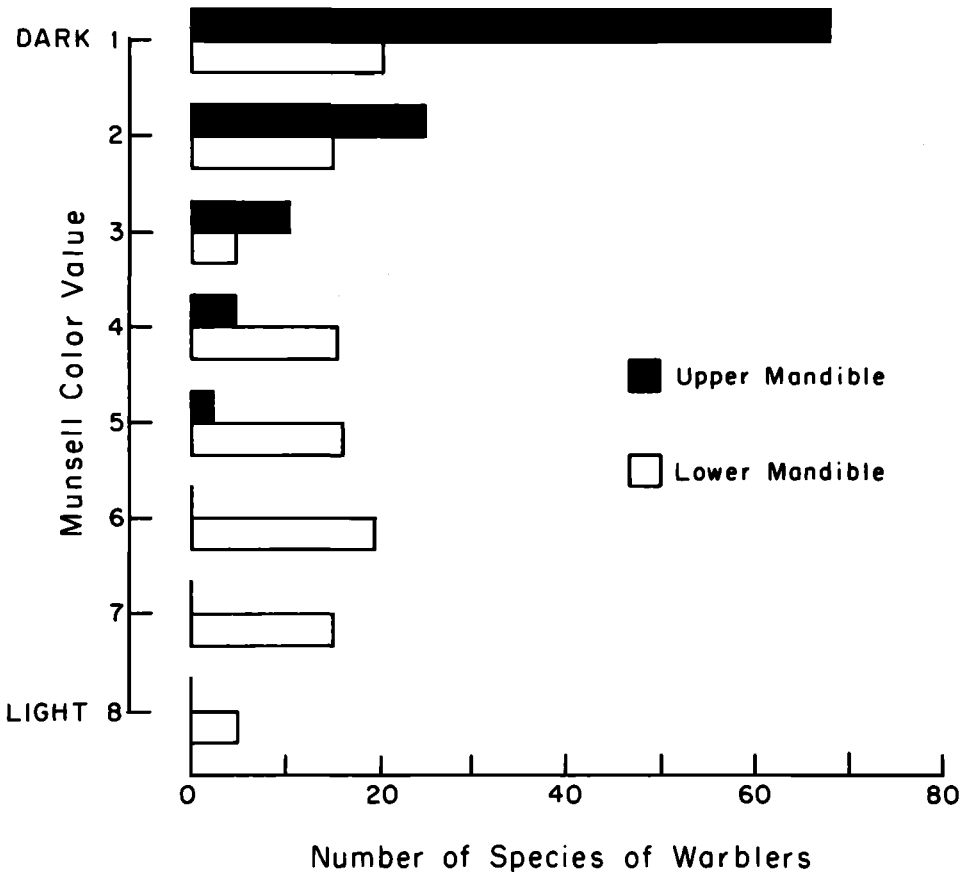


FIGURE 6. Munsell color values of the upper and lower mandibles of females of 106 species of wood-warblers.

a Munsell color value of 8 (lightest). The difference between color values 2 and 4 appeared greater than the difference between 4 and 6 or 6 and 8. Thus legs with color values 4, 6, and 8 are collectively referred to as light, legs with color value 2 are referred to as dark.

The Wilcoxon Matched-Pairs, Signed-Ranks statistic was used to evaluate color values of upper and lower mandibles of 115 species of wood-warblers (Fig. 5). Species with uniform bill color were counted toward retention of the null hypothesis of no difference in color value of upper and lower mandibles. Nevertheless, the upper mandible is significantly darker than the lower among both males ($\chi^2 = 480.5$, $N = 115$, $P < 0.001$) and females (Fig. 6, $\chi^2 = 264.5$, $N = 108$, $P < 0.001$).

COLOR VARIATION OF THE LEGS

Leg coloration was evaluated by grouping specimens by age, sex, and season of collection as indicated on the museum label. Only groups that contained eight or more specimens were compared intraspecifically. Because the data were ordinal, the Kolmogorov-Smirnov statistic (Sokal and Rohlf 1969) was used to evaluate

TABLE 5
INTRASPECIFIC COMPARISON BY SEASON OF MUNSELL COLOR VALUES OF LEGS BASED ON THE KOLMOGOROV-SMIRNOV STATISTIC¹

Leg color	Sex, age	Spring vs summer	Spring vs autumn	Spring vs winter	Summer vs autumn	Summer vs winter	Autumn vs winter
Dark	Male	1/39 Prairie 2,1	1/26 Palm 2,1	0/31	0/29	2/29 Pine 2,2 Vitelline 1,2 0/19	2/21 Palm Slate-throated Redstart 1,2 0/16
	Female	2/33 Prairie 2,1 Vitelline 1,2	2/20 Blackburnian 2,1 Palm 2,1	3/17 Prairie 2,2 Palm 2,2 Pine 2,2	0/17		
	Juvenile	0/2	1/1 Black-and-white	0/0	1/15 Townsend's 2,1	0/4	1/4 Palm
Light	Male	2/31 Yellow 4,4 Blackpoll 6,4	3/24 Northern Parula 4,2 Blackpoll 6,4 C. Yellowthroat 6,4	0/24	0/23	1/24 Yellow 4,4	2/20 Northern Parula 2,4 Tropical Parula 6,2
	Female	2/27 Yellow 4,4 Blackpoll 6,4	2/19 Blackpoll 6,4 C. Yellowthroat 6,6	1/19 Blackpoll 6,6	0/18	1/21 Yellow 4,4	0/14
	Juvenile	0/3	0/2	0/0	0/10	0/1	0/1

¹ The numerator is the number of species with a significant difference in coloration of the legs between indicated groups. The denominator is the total number of species compared. Listed below the numerical comparison are the species, if any, in which leg color differed significantly and the modal color values of the seasonal groups compared. Color values are given in the order of the column heading. Smaller color values indicate darker legs.

differences in modal color value or variance in color values between two groups. The hypothesis of no difference was rejected whenever the probability of no difference was below 0.05.

Males and females of all species had the same leg color (Table 4). Adults and juveniles differed significantly in only eight species (Table 4). In three of these the modal color value was the same, but significantly more variation was found among juveniles. In the remaining five species the legs of juveniles were lighter than the legs of adults. The color of the legs shows significant seasonal variation in very few species (Table 5), fewer than would be expected from Type II error. Furthermore, where significant variation occurs, it is inconsistent or involves the range of variation not the modal leg color. Some species have darker legs in autumn, others in spring, or summer, or winter.

The slight, but significant, tendency for juveniles to have lighter legs than adults ($P < 0.05$, Sign Test) and lighter legs early in the year results from nestling wood-warblers having fleshy legs until fledging, when the integument dehydrates (Ricklefs 1967, 1968, 1974) and, in dark-legged species, becomes impregnated with melanin. Among adult wood-warblers coloration of the legs does not vary with sex (Table 4) or season (Table 5).

CHAPTER 3

DURABILITY

“There is only one important exception to the generalization that desert animals resemble in color the soil on which they live, but it is a most remarkable one, in many deserts a number of indigenous animals are black.”

(Buxton 1923:150)

Different biochromes affect the structure of feathers differently (Desselberger 1930; Danforth 1958; Brush and Allen 1963; Brush 1965a, 1981; Voitkevich 1966). If durability depends on the feather's structure, then differently colored feathers exposed to a constant amount of wear should show different amounts of damage. If potential damage to the plumage differs significantly in different parts of the body or in different habitats, then the frequency of differently colored feathers with different durabilities should reflect differences in potential damage.

Dwight (1900) appears to have been the first to associate differential durability with differently colored barbs, although much earlier Bachman (1839) concluded that birds change color without molting simply by wearing away the differently colored edges of feathers. Averill (1923) observed that white barbs of recently shed primaries of gulls are destroyed whereas black barbs, although damaged, remain functional. His observation was repeated by Test (1940) on the remiges of Common Flickers (*Colaptes auritus*) and experimentally replicated by Bergman (1982) on the remiges of Scandinavian Lesser Black-backed Gulls (*Larus f. fuscus*). These observations suggest that black feathers are more durable than white feathers. Because melanin is the source of the black color, they further imply that feathers containing melanin are more durable than feathers lacking it. Averill and Test compared black and white barbs, but they failed to mention other colors or to quantify the differences in durability of differently colored feathers. This is important because the color of melanic feathers varies with the density of melanoprotein granules (Bowers 1959) and the structure and arrangement of granules (Auber 1957; Greenewalt et al. 1960; Durrer and Villiger 1962; Dyck 1971, 1976).

Damage to feathers may result from collision with large (e.g., twigs, stones) or small (e.g., airborne particles) objects, from repeated bending, or from over-extension. The hypothesis that differently colored feathers resist damage differently was tested by subjecting feathers of different colors to experimental abrasion by airborne particles. Microscopic analysis suggests that experimental abrasion of feathers is qualitatively similar to natural abrasion. A mathematical model of particulate abrasion was developed to predict the distribution of abrasion-resistant plumage on a wood-warbler's body and the frequency of abrasion-resistant plumage among species in habitats with different abrasive properties. Predictions were compared with the observed color patterns of wood-warblers and the frequency of abrasion-resistant plumage among species in different habitats.

HOW NATURAL IS EXPERIMENTAL ABRASION?

Natural abrasion of feathers requires months under unstudied conditions. Experimental abrasion requires seconds under conditions that can be quantified, but does experimental abrasion approximate the natural process? To address this question, feathers plucked just prior to molt were compared microscopically with feathers experimentally abraded with airborne silicon particles.

Methods.—The outermost left rectrix and the left medial rectrix were plucked from wood-warblers and other small songbirds captured at the Delaware Wildlife Refuge during the summer of 1981. Because abrasion was most evident on the medial rectrices, they were selected for microscopic study. None of the species whose feathers were experimentally abraded was captured during 1981; therefore, experimentally abraded feathers of the Ovenbird and naturally abraded feathers of the Song Sparrow (*Melospiza melodia*) were selected for comparison. Feathers of both species are uniformly brown and of similar size and microstructure.

Ovenbird feathers were exposed for one min to a stream of silicon carbide particles, 20 μm or less in diameter. To prevent the feather from moving in the air stream it was clamped with its ventral surface against a metal plate. Feather and plate were mounted perpendicular to the stream of particles with the dorsal surface of the feather 10 cm from the source of the air stream. During the one-min exposure period, 0.4 g of silicon carbide hit the feather.

The distal 8 mm of feather was chosen as a readily identifiable portion that was representative of the feather's vane. Ten abraded feathers of each species were uniformly coated with a 500 Å layer of gold in a Technics Hummer V triode sputter-coater. Specimens were examined with an Hitachi scanning electron microscope, model S-500, at 20 kV accelerating voltage and a focal length of 10 mm.

Comparison.—Several structural changes in feathers result from wear (Fig. 7 A, D, G, vs B, E, H, or H, C, I). The vast majority of barbules have been broken (Fig. 7 B, C, E, F), many of them within 10 μm of the barb. The broken edges (Fig. 7 E, F, and H) are jagged suggesting that the distal portion of the barbule was torn off, not gradually rubbed away. The barbs and rachis of both the Ovenbird (Fig. 7 B, E) and Song Sparrow (Fig. 7 C, F) show cracks and some splitting that reveal the internal structure of the barb (Fig. 7 H). Similarities between naturally (Fig. 7 C, F, I) and experimentally (Fig. 7 B, E, H) abraded feathers suggest that experimental abrasion is a reasonable approximation to natural wear.

Abrasive particles are found on feathers that were collected in the wild (Fig. 7 D, G, F, I) and feathers that were experimentally abraded (Fig. 7 E, H). The presence of abrasive particles and similarities in damage to Ovenbird and Song Sparrow feathers suggest that particulate abrasion may be an important source of feather wear.

EXPERIMENTAL ABRASION OF WOOD-WARBLER FEATHERS

Present knowledge of the structure of biochromes and their effects on feather structure allows us to predict the relative extent of damage to differently colored feathers subjected to equal amounts of wear. Melanin is a polymer of high molecular weight that binds to protein (Nicolaus 1968; Needham 1974) to form an insoluble granule about 0.2 μm in diameter. Deposition of melanoprotein granules

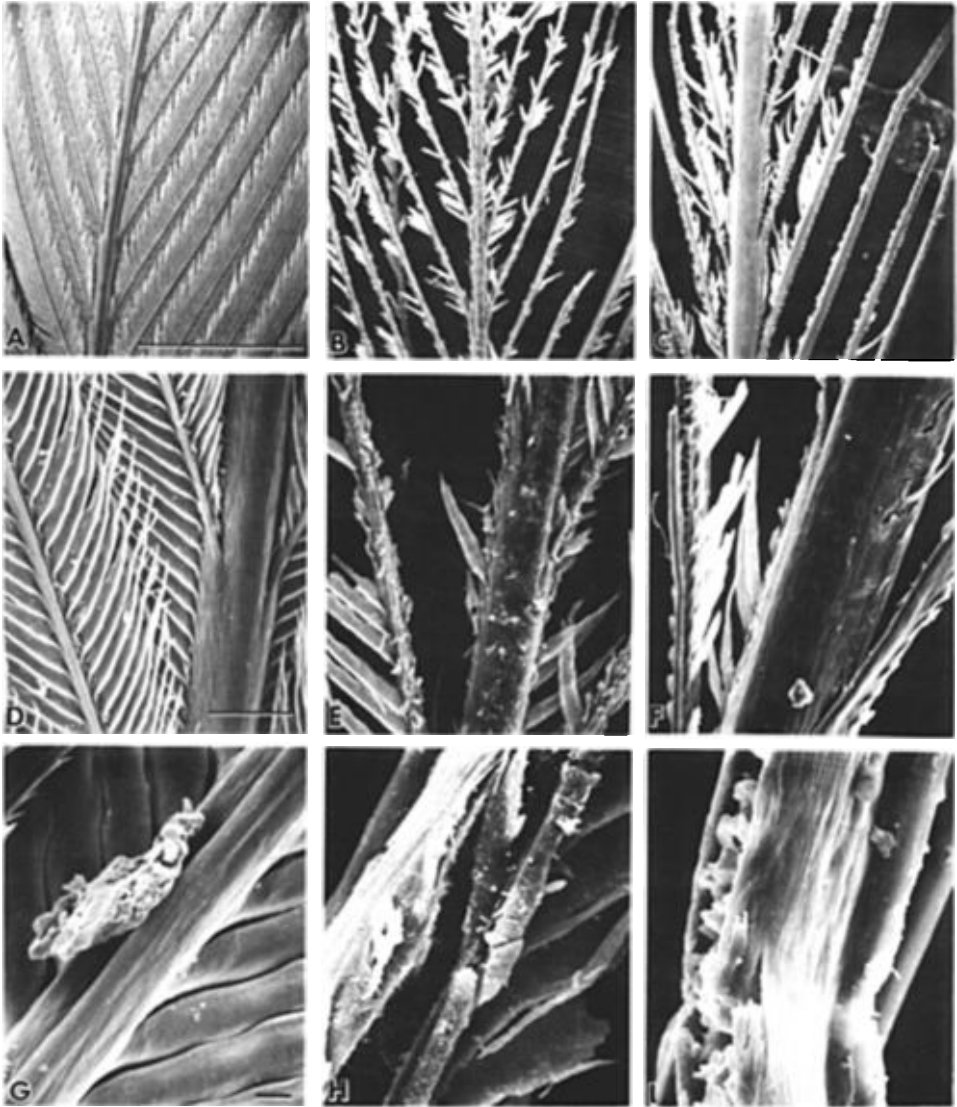


FIGURE 7. Undamaged (A, D, G) and experimentally abraded (B, E, H) Ovenbird left outermost rectrices are shown in the left and middle columns respectively. A naturally worn Song Sparrow medial rectrix is shown in the right (C, F, I) column. The rachis is the largest, most nearly vertical structure in A–F. The large branches from the rachis are barbs with the barbules being the flattened branches off the barb. Barbicels are the hooklike structures visible along the right side of D. In all pictures, the proximal portion of the feather is at the bottom of the picture and the distal portion at the top of the picture. The scale for each horizontal row of photographs is represented by a horizontal bar in the lefthand photograph: (A) 500 μm , (D) 50 μm , and (G) 5 μm .

in the feather's cortex (Lucas and Stettenheim 1972) is associated with thickening of the cortical layer (Spottel 1914; Voitkevich 1966). Carotenes and xanthophylls are diffuse biochromes and in moderate concentrations, such as found in wood-warbler feathers (Brush and Johnson 1976), have little effect on the structure of

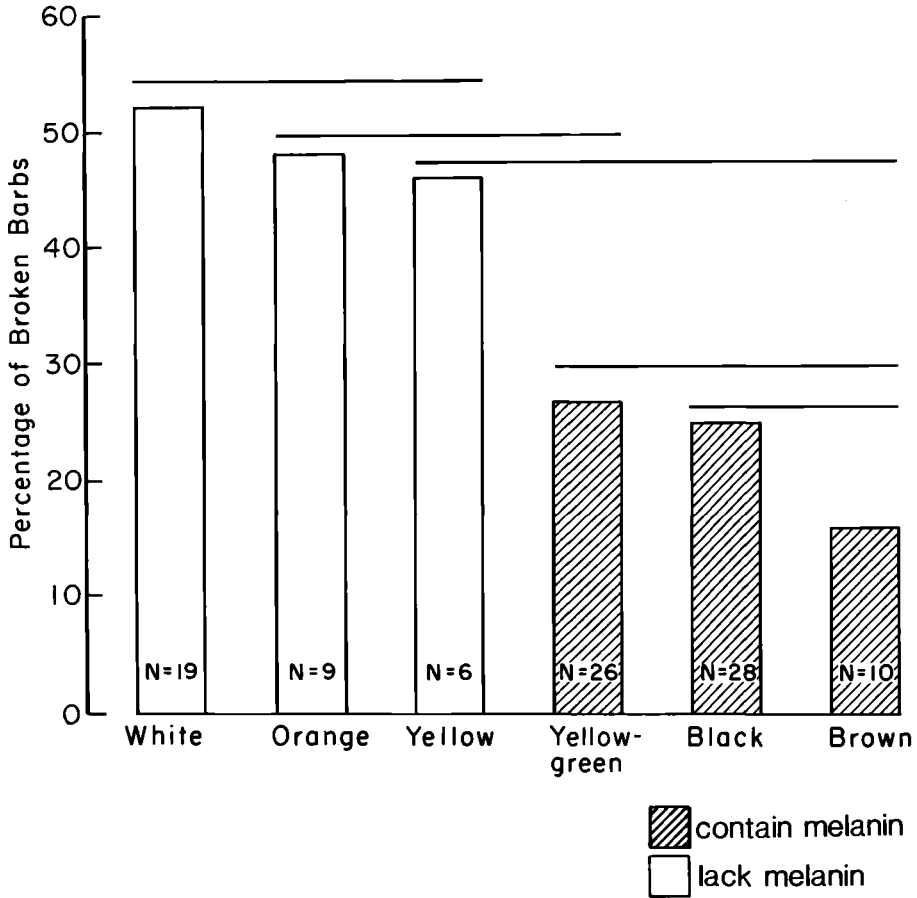


FIGURE 8. The mean percentage of broken barbs in feathers of different colors exposed to equal amounts of particulate abrasion. N = number of feathers abraded. The horizontal lines group colors whose mean percentage of broken barbs do not differ significantly.

barbs and barbules (Brush and Siefried 1968). In wood-warblers white is due to reflection and scattering of all wavelengths from closely packed, colorless fibers in barbs and barbules. Only in feathers that contain melanin are there structural reasons to expect increased durability. Therefore, *prediction 3.1*: among differently colored feathers, those impregnated with melanin should be most resistant to wear.

Methods.—The outermost left rectrix was plucked from wood-warblers killed at television transmitting towers in Madison, Wisconsin, on 26–28 September 1973. This feather was chosen because it was readily identifiable, easily removed, frequently contained a contrastingly colored patch, and occurred in six different colors in different species.

Prior to abrasion all feathers were examined to ensure that there were no broken barbs or missing barbules. Only feathers in perfect condition were used. Feathers were individually tagged and traced so that the area of each feather or colored patch could be used.

TABLE 6
 PROBABILITIES¹ THAT THE DIFFERENCE IN PERCENTAGE OF BROKEN BARBS
 BETWEEN ANY TWO FEATHER COLORS IS DUE TO CHANCE

Feather color	White	Orange	Yellow	Yellow-green	Black
Brown	<0.001	<0.02	>0.1	>0.5	>0.5
Black	<0.005	<0.05	>0.5	>0.5	
Yellow-green	<0.005	>0.1	>0.5		
Yellow	>0.5	>0.5			
Orange	>0.5				

¹ Based on analysis of variance and Scheffé test.

All feathers were experimentally abraded as described above. Following abrasion the percentage of broken barbs was determined for each feather. I calculated a mean percentage of broken barbs for each color and used an analysis of variance to compare all means. The difference between pairs of means was evaluated with the Scheffé test (Roscoe 1975).

Following abrasion, each feather was again traced. A Keuffel and Esser compensating polar planimeter, model 620005, was used to find the area from the tracings of each feather before and after abrasion. Readings were in square centimeters and accurate to 0.1 cm². Because size of the differently colored feathers varied, I calculated the area destroyed by abrasion as a percentage. The analysis of variance was used to evaluate the difference among means and the Scheffé test to evaluate the differences between all pairs of means.

Results.—The mean percentages of broken barbs vary significantly with color ($F = 9.32$; d.f. = 5,95; $P < 0.001$; Fig. 8; Table 6). Black, brown, and yellow-green feathers, the only feathers that contain melanin, have a significantly lower percentage of broken barbs than white, which contains no biochrome. Black and brown feathers also have a significantly lower percentage of broken barbs than orange feathers which contain a carotenoid, but no melanin. The percentage of broken barbs is not significantly different among black, brown, and yellow-green feathers, all of which contain melanin, nor do yellow, orange, and white feathers, none of which contain melanin, differ significantly.

The mean percentages of area of differently colored feathers destroyed by abrasion differ significantly ($F = 37.65$; d.f. = 5,95; $P < 0.001$; Fig. 9; Table 7). Brown and yellow-green feathers lost a significantly smaller percentage of area than did yellow and white feathers. The percentage of surface area lost by brown, black, and yellow-green feathers is not significantly different nor do percentages of surface area lost by orange, yellow, and white feathers differ significantly.

The percentage area lost during abrasion is highly correlated with the percentage of broken barbs (Fig. 10: $r = 0.91$). However, future discussion is based on the percentage of area lost because loss of surface area is critical to proper functioning of the wings and tail. A barb that breaks at the tip will have less aerodynamic effect on the bird than a barb that breaks near its base.

Discussion.—The hypothesis that differently colored feathers exposed to a constant amount of abrasion show different amounts of damage is strongly supported by the data. Feathers whose color is wholly (black, brown) or partially (yellow-green) the result of melanin-impregnation are more abrasion-resistant than feathers

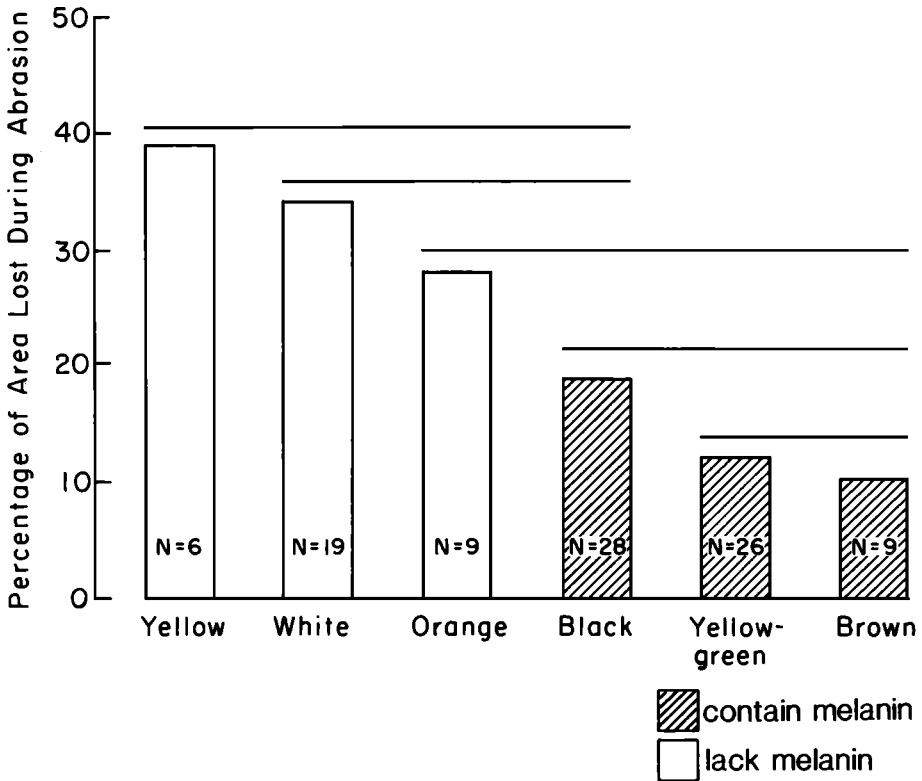


FIGURE 9. The percentage of area lost by differently colored feathers exposed to equal amounts of particulate abrasion. N = number of abraded feathers. The horizontal lines group colors whose mean percentages of area lost do not differ significantly.

lacking melanin (*prediction 3.1*). The addition of moderate amounts of carotenoid to melanic feathers, as in the yellow-green feathers of wood-warblers, has no significant effect on abrasion resistance. The data suggest no difference in the abrasion resistance of carotenoid colored and white feathers. However, concentration of carotenoids greater than those found in wood-warbler feathers can affect the structure of feather barb and barbules. Externally the barbules may be lacking and the barb laterally flattened (Frank 1939; Rawles 1960; Brush and Seifreid

TABLE 7

PROBABILITIES¹ THAT THE DIFFERENCE IN PERCENTAGE OF SURFACE AREA LOST BETWEEN ANY TWO FEATHER COLORS IS DUE TO CHANCE

Feather color	Yellow	White	Orange	Black	Yellow-green
Brown	<0.05	<0.02	>0.5	>0.5	>0.5
Yellow-green	<0.05	<0.005	>0.5	>0.5	
Black	>0.5	>0.5	>0.5		
Orange	>0.5	>0.5			
White	>0.5				

¹ Based on analysis of variance and Scheffé test.

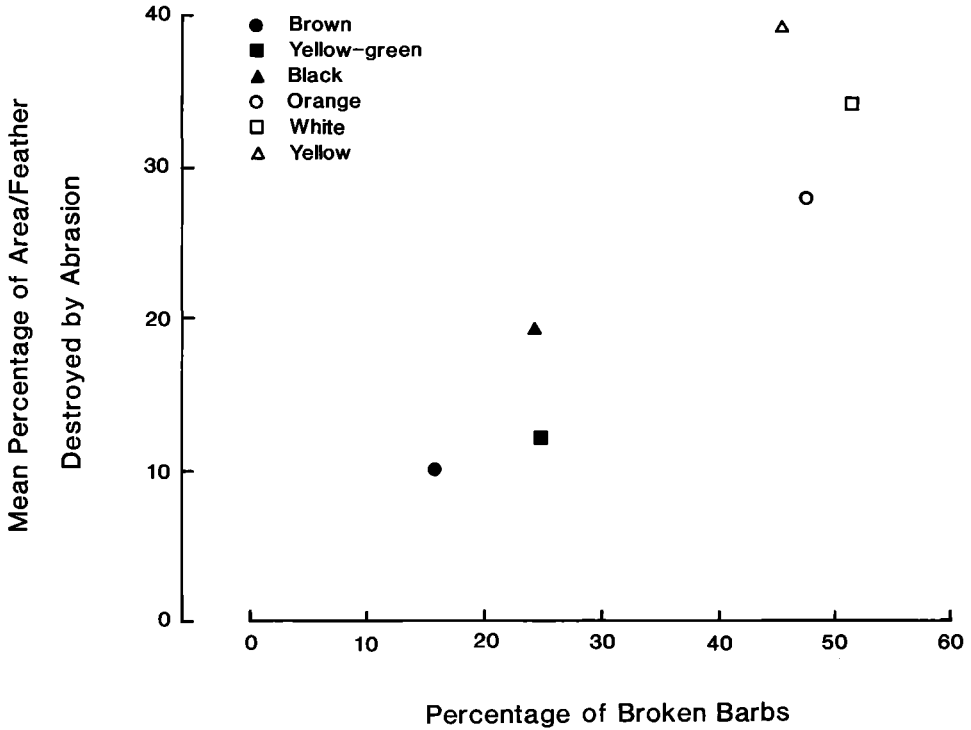


FIGURE 10. Percentage of area lost during abrasion plotted as a function of the percentage of broken barbs.

1968; Olson 1970; Johnson and Brush 1972; Troy and Brush 1983). Internally the medulla may be reduced or absent, although the cortical cells, which contain the biochrome, remain distinct and a thickened exterior cuticle is present (Olson 1970). How such modifications affect abrasion resistance is unknown.

ABRASION BY AIRBORNE PARTICLES

The damage, (D), that results from the collision of airplane wings with airborne particles is proportional to the kinetic energy ($K.E.$) and number (n) of colliding particles (Probstein and Fasso 1970; Waldman and Reinecke 1971; Smith, D. H. 1976):

$$D = cn(K.E.) \quad 3.1$$

where c is a constant of proportionality. I assume that the same relationship describes the collision of airborne particles with the wings of birds. The non-elasticity of such collisions is shown by the presence of particles embedded in the variously damaged barbs and barbules (Fig. 7 B, C, E, F, H, and I). The energy transferred from the particle to the barb or barbule struck is dissipated as heat or by destruction of the keratin fibers.

Kinetic energy is energy due to motion. It is defined by:

$$K.E. = \frac{1}{2}mv^2 \quad 3.2$$

where m is the mass of the particle and v its velocity in any direction. Substituting equation 3.2 for $K.E.$ in equation 3.1 gives the following relationship:

$$D = \frac{c}{2}nmv^2 \quad 3.3$$

Damage from the abrasion of airborne particles is proportional to the number of collisions, the mass of the colliding particles, and the velocity of the particles.

If a habitat has a uniform density of particles with a characteristic, average mass—for example the air of boreal forests that might contain conifer pollen as its primary particulate—, then variations in the kinetic energy of particles depend only on variations in the velocity of the particles at the moment of collision with the feather barbs or barbules (equation 3.3).

The mass of an average particle traveling toward collision with a barb or barbule is small compared to the mass of the feather. Therefore, if the feather to be hit is taken as the reference point, all changes in velocity of either the feather or the particle will appear as changes in the velocity of the particle only. Airborne particles will appear to approach a flying bird along its line of flight at a velocity equal and opposite to the bird's velocity, assuming still air. Airborne particles will approach a perched bird from the direction of and at the same velocity as the wind.

If the velocity of the bird were the only factor that determined the velocity of the particles at the point of collision, then the head, neck, breast, shoulders, and leading edge of the wings would receive the most abrasion. However, the airfoil shape of the wings, and possibly of the body as well, means that air moving across the dorsum has a higher velocity than air moving across the venter. Turbulence around the wings and tail means that these are areas of rapid air movement, and the wings move thereby contributing their own kinetic energy to the collision. Because the velocity of air moving past a flying bird varies according to a predictable pattern, the kinetic energy of airborne particles colliding with the feathers varies predictably, as does the potential damage caused by particulate abrasion.

PREDICTIONS BASED ON VELOCITY OF PARTICLES

The following predictions are based on the airflow pattern around a flying bird.

Dorsal color.—If the body shape of a flying bird deviates from teardrop, then air flow is not equal over all body surfaces. In fact, the flight-profile of most birds suggests an airfoil. Where the body profile approximates an airfoil, the velocity of airborne particles moving across the dorsum is faster than the velocity of particles moving across the venter, and the kinetic energy of particles is greater. The wing *must* be an airfoil in birds that fly, and, therefore, airborne particles moving across the dorsal surface of the wing have a higher kinetic energy than particles moving across the ventral surface. Thus, *prediction 3.2*: the dorsum is more likely to be melanin-impregnated than the venter.

Rectrix color.—The rectrices supplement the control movements of the wings, especially in the rapid aerial maneuvers of wood-warblers. During such maneuvers the rectrices are spread to form an auxiliary surface behind and below the wings. Such a surface draws air over the main surface of the wings and so keeps the flow attached to the wings at high angles of attack, thereby increasing the maximum

lift coefficient of the wing and lowering the stalling speed (Pennycuick 1972, 1975). Such use of the tail subjects the entire tail to rapidly moving air similar to the rapid flow of air across the dorsum, but also subjects the lateral and trailing edges to turbulence. The velocity of particles in areas of turbulence is greater than that of particles in the air moving across the dorsum or the dorsal surface of the tail because the air in the turbulence is moving relative to the non-turbulent flow of air. Where the velocity is greater, the kinetic energy of the particles is greater, and the damage from abrasion is greater (equation 3.3). The tail is subjected to abrasion from two sources: rapidly moving air and turbulence. Thus, *prediction 3.3*: the tail, and particularly the lateral and trailing edges of the tail, is more likely to be melanin-impregnated than the dorsum.

When the tail is expanded, the more medial feathers overlies the adjacent, more lateral feathers with the lateral barbs of each feather above the medial barbs of the adjacent feather. Therefore, particles in the rapidly moving, dorsal airflow will abrade the overlying medial tail feathers more than the lateral feathers and the overlying lateral barbs of each feather more than the medial barbs. When the tail is furled in rapid flight, the medial feathers are uppermost with the most lateral feathers on the bottom. During such flight, only the medial feathers of the tail and the lateral edges of the underlying feathers will be exposed to abrasion from airborne particles moving around the tail. Thus, *prediction 3.4*: medial feathers and the lateral edges of all tail feathers are more likely to contain melanin than other parts of the tail.

Remex color.—The remiges are abraded by rapidly moving airborne particles. Such abrasion is similar to that occurring on the dorsum and tail. The remiges are also subject to turbulence both at their trailing edges and at the wing tip. Unlike the dorsum and rectrices, the remiges, particularly the distal remiges or primaries, are moving. From our reference point on the feather such movement appears as changes in the velocity of the particle. Since the wing moves at an angle with respect to the line of flight, the apparent change in the velocity of the particle is equal and opposite to a vector of the velocity of the remiges that is parallel to the line of flight. So the velocity of a particle approaching the remiges has increased velocity due to movement over an airfoil, increased velocity due to turbulence, and increased velocity due to flapping of the remiges. As a result, *prediction 3.5*: the remiges are more likely to be melanin-impregnated than either the dorsum or the tail.

PARTICULATE ABRASION OF PERCHED BIRDS

The small size of most airborne particles ($<5 \mu\text{m}$) means that they are carried with the wind. However, the extent to which foraging birds expose themselves to wind is poorly known. At low temperatures birds seek sheltered foraging sites (Grubb 1975, 1977, 1978, 1979), but we know little about the exposure of foraging birds under other conditions, and exposure is not the only factor. Does a foraging bird orient with respect to the wind, and if so, how? Without empirical knowledge of the exposure and orientation of foraging wood-warblers with respect to the wind, it is impossible to predict the extent to which different areas of the body are abraded by windblown particles. Birds that are resting or incubating in windy locations commonly face the wind (Austin 1929; Gochfield 1978). Therefore, the

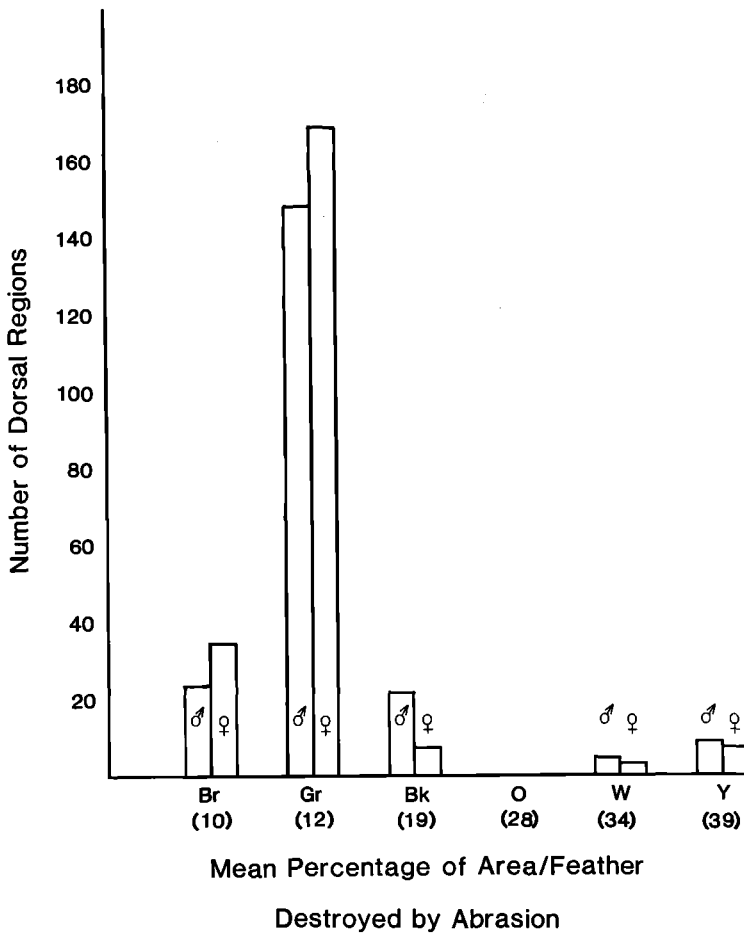


FIGURE 11. The frequency of feather colors among dorsal regions plotted as a function of abrasion resistance of those same feather colors measured in terms of area destroyed by experimental abrasion (see Fig. 10). For males 208 regions are plotted, 219 regions for females.

only consistent orientation of perched birds with respect to the wind is similar to the orientation found with respect to relative wind in flying birds. However, the absolute amount of abrasion is probably much less in a perched bird than in a flying bird because the velocity of particles would depend only on absolute wind speed which would rarely equal the speed of a flying bird.

OBSERVED TOPOGRAPHY OF ABRASION-RESISTANT COLORS

I have quantified abrasion resistance for black, brown, yellow-green, yellow, orange, and white feathers of wood-warblers. I have developed a model of abrasion based on the different velocities of airborne particles moving around a bird in flapping flight. The model predicts more severe abrasion in some areas of the body than in other areas. I now look at the frequency of abrasion-resistant colors in different areas of the body based on the color frequencies in Tables 2 and 3.

As predicted (*prediction 3.2*) the most abrasion-resistant colors (brown, yellow-

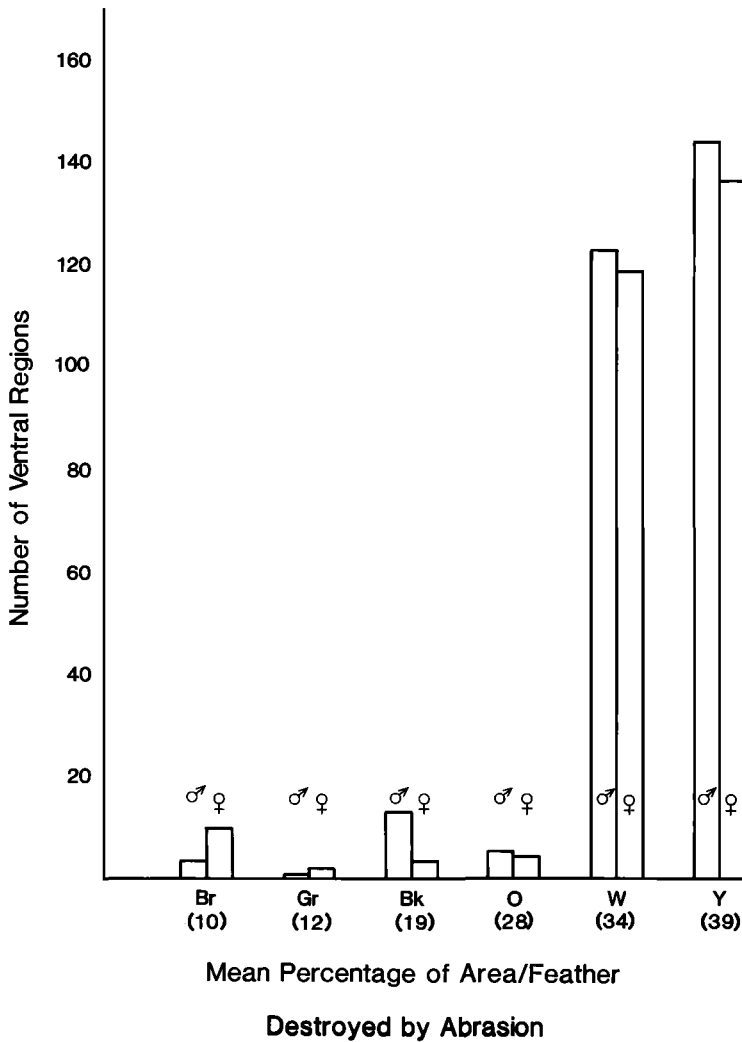


FIGURE 12. The frequency of feather colors among ventral regions plotted as a function of abrasion resistance of those same feather colors measured in terms of area destroyed by experimental abrasion (see Fig. 10). For males 292 ventral regions are plotted, 276 ventral regions for females.

green, and black) predominate on the dorsum of wood-warblers (Fig. 11), whereas white and yellow predominate on the venter (Fig. 12) but occur rarely on the dorsum. Because the dorsum consists of three regions, males of 113 species have 339 dorsal regions of which 131 consist of colored feathers whose abrasion resistance is unknown. However, colors in all but one of these regions are based on melanins and, therefore, should be abrasion-resistant. Females of 106 species have 318 dorsal regions of which 99 consist of feather colors whose abrasion resistance is unknown. As with males, colors in all but one of the regions are based on melanins. Thus, the predominance of abrasion-resistant feather colors on the dorsum is further supported by the predominance of melanic colors among the dorsal regions whose feather colors were not measured for abrasion resistance.

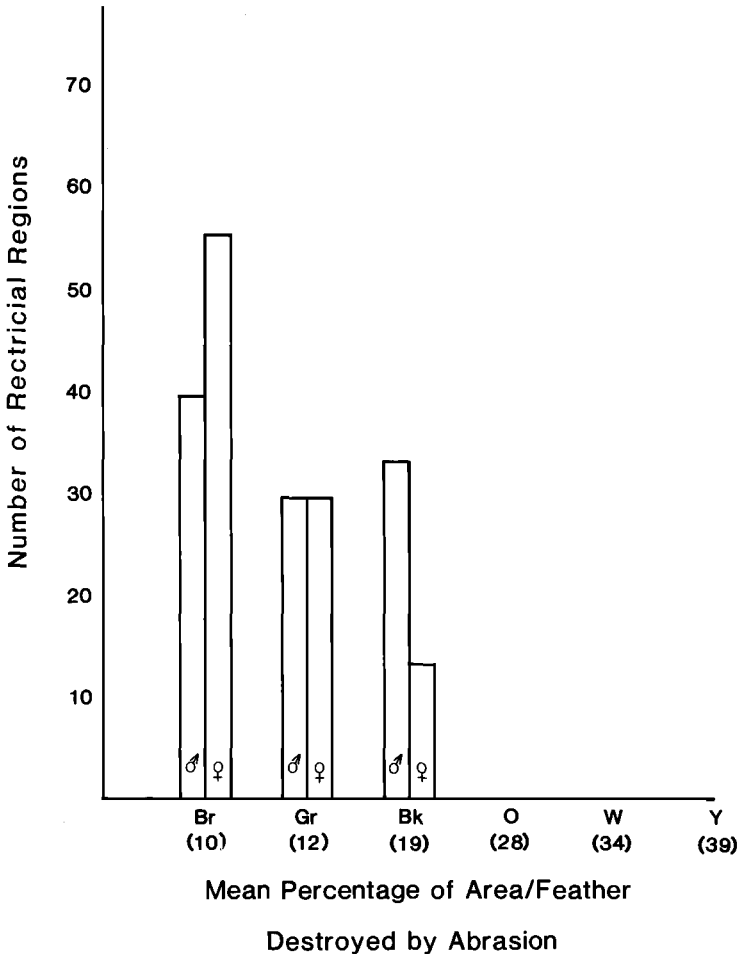


FIGURE 13. The frequency of tail (rectricial) colors of 112 species of wood-warblers, exclusive of tailspots, plotted as a function of abrasion resistance measured in terms of area destroyed by experimental abrasion (see Fig. 10).

The rectrices show a much greater tendency toward abrasion-resistant coloration than the dorsum (*prediction 3.3*). No species have predominantly orange, white, or yellow rectrices (Fig. 13). Males of 11 species and females of nine species have gray rectrices whose abrasion resistance is unknown. However, gray is based on melanin; hence the rectrices of these species should be abrasion-resistant.

Many wood-warblers have tailspots that are colored differently from the surrounding rectrices. However, as predicted (*prediction 3.4*) the medial rectrices are always melanic as are most of the distal barbs of feathers that possess light patches (*prediction 3.3*). The right outermost rectrices of the eastern North American wood-warblers shown in Figure 14 illustrate this latter point, and in 18 of the 23 species pictured the light-colored barbs are restricted to the medial side as predicted (*predictions 3.3 and 3.4*).

Remiges (*prediction 3.5*) show the greatest tendency toward abrasion-resistant color (Fig. 15). No species of wood-warbler has white, yellow, or orange remiges.

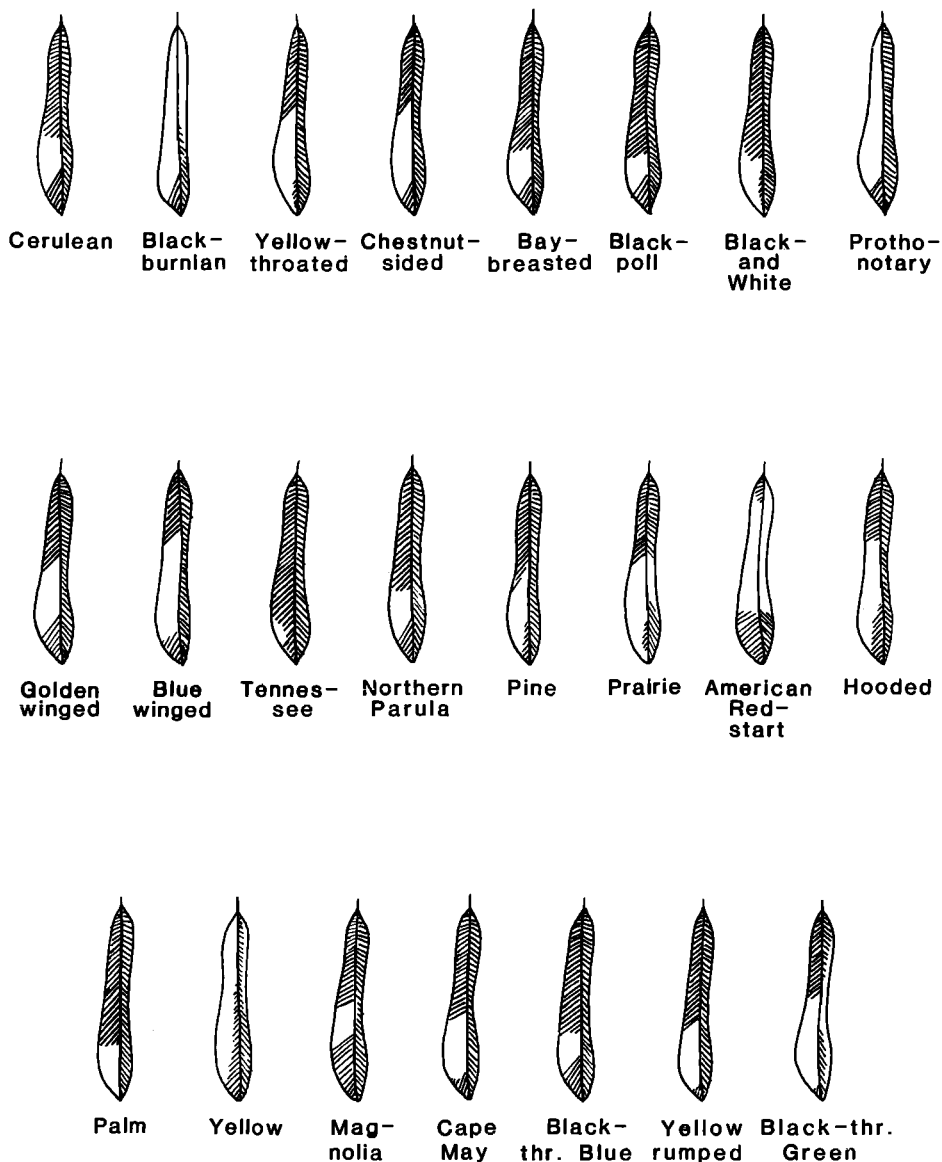


FIGURE 14. Right outermost rectrix of some eastern North American wood-warblers (adapted from Blake 1966).

Many species have white, yellow, or orange wingbars, but these are located on the primary and secondary coverts or proximal surface of the remiges where air flow, although rapid, is not turbulent and where movement caused by flapping is minimal. In other words the location of wingbars (which probably function in communication, see Chap. 6) may be dictated by the need to minimize particulate abrasion to non-melanic, easily abraded feathers.

The importance of melanic remiges is suggested by a comparison of worn white and melanic feathers from the wings of a partially albinistic Yellow-rumped War-

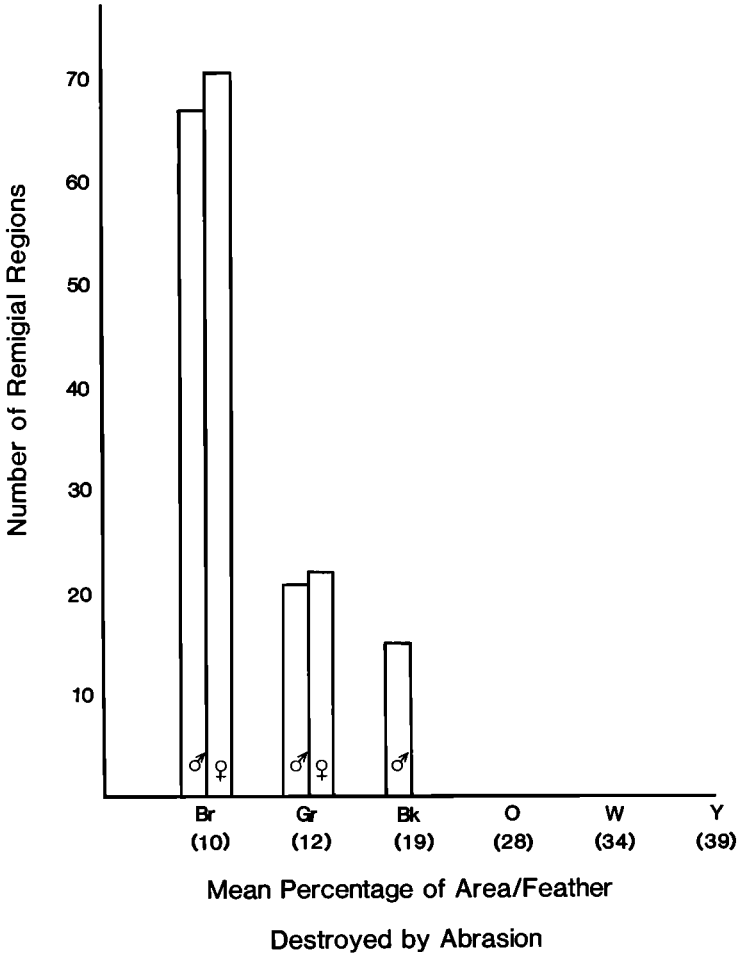


FIGURE 15. The frequency of wing (remigial) colors of 112 species of wood-warblers plotted as a function of abrasion resistance measured in terms of area destroyed by experimental abrasion (see Fig. 10).

bler (Barrowclough and Sibley 1980). The white remiges had significantly less surface area than the melanic remiges. If all the bird's flight feathers had been white, the surface area of the wings would have been 16 percent less than in a wood-warbler with melanic remiges, the power required for sustained flight would be increased by 4 percent, with a 9 percent increase in the power required for aerial maneuvers. These results confirm the increased durability of melanic feathers under field conditions and provide an estimate of the importance to the bird of reduced abrasive damage to the feathers.

A bird's wings and body generate lift by the difference in velocity of air moving over and under them and by their inclination relative to the air stream. When inclined the body and wings present the ventral surface to the air stream, thus abrasion would be more severe on the ventral surface than the dorsal surface and abrasion-resistant plumage should be common on the ventral surface of the body

TABLE 8
 SIZE¹ AND DENSITY OF AIRBORNE PARTICLES RECORDED IN DIFFERENT HABITATS

Habitat	Diameter of airborne particles (μm)	Density of airborne particles ($\mu\text{g m}^{-3}$)	Source
Desert	150-300	—	Bagnold 1941
	50-500	—	Smalley and Vita-Finzi 1968
	1-70	—	Schuete as cited by Gillette et al. 1972
Semi-desert	31.2-62.5	—	Swineford and Frye 1945
	62.5-125	—	Warn and Cox 1951
	49-53	—	Chepil and Woodruff 1957
	—	3.2×10^3 - 1.3×10^6	Chepil 1957
Eroding field	0.6-40	—	Gillette et al. 1972
Continental coasts	20	22	Prospero and Carlson 1972
	—	12.1	Prospero 1979
Polar	5	—	Darbey et al. 1974
	0.2-2	2-12	Heintzenberg 1980
	2	—	Thompson and Mosley-Thompson 1981
Ocean	—	0.35-0.69	Prospero 1979
	0.4-4.0	0.02-2.3	Duce et al. 1980

¹ Abrasive damage is related to the mass of airborne particles (equation 3.3) not their diameter. However, quartz (SiO_2) particles comprise 70-80 percent of all airborne dust (Smalley 1966; Smalley and Vita-Finzi 1968; Delany et al. 1973; Haeberli 1978). Because their mineral composition is similar, large particles will have a larger mass than smaller particles.

and wings. The rarity of melanic venters (Fig. 12) may argue against the importance of lift generated by inclination or against the importance of particulate abrasion.

Countershading to reduce three dimensionality (Thayer 1909; Cott 1957) has long been the accepted explanation of the dark dorsal, light ventral pattern. The effectiveness of countershading has been demonstrated experimentally (Ruiter 1956), but the data presented here establish abrasion resistance as a possible additional advantage to the dark dorsal, light ventral pattern common among birds.

PREDICTIONS BASED ON NUMBER AND SIZE OF PARTICLES

Different habitats have different densities of airborne particles and different characteristic masses (Table 8). Where the mass and density of airborne particles is high, abrasive damage to the plumage may be severe (equation 3.3). Where the mass and density of particles are low, abrasive damage to the plumage is slight (equation 3.3). If wind speeds over deserts and oceans are within an order of magnitude of each other, then abrasion from airborne particles will be far more severe in deserts where particles are larger and more numerous (Table 8) than over oceans where particles are smaller and less numerous (Table 8). Because melanic feathers are more abrasion-resistant than non-melanic feathers, *prediction 3.6*: more desert-dwelling species have a high proportion of melanic plumage than oceanic species.

HABITAT DIFFERENCES IN THE NUMBER OF SPECIES WITH DIFFERENT PROPORTIONS OF MELANIC PLUMAGE

Wood-warblers cannot provide a comparative test of *prediction 3.6*. Therefore, I compared a sample of desert-dwelling species based on Meinertzhagen (1954)

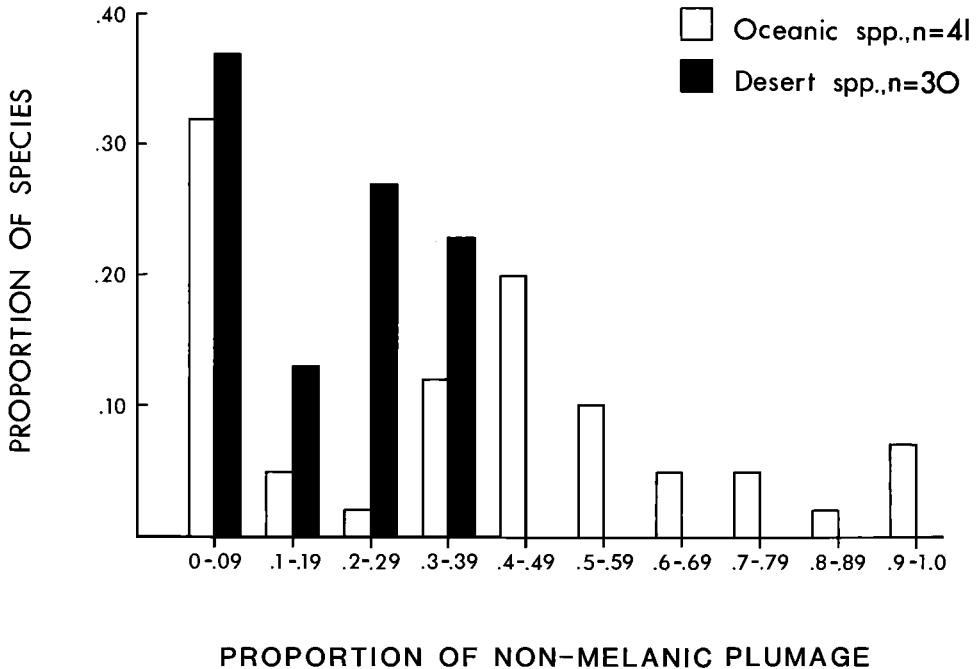


FIGURE 16. The proportion of oceanic (41 species or color morphs) or desert-dwelling (30 species) species plotted as a function of the proportion of non-melanic plumage.

and a sample of oceanic birds based on Alexander (1954), Mayr and Cottrell (1979), and Peters (1934). Desert-dwelling species were those confined to the interior of the Arabian peninsula, not strictly confined to vegetated oases, and frequently exposed to blowing sand. Oceanic species included those that remain 50 km or more from land except when breeding or whose range is confined to oceanic islands (e.g., Ascension Frigatebird *Fregata aquila*) where airborne particles have the same characteristics as those in oceanic air (Duce et al. 1980). Not used were species that dive for food or dig nesting burrows because both activities involve nonparticulate wear of feathers. When information on nesting and foraging habits was unknown, species were rejected if their congeners dive or burrow. Information on foraging and nesting habits of oceanic birds was taken from Alexander (1954), Palmer (1962), Watson (1966), Stokes and Shackleton (1968), Burt (1974), Brown et al. (1978), Tuck and Heinzel (1979) and John Warham (pers. comm.).

Color morphs were treated as separate species. Only the winter plumage of phalaropes was included because this plumage is worn at sea. My sample of oceanic species includes all avian species that meet the criteria. My sample of desert-dwelling species includes only those inhabiting the Arabian desert because distributional information for these species is more complete than for comparable species in other deserts.

The proportion of melanic plumage was estimated for specimens in the Museum of Comparative Zoology at Harvard University. The same topographical regions were used as for wood-warblers (Fig. 1). The color of each region was estimated by comparing the specimen with Munsell color swatches. The relative area of

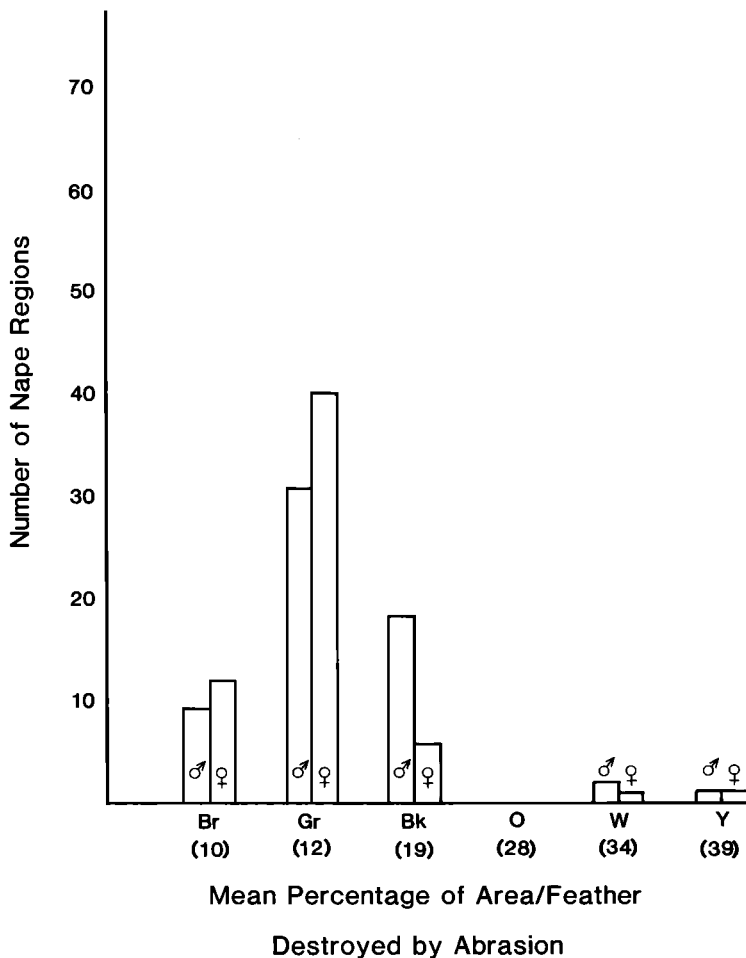


FIGURE 17. The frequency of nape colors of 112 species of wood-warblers plotted as a function of abrasion resistance measured in terms of area destroyed by experimental abrasion (see Fig. 10).

each feathered region was assumed to be the same for all species considered. Areas were estimated by tracing the outline of each region on the spread skin of a House Sparrow (*Passer domesticus*) with a Keuffel and Esser compensating polar planimeter, model 620005. The relative area of each region was calculated by dividing its absolute area by the total surface area of the House Sparrow (see Appendix II-1 for relative areas). The proportion of surface covered by melanic plumage is given in Appendix II-2 for each species sampled.

The hypothesis that desert-dwelling and oceanic species have equal proportions of melanic plumage was evaluated with the chi-square statistic. Species with more than 40% non-melanic plumage were treated as one statistical category in order to avoid chi-square cells with fewer than five expected species.

Desert-dwelling birds have a significantly ($\chi^2 = 25.69$, d.f. = 4, $P < 0.005$) lower proportion of non-melanic plumage than oceanic species (*prediction 3.6*, Fig. 16). No desert-dwelling species has more than 40 percent non-melanic plumage

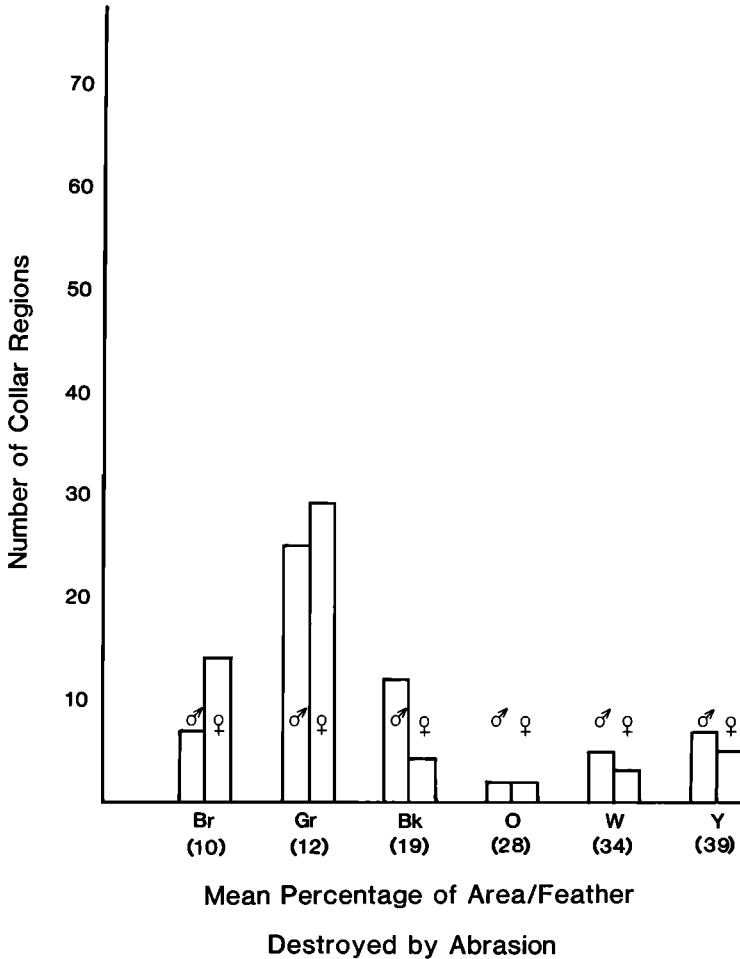


FIGURE 18. The frequency of collar colors of 112 species of wood-warblers plotted as a function of abrasion resistance measured in terms of area destroyed by experimental abrasion (see Fig. 10).

whereas almost half of the oceanic species have 40 percent or more non-melanic plumage, and three species lack melanic plumage (Fig. 16).

The comparison between oceanic and desert-dwelling birds suggests that color may be influenced by the number and size of airborne particles characteristic of different habitats. Deserts are particularly abrasive habitats, and the large number of black species found in deserts (Buxton 1923) may reflect the importance of abrasion resistance, a selective force that has received scant attention (e.g., Cloudsley-Thompson 1976) in the debate over coloration of desert-dwelling animals. The problem of abrasion resistance is not restricted to birds. Hamilton (1973) notes that desert-dwelling beetles with white exoskeletons have more skeletal damage than black congeners. Observations from other taxa are lacking.

Several authors (Norris 1967; Hamilton 1973; Porter et al. 1973) have suggested that black optimizes energy balance of desert species, although, for birds and mammals piloerection and behavior appear more important to energy balance

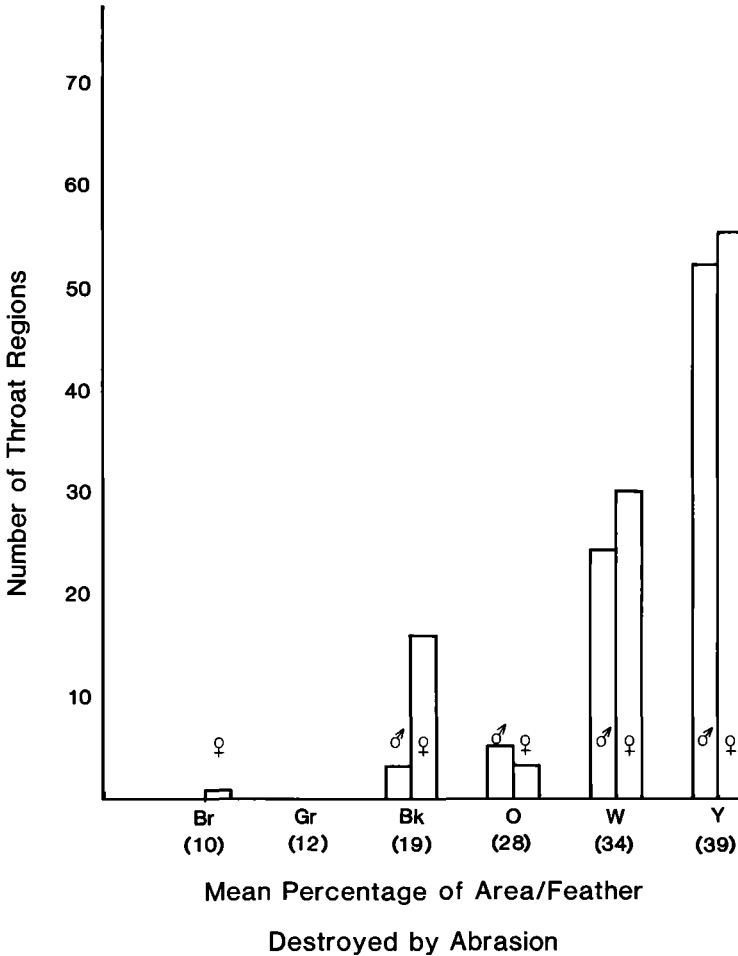


FIGURE 19. The frequency of throat colors of 112 species of wood-warblers plotted as a function of abrasion resistance measured in terms of area destroyed by experimental abrasion (see Fig. 10).

than color (Walsberg 1983). Hailman (1977a) has shown that in bright habitats, such as deserts and oceans, black provides high contrast for optical signalling. Thus black may have several important advantages for desert-dwelling species, not the least of which is increased abrasion resistance.

PREDICTIONS BASED ON RESISTANCE TO FRICTION

The friction of two or more feathers rubbing against each other may also cause abrasion. Such abrasion occurs at the joints and wherever feathers fold over each other. Thus, *prediction 3.7*: feathers located at joints are melanin-impregnated to resist abrasion due to rubbing of the feathers against each other.

Similar friction results when part of the body scrapes against a rough substrate (e.g., perches, nearby twigs). Thus, *prediction 3.8*: body parts that are frequently scraped against rough substrates should also be melanin-impregnated.

OBSERVED COLOR TOPOGRAPHY IN RESPONSE TO FRICTION

The feathers covering the dorsal surface of the shoulder are included in the back which is always yellow-green, brown or black (Tables 1, 2, *prediction 3.7*). When yellow, white, or orange feathers occur on the dorsum (Fig. 11), they are confined to the rump or upper tail coverts where no joints are found.

The other major joint where color was noted is the neck. White, yellow, and orange commonly occur on the neck (Tables 1, 2, *contra prediction 3.7*) where they are found rarely on the nape (Fig. 17), occur more frequently on the collars (Fig. 18), and dominate throat color (Fig. 19). The throat is prominently displayed during singing and probably acts as an optical signal, colored to maximize its conspicuousness (Chap. 7). However, the effect of abrasion on throat feathers is countered in many species of wood-warblers by semiannual molt of the feathers of the head and throat (Dwight 1900). Feathers elsewhere on the body, particularly the remiges and rectrices, are molted only once annually.

Abrasive contacts with a substrate could not be quantified. However, many ground-dwelling birds that constantly push their way through vegetation are brown, an abrasion-resistant color, and molt twice annually (Dwight 1900, Sievert Rohwer pers. comm.), suggesting extreme abrasion within the microhabitat of these species. Contact with substrates is an important source of abrasion that needs further study.

CONCLUSIONS REGARDING DURABILITY

Experimental results show unequivocally that melanic feathers are more resistant to abrasion by airborne particles than non-melanic feathers. Particulate abrasion apparently depends on the number, mass, and velocity of airborne particles. Because of unequal airflow around a flying bird, some parts of the body are exposed to higher velocity particles, hence more abrasion, than other parts of the body. Melanic plumage covers areas most exposed to abrasion. In deserts large and numerous airborne particles create severe abrasion, and desert-dwelling birds have high proportions of melanic plumage. Over oceans, where airborne particles are small and scarce, abrasion is slight, and many oceanic birds show little melanic plumage. These results are consistent with the hypothesis that one selection pressure acting on color and its pattern arises from the need to protect feathers from abrasion by airborne particles.

Feathers are also abraded by contact with vegetation. Such abrasion is difficult to study quantitatively, but may be an important selective pressure in the evolution of color. For example, grassland birds are commonly brown, an abrasion-resistant color, instead of green, a more cryptic color, and grassland species molt more frequently than forest-dwelling species (Dwight 1900). Evidently, the need for durable feathers combined with the chemistry of biochromes and keratin may dictate the distribution of biochromes. Thus durability may be one selective factor in the evolution of color and its pattern.

The dark dorsum predicted by the need for abrasion resistance is also predicted by the need for ultraviolet shielding. Protection from intense ultraviolet radiation may result from: (1) tolerance through repair or replacement mechanisms (Harm 1980) or (2) shielding. Melanic feathers absorb significantly more ultraviolet radiation than carotenoid-containing feathers that absorb significantly more ultra-

violet radiation than feathers without biochromes (Burt 1979). The dorsum of wood-warblers is generally melanic and, of all body surfaces, is most exposed to ultraviolet radiation; hence its color could have evolved to shield internal organs from potentially harmful radiation. Although it cannot be ruled out, ultraviolet shielding may not be an important determinant of external coloration. Feathers are nonliving structures that are not seriously damaged by ultraviolet radiation (but see Bergman 1982). The shield need only protect easily damaged cells in the nervous and reproductive systems and, therefore, may lie in the skin or immediately around sensitive organs (Porter 1967; Porter and Norris 1969). When the ultraviolet shield is internal, external color may conform to other selection pressures.

Countershading is yet another explanation for the dark dorsal, light ventral pattern common among wood-warblers. A. H. Thayer (1896) suggested countershading, in which the dorsum has lower reflectivity than the venter, as a means of reducing the dorso-ventral contrast caused by the animal's own shadow. The idea was developed by G. H. Thayer (1909) and Cott (1957). Later Ruitter (1956) demonstrated the importance of countershading to the concealment of caterpillars from predatory jays. Predation is the selective force behind countershading. Predation on wood-warblers occurs (Bent 1937, 1953; Rusch and Doerr 1972; Fogarty and Hetrick 1973; Ogden 1974; Johnson and Johnson 1976; Dodrill and Gilmore 1978; Mueller et al. 1981), but is it sufficient to select for countershading? At present the question is unanswerable, but important. Endler (1980) has shown that in the same species color patterns that evolve in the absence of predation are quite different from those that evolve in the presence of predation.

The dark dorsal, light ventral color pattern may reduce both dorso-ventral contrast and abrasion of dorsal feathers. Selection for countershading may predate selection for abrasion resistance, since reduced shadow contrast would seem more important to a small, terrestrial reptile dependent on crypsis than to a small, aerial bird dependent on flight. Selection may have shifted from countershading to abrasion resistance as reptiles evolved into birds. Future work may suggest ways of separating the hypotheses; until then both must be considered potential explanations for the dark dorsum of wood-warblers.

CHAPTER 4

COLOR AND ENERGY BALANCE

“White dresses are worn in summer, because they are found to be cooler than dark ones. The celebrated Benjamin Franklin placed bits of cloth of various colors upon snow, exposed them to direct sunshine, and found that they sank to different depths in the snow. The black cloth sank deepest, the white did not sink at all. Franklin inferred from this experiment that black bodies are the best absorbers, and white ones the worst absorbers of radiant heat.”

(Tyndall 1897:225–226)

Does coloration significantly affect energy-balance between a bird and its environment? Is coloration a significant predictor of avian behavior? Conclusive answers to these questions require a detailed thermodynamic model of the bird. However, 10 to 56 percent of a resting bird's heat loss occurs through the legs (Deighton and Hutchinson 1940; Veghte and Herreid 1965; Baudinette et al. 1976; Chappell 1980a) with an additional 5 to 10 percent loss from the mandibles (Deighton and Hutchinson 1940; Veghte and Herreid 1965; Hill et al. 1980); hence these unfeathered surfaces account for a significant part of a bird's total heat loss. Additionally, energy flow is more easily modeled for the legs and mandibles than for the feathered body. In this chapter I examine energy flow for the legs and mandibles of wood-warblers with particular attention to the hypothesis that coloration of the legs and mandibles is a factor in the wood-warbler's behavioral energetics.

Absorption of solar energy by dark plumage has been associated with increased heat gain (Lustick et al. 1978, 1979; Finch et al. 1980) and reduced metabolic rates (Enger 1957; Hamilton and Heppner 1967; Lustick 1969; Heppner 1970; Marder 1973; MacMillen et al. 1977; Wunder 1979; Ellis 1980). However, Kovarik (1964) and Walsberg et al. (1978) calculated that dark feathers could reduce the amount of energy that penetrates to and is absorbed by the skin. These calculations were verified experimentally by Walsberg et al. (1978) who showed that with fully erect plumage and moderate wind speeds (≥ 3 m/s) a dark bird would absorb solar radiation at its outermost surface where convection and reradiation would remove the heat before it could be conducted to the skin. Behavioral verification is provided by the work of Howell et al. (1974) on the Chilean Gray Gull (*Larus modestus*) which nests on deserts devoid of shade. The gull's dark feathers are sleeked in the cold, early morning when absorption of solar heat close to the skin is advantageous. In early afternoon, when temperatures and insolation are extreme, the feathers are fluffed, reducing penetration of solar radiation and providing high thermal resistance. A bird can also regulate its heat gain by its orientation to the sun (Lustick et al. 1978; Mugaas and King 1981; Walsberg 1982) or selection of a suitable microclimate (Calder 1973; Grubb 1975, 1977, 1978; Mugaas and King 1981; Walsberg 1982). Therefore, color of the plumage appears less important to energy balance than behavior and ptiloerection.

Plumage is not a factor in energy absorption by birds' legs which provide a surface for rapid heat exchange (Kahl 1963; Brush 1965b; Johansen and Millard 1973; Murrish and Guard 1976; Lustick et al. 1979; Chappell 1980a; Hill et al. 1980). When heat stressed, birds flush their legs and feet with blood, thereby increasing conductive heat loss (Murrish and Guard 1976). When cold stressed, birds of temperate regions perch with one or both feet tucked into the belly feathers (Madsen 1945; Hill et al. 1980). These studies suggest the energetic importance of the legs, but fail to address the potential effect of tarsal color on energy flow in the legs.

ENERGY BALANCE: A GENERAL EQUATION

The "legs" of wood-warblers from the heel joint distally are the biological energy system under consideration. Transfer of energy between the legs and their environment, which includes the wood-warbler's body, occurs by radiation, evaporation, convection, and conduction. Additionally, thermal energy is generated by the legs.

Radiation energy is absorbed into sunlit legs from two different regions of the electro-magnetic spectrum. Solar radiation in the form of direct, reflected, and scattered sunlight has a spectrum at sea level that extends from 290 nm in the ultraviolet to roughly 2600 nm in the middle infrared (Gates 1962, 1963, 1980). That range contains about 97 percent of the solar energy incident on the earth's surface (Gates 1965b). Thermal radiation from the ground and sky and from plants and animals in the environment has a spectrum whose shortest wavelengths are about 4000 nm (Gates 1963, 1965a, 1980; Monteith 1973). Differently colored surfaces absorb different amounts of solar radiation (Porter and Gates 1969; Porter et al. 1973) whereas thermal radiation is absorbed well by all biological tissue regardless of color (Hammel 1956; Buettner and Kern 1965; Birkebak 1966; Fuchs and Tanner 1966; Gates 1968, 1969, 1970). For these reasons absorbed radiation is represented by two terms, S_a , absorbed shortwave (solar) radiation, and L_a , absorbed longwave (thermal) radiation.

Thermal energy is radiated from the legs, L_r , with wavelengths in excess of 4000 nm. The legs and environment also exchange energy by evaporation, convection, and conduction. In general, convection, C , represents a net loss from the legs, but when the temperature of the air exceeds the temperature of the legs, thermal energy enters the legs by convection. Conduction, K , represents a net loss of energy unless the substrate is warmer than the legs in which case energy is conducted into the legs. Conversion of a liquid to a gas (evaporation), E , requires energy and represents energy loss from the legs. Energy stored, St , within the legs, whether as chemical energy or latent heat is temporarily unusable. In general, energy flowing into the legs must equal energy flowing out of the legs. Based on the above discussion the equality may be stated as:

$$S_a + L_a + M = L_r \pm C \pm K + E \pm St \quad 4.1$$

where M is thermal energy generated by metabolism. This is a general statement of energy balance. To predict the behavior of wood-warblers with differently colored legs, equation 4.1 must be expressed in more specific terms.

ENERGY BALANCE IN THE LEGS OF WOOD-WARBLERS

Each of the terms in equation 4.1 is stated below in variables that are measurable and applied specifically to the legs. Definition of the terms and derivation of the expressions shown below are explained in Appendix IV.

Absorbed solar energy, S_a ($\mu\text{W cm}^{-2}$) is calculated from:

$$S_a = \alpha_s \left[\sin \theta \frac{1}{\pi} S_p + 0.5 S_s + 0.5 \rho_g (S_p + S_s) \right] \quad 4.2$$

where α_s is the mean absorptivity to shortwave (solar) radiation, S_p is direct solar irradiance ($\mu\text{W cm}^{-2}$), S_s is scattered solar irradiance (skylight) ($\mu\text{W cm}^{-2}$), θ is the angle between the direct solar beam and the long axis of the leg, π is a constant, and ρ_g is the reflectance of the ground to shortwave irradiance.

Absorbed longwave (thermal) energy is calculated from:

$$L_a = 2.84 \times 10^{-6} [T_g^4 + (T_a - 20)^4] \quad 4.3$$

where T_g is the temperature of the ground ($^{\circ}\text{K}$) and T_a is the temperature of the air ($^{\circ}\text{K}$). The constant, $2.84 \times 10^{-6} \mu\text{W cm}^{-2} \text{ } ^{\circ}\text{K}^{-1}$, is one-half the Stephan-Boltzmann constant (Appendix IV). Metabolic heat, M , generated in the legs or carried into them is negligible (Appendix IV).

Energy is lost from the legs by radiation, convection, and evaporation. Energy conducted from the legs to the substrate, K , is not calculable for wood-warblers' legs and is omitted from further consideration (Appendix IV). Energy radiated from the legs is given by the equation:

$$L_r = 5.56 \times 10^{-6} T_c^4 \quad 4.4$$

where the constant, 5.56×10^{-6} , has units $\mu\text{W cm}^{-2} \text{ } ^{\circ}\text{K}^{-1}$, and T_c is the core temperature of the legs ($^{\circ}\text{K}$). Convective energy loss is calculated from:

$$C = 4.32 \times 10^2 [u/d]^{0.5} [T_c - T_a] \quad 4.5$$

Gates (1962) calculated the constant, $4.32 \times 10^2 \text{ J cm}^{-2} \text{ } ^{\circ}\text{K}^{-1}$, for a smooth cylinder with its long axis perpendicular to the direction of wind flow (Appendix IV); the wind speed is u (cm/s), and d is the diameter of the legs (cm). Evaporative energy loss is E' ($\mu\text{W cm}^{-2}$).

Substituting in equation 4.1 the precise expressions stated above and derived in Appendix IV, one obtains the following statement of energy-balance in the legs of wood-warblers:

$$\begin{aligned} \alpha_s \left[\sin \theta \frac{1}{\pi} S_p + 0.5 S_s + 0.5 \rho_g (S_p + S_s) \right] + 2.84 \times 10^{-6} [T_g^4 + (T_a - 20)^4] \\ = 5.56 \times 10^{-6} T_c^4 + 4.32 \times 10^2 [u/d]^{0.5} [T_c - T_a] + E' \end{aligned} \quad 4.6$$

Of the eleven variables in equation 4.6, only four, θ , ρ_g , T_g , and T_c , were not measured. Species were observed under conditions where θ and ρ_g can be assumed similar for all species. Throughout the study of energetics in the legs of wood-warblers, focus is on differences among species—not absolute values of variables—; hence observation under similar conditions is a valid alternative to direct measurement. I assumed that because of their physiological and morphological similarities, all species of wood-warblers must maintain the same minimal temperature in the

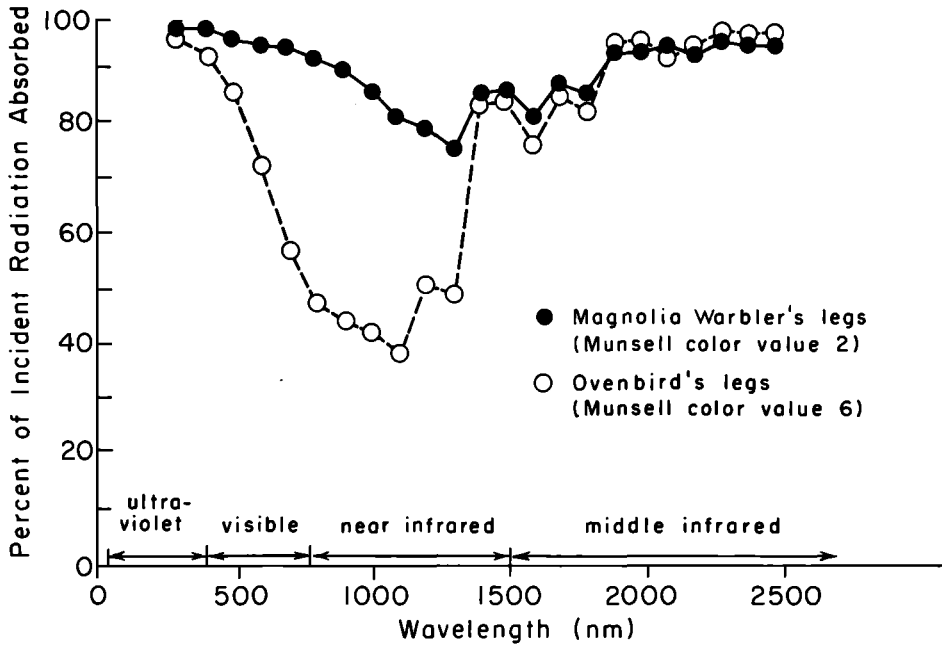


FIGURE 20. Absorption spectra of representative wood-warblers' legs.

legs (T_c). If the temperature of the legs is the same in all wood-warblers, then a difference among species in one variable—for example, leg color (α_s)—means that a counter-balancing difference must occur in some other variable. Equation 4.6 is used to test the hypothesis that color of the legs measurably affects the energy balance of wood-warblers and therefore predicts their behavior.

MEASUREMENT OF THERMODYNAMIC VARIABLES

Mean solar absorptivity.—Little intraspecific variation is found in tarsal color of wood-warblers (Tables 4, 5) despite significant interspecific variation. Coloration results from the differential absorption of visible light. In this section I present absorption spectra of wood-warblers' legs and quantify differences in color among species.

The absorption spectrum of wood-warblers' legs is derived from the following relationship:

$$\alpha_\lambda + \rho_\lambda + \tau_\lambda = 1 \quad 4.7$$

in which reflectance, ρ_λ , and transmittance, τ_λ , of wavelength λ can be measured (Chap. 2). The computer program SOLRAD (McCullough and Porter 1971) integrates the absorption spectrum to give the mean absorptivities of differently colored legs. Reflection and transmission spectra were measured in five dark-legged species (Munsell color value 2) and two light-legged species (Munsell color value 6).

The absorption spectra of the Ovenbird, a light-legged species, and the Magnolia Warbler, a dark-legged species, are compared in Figure 20. Absorption reaches a maximum difference of 40 percent in the near infrared region of the spectrum

TABLE 9
MEAN ABSORPTIVITY OF SUNLIGHT BY WOOD-WARBLER LEGS¹

Species	Mean absorptivity (α)
Munsell color value 6 (light)	
Ovenbird	0.67
Mourning	0.71
Munsell color value 2 (dark)	
Black-and-white	0.90
Tennessee	0.89
Magnolia	0.90
Chestnut-sided	0.89
Bay-breasted	0.85

¹ At 43°N latitude on 21 June at 1200 h as calculated from SOLRAD (McCullough and Porter 1971). The optical air mass is 1.0, the bird's altitude is 1 km, the dust is 200 particles cm⁻³, the precipitable water vapor is 1 cm (Gates and Harrop 1963), and total ozone is 0.35 cm.

where the dark legs of the Magnolia Warbler absorb about twice as much energy as the light legs of the Ovenbird. The mean absorptivity to sunlight (290–2600 nm) is 0.85 to 0.90 in five dark-legged species and 0.67 and 0.71 in two light-legged species (Table 9).

The mean absorptivities, α_s , of dark- and light-legged wood-warblers differ considerably, with dark-legged species absorbing more incident solar energy than light-legged species, but absorption of energy depends on mean absorptivity and irradiance. Irradiance is examined next.

Incident sunlight.—Irradiance of the legs by direct (S_p), scattered (S_s), and reflected [$\rho_g(S_p + S_s)$], sunlight (equation 4.6) varies with latitude, season, and time of day. All species were compared at the same latitudes, seasons, and times of day. Therefore, the relevant observation is not total irradiance, but whether wood-warblers expose their legs to direct sunlight or confine them to shadow where only scattered and reflected sunlight are incident.

To determine irradiance of the legs, I located a wood-warbler, identified its species, waited 10 sec, and noted whether its legs were in sunlight or shadow. Each bird was observed only once. Dark-legged species (Munsell color value 2) had their legs in sun on 44 of 513 observations and light-legged species (Munsell color value 4, 6, or 8) had their legs in the sun on 25 of 194 observations. The difference is not significant ($\chi^2 = 2.90$, d.f. = 1, $0.10 > P > 0.05$); hence the difference in energy entering the legs depends on differences in color (α_s , equation 4.6), not on differences in exposure to sunlight.

Thermal absorptivity.—The total absorbed energy is derived from five sources: (1) direct sunlight, (2) scattered sunlight, (3) reflected sunlight, (4) thermal radiation from the ground, and (5) thermal radiation from the sky. All variables that affect absorption of sunlight have been discussed. If the average angle of the legs with respect to the sun's rays (θ) and the average reflectance from the ground (ρ_g) are the same for all species of wood-warblers, then the only term of equation 4.6 that varies among species is solar absorptivity (α_s).

Absorption of sunlight depends entirely on the difference in the mean absorptivity of differently colored legs. What of thermal absorptivity? Legs, regardless of color, absorb all incident thermal energy (Porter et al. 1973; Gates 1980).

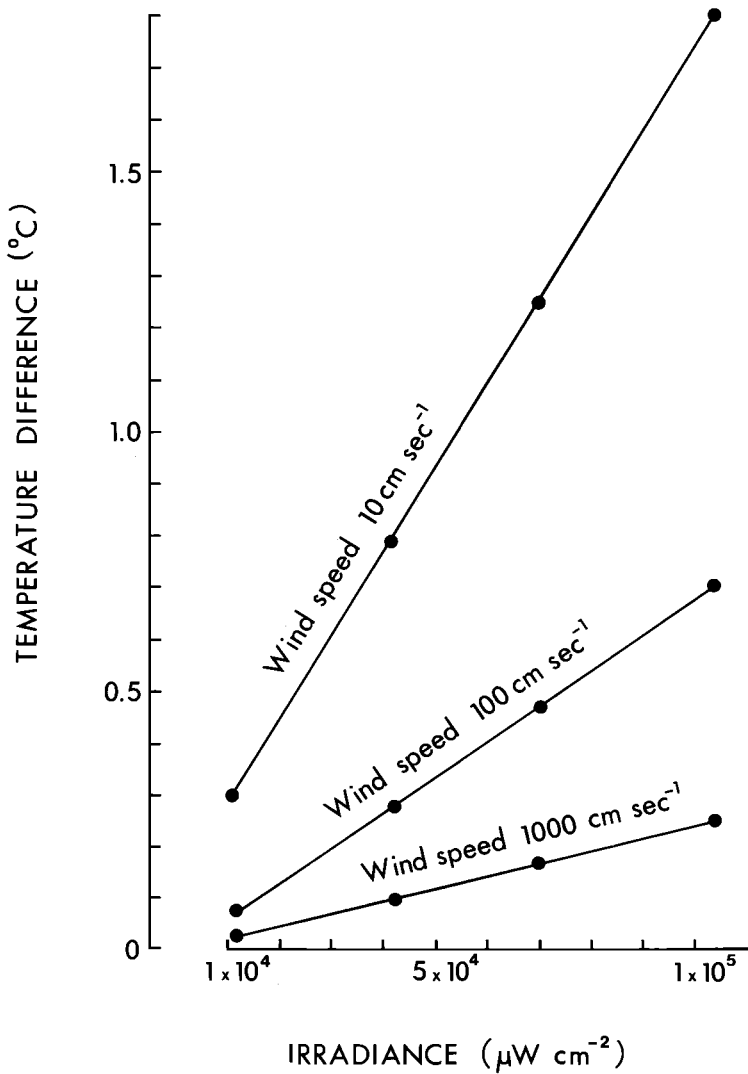


FIGURE 21. The temperature difference (ΔT) between dark and light legs plotted as a function of solar irradiance at three different wind speeds with air and ground temperatures at 0°C .

Absorption of thermal energy depends entirely on the temperatures of the sky and the ground (equation 4.6).

Equilibrium-temperature.—The equilibrium-temperature of the legs is the core temperature (T_c) at which energy loss from reradiation, convection, and evaporation (see equation 4.6 above) exactly balances the solar and thermal energy absorbed. Over a sufficient period of time energy absorbed must equal energy lost: a net increase results in death of the tissue from over-heating, whereas a net loss results in tissue death from freezing. The core temperature of differently colored legs (T_c) at equilibrium is found by solving equation 4.6 iteratively for T_c .

The equation is repeated here for reference:

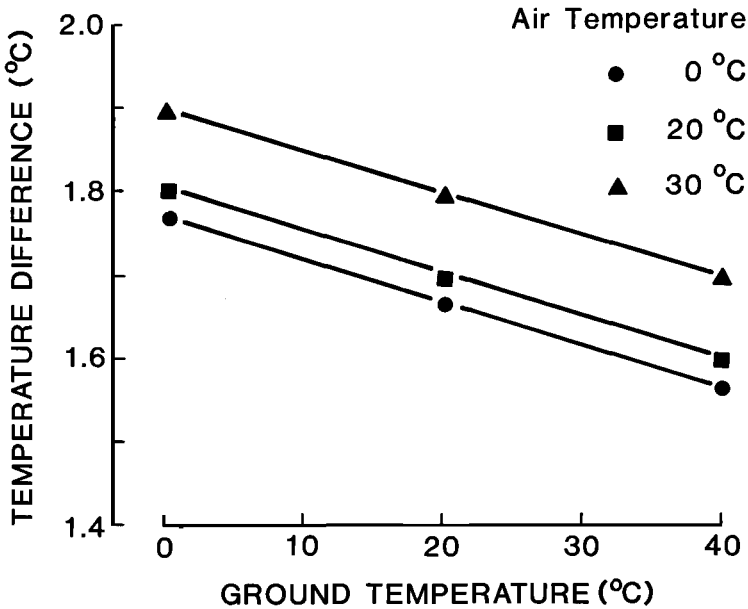


FIGURE 22. The temperature difference (ΔT) between dark and light legs plotted as a function of ground temperature at three different air temperatures and at constant wind speed (10 cm sec^{-1}) and solar irradiance ($10.4 \times 10^4 \mu\text{W cm}^{-2}$).

$$\alpha_s \left[\sin \theta \frac{1}{\pi} S_p + 0.5 S_s + 0.5 \rho_g (S_p + S_s) \right] + 2.84 \times 10^{-6} [T_g^4 + (T_a - 20)^4]$$

$$= 5.56 \times 10^{-6} T_c^4 + 4.32 \times 10^2 [u/d]^{0.5} [T_c - T_a] + E' \quad 4.6$$

The average angle between the sun's rays and the legs (θ) is assumed to be 45° . Reflectance, ρ_g , from a northern, temperate zone mixed forest is approximately 0.20 (Barry and Chambers 1966; Stanhill 1970). The leg's equilibrium-temperature was calculated for ground temperatures (T_g) of 0°C , 20°C , and 40°C , air temperatures (T_a) of 0°C , 20°C , and 30°C and wind speeds (u) of 10, 100, and 1000 cm sec^{-1} . Irradiance from direct (S_p) and scattered (S_s) sunlight varied from 1.4 to 4.2, 7.0, and $9.8 \times 10^4 \mu\text{W cm}^{-2}$. The equation is solved for air saturated with water vapor so that evaporative water loss (E') is assumed to be zero. Absorptivity (α_s) and the characteristic dimension of the legs, their diameter (d in cm, see below), are assigned the measurements of the Magnolia Warbler (dark-legged species) and the Ovenbird (light-legged species).

I subtracted the equilibrium-temperature of the Ovenbird's legs (T_o) from the equilibrium-temperature of the Magnolia Warbler's legs (T_m) and plotted the difference (ΔT) (Figs. 21, 22).

$$\Delta T = T_m - T_o \quad 4.8$$

At air and ground temperatures of 0°C , increasing the irradiance of direct and scattered sunlight increases the temperature difference (ΔT , Fig. 21) between dark and light legs. Under the same constant conditions, as wind speed increases the temperature difference between dark and light legs decreases (Fig. 21). With a

wind speed of 10 cm sec^{-1} and solar irradiance of $10.4 \times 10^4 \mu\text{W cm}^{-2}$, the temperature difference between dark and light legs decreases as air or ground temperature, or both, increase (Fig. 22). On an overcast day with a strong wind the temperature difference between dark and light legs is small, probably negligible. On a calm, sunny day the dark legs have a calculated equilibrium-temperature almost 2°C warmer than light legs. Variation in air and ground temperatures has less effect (Fig. 22) on the difference in equilibrium-temperature than variation in irradiance and wind speed (Fig. 21).

When the temperature of the leg approaches 0°C , birds either withdraw the legs into the fluffed plumage (Hill et al. 1980) or dump metabolic heat into the legs (Lustick et al. 1979). Because absorbed solar energy heats the legs, air and ground temperatures must drop below 0°C before the legs approach 0°C , and behavioral or physiological adjustments are required to prevent a further temperature decline. The greater the amount of incident solar radiation, the lower the air and ground temperatures must be before adjustments are required. These generalizations apply equally to legs of any color as long as they are exposed to direct, scattered, or reflected sunlight.

Because dark legs maintain a higher equilibrium-temperature than light legs under all conditions, they can tolerate lower air and ground temperatures before behavioral or physiological adjustments become necessary. Therefore, dark-legged species are more tolerant than light-legged species of conditions that increase energy loss from the legs.

What is the energetic advantage of light legs? Light legs invariably have a lower equilibrium-temperature than dark legs. Because unfeathered legs lose heat rapidly (Deighton and Hutchinson 1940; Baudinette et al. 1976; Lustick et al. 1979), light legs could act as a significant heat sink for species that overheat. Overheating may result from living in a hot climate, a habitat exposed to direct sunlight where shade is scarce, or from the exertion of constant flying. In a wood-warbler that occupies a habitat exposed to intense sunlight light legs are better heat sinks than dark legs because the difference between the temperature of the light legs and the body is greater. Blood flowing through light legs would lose more heat than blood flowing through dark legs.

Evaporative energy loss.—Differences in energy absorbed by dark and light legs are not evident in behavioral responses to evaporation (E' , equation 4.6). Wood-warblers can prevent evaporative energy loss by withdrawing the legs into the ventral feathers. Data on posture during overcast and rainy weather were collected during the summers of 1973 and 1974 at Itasca, Minnesota, and during the spring and autumn of 1973–1975 in Madison, Wisconsin. I located a wood-warbler, identified its species, waited 10 sec, and on the tenth sec noted whether it was perched with both legs, one leg, or neither leg outside the ventral feathers.

In rain, dark-legged wood-warblers extended both legs on 55 of 83 observations, whereas light-legged wood-warblers extended both legs on 5 of 7 observations. The difference is not significant ($\chi^2 = 0.71$, d.f. = 1, $P > 0.25$). Low levels of irradiance during storms greatly reduce the thermal advantage of dark legs (Fig. 21), which may account for the nonsignificant difference. Wood-warblers perched under overcast skies extended both legs on 162 of 229 observations, whereas wood-warblers perched under overcast skies and in rain extended both legs in 60 of 90 observations. Again, the difference was not significant ($\chi^2 = 0.25$, d.f. = 1,

$P > 0.50$). Apparently evaporative energy loss is not a significant factor in energy balance of the legs, probably because the high relative humidity during rain would minimize evaporation.

Convective energy loss: postural changes.—When energy loss exceeds energy gain, the wood-warbler must adjust either gain or loss in order to survive. A major imbalance necessitates drastic correction, for example migration, the subject of the next section. A minor imbalance can be corrected either by allowing metabolic heat to flow into the legs (Lustick et al. 1979) or by a postural change such as drawing the legs into the ventral feathers where they are insulated and warmed by conduction from the body (Hill et al. 1980). The second strategy is advantageous because metabolism need not be increased, but disadvantageous because the legs are practically useless for locomotion.

If metabolic energy is not increased, then equation 4.6 predicts that; *prediction 4.1*: as convective energy loss increases, the probability that one or both legs are drawn into the belly feathers also increases and *prediction 4.2*: because dark legs maintain a higher equilibrium temperature than light legs, species with dark legs have a lower probability of drawing the legs into the belly feathers than light-legged species under the same conditions of convective energy loss.

Data were collected during the summers of 1973 and 1974 at Itasca, Minnesota, and during the spring and autumn of 1973–1975 in Madison, Wisconsin. I identified each wood-warbler, waited 10 sec, and on the tenth sec recorded whether it had both legs, one leg, or neither leg outside the ventral plumage, the height at which it perched, and the height of the tree in which it perched. The position of the legs was recorded only once for each bird. No more than 10 observations were made on any one species in the same locality in one week so as to limit the potential contribution of a particular individual to the sample.

Wind speed was recorded hourly. The wind speed for each observation was assumed to equal the most recently preceding wind measurement. When a bird perched below the top of the canopy, I assumed that the wind speed was the same as 2 m above the forest floor, which was the height of my measurements. If the bird was at the top of the canopy, wind speed measured in the open was used; this wind speed was measured at least every 3 h.

For purposes of thermodynamic modeling I assumed the leg to be cylindrical and measured its diameter at the midpoint of the tarsometatarsus in 18 species of wood-warblers (see page 48). Using the observed wind speed, u (cm sec⁻¹), and the leg diameter, d (cm), of the species or its closest, measured relative, I calculated the potential convective energy loss for each observation from the term for convective heat loss in equation 4.7:

$$C = 4.32 \times 10^2 [u/d]^{0.5} [T_c - T_a] \quad 4.9$$

At air temperatures between 0°C and 30°C birds' legs maintain a core temperature a few degrees above air temperature (Lustick et al. 1979; Hill et al. 1980) due to absorption of solar and thermal radiation and incomplete energy exchange in the blood flowing to and from the legs. Throughout the calculations I assumed that the legs were 4°C warmer than the air regardless of air temperature or color of the legs.

Observations of 30 species of wood-warblers were grouped according to the

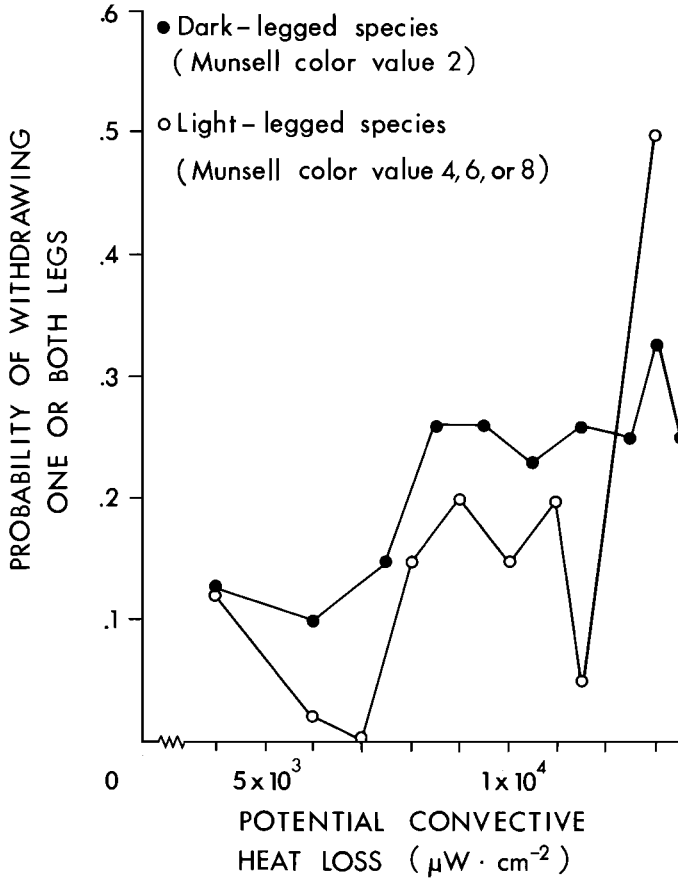


FIGURE 23. The probability of drawing one or both legs into the ventral feathers plotted as a function of potential convective energy loss from the legs of wood-warblers with dark and light legs.

potential convective energy loss calculated for each observation. The calculated convective energy loss was rounded to the nearest $5 \times 10^2 \mu\text{W cm}^{-2}$. The probability of drawing one or both legs into the ventral feathers was calculated for wood-warblers with dark legs (Munsell color value 2) and those with light legs (Munsell color values 4, 6, or 8). Data were too few to permit separation among the light-legged species by Munsell color values or statistical comparison of dark-legged and light-legged species.

The probability of drawing one or both legs into the ventral feathers (Fig. 23) increases as convective heat loss increases (*prediction 4.1*), but the increase is similar for dark-legged and light-legged wood-warblers (*contra prediction 4.2*). The lack of difference between dark-legged and light-legged species despite greater absorption of energy by dark-legged species suggests that species with light legs make up the difference by sending metabolic heat into the legs. Alternatively, wood-warblers with light legs may tolerate a lower temperature in the legs, but such a course has its limits as the temperature of the legs approaches zero.

Convective energy loss: diameter of the legs.—Convective energy loss depends,

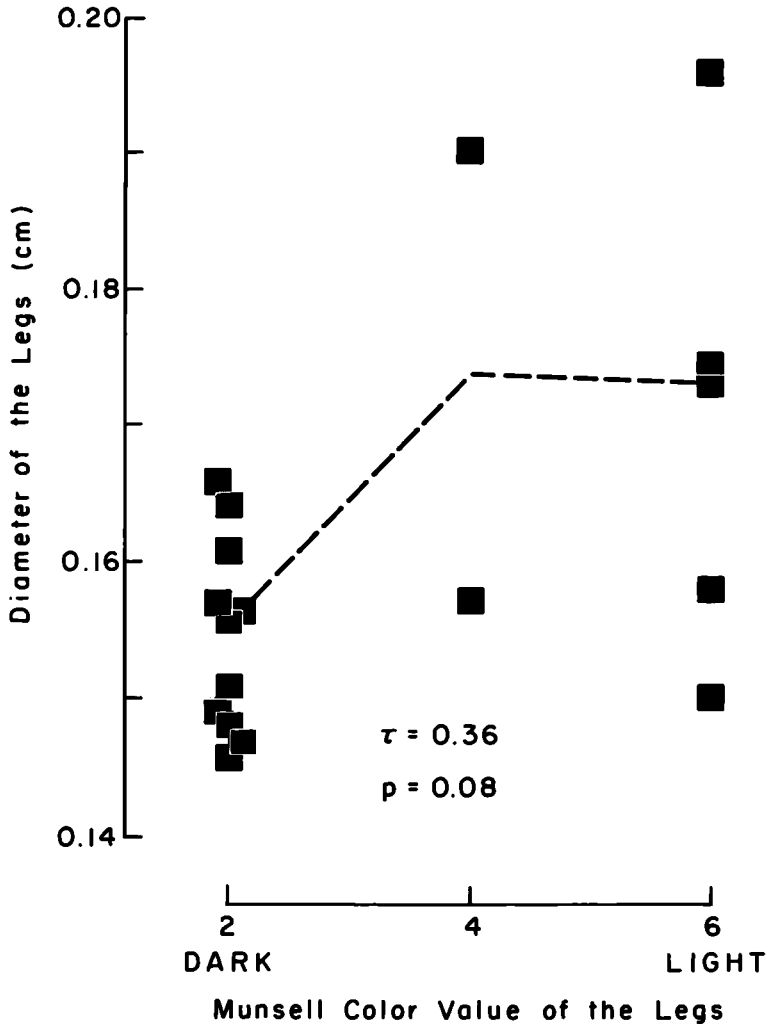


FIGURE 24. Diameter of the legs plotted against their Munsell color value. The dashed line connects the median values of species of wood-warblers.

in part, on the characteristic dimension (equation 4.9) which is the length of an object's axis parallel to the wind. Wood-warblers perch upright; therefore, the characteristic dimension of a wood-warbler's leg approximates its diameter. Decreasing the diameter of the leg decreases the thickness of the surrounding boundary layer of air which in turn increases convective energy loss. Because of increased energy loss, small diameter legs should maximize energy absorption by being dark. Because large diameter increases the boundary layer and reduces convective energy loss, legs with a large diameter can afford the reduced absorption of a light color. Thus, *prediction 4.3*: legs with a small diameter should be dark (low Munsell color value) whereas legs with a large diameter could be light (high Munsell color value).

For 18 species of wood-warblers the correlation between leg diameter and Munsell color value is not significant (*contra prediction 4.3*) (Fig. 24), but the

prediction's failure appears to lie in the similarity of legs with Munsell color values of 4 and 6. A Mann-Whitney U -test shows a significant difference ($U = 15.5$, $P = 0.015$) between the diameter of legs with Munsell color value 2 and legs with Munsell color values 4 and 6. Thus smaller diameter is correlated with increased energy absorption (*prediction 4.3*).

AIR TEMPERATURE AND DISTRIBUTION OF WOOD-WARBLERS

Behavioral and physiological adaptations enable birds to prevent the temperature of the legs from dropping below 0°C (Scholander 1957; Lustick et al. 1979; Hill et al. 1980). However, as the air temperature drops, convective energy loss from the legs increases (equation 4.9). A temporary imbalance can be corrected by drawing the legs into the belly feathers, a posture correlated with potential convective energy loss (Fig. 23). Such a posture virtually eliminates radiative and convective energy loss, but precludes locomotion. The imbalance may be avoided by moving to a more favorable microhabitat (Grubb 1975, 1977, 1978) or alternating between favorable and unfavorable microhabitats (Mugaas and King 1981). When the imbalance becomes prolonged or large, or when favorable microhabitats are too few, birds must migrate to more favorable habitats. Air temperature fluctuates seasonally in temperate regions. When air temperature falls, energy absorption decreases because of reduced thermal radiation from the sky and ground, while energy loss increases because of increased convective energy loss. Dark and light legs absorb different amounts of solar energy independently of air, ground, and sky temperatures. Because they absorb less solar energy, light legs can tolerate less reduction in absorbed thermal energy and less increase in convective energy loss than dark legs. Therefore, *prediction 4.4*: light-legged wood-warblers arrive north in spring at higher air temperatures (i.e., later) than dark-legged wood-warblers. *Prediction 4.5*: light-legged wood-warblers depart south in the autumn at warmer air temperatures (i.e., earlier) than dark-legged wood-warblers. *Prediction 4.6*: light-legged wood-warblers winter in warmer environments than dark-legged wood-warblers.

Migratory patterns.—For the area within 33 km of Madison, Wisconsin I recorded the arrival date of the first individual of the species (1971–1975) and the departure date of the last individual of the species (1972–1974). Similarly, I recorded the arrival of the first individual of each species within 33 km of Itasca (1973–1974).

From these data I determined the mean earliest arrival date and mean latest departure date for all species seen in at least one half of the years for which I have records at each location. The 30-yr mean minimum daily temperatures were obtained for spring and autumn for Madison and Fargo, North Dakota (the closest weather bureau station to Itasca). Temperature on the date of spring arrival was plotted as a function of Munsell color value of the legs and Kendall's tau (Siegel 1956) was used to calculate the significance of the observed rank correlation.

The mean minimum temperature on the mean earliest date of arrival is significantly correlated with the Munsell color value of the legs for species arriving at Madison ($\tau = 0.35$, $P = 0.003$, Fig. 25) and for species arriving at Itasca ($\tau = 0.41$, $P = 0.005$, Fig. 26). Likewise the mean minimum temperature on the mean latest date of departure is significantly correlated with the Munsell color value of the legs ($\tau = 0.31$, $P = 0.02$, Fig. 27). Species and temperatures are listed in Ap-

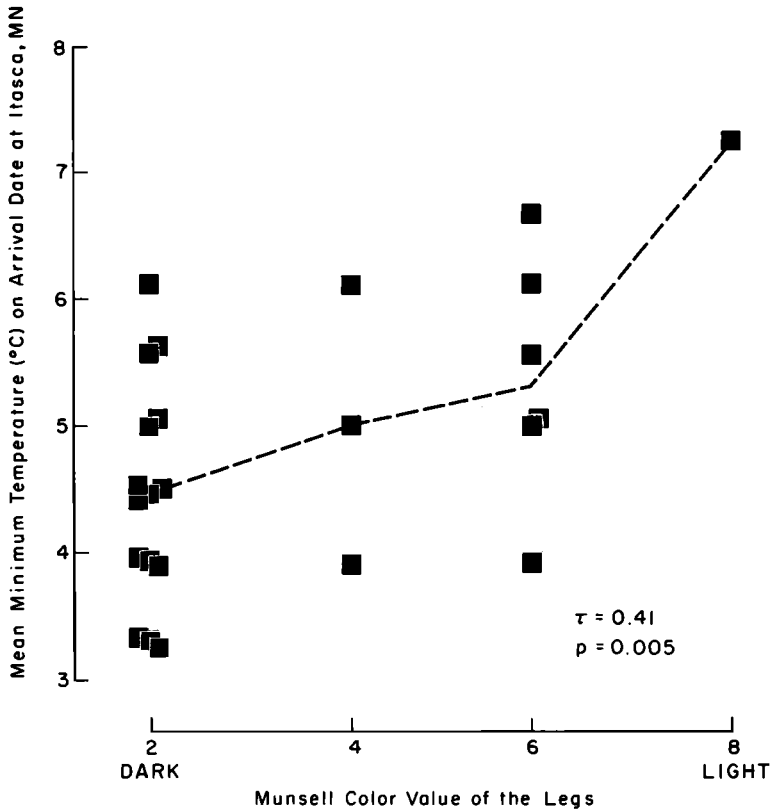


FIGURE 26. Mean minimum air temperature on the mean earliest arrival date for each species of wood-warbler seen at Itasca, Minnesota, 1973, 1974, plotted as a function of the Munsell color value of its legs. The dashed line connects median values.

any contribution to energy balance may be critical. Because dark legs have a higher energy gain than light legs, they can tolerate greater energy loss than light legs. Thus dark-legged wood-warblers are able to arrive earlier and remain later on their northern breeding grounds, a fact noted almost two hundred years ago among European warblers:

I make no doubt but there are three species of the willow-wrens: two I know perfectly; . . . for the one has a joyous, easy, laughing note; the other a harsh loud chirp. . . the songster is one-fifth heavier than the chirper. The chirper (being the first summer bird of passage that is heard, the wryneck sometimes excepted) begins his two notes in the middle of March, . . . the legs of the larger of these two (the willow warbler, *Phylloscopus trochilis*) are flesh-coloured; of the less (the chiff-chaff, *P. collybita*) black. (White 1789:47-48)

December distribution of North American Parulinae.—In winter the temperature range in North America varies geographically from well above the cold tolerance of wood-warblers in the warm southwestern and gulf coast states to far below their tolerance in the bitterly cold northern states and Canada. Therefore, light-legged species should inhabit warmer environments in winter than dark-legged species (*prediction 4.6*).

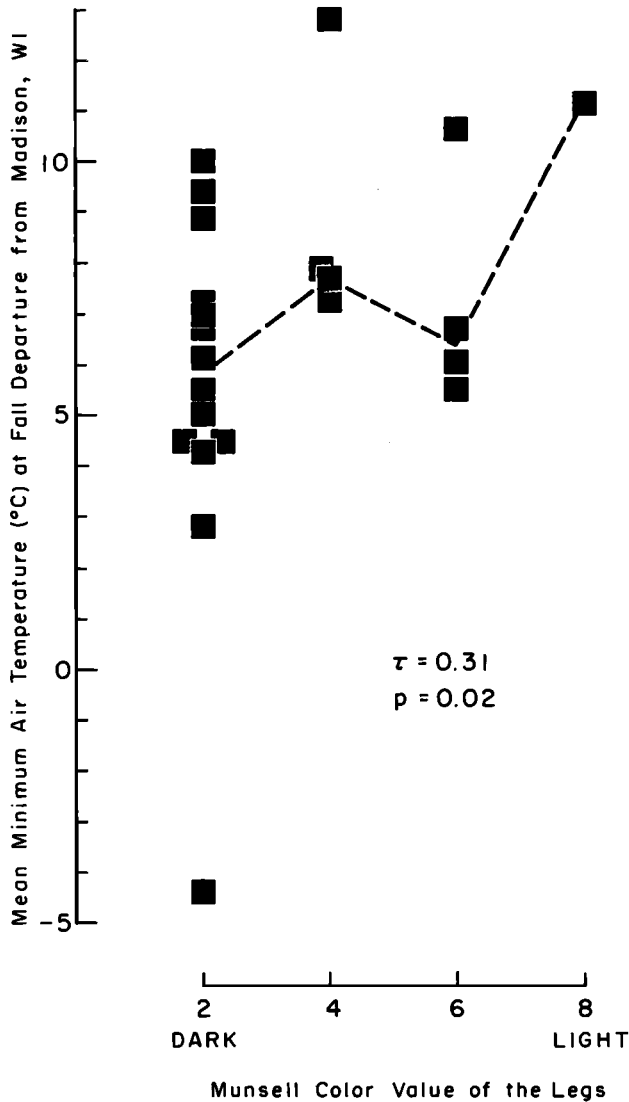


FIGURE 27. Mean minimum air temperature on the mean latest departure date for each species of wood-warbler seen at Madison, Wisconsin, 1972–1974, plotted as a function of the Munsell color value of its legs. The dashed line connects median values.

The prediction was tested by plotting the winter range of each species as determined by the 1947–1973 Audubon Christmas Bird Counts. A count-area was defined as being at the northern limit of the species' winter range if the same area was counted in at least five years and the species occurred on at least one half (more than "accidental" occurrence) and not more than three-fourths of the counts made. Occasional absence from a site suggests that winter conditions at the site could stress the species beyond its endurance, such that adaptations contributing to cold tolerance would be important. The number of individuals recorded was not considered, only presence or absence of the species.

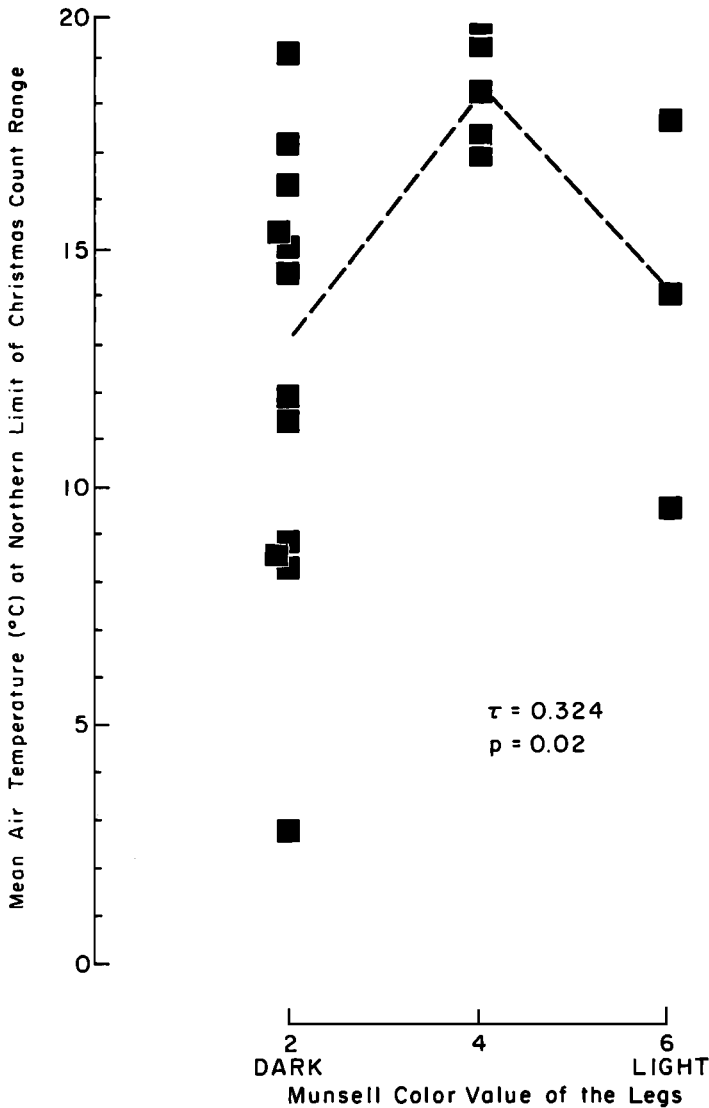


FIGURE 28. Mean air temperature at the northern limit of the species' range (Audubon Christmas Bird Count) plotted as a function of the Munsell color value of its legs. The dashed line connects median values.

For each count area the mean December temperature was obtained from 1945 to 1970 as recorded at the nearest weather station on the same isotherm. The temperature at the northern limit of the species' winter range was the mean of the mean temperatures from all count areas where the species occurred on one half to three-fourths of the counts. Kendall's tau (Siegel 1956) was used to test the significance of the correlation between leg color and temperature at the northern limit of the Christmas count range.

Wood-warblers with light legs winter in the warmest parts of North America (Fig. 28) or leave North America altogether (*prediction 4.6*). No wood-warblers

whose legs have a Munsell color value of 8 (very light) occur in North America in December. Most species of wood-warblers that winter in North America and especially in the coldest environments are dark-legged (Fig. 28). As with arrival and departure sequences, leg color is only one factor among many that enable a wood-warbler to maintain energy balance under cold conditions.

CONFOUNDING VARIABLES

Colder climates tend to be occupied by larger members within a species than warmer climates (Bergmann's Rule). Even among migratory species, larger individuals tend to remain in colder, more northerly habitats than smaller individuals (e.g., western subspecies of Song Sparrow [Aldrich 1984]). The occurrence of dark-legged wood-warblers in cold climates may be correlated with larger size, color of the legs being only an incidental variable.

Determination of arrival and departure sequences and the northern limit of the December range are described above. Weights are of adult males captured at the Powdermill observatory (Clench and Leberman 1978). Arrival sequences were correlated with spring weights, departure sequence and December distribution with autumnal weights. Pearson's Product Moment Correlation (Roscoe 1975) was used for all correlations except that between mass and color of the legs for which Kendall's tau (Siegel 1956) was used.

The weight of wood-warblers is not significantly correlated with air temperature upon arrival at Madison, Wisconsin ($r = 0.12$) or at Itasca, Minnesota ($r = 0.13$) or with air temperature upon departure from Madison ($r = -0.16$) or with air temperature at the northern limit of the North American December distribution ($r = 0.04$). Indeed, color of the legs is not correlated with weight ($r = 0.17$, $P = 0.19$). Thus neither migratory sequence nor December distribution are correlated with weight. Color of the legs appears to be a thermal adaptation independent of body mass.

MANDIBULAR COLOR AND BEHAVIOR OF WOOD-WARBLEDERS

The mandibles are uninsulated and warm even at low air temperatures (Calder and King 1974; Hill et al. 1980). Deighton and Hutchinson (1940) found that chickens reduced their heat loss 5–10 percent by placing the bill among the scapular feathers. Whether reduction in energy loss came from breathing warm air or from reducing radiative and convective energy loss is unknown. The following section examines the hypothesis that mandibular coloration is a factor in a wood-warbler's thermal and behavioral energetics.

Absorbed energy.—In general, equation 4.7 applies to the bill as well as the legs, but because the bill is not cylindrical neither the silhouette area, A_p (cm^2), nor the convection coefficient, h_c ($\mu\text{W cm}^{-2} \text{K}^{-1}$), can be simplified. Without these simplifications equation 4.7 is written:

$$\begin{aligned} \alpha_s[S_p(A_p/A_t) + 0.5S_s + 0.5\rho_g(S_p + S_s)] + 2.84 \times 10^{-6}[T_g^4 + (T_a - 20)^4] \\ = 5.56 \times 10^{-6}T_c^4 + h_c(T_c - T_a) + E' \end{aligned} \quad 4.10$$

where α_s is the mean absorptivity to shortwave (solar) radiation, S_p is direct solar irradiance ($\mu\text{W cm}^{-2}$), A_t is the total surface area of the mandibles (cm^2), S_s is

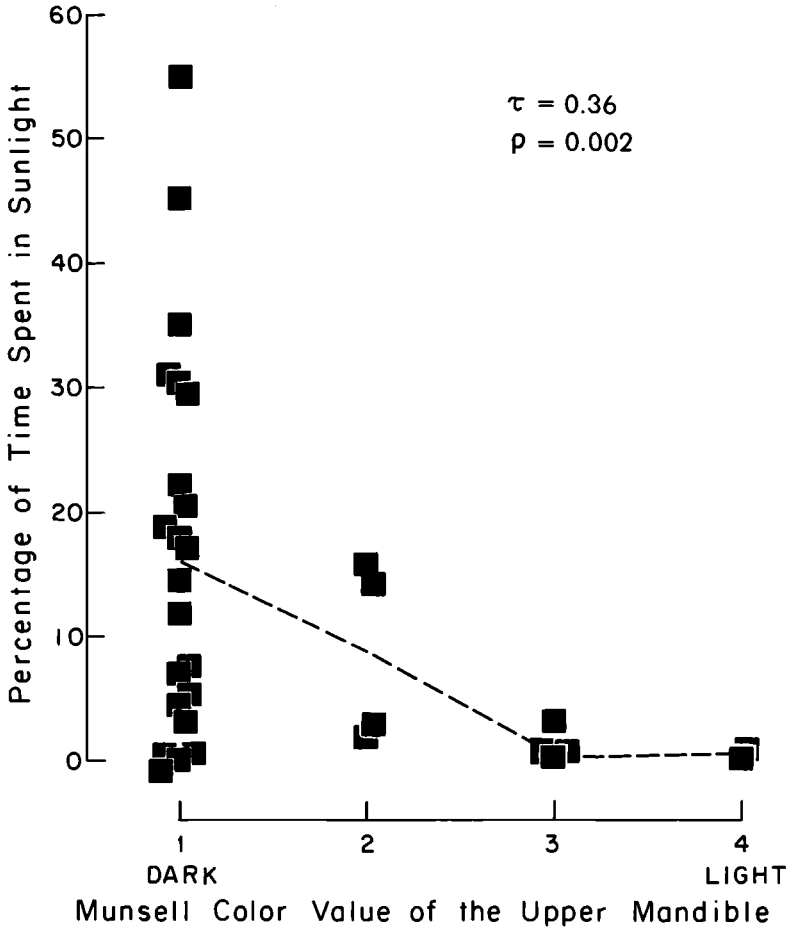


FIGURE 29. The percentage of time spent in sunlight by various species of wood-warblers plotted against the Munsell color value of the upper mandibles. The dashed line connects median values.

scattered solar irradiance ($\mu\text{W cm}^{-2}$), ρ_g is reflectance from the ground, T_g is the temperature of the ground ($^{\circ}\text{K}$), T_c is the temperature ($^{\circ}\text{K}$) of the mandibles (bill), and E' is the evaporative water loss ($\mu\text{W cm}^{-2}$).

The mean absorptivity of the mandibles (α_s) is the same for all members of a species, but varies interspecifically (Chap. 2). The predominance of dark upper mandibles (Figs. 5 and 6) suggests that wood-warblers have maximized energy absorption by the mandibles.

The ratio A_p/A_t cannot be measured in the field. Therefore, I assume that the distribution of values of the ratio is similar among species of wood-warblers.

The remaining variables that determine absorption of solar energy are the irradiance from direct (S_p), scattered (S_s), and reflected [$\rho_g(S_p + S_s)$] sunlight. Because all species were observed at the same latitudes, during the same seasons, and throughout the day, the solar irradiance to which the mandibles were exposed is similar for all species. The amount of solar energy absorbed depends on the frequency with which the mandibles are in direct sunlight.

TABLE 10
COMPARISON OF THE MUNSELL COLOR VALUE OF THE UPPER MANDIBLE WITH
THE LEGS IN MALES OF 115 SPECIES OF WOOD-WARBLERS

Munsell color value of the upper mandible		Munsell color value of the legs			
		Dark		Light	
		2	4	6	8
Dark	2	58	16	18	12
	4	0	1	6	4
	6	0	0	0	0
Light	8	0	0	0	0

When the body is in sunlight I assume the mandibles are in sunlight. Three light zones were identified: sunlight, when the body was entirely illuminated; shade, when the body was entirely in shadow; and dappled, when the body was simultaneously in shadow and sunlight. I located a wood-warbler, identified its species, waited 10 sec, then recorded the light zone occupied by the bird. Kendall's tau was the correlation measure for the percentage of time spent in sunlight (number of observations of the body in sunlight divided by the total number of observations made under sunlit conditions) plotted as a function of Munsell color value of the upper and lower mandibles.

The probability of exposing the mandibles to sunlight is significantly correlated with the color of the upper mandible (Fig. 29). Species with light mandibles are less frequently in sunlight. Exposure to sunlight and color of the lower mandibles are not correlated ($r = 0.02$, $P > 0.10$).

Light upper mandibles not only absorb less incident energy than dark upper mandibles, but light upper mandibles are exposed to direct solar radiation less frequently than dark upper mandibles. Because light mandibles absorb less energy than dark mandibles, light mandibles can also tolerate less energy loss than dark mandibles. If color of the upper mandibles affects the wood-warbler's energy balance, then species with light upper mandibles will be less cold tolerant than species with dark upper mandibles.

Energy loss.—During the day, wood-warblers never hid their bills in their scapular feathers, a behavioral pattern comparable to drawing the legs into the belly feathers. Therefore only migratory behavior and winter distribution can be used as measures of the importance of mandibular coloration to energy loss: *prediction 4.7*: species with light mandibles arrive north in the spring at higher air temperatures than species with dark mandibles; *prediction 4.8*: species with light mandibles depart south in the autumn at higher air temperatures than species with dark mandibles; *prediction 4.9*: species with light mandibles overwinter in warmer environments than species with dark mandibles.

The data and statistical tests are the same as those used to examine correlation between color of the legs and winter distribution and migratory sequence. Pearson's Product Moment Correlation was used to examine correlation of leg color with color of the upper and lower mandibles.

Color of the legs correlates poorly with color of the upper mandibles ($r = 0.42$) and even more poorly with color of the lower mandible ($r = 0.19$). Color of the upper mandible is not correlated with the mean temperature on the earliest arrival

date in Madison, Wisconsin ($\tau = 0.12$, $P > 0.10$) or at Itasca, Minnesota ($\tau = 0.08$, $P > 0.10$) nor is it correlated with the mean temperature on the mean latest departure date from Madison ($\tau = 0.20$, $P > 0.10$). Wood-warblers with dark upper mandibles do not winter in colder climates ($\tau = 0.13$, $P > 0.10$). Like the upper mandible, color of the lower mandible is not correlated with temperature variation.

The failure of mandibular color as a predictor of migration and winter range may be due to the relatively low proportion of heat lost from the mandibles, 5 to 10 percent, compared to the relatively high proportion from the legs, 10 to 56 percent (Deighton and Hutchinson 1940; Veghte and Herreid 1965; Baudinette et al. 1976; Chappell 1980a; Hill et al. 1980). Alternatively, mandibular color might have evolved to meet selection pressures unrelated to energy flow. However, the upper mandible is extremely dark with much less color variation than the legs (Table 10) suggesting that energy gain has been maximized.

CHAPTER 5

REDUCED VISUAL INTERFERENCE

“ . . . the first rays, shooting across the level water-meadows, took the animals full in the eyes and dazzled them.”

(Grahame 1933:127)

The wood-warbler's bill and facial feathers could reflect light into its eyes. Such reflected light might have several undesirable effects on the bird's vision, for example, blinding glare or dazzle, high luminance in parts of the visual field that diminishes contrast in other parts of the field, and adaptation to a higher illuminance level than is appropriate for the remainder of the visual field. Neither the bill nor the head transmits light; therefore, light incident on the bill or face is absorbed or reflected. Reflection from the face and bill is reduced by dark coloration. Ficken et al. (1971) state that dark patches or stripes around, about, or across the eye are frequently found in birds or mammals that inhabit bright environments, but they provide only anecdotal evidence.

Relative luminance was calculated for differently colored feathers and Munsell color value used to estimate the bill's relative luminance. If coloration of the bill and face evolved to reduce reflection to the eyes, then those colors with the lowest relative luminance should occur on the face and bill. The prediction is compared with the observed coloration of wood-warblers. Where mandibular and facial color vary, the percent of foraging time spent in sunlight was compared in differently colored species. The chapter concludes by reevaluating the hypothesis that facial color is an adaptation to minimize reflectance that interferes with vision.

COLORATION TO REDUCE REFLECTANCE

Coloration to reduce reflectance and the pattern of such color can be predicted only after two questions are answered: (1) reflectance from what regions most critically affects the vision of wood-warblers, and (2) which colors minimize reflectance.

Regions that reflect into the eyes. — The regions whose reflectance most critically interferes with vision are those within the wood-warbler's visual field regardless of how it holds its head. The eyebrow stripe, eyeline, and eye-ring are the only feathered regions always within the wood-warbler's visual field. The upper mandible is well within the visual field of the Barn Swallow (*Hirundo rustica*, Polyak 1957) and is probably in the visual field of wood-warblers. Because the eyes of wood-warblers are posterior and dorsal to the mandibles, and because the upper mandible overlaps the lower mandible slightly, only the upper mandible will reflect light to the pupils when the mandibles are closed. Hence, the hypothesis of coloration to reduce reflectance applies to the coloration of four regions: the eyebrow stripe, eyeline, eye-ring, and upper mandible.

Reflectance of differently colored feathers. — The apparent brightness of reflected light determines its effect on vision. The apparent brightness of a stimulus depends

upon its absolute energy flux as a function of spectral position and upon the receiver's spectral sensitivity. A photometrically defined scale approximates human brightness perception by using a conversion function (the curve of the standard observer), whereby a spectroradiometrically defined stimulus can be expressed in photometric terms (e.g., cd/m^2 , Appendix III). Because photopic spectral sensitivity curves of many diurnal vertebrates are similar (but see Chap. 7), it is possible to use a photometric scale as a general approximation of the phenomenal brightness of a stimulus.

The luminance of a surface is a photometric expression of the surface brightness. For differently colored feathers the logarithm of the luminance is calculated by a computer program from the reflectance data of the stimulus (power density vs frequency). To normalize luminance for a given habitat's illumination, I calculated the range of possible values and the position of the stimulus luminance within the range. The extremes of the luminance range are represented by the logarithm of the luminance of a maximally reflecting white surface (BaSO_4 ; Weast 1976) and the logarithm of the luminance of a minimally reflecting black surface (powdered carbon; Weast 1976). The reason for logarithms is explained in Chapter 7 where luminance is discussed in detail. The luminance of the stimulus relative to the range of possible luminances is expressed by the following ratio:

$$RL = (SL - BL)/(WL - BL) \quad 5.1$$

where SL is the logarithm of the stimulus' luminance, BL is the logarithm of the luminance from a minimally reflecting black surface, and WL is the logarithm of the luminance from a maximally reflecting white surface. The relative luminance, RL , is a dimensionless value that ranges from zero (minimally reflecting black surface) to one (maximally reflecting white surface).

The relative luminance values for differently colored feathers are: black (0.51); blue (0.65); brown (0.65); gray (0.67); yellow-green (0.69); chestnut (0.73); orange (0.84); yellow (0.91); and white (0.93). Because legs with a Munsell color value of 2 reflect less visible (400–750 nm) light than legs with a Munsell color value of 6 (Fig. 4, Chap. 2), I have assumed that Munsell color value is correlated with relative luminance. As Munsell color value increases, relative luminance increases. Nonetheless, I have been unable to calculate the relative luminance of Munsell color values; thus, the values themselves are used as an ordinal estimate of relative luminance from unfeathered surfaces.

If coloration is an adaptation to reduce reflection that interferes with vision, then the above data suggest that, *prediction 5.1*: the eyebrow stripe, eyeline, eye-ring, and upper mandible should be black to minimize relative luminance.

Observed facial coloration.—The expected frequency of feather colors (Table 11) is calculated by assuming that they occur in the same proportion as on all 19 feathered regions of the body in all species of wood-warblers (Tables 2 and 3, Chap. 2). The expected frequency is calculated separately for males and females. The chi-square Goodness of Fit statistic (Roscoe 1975) was used to estimate agreement between expected and observed color frequencies. Color of the upper mandible, which is in the visual field, is compared to color of the lower mandible and legs, which are unfeathered and outside the visual field. Comparisons are based on the Wilcoxon Matched-Pairs Signed-Ranks test where T is the calculated

TABLE 11
 NUMBER OF SPECIES IN WHICH MALES OR FEMALES HAVE EYEBROW STRIPES,
 EYE-RINGS, OR EYELINES OF THE INDICATED COLOR

Color	Males				Females			
	Ex-pected	Observed			Ex-pected	Observed		
		Eye-ring	Eyebrow stripe	Eyeline		Eye-ring	Eyebrow stripe	Eyeline
White	17	31	26	4	17	29	23	4
Yellow	18	23	33	14	16	29	18	11
Orange	1	2	3	0	1	4	2	0
Red	2	3	2	1	2	2	3	1
Chestnut	3	3	2	6	2	3	1	4
Yellow-green	20	6	2	11	24	15	13	20
Gray	19	8	15	24	20	22	20	41
Brown	12	3	2	5	17	8	6	11
Blue	3	2	4	1	1	0	3	0
Black	17	31	22	45	6	8	5	14
χ^2		50.3	49.5	18.0		17.8	38.0	48.6
<i>P</i>		<0.005	<0.005	<0.05		<0.05	<0.005	<0.005

statistic (Roscoe 1975). Species whose upper mandible had Munsell color values of 1 or 3 were lumped with species whose upper mandible had the next higher Munsell color value. Such a procedure is conservative because it increases the number of species whose upper mandible and legs have the same Munsell color value. Tie scores favor the hypothesis of no difference.

The eyebrow stripe, eyeline, and eye-ring are not exclusively black (Table 11, *contra prediction 5.1*). Nevertheless, color of the eyeline in both sexes is significantly darker than expected whereas the eyebrow stripe and eye-ring are significantly lighter than expected.

Males in 101 of 115 species and females in 86 of 106 species have upper mandibles that are black or nearly black (Munsell color values 1 or 2, Figs. 5 and 6; *prediction 5.1*). Such coloration is not characteristic of other unfeathered surfaces. The upper mandible is significantly darker than the lower mandible (Figs. 5 and 6; $T = 225$, d.f. = 115, $P < 0.001$) and the legs (Table 10; $T = 712$, d.f. = 113, $P < 0.001$).

BEHAVIOR TO REDUCE REFLECTANCE

If the facial feathers or upper mandible are lightly colored, the species may frequent shade where illuminance is low. In dim light, reflection from the upper mandible or facial feathers may be insufficient to adversely affect the wood-warbler's vision; therefore, *prediction 5.2*: the higher the relative luminance of the face or upper mandible, the less time the species spends in sunlight.

Data on the behavior of wood-warblers fall into three broad categories: display, foraging, and maintenance. A wood-warbler can probably display and sing despite imperfect vision. It can certainly bathe and preen without observing itself, but in order to forage successfully optimal visual conditions are probably essential. Therefore, *prediction 5.2* is applied to foraging behavior only.

I located a wood-warbler, identified its species, waited 10 sec, then recorded on a continuously running tape recorder the behavioral patterns of wood-warbler

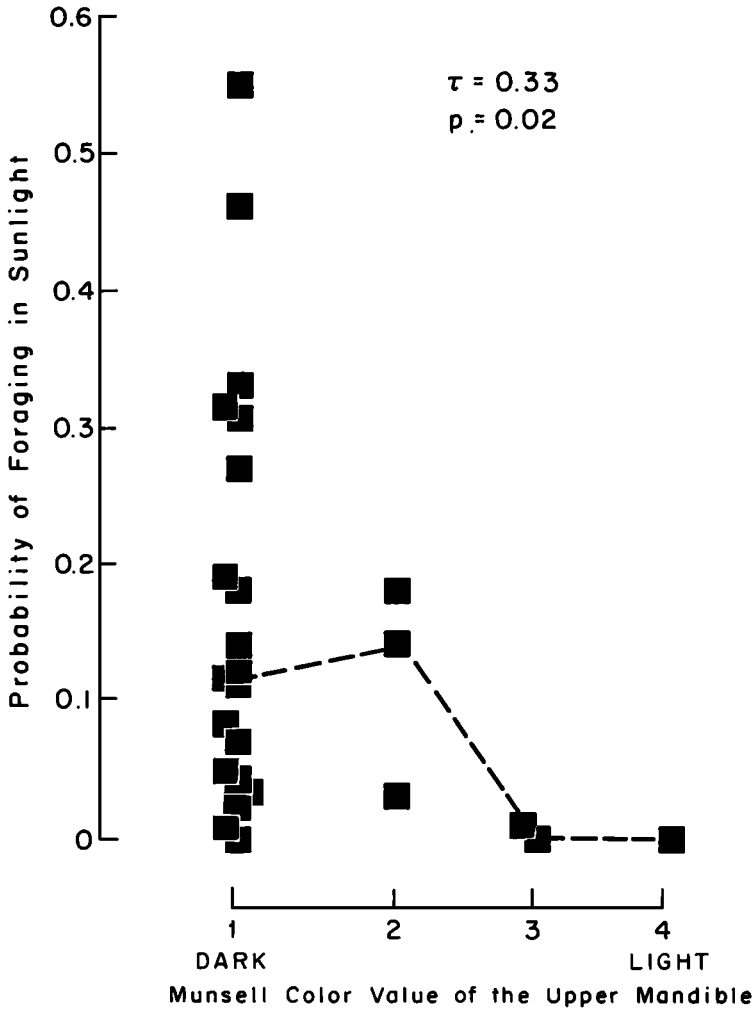


FIGURE 30. Probability of foraging in sunlight plotted against the Munsell color value of the upper mandible for various species of wood-warblers. The dashed line connects median values.

and each change of light zone (Chap. 4). I determined the time spent in each light zone with a stopwatch when I replayed the tape. Foraging behavior consists of three action patterns (names from Fitzpatrick 1980), two of which involve flight. Flight occurred whenever the wings were unfolded and the feet were not in contact with the substrate. *Aerial hawks* were those flights that deviated from a straight-line path where the deviation was not necessitated by an obstruction. *Sally-gleans* occurred when the bird while in flight contacted a substrate with its bill. *Gleaning* occurred when the perched bird jabbed at and contacted the substrate with its bill. Foraging began when the bird performed its first foraging action pattern. If consecutive foraging patterns were separated by 60 sec or less, then I included the time between patterns as foraging time. Such time was often spent searching leaves or twigs.

Let f_s be the time spent foraging in the sunlight and S be the total time the species spent foraging with the sun shining. The probability of foraging in sunlight, F , is:

$$F = f_s/S \quad 5.2$$

The Pearson Product-Moment Correlation Coefficient was used to express the correlation between the probability of foraging in sunlight and reflectance from the eyeline, eye-ring, and eyebrow stripe. Kendall's tau was used to measure the correlation between probability of foraging in sunlight and the Munsell color value of the upper mandible.

The probability of foraging in sunlight and reflectance from the eyeline ($r^2 = 0.06$), eyebrow stripe ($r^2 = 0.02$), or eye-ring ($r^2 = 0.03$) are not correlated. However, correlation between the Munsell color value of the upper mandible and the probability of foraging in sunlight is significant ($\tau = 0.33$, $P = 0.02$, Fig. 30). Species whose upper mandible has a Munsell color value of 3 or 4 never forage in sunlight.

CONCLUSIONS

Most objects, feathers for example, have a matte finish that reflects light according to Lambert's Law, which states that when illumination is normal to the surface, the magnitude of reflection at various angles is proportional to the cosine of the angle with respect to the normal (Monk 1963). If surface irregularities are small in comparison with the wavelength of light, the surface is polished and reflectance is of a simpler type, called specular, in which the angle of reflection of the light beam equals the angle of incidence. If we consider only the intensity of reflected light at a particular point, the pupil of the eye, for example, then interference from reflected light is minimized by reflection from a matte surface. This is because with the same intensity of incident light and the same reflection spectrum, the polished surface reflects all light in the same direction whereas the matte surface scatters light in all directions.

Among wood-warblers, the feathered surfaces near the eye approximate a matte surface whereas the upper mandible approximates a polished surface. Reflectance from feathered regions is diffuse and the intensity of reflected light at the pupil is low compared to the maximum intensity possible with specular reflectance. Reflectance from the eyeline, eyebrow stripe, and eye-ring is reduced by the matte surface and color may serve functions unrelated to reducing reflectance.

Ficken et al. (1971) suggested that eye-rings, which are invariably light-colored, increase the light-gathering potential of the eye. However, reflection into the eye from nearby feathers only increases the amount of scattered light entering the eye. Such light cannot be resolved into an image and therefore only causes the eye to adapt to a higher level of illuminance than is appropriate to the visual field.

Polyak (1957) apparently was the first to suggest that eyelines of vertebrates serve as lines of sight. The hypothesis was stated more precisely by Ficken and Wilmot (1968) who offered supporting data from a comparative study of North American songbirds. If eyelines are sighting lines, then the line from the eye to the mouth must have at least one contrasting edge. Among wood-warblers the eyebrow stripe is usually light and the eyeline dark, thus providing the contrasting

edge along which to sight prey. If wood-warblers sight along such lines, however, both the line and the prey must be roughly in focus at the same time, a seemingly unlikely event. Furthermore, sighting could be done by aligning the tip of the bill with the prey, the bill tip being farther from the eye than the eyeline.

Dark faces may mask the eye enabling wood-warblers to approach their insect prey closely before startling it (Cott 1957; Gavish and Gavish 1982). However, only 55 of 112 species of wood-warblers have faces dark enough to mask the eye and 22 of the 55 species have a light eye-ring that contrasts markedly with the dark face and eye. These data cannot rule out the possibility that a dark face masks the eye, but most wood-warblers have a brightly colored face or eye-ring that contrasts with and highlights the eye.

Dark coloration of the eyeline reduces even diffuse reflectance along this most important line of sight. Furthermore, subadult male American Redstarts exchange their light gray facial features for black in a prealternate molt restricted to the rictal bristles and facial feathers (Rohwer et al. 1983). The molt would reduce reflectance near the eye, but its pattern is too irregular to mask the eye or provide a sighting line. Color of feathers surrounding the eye remains largely unexplained with reduction of reflectance one of the few realistic possibilities.

The hard, polished surface of the mandibles may be important in feeding and manipulative tasks, but specular reflectance from the upper mandible may be intense under certain conditions. If the surface structure cannot be altered, then the only means of reducing reflection is absorption of light by a dark biochrome. Color of the upper mandible, and behavior of species with differently colored upper mandibles is consistent with the need to minimize specular reflectance.

Recent experimental evidence (Burt 1984) also supports the need to minimize specular reflectance from the upper mandible. When the dark upper mandible of Willow Flycatchers (*Empidonax traillii*) was painted white, they increased the proportion of foraging time spent in shade. Furthermore, the experimental result is not expected if mandibular color is an adaptation to energy gain (Chap. 4). Thus, the comparative data from wood-warblers and the experimental data from flycatchers favor the hypothesis that color of the upper mandible is an adaptation to minimize reflectance that interferes with vision.

CHAPTER 6

COLOR PATTERNS THAT INCREASE VISIBILITY

"... our woods are thronged with birds as exquisitely colored as the daintiest tropical forms Entering an apparently deserted bit of woods, we hear faint voices, lisping *tseeps*, and soon discover that the tree tops are animated with flitting forms."

(Chapman 1912:430)

Many species communicate optically. Striking examples of optical signals include the brilliant colors and stereotyped, often grotesque, postures associated with the reproductive displays of many species. However, anything about one animal that is perceived by another animal is a potential optical signal, for example, a barely perceptible color pattern or routine, ongoing behavior (Hailman 1977a). The first hypothesis examined in this chapter is that conspicuous color patterns of wood-warblers create optical signals broadcast during routine behavior.

A display is any behavioral pattern whose evolution has been influenced by its function as a signal to other animals. Displays may evolve from noncommunicative action patterns or incipient portions of action patterns (intention movements) by the evolutionary process of ritualization (Huxley 1914, 1923; Daanje 1950). Tinbergen (1952) suggested that during ritualization, conspicuous structures or colors evolve to accentuate communicative movements (and *vice versa*). For example, the broad, orange feather among the green secondaries of the male Mandarin Duck (*Aix galericulata*) dramatizes courtship preening in which the male's bill emphatically touches the modified feather (Lorenz 1941), and the Eurasian Robin's (*Erithacus rubecula*) red breast emphasizes postures used in territorial defense (Lack 1965). The second hypothesis examined in this chapter is that patterns of color create optical signals associated with the display behavior of wood-warblers.

Wingbars and tailspots are simple, well-defined color patterns that are widespread among wood-warblers and ideally suited to an examination of the above hypotheses. I look first at the occurrence of wingbars and tailspots in the subfamily Parulinae. Next I examine the first hypothesis, that wingbars and tailspots create optical signals broadcast during routine behavior. Routine behavior that reveals the wingbars or tailspots includes aerial foraging, flying, and maintenance. The occurrence and frequency of such behavior are compared in species that have wingbars, or tailspots, both, or neither. The second hypothesis that patterns of color are optical signals associated with display behavior is tested by comparing the display behavior and its frequency of occurrence in wood-warblers that have wingbars, or tailspots, both, or neither.

WINGBARS AND TAILSPOTS

I determined the presence or absence of wingbars and tailspots in 113 species of wood-warblers and the independence of these markings from one another.

Only four regions of the bird's body concern us here, the remiges and wingbars and the rectrices and tailspots (Fig. 1). Wingbars are present when the remiges

and wingbars are differently colored. Similarly, tailspots are differently colored from the rectrices in species that possess tailspots. I evaluated the hypothesis that the presence of wingbars is independent of the presence of tailspots with a chi-square Test of Independence (Roscoe 1975).

Of 113 species of wood-warblers, 52 have tailspots and 34 have wingbars. Wood-warblers show a significant tendency to have both wingbars and tailspots (32 species) or neither (59 species; $\chi^2 = 45.27$, d.f. = 1, $P < 0.005$). Only 20 of 52 species with tailspots lack wingbars. Only two species with wingbars lack tailspots. Within species no sex- or age-related differences were found in the pattern of wingbars or tailspots.

Wingbars and tailspots are revealed by spreading the wings and tail on takeoff and landing, and the tail is spread during mid-flight maneuvers. The tendency of the two patterns to occur together or not at all probably results from the fact that both patterns are revealed by the same behavior. In the analysis that follows functions of wingbars and tailspots are evaluated.

REVEALING BEHAVIOR

Wingbars are best revealed by fanning the wings; likewise tailspots are best revealed by fanning the tail. The wings and tail are fanned on all flights at takeoff and landing. Some foraging flights also reveal the tailspots during erratic, mid-flight maneuvers. Thus routine flights reveal the wingbars and tailspots, but lack the stereotypy of ritualized aerial displays. If wingbars and tailspots create optical signals that are broadcast during routine flights then, *prediction 6.1*: wood-warblers with wingbars or tailspots fly more frequently than species with neither wingbars nor tailspots.

Methods.—The behavior of singing males was recorded at Itasca, Minnesota (1974), Chapel Hill, North Carolina (1975), and Madison, Wisconsin (1974, 1975). Song provided a behavioral marker with which to begin observations, a marker that was as independent as possible from behavior related to optical signaling. I located a wood-warbler by its song, identified it visually, waited 10 sec, and then described its behavior on a continuously running tape. An individual was followed for as long as possible, up to 10 min, but never less than 10 sec. When I transcribed a tape, I wrote down all behavior that occurred, when it occurred, its duration, and the interval between occurrences. I compared the frequency of flight in wood-warblers with both wingbars and tailspots, tailspots only, and neither wingbars nor tailspots. Flights that revealed the wingbars, tailspots, or both were divided into routine flights and aerial display.

Flight occurred whenever the wings were spread and the feet not in contact with the substrate. *Commutes* occurred when the bird flew the most direct route between perches. *Aerial hawks* occurred when the bird deviated from the most direct route. *Sally-gleans* occurred when the bird while in flight contacted a substrate with its bill. *Aerial displays*, described later, are discussed in relation to the second hypothesis, that wingbars and tailspots are associated with display behavior. Takeoff was indicated on the tape recording by the word "up," landing by the word "down," and I recorded the type of flight after the word "down." If the bird flew out of sight, the observation was terminated with the takeoff and the final flight ignored.

TABLE 12
 FREQUENCY OF FLIGHT AMONG WOOD-WARBLED LOCATED BY SONG

Number of intervals	Species	Mean interval (sec) between takeoffs	Wingbars	Tailspots
50	Golden-winged	5.5	+	+
22	Cape May	7.8	+	+
33	Prairie	9.0	+	+
33	Yellow-throated	10.0	+	+
15	Tennessee	10.0	-	+
12	Hooded	11.7	-	+
121	Nashville	11.8	-	-
59	Magnolia	12.7	+	+
6	Blue-winged	13.0	+	+
46	Black-and-white	14.5	+	+
221	Chestnut-sided	16.0	+	+
521	Am. Redstart	16.4	+	+
11	Palm	16.8	-	+
130	Northern Parula	18.1	+	+
117	Pine	18.2	+	+
98	Black-thr. Green	18.2	+	+
14	Prothonotary	19.6	-	+
30	Canada	20.4	-	-
87	Yellow	21.5	+	+
58	Yellow-rumped	24.0	+	+
236	Blackburnian	25.3	+	+
4	Blackpoll	27.8	+	+
15	Cerulean	35.7	+	+
27	Kentucky	40.8	-	-
100	Common Yellowthroat	65.6	-	-
6	La. Waterthrush	73.0	-	-
19	Mourning	110.3	-	-
5	Connecticut	117.8	-	-
27	Ovenbird	245.6	-	-

The frequency of flight was high enough to calculate the mean interval between consecutive takeoffs for all species for all flights and for some species for each of the four types of flight. The mean interval between consecutive takeoffs was calculated and the Kruskal and Wallis statistic (Langley 1971) used to compare ranks of species with both wingbars and tailspots, species with only tailspots and species with neither wingbars nor tailspots. The difference between each pair of the above three groups was examined with the Wilcoxon Sum of Ranks test (Langley 1971). Sampling bias was checked by comparing the mean interval of observation with the frequency of all flights. Comparison is based on the Pearson Product-Moment Correlation Coefficient.

Results.—Overall the difference in ranks is significant (Table 12, $\chi^2 = 9.95$, d.f. = 2, $0.01 > P > 0.001$). The ranks of wood-warblers with both wingbars and tailspots are not significantly different from the ranks of those with only tailspots ($r = 39$, $P > 0.10$). Species with neither wingbars nor tailspots have significantly longer intervals between consecutive takeoffs than species with tailspots only ($r = 12$, $P = 0.01$) or species with both wingbars and tailspots ($r = 54$, $0.01 > P > 0.002$).

Species might appear to fly infrequently because of many short observation periods in which no flights were seen. Such a bias would be indicated by a negative correlation between the mean interflight interval and the mean length of obser-

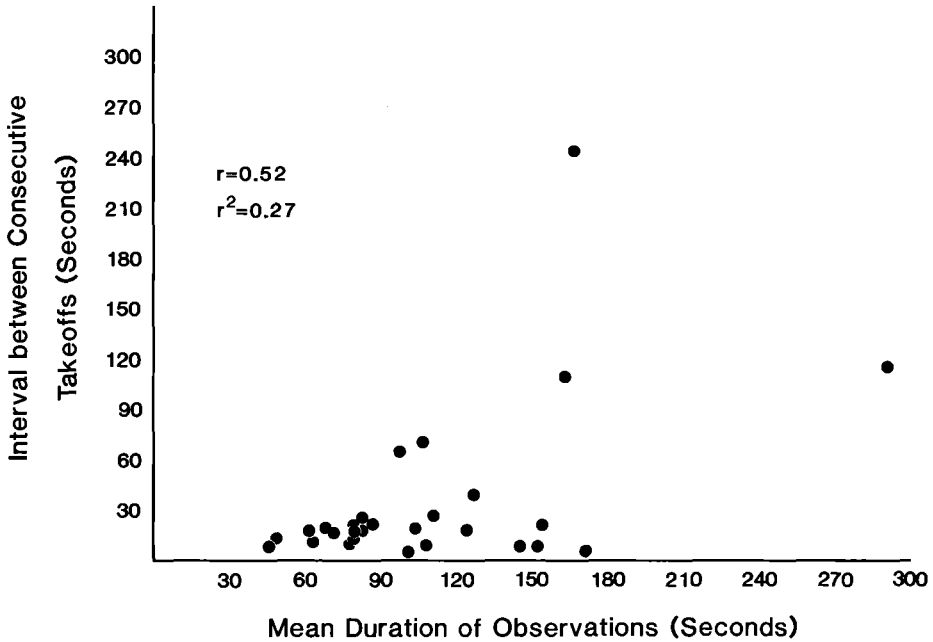


FIGURE 31. Interval between consecutive flights plotted as a function of the mean length of continuous observation of species listed in Table 11.

vation periods. However, the correlation is low, but positive, indicating that species with long intervals between consecutive flights tended to be observed for longer periods (Fig. 31) than species with short intervals between flights. Hence, the long interflight intervals are real, the result of long periods of observation in which flights were infrequent.

Wood-warblers that lack wingbars and tailspots might still fan the tail and wings as often as those with one or both patterns by engaging in longer flights or more frequent erratic flights (*aerial hawks* or *sally-gleans*). However, species with neither wingbars nor tailspots have flights of about the same duration as species with patterned wings or tails (Table 13, $\chi^2 = 4.30$, d.f. = 2, $P = 0.25$) based on the Kruskal and Wallis statistic. The ranks of wood-warblers with both wingbars and tailspots are not significantly different from the ranks of species with only tailspots ($r = 23$, $0.10 > P > 0.05$) nor are they significantly different from the ranks of species with neither wingbars nor tailspots ($r = 80$, $P > 0.10$). The ranks of wood-warblers with only tailspots are not significantly different from the ranks of those that lack both patterns ($r = 24$, $P > 0.10$). Some bias is introduced into these results by the fact that 0.5 sec was the briefest time interval that could be measured. Briefer flights were assigned a duration of 0.5 sec.

The length of the interval between *commutes* is significantly different in differently patterned wood-warblers (Table 14, $\chi^2 = 9.47$, d.f. = 2, $0.01 > P > 0.002$). Species with both wingbars and tailspots have significantly shorter intervals than species with neither wingbars nor tailspots ($r = 55$, $0.01 > P > 0.002$). Wood-warblers with only tailspots also have intervals between *commutes* that are significantly shorter than intervals of species with neither wingbars nor tailspots ($r =$

TABLE 13
FLIGHT DURATION OF WOOD-WARBLED LOCATED BY SONG

Number of flights	Species	Mean flight duration (sec)	Wingbars	Tailspots
4	Blackpoll	0.50	+	+
50	Golden-winged	0.57	+	+
6	Blue-winged	0.58	+	+
30	Canada	0.60	-	-
46	Black-and-white	0.62	+	+
130	Northern Parula	0.64	+	+
121	Nashville	0.66	-	-
59	Magnolia	0.67	+	+
98	Black-thr. Green	0.68	+	+
33	Yellow-throated	0.70	+	+
5	Connecticut	0.70	-	-
22	Cape May	0.73	+	+
521	Am. Redstart	0.75	+	+
14	Prothonotary	0.75	-	+
117	Pine	0.76	+	+
236	Blackburnian	0.78	+	+
221	Chestnut-sided	0.79	+	+
27	Kentucky	0.83	-	-
15	Cerulean	0.83	+	+
11	Palm	0.85	-	+
100	Common Yellowthroat	0.89	-	-
33	Prairie	0.89	+	+
12	Hooded	0.95	-	+
19	Mourning	0.97	-	-
87	Yellow	1.27	+	+
15	Tennessee	1.27	-	+
58	Yellow-rumped	1.32	+	+
27	Ovenbird	1.50	-	-
6	La. Waterthrush	2.50	-	-

14, $P = 0.05$). Intervals between *commutes* in wood-warblers with only tailspots are not significantly different from intervals between *commutes* of those with both wingbars and tailspots ($r = 42$, $P > 0.10$).

When *commuting* the tail is fanned only on takeoff and landing, but *aerial hawking* requires the tail to be fanned during aerial maneuvers. The length of the interval between *aerial hawks* differs significantly (Table 15, $\chi^2 = 9.71$, d.f. = 2, $0.05 > P > 0.01$) among species with differently patterned wings and tails. Species with both wingbars and tailspots have significantly shorter intervals between *aerial hawks* than species with neither wingbars nor tailspots ($r = 26$, $0.01 > P > 0.002$). In species with only tailspots, intervals between *aerial hawks* are not significantly different from those of species with both wingbars and tailspots ($r = 26$, $P > 0.10$). Too few species are available for comparison between those with only tailspots and those with neither wingbars nor tailspots, but the three species with only tailspots all have shorter intervals between *aerial hawks* than the six species with neither wingbars nor tailspots.

No significant difference was found in the interval between *sally-gleans* (Table 16) in birds with differently patterned wings and tails ($\chi^2 = 5.48$, d.f. = 2, $0.10 > P > 0.05$). The total time species with only tailspots were observed is small, and the short intervals may be artifacts; however, Prothonotary and Hooded warblers often occupy similar habitats and may be expected to show similar behavior.

TABLE 14
 FREQUENCY OF COMMUTES AMONG WOOD-WARBLERS LOCATED BY SONG

Number of intervals	Species	Mean interval (sec) between takeoffs of commutes	Wingbars	Tailspots
50	Golden-winged	5.5	+	+
32	Prairie	9.6	+	+
17	Cape May	10.1	+	+
33	Yellow-throated	10.6	+	+
14	Tennessee	10.7	—	+
6	Blue-winged	13.0	+	+
105	Nashville	13.6	—	—
10	Hooded	14.1	—	+
45	Black-and-white	14.9	+	+
50	Magnolia	15.0	+	+
198	Chestnut-sided	17.8	+	+
121	Northern Parula	19.5	+	+
104	Pine	20.4	+	+
408	Am. Redstart	21.0	+	+
11	Prothonotary	21.6	—	+
81	Black-thr. Green	22.0	+	+
26	Canada	23.6	—	—
7	Palm	26.3	—	+
68	Yellow	27.5	+	+
4	Blackpoll	27.8	+	+
205	Blackburnian	29.1	+	+
37	Yellow-rumped	37.6	+	+
14	Cerulean	38.3	+	+
23	Kentucky	48.0	—	—
93	Common Yellowthroat	70.5	—	—
5	La. Waterthrush	87.5	—	—
5	Connecticut	117.8	—	—
17	Mourning	123.3	—	—
26	Ovenbird	255.0	—	—

Discussion.—The intervals between successive *commutes* and between successive *aerial hawks* are significantly shorter in species with both wingbars and tailspots or only tailspots than in species with neither pattern (*prediction 6.1*). The similar behavior of species with both wingbars and tailspots and species with tailspots only suggests that during routine flights around the territory tailspots create the important optical signal.

The results also suggest that color patterns emphasize conspicuous movements in routine, unritualized behavior. Discovery and capture of prey remain the primary function of foraging flights, but the increased frequency of such flights among species with tailspots suggests a secondary signalling function for the flights. Whether the pattern or the behavior changed first is open to speculation. However, Nashville and Canada warblers lack wingbars and tailspots, but have the high frequency of foraging flights characteristic of species with one or both flash patterns, suggesting that color evolved to emphasize existing behavior.

The interval between successive *sally-gleans* is not correlated with the presence or absence of wingbars and tailspots (*contra prediction 6.1*). Although *sally-gleans* occur infrequently, the lack of correlation is surprising and inexplicable.

All species within *Dendroica* have wingbars or tailspots whereas no species within *Geothlypis* and *Seiurus* have wingbars or tailspots. Such lack of intrageneric

TABLE 15
 FREQUENCY OF AERIAL HAWKING AMONG WOOD-WARBLED LOCATED BY SONG

Number of intervals	Species	Mean interval (sec) between takeoffs of aerial hawks	Wingbars	Tailspots
5	Cape May	34.4	+	+
19	Yellow-rumped	73.1	+	+
79	Am. Redstart	108.5	+	+
16	Yellow	116.9	+	+
6	Magnolia	124.8	+	+
1	Hooded	141.0	-	+
11	Black-thr. Green	162.1	+	+
2	Yellow-throated	164.8	+	+
1	Palm	184.5	-	+
15	Chestnut-sided	235.4	+	+
1	Prothonotary	237.5	-	+
5	Nashville	285.3	-	-
7	Pine	303.9	+	+
7	Northern Parula	336.8	+	+
17	Blackburnian	351.1	+	+
1	Canada	612.5	-	-
1	Black-and-white	669.0	+	+
2	Mourning	1048.2	-	-
1	Kentucky	1101.0	-	-
4	Common Yellowthroat	1639.1	-	-
1	Ovenbird	6631.0	-	-

variation suggests a single phylogenetic origin for the correlation of color pattern with short interflight intervals. However, wingbars or tailspots are present in *Mniotilta*, *Setophaga*, and *Protonotaria* all of which have short interflight intervals comparable to those of *Dendroica* (Table 17) despite being generically distinct (Avisé et al. 1980). In fact, the mean genetic distances (Nei's D) between genera of Parulinae (Avisé et al. 1980:307) suggest that *Mniotilta* is more distantly related to *Dendroica*, despite similarities in color pattern and behavior, than *Seiurus* and *Geothlypis* which lack flash patterns and have long interflight intervals (Table 17). Apparently the correlation of wingbars and tailspots with short interflight intervals has evolved more than once within the Parulinae.

The presence of flash patterns varies intragenerically in *Wilsonia* and *Vermivora*. Within *Wilsonia*, the Hooded Warbler has tailspots and a shorter mean interval between takeoffs (11.7 sec) than the Canada Warbler (20.4 sec) which lacks wingbars and tailspots. Within *Vermivora*, the three species with flash patterns (Blue-winged, Golden-winged, and Tennessee warblers, have a combined mean interval between takeoffs (7.1 sec) that is shorter than the mean interval of the Nashville Warbler (11.8 sec) which lacks wingbars and tailspots. The variability within *Vermivora* and *Wilsonia* suggests that within these genera the association between color and behavior arose independently of *Dendroica* and perhaps more recently because both genera contain species that fly frequently, but lack flash patterns.

The similarity of wingbars and tailspots among species of wood-warblers (Fig. 14) may be an example of social mimicry (Moynihan 1968, 1981), Batesian mimicry (Barnard 1979, 1982), or the similarity of physical constraints on the placement and color of optical signals (Chap. 3 and 7; Burtt and Gatz 1982). Whatever the information communicated by showing the wingbars and tailspots,

TABLE 16
 FREQUENCY OF SALLY-GLEANING AMONG WOOD-WARBLEDERS LOCATED BY SONG

Number of intervals	Species	Mean interval (sec) between takeoffs of sally-gleans	Wingbars	Tailspots
2	Prothonotary	118.5	—	+
1	Hooded	141.0	—	+
9	Nashville	158.5	—	—
3	Canada	204.2	—	—
3	Magnolia	249.7	+	+
29	Am. Redstart	295.6	+	+
1	Prairie	306.5	+	+
6	Pine	354.5	+	+
5	Black-thr. Green	356.6	+	+
3	Kentucky	368.0	—	—
1	La. Waterthrush	437.5	—	—
4	Yellow	467.8	+	+
12	Blackburnian	497.4	+	+
1	Cerulean	536.0	+	+
8	Chestnut-sided	882.8	+	+
1	Yellow-rumped	1389.5	+	+
1	Northern Parula	2357.5	+	+
2	Common Yellowthroat	3278.2	—	—

both patterns appear to create optical signals that are given during routine behavior such as foraging or moving about the territory.

DISPLAY BEHAVIOR

If wingbars and tailspots create optical signals associated with the display behavior of wood-warblers then, *prediction 6.2*: display behavior of species with wingbars and tailspots will include fanning the wings, tail, or both to reveal these flash patterns.

The optical displays of wood-warblers that reveal wingbars, tailspots, or both consist of a variety of aerial and non-aerial action patterns. The names of the displays and their descriptions are from Ficken and Ficken (1962b, 1968a, b), Ficken (1962), and Baird (1967), except for song flight, which is based on my own field notes. Occurrence of aerial and non-aerial displays among wood-warblers is summarized in Table 18.

TABLE 17
 FREQUENCY OF FLIGHT AMONG GENERA OF WOOD-WARBLEDERS

Number of intervals	Genus	Number of species analyzed	Mean interval between takeoffs (sec)	Wingbars or tailspots
46	<i>Mniotilta</i>	1	14.5	present
521	<i>Setophaga</i>	1	16.4	present
994	<i>Dendroica</i>	13	19.2	present
14	<i>Protonotaria</i>	1	19.6	present
151	<i>Geothlypis</i>	4	68.5	absent
33	<i>Seiurus</i>	2	214.2	absent

Circle flight.—The male flies from his perch, approaches a male or female conspecific, and returns to the vicinity of his original perch. The flight path is horizontal and semicircular.

Glide.—The male glides 3–7 m with wings outstretched and tail spread. Occasionally a few small-amplitude wing beats occur.

Moth flight.—The male flies slowly away from the female with large-amplitude wing beats; the head is held high above the back.

Hover.—The male raises and fans his tail, raises the wings, and flies with rapid, small-amplitude wing beats. The breast feathers are fluffed, the head held high above the back, and the crown feathers raised. The male flies toward the female, hovers before her, and may fly in an arc around her. The display is known only from Golden-winged and Blue-winged warblers (Table 18).

Song flight.—In Common Yellowthroats the male flies up at a 45° angle with the horizontal. About 10 m above the ground, the male tilts his head so that the bill points vertically up; the tail is cocked vertically over the back, and as the male sings, he descends at about a 45° angle on stiffly beating wings. Less ritualized song flights are found in many species of wood-warblers (Table 18).

Supplant.—The wood-warbler flies at a conspecific or rarely an individual of another species, but instead of following the fleeing conspecific the wood-warbler alights on the vacated perch.

Chase.—Chases occur when a wood-warbler flies toward a conspecific (rarely an individual of another species) which turns and flees with the wood-warbler pursuing. In Prairie Warblers and American Redstarts both pursuer and pursued fly slowly and often side by side, suggesting that, in these species at least, the chase is ritualized (Ficken 1962; Nolan 1978).

Wings-out.—“The contour feathers are sleeked, the body held horizontal, and the bird faces its opponent. The wings are lifted horizontally out from the body” (Ficken 1962:625).

Tail-spread.—The tail feathers are fanned to a variable degree while the tail is held parallel to the body's long axis or less frequently cocked upward. The duration of the tail-spread varies from minutes in the American Redstart to less than one sec in the Hooded and Magnolia warblers (pers. obs.).

Although display behavior of wood-warblers with wingbars or tailspots includes fanning the wings, tail, or both (Table 18) as predicted (*prediction 6.2*), such displays are also found among species that lack wingbars and tailspots (Table 18). The widespread nature of the displays suggests that they are ancestral to the more taxonomically restricted wingbars and tailspots. However, displays may be more exaggerated or more frequently performed in species with wingbars or tailspots than in species lacking flash patterns. To evaluate the frequency of displays I located a wood-warbler by its song, identified it visually, waited 10 sec, and then described its behavior on a continuously running tape. An individual was followed for as long as possible, up to 10 min, but never less than 10 sec. During transcription I noted the type of display, its duration, and the interval between any two consecutive displays.

The data on the interval between successive aerial displays are too few for statistical analysis (Table 19). Nonetheless aerial display is rare in species with neither wingbars nor tailspots, occurring infrequently in only one out of eight

TABLE 18
 OCCURRENCE OF AERIAL AND NON-AERIAL DISPLAYS AMONG WOOD-WARBLEDERS

Species	Color pattern		Aerial display ¹					Non-aerial display		Source		
	Wing-bars	Tail-spots	Circle flight	Glide	Moth flight	Hover flight	Song flight	Sup-plant	Chase		Wings out	Tail spread
Golden-winged	+	+	x	x	x	x	x	x	x	x	x	E.H.B.; Baird 1967; Ficken and Ficken 1968a, 1968b
Blue-winged	+	+			x	x			x	x		Ficken and Ficken 1962b
Tennessee	-	-	x						x			E.H.B.
Nashville	+	+					x		x			E.H.B.; Bowles and Bowles 1906; Chapman 1907
Northern Parula	+	+	x						x			E.H.B.; Morse 1967
Yellow	+	+	x				x		x			E.H.B.
Magnolia	+	+	x						x			E.H.B.; Kendeigh 1945; Bent 1953; Morse 1976
Cape May	+	+							x			E.H.B.
Yellow-rumped	+	+	x						x			E.H.B.; Morse 1976
Black-thr. Green	+	+	x						x			E.H.B.; Kendeigh 1945; Morse 1976
Blackburnian	+	+			x				x			E.H.B.; Morse 1976
Chestnut-sided	+	+	x		x				x			E.H.B.; Ficken and Ficken 1962b
Pine	+	+	x						x			E.H.B.
Kirtland's	+	+					x					Mayfield 1960
Prairie	+	+			x				x			E.H.B.; Nolan 1978
Black-and-white	+	+							x			E.H.B.
Am. Redstart	+	+	x						x			E.H.B.; Ficken and Ficken 1962b; Ficken 1962
Prothonotary	-	-					x					Brewster 1878
Worm-eating	-	-					x					Chapman 1907
Ovenbird	-	-	x						x			E.H.B.; Chapman 1907; Hann 1937; Freeman 1950; Eaton 1958; Bent 1953; Ficken and Ficken 1962b; Lein 1981
Northern Waterthrush	-	-					x					Eaton 1958
Louisiana Waterthrush	-	-	x									Ficken and Ficken 1962b; Eaton 1958
Kentucky	-	-					x					Chapman 1907
Mourning	-	-					x		x			E.H.B.; Bent 1953; Cox 1960
MacGillivray's	-	-					x		x			Chapman 1907
Common Yellowthroat	-	-					x					E.H.B.; Bent 1953
Hooded	-	-					x					E.H.B.; Bent 1953
Canada	-	-										Ficken and Ficken 1962b
Painted Redstart	+	+							x			Chapman 1907
Slate-throated Redstart	-	-										Skutch 1954

¹ x = reported, no mark = unreported.

TABLE 19
 FREQUENCY OF AERIAL DISPLAYS AMONG WOOD-WARBLED LOCATED BY SONG

Number of intervals	Species	Mean interval (sec) between takeoffs of aerial displays	Wingbars	Tailspots
3	Palm	61.5	—	+
1	Tennessee	149.5	—	+
1	Yellow-rumped	1389.5	+	+
5	Am. Redstart	1714.4	+	+
3	Blackburnian	1989.5	+	+
1	Northern Parula	2357.5	+	+
1	Common Yellowthroat	6556.5	—	—

species observed. Aerial displays were observed in six of 21 species with wingbars or tailspots, and aerial displays occurred more frequently in those species than in the Common Yellowthroat which lacks wingbars and tailspots. Three non-aerial displays were observed in wood-warblers located by song; all were in species with wingbars and tailspots.

CONCLUSIONS

Aerial displays reveal wingbars and tailspots simultaneously. That would seem to explain the tendency of the patterns to occur together or not at all, although species with only tailspots use the same displays and display just as often as species with both wingbars and tailspots. Perhaps different displays show the wings and tail differently, and species with only tailspots use displays that emphasize the tail.

Weidman (1964) has argued that when the same movement reveals different patterns of color in closely related species, the pattern of color has evolved to dramatize the movement. When the same pattern of color is revealed by different display movements in closely related species, the movement has evolved to reveal the pattern of color. In wood-warblers aerial and non-aerial displays are found in species with and without wingbars and tailspots (*contra prediction 6.2*, Table 18). These data suggest that evolution of the display preceded evolution of the color pattern. However, wood-warblers with wingbars and tailspots or only tailspots display more frequently (Table 19) and their displays appear to be more exaggerated (Ficken 1962; Ficken and Ficken 1962b; Nolan 1978) than species with neither wingbars nor tailspots (*prediction 6.2*). These data suggest that displays evolved to reveal the pattern of color.

Has the pattern of color evolved to dramatize the display or has the display evolved to dramatize the pattern of color? The answer appears to be that both evolutionary sequences occur. Each sequence reinforces the other. Evolution of a color pattern that dramatizes a display movement leads to evolution of a more exaggerated movement which leads to a more dramatic color pattern and so forth. The hypothesis that patterns of color are associated with display movements is supported by the data, but the relationship between patterns of color and display movements is more complicated than the hypothesis suggests.

CHAPTER 7

COLOR OF OPTICAL SIGNALS

"It's like this," he said. "When you go after honey with a balloon, the great thing is not to let the bees know you're coming. Now if you have a green balloon, they might think you were only part of the tree, and not notice you, and if you have a blue balloon, they might think you were only part of the sky, and not notice you, and the question is: which is most likely?"

"Wouldn't they notice you beneath the balloon?" you asked.

"They might or they might not," said Winnie-the-Pooh. "You never can tell with bees." He thought for a moment and said, "I shall try to look like a small black cloud. That will deceive them."

"Then you had better have the blue balloon," you said; and so it was decided.

(Milne 1926:16-17)

Contrast is important to a signal's visibility, but contrast is not a property of color; contrast is a property of a color seen under specified ambient irradiance and against a spectrally defined background. Contrast also depends on the optical sensitivity of the perceiving organism. If contrast between the color of a signal (e.g., the balloon) and its background (e.g., the tree or the sky) can be quantified, then it is possible to predict the most or least contrasting colors under specified conditions. In this chapter I describe a method that quantifies contrast between a colored signal and its background under known light conditions. I calculate the contrast between differently colored feathers of wood-warblers and coloration of their habitats, predict the color of tailspots and wingbars of Parulinae, and test the predictions.

CALCULATION OF CONTRAST

Irradiance.—Most biological, optical signals depend on light reflected from the animal (Fig. 32). Therefore, the receiver's perception of the signal depends on the characteristics of the ambient irradiance which, in a real habitat, depend upon such variables as the time of year, time of day, amount of cloud cover, amount of vegetation between the light source and the optical signal, and the spectral radiance of the habitat (Fig. 32). Although irradiance under a clear sky has been successfully modeled (McCullough and Porter 1971), attempts to model irradiance within a forest have been unsuccessful (Hailman 1979). Thus irradiance within a forest must be measured directly (see p. 83).

Spectral irradiance is the "amount" of light incident on a surface expressed per wavelength or hertz throughout the visible spectrum. The "amount" of light is measured according to energy and its spectral position by frequency. Spectral radiance is light emitted or reflected from a surface. Measurements are expressed as a power density function of spectral position (i.e., $\mu\text{W cm}^{-2} \text{THz}^{-1}$ vs THz).

Surface reflection.—The information-carrying light that reaches the receiver is a function of the ambient irradiance on the reflecting surface, the reflecting properties of the surface, and changes that occur in the reflected light between the surface and the observer. For present purposes I consider the medium between

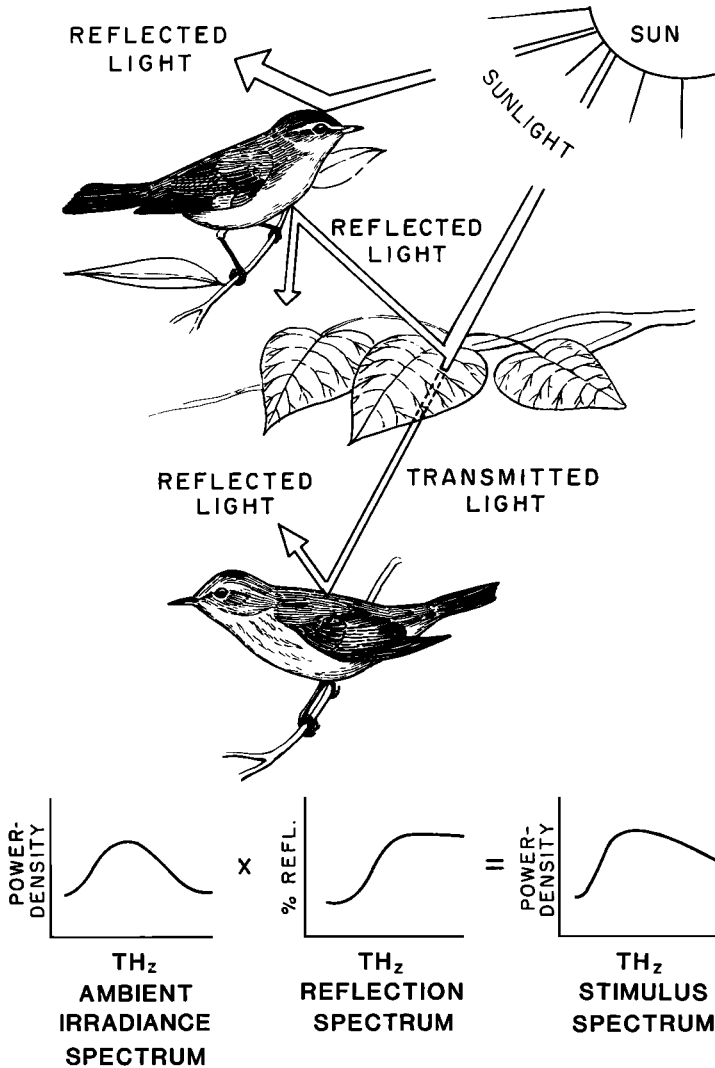


FIGURE 32. Coloration of an optical signal (expressed as a power-density function of spectral position) as a product of ambient irradiance, itself the interaction of sunlight with the habitat, and the signal's reflection spectrum measured spectrophotometrically (THz = Terahertz = 10^{12} Hz).

surface and receiver to be totally transparent even though, in terrestrial habitats, the light may be altered by fog or dust and, in water, by turbidity or absorption and scattering by water molecules themselves. Assuming total transparency, the light reaching the eye is a function only of the ambient illumination and the reflecting properties of the surface.

I ignore special properties of surfaces that alter light reflected as a function of the viewing angle: specular reflectance, dichromaticity, and iridescence. I assume the reflecting surface to be a matte surface (e.g., feathers) whose reflecting properties are described by the function relating reflectance and spectral position (e.g., the curve of % reflectance vs THz, Fig. 32). This function is determined spec-

trophotometrically by measuring the surface in a laboratory spectrophotometer; such determinations must be made for the signal-surface and for the surfaces of objects that constitute the visual background of the optical signal (leaves, rocks, tree trunks, branches). The physical stimulus reaching the eye of the receiver is the product of the ambient irradiance and the surface reflection, expressed as a power-density function of spectral position (e.g., $\mu\text{W cm}^{-2} \text{THz}^{-1}$ vs THz, Fig. 32).

Dominant frequency.—From the physical definition of the stimulus reaching the eye three perceptual parameters of the stimulus are extracted. The first may loosely be called the apparent color, expressed more precisely as the dominant frequency. The *dominant frequency* (or wavelength) is the monochromatic frequency that, when mixed with an appropriate amount of white light, provides a phenomenal match with the stimulus (purple hues excepted). The empirical matching experiments that allow calculation of dominant frequency of any stimulus have been performed only for humans and honeybees (*Apis mellifera*).

Color vision systems of diurnal vertebrates are morphologically similar (Walls 1942; Gruber 1979). Microspectrophotometry shows that these animals have three distinct populations of color receptors (“cones”) characterized by visual pigments whose absorption spectra are separated in the visual spectrum (Fuortes 1972; but see Harosi and Hashimoto 1983). Spectral sensitivities may differ. Humans are insensitive to ultraviolet light whereas birds appear to possess ultraviolet sensitivity (Kreithen and Eisener 1978; Goldsmith 1980; Parrish et al. 1981; Chen et al. 1984, Parrish et al. 1984). However, psychophysical experiments reveal that, within the visible spectrum, photopic spectral sensitivities of diurnal vertebrates are similar, and spectral discrimination studies show similar curves for the Bullfrog (*Rana catesbiana*), Rock Dove (*Columba livia*), Rhesus Macaque (*Macaca mulatta*), and Human (*Homo sapiens*, Hailman 1967, 1979). Therefore, lacking any other colorimetric system among vertebrates, the method described below uses the chromaticity system developed for humans, explicitly recognizing that some measure of error may be introduced when application to non-human vertebrates is made.

From any spectral-energy distribution function describing a stimulus the dominant wavelength may be calculated using commonly tabulated values. These yield the “x” and “y” coordinates of a stimulus on a standard Commission Internationale de l’Eclairage (C.I.E.) chromaticity diagram, and the dominant wavelength may be found geometrically by extending a line from the white point through the sample point to the spectral locus (Fig. 33). The wavelength at the intersection of the line and the curve is the dominant wavelength of the sample (~ 516 nm in Fig. 33). A computer program performed the geometric determination mathematically, thus extracting the dominant wavelength (which may also be expressed in frequency terms) from the defined stimulus.

The calculation (by any method) of dominant wavelength (or frequency) in colorimetry depends upon definition of the white point of the chromaticity diagram. Different white points yield slightly different dominant frequencies. The white point used in Figure 33 is equal energy white which has “x” and “y” chromaticity coordinates, 0.33 and 0.33. Equal energy white, as the name implies, is white light that has equal energy at all frequencies.

Excitation purity.—The second of the three parameters defining a visual stim-

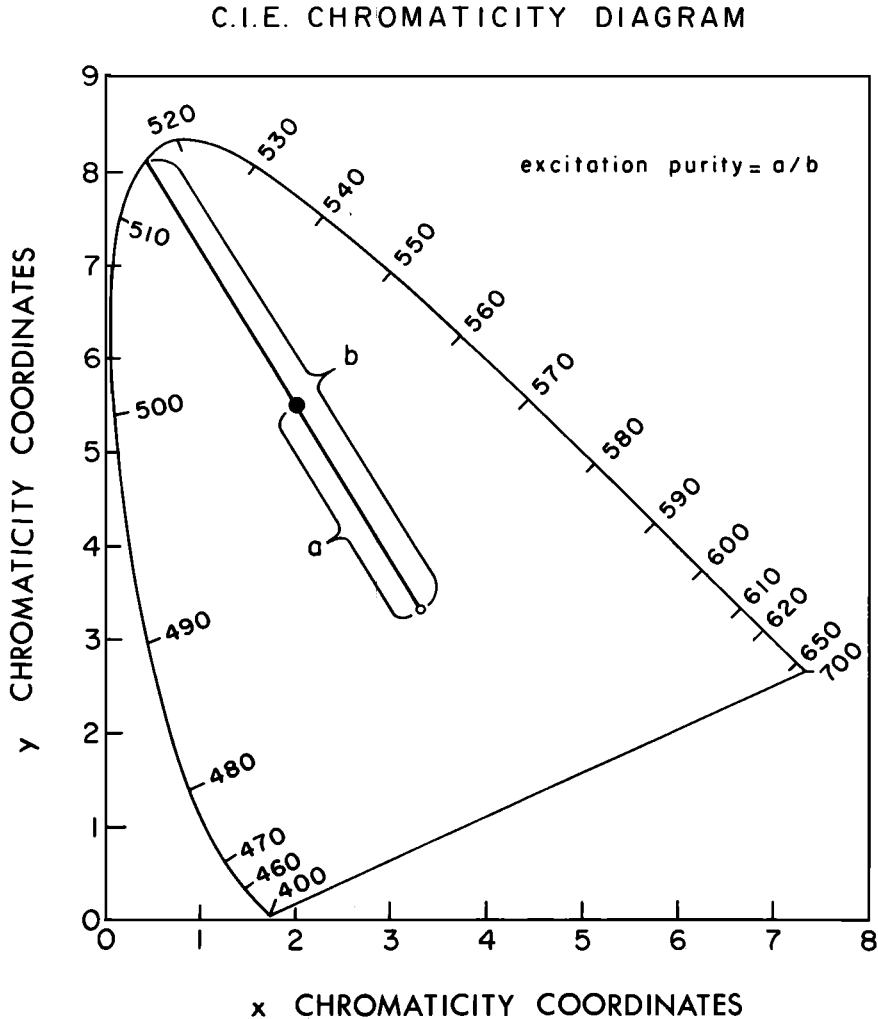


FIGURE 33. Commission Internationale de l'Eclairage (C.I.E.) chromaticity diagram based on the two degree color matching functions (Billmeyer and Saltzman 1966; Nimeroff 1968). The numbers along the outer rectangle indicate the magnitude of the x and y chromaticity coordinates. The curved line represents monochromatic (saturated) colors whose wavelength (nm) is indicated by the numbers along the curve. The line connecting 400 and 700 nm is the purple locus. White light of equal energy is plotted as an open circle with coordinates (0.33, 0.33).

ulus is the excitation purity, which is an expression of the saturation or apparent color purity of a stimulus. More exactly, excitation purity is a (reciprocal) measure of the amount of white that must be mixed with the monochromatic dominant frequency in order to create a subjective match to the stimulus. Excitation purity of the sample represented in Figure 33 is the ratio of "a" to "b" where "a" is the distance from the white point to the sample and "b" is the distance from the white point to the spectral locus. The ratio is a dimensionless value that varies between zero (pure white) and one (pure monochromatic light). The excitation purity was calculated by computer in the present method. Two stimuli that have

the same dominant frequency but differ considerably in excitation purity are readily discriminated, so that this parameter is an important aspect of surface-contrast of optical stimuli.

Relative luminance.—The calculation of relative luminance, explained in Chapter 5, is summarized below because calculation of the relative luminance is crucial to the quantification of contrast.

The apparent brightness of a stimulus depends upon its absolute energy flux as a function of spectral position and upon the receiver's differential sensitivity across the spectrum. There is a photometrically defined scale that approximates human brightness perception (Appendix III) by using a conversion function (the curve of the standard observer) whereby a spectroradiometrically defined stimulus can be expressed in photometric terms. Because photopic spectral sensitivity curves of many diurnal vertebrates are similar, it is possible to use a photometric scale as a general approximation of the phenomenal brightness of a stimulus.

The luminance of a surface is a photometric expression (in cd m^{-2}) of the surface brightness. For stimuli under consideration in this chapter, the logarithm of the luminance is calculated by computer program from the reflectance data of the stimulus (power density vs frequency). To normalize luminance for a given habitat's illumination, I calculated the range of possible values and the position of the stimulus luminance within that range. The extremes of the luminance range are represented by the logarithm of the luminance of a maximally reflecting white surface (BaSO_4 ; Weast 1976) and the logarithm of the luminance of a minimally reflecting black surface (powdered carbon; Weast 1976). The luminance of the stimulus relative to the range of possible luminances is expressed by the following ratio:

$$RL = (SL - BL)/(WL - BL) \quad 7.1$$

where SL is the logarithm of the stimulus' luminance, BL is the logarithm of the luminance from a minimally reflecting black surface and WL is the logarithm of the luminance from a maximally reflecting white surface. The relative luminance, RL , is a dimensionless value that ranges from zero (minimally reflecting black surface) to one (maximally reflecting white surface).

Discriminability scaling of purity and luminance.—At this point an optical stimulus emanating from a reflecting surface may be characterized by three parameters: dominant frequency, excitation purity, and relative luminance. These three are used to define a three-dimensional stimulus-space within which individual stimuli plot as points. It is now necessary to define the scaling intervals and ranges of the variables in order to create the bounded space within which stimuli plot as points.

The most straightforward way to plot the three variables is on linear scales, but this method fails to account for non-linearities of discriminability. No animals exist for which the discriminability function of excitation purity is known. For example, one does not know whether two stimuli of the same dominant frequency and relative luminance but differing in excitation purity are discriminable with equal ease throughout the scale of excitation purity: is a purity-difference of 0.9 vs 0.8 as discriminable as a difference of 0.4 vs 0.3? In the absence of relevant discriminability data, excitation purity is scaled linearly.

The discriminability of relative luminances is definitely nonlinear, although the

function relating the value of discriminable differences at different relative luminances is disputed (Hailman and Jaeger 1976). The problem can be rephrased in terms of the function relating the growth of the brightness sensation to the increase in physical intensity. Hailman (pers. comm.) believes the best fitting function is the integral of a normal probability-density function, but over a large range, a power-function provides a good fit, and over the middle part of the range a logarithmic function (Weber-Fechner relation) provides a reasonable fit (Hailman and Jaeger 1976). In fact, over the central part of the range, the function is approximately linear with the logarithm of intensity, and the theoretical approach of Hailman and Jaeger (1974; Jaeger and Hailman 1973, 1976) suggests that visual processes work to keep an animal's sensitivity adjusted so that its midpoint of brightness function is near the optimum ambient illumination. In other words, over normal ranges of viewing real, reflecting objects in the environment, discriminability of luminances is approximately linear with the logarithms in the calculation of relative luminance.

Discriminability scaling of frequency.—The scaling of the last of the three parameters, dominant frequency, was made nonlinear to account for spectral discriminability. The just noticeable difference (JND) is a perceptual measure of spectral discriminability. Among diurnal vertebrates JNDs tend to be large at low and high frequencies, indicating poor discrimination among the reds and violets, whereas JNDs are small among middle frequencies indicating the potential for fine color discriminations in the yellow-green range. Plots of JNDs as a function of spectral frequency are available for several species including the Rock Dove or "pigeon" (Hailman 1967; DeValois and Morgan 1974). Because the present color-space was designed to be tested with birds, the Rock Dove's curve was selected as the basis for frequency scaling.

The relative discriminability (in terms of change of frequency necessary for criterion discrimination by the pigeon [Hamilton and Coleman 1933; Hailman 1967]) was determined between adjacent frequency data points throughout the spectrum. The discriminability value at the lowest frequency was averaged with the discriminability value in the interval between the two frequencies. This average value (v_{xy}) is thus defined by:

$$v_{xy} = (\Delta v_x + \Delta v_y)/2 \quad 7.2$$

where x and y are the frequencies at which the discriminability was measured. Hamilton and Coleman (1933) located 31 points along the pigeon's discriminability curve. To complete the visible spectrum I calculated a thirty-second point at 750 THz by extrapolation, so that 31 intervals exist, each with its own calculated value of v_{xy} .

To create a scale that has intervals of equal discriminability the reciprocal of v_{xy} may be used as the basis of the scaling-interval between the two frequencies x and y . Because the spectral separation of x and y differs in the empirical experiments from which the data are derived (Hamilton and Coleman 1933), it is necessary to define the *relative scaling interval* (RSI) between them as:

$$RSI = \frac{x - y}{v_{xy}} \quad 7.3$$

where both numerator and denominator are in THz so that the scaling interval is physically dimensionless. Lastly, to normalize the scale, the entire interval of the visible spectrum (400 to 700 nm of wavelength, or 750 to 428.6 THz of frequency) was taken as unity. The 31 RSI values were summed and each RSI value (equation 7.3) expressed as a fraction of the sum, called the *standardized scaling interval* (SSI):

$$SSI = \frac{RSI}{\sum RSI} \quad 7.4$$

This procedure defines the entire visible spectrum in a range from zero (750 THz) to one (428.6 THz), in which the interval of scaling is that of equal discriminability. Two monochromatic lights equally spaced on this scale are approximately equally discriminable by the pigeon. The nonlinearity of the underlying function is not expressed between adjacent data points, but because the scale includes 32 points, the error introduced by this nonlinearity is small. Once the scale is defined, any frequency may be plotted by finding the position of the stimulus frequency through a computer program that sorts for the interval in which the frequency falls and linearly interpolates within that interval.

A scale that arranges hues by frequency is a physical, not a perceptual, scale. The present scale, based on frequency, implies that red and violet, which are at opposite extremes of the scale, are more easily discriminated than red and green, but there is no perceptual basis for that implication. Other methods of scaling hue have been considered, but none of the alternatives relate hues to one another in a perceptually meaningful way (but see Billmeyer and Saltzman 1966; Nimeroff 1968; Hailman 1979). Therefore, I have used a frequency scale corrected for the discriminability of similar frequencies.

Another difficulty with the dominant frequency approach to defining visual stimuli is that purple stimuli (mixtures of energy at spectral extremes) will not plot on the standardized scale just described. A purple stimulus is described by the dominant frequency of its complement: the monochromatic light that must be subtracted from white to provide a metameric match. In fact, among birds and fishes (the two groups of vertebrates showing the highest diversity of signal coloration) few species appear purple to the human observer. Therefore, the exclusion of purple may not be serious for purposes of analyzing optical signals.

Color-space.—Having defined scales for the three perceptual parameters of a stimulus, a three-dimensional color-space is defined by arranging the three scales on rectilinear coordinates. Despite recent advances in our knowledge of visual processing (Favreau and Cavanagh 1981), empirical data on the discriminability of the three parameters relative to one another are lacking; hence, the ranges of all three are made equal. That is, two stimuli that differ in dominant frequency by, for example, one-third of the range of the frequency scale are thus considered to be as discriminable as two stimuli whose difference in relative luminance is one-third of that scale. The space defined is, therefore, a cube within which every non-purple stimulus may be plotted as a single point.

Within the cubic color-space the shortest distance between two stimulus points is found geometrically by computer, using the triple coordinates of the two points (Fig. 34). Because the color-space is a cube whose sides are unitary, the maximum

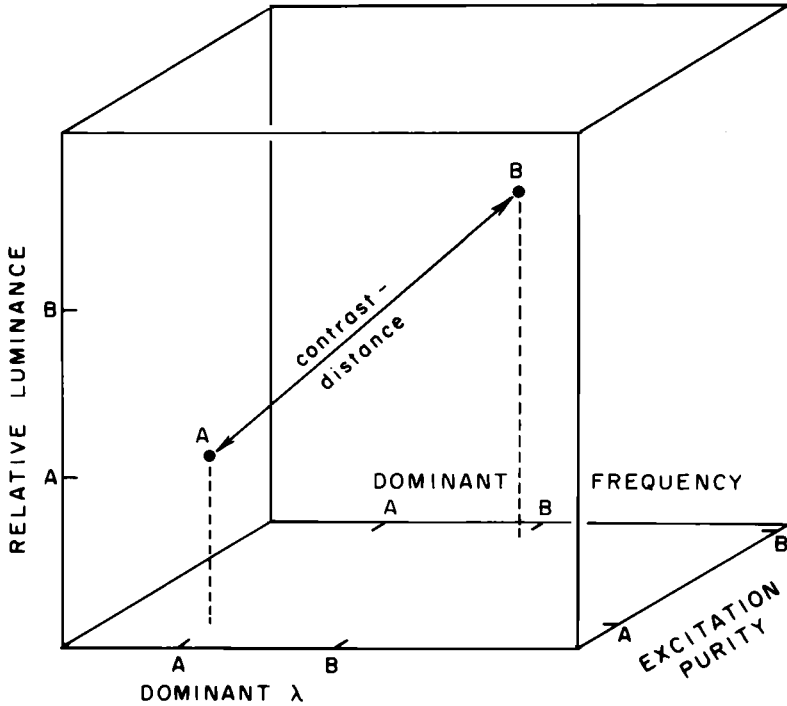


FIGURE 34. The cubic color-space defined by three perceptual parameters of a visual stimulus arranged as rectilinear coordinates of unitary length. Points A and B differ in all three parameters. The shortest distance between them is the contrast-distance. The projection of the points vertically onto the base of the cube helps locate the points in space and define their coordinates of dominant frequency and excitation purity; the length of the projection line expresses relative luminance.

distance between two points is the line diagonally connecting opposite corners of the cube, which line has a length of 1.732 arbitrary units. For example, an extremely dark, nearly achromatic violet stimulus will plot very near one corner (luminance, purity and frequency coordinates nearly zero). A very bright, monochromatically pure far-red stimulus will plot very near the diagonally opposite corner (luminance, purity and frequency coordinates nearly one).

The shortest distance between two points within the cubic color-space is the *contrast-distance*. When the contrast-distance is small, the colored surfaces appear similar. For example, a leaf and a greenish bird (e.g., Orange-crowned Warbler) have a small contrast-distance and appear similar. When the contrast-distance is large (whether due to purity, luminance, or frequency differences), the surfaces appear dissimilar. A leaf and a bright red bird (e.g., Northern Cardinal, *Cardinalis cardinalis*), for example, have a large contrast-distance and appear dissimilar. It is, therefore, possible to measure by a single value the relative visual contrast between two stimuli on a scale that goes from zero (no contrast) to 1.732 (maximum contrast) on the basis of their surface properties illuminated in a defined light environment and viewed by an animal whose visual characteristics are known.

I am keenly aware of the arbitrary nature of these calculations. I have tried to indicate the assumptions of construction at each step: similarity of visual systems

among diurnal, terrestrial vertebrates; linearity of variables; and so on. Ideally, the principles of construction should be used to create a color-space for each observing species, assuming that many investigators would be willing to spend their lives determining the relevant psychophysical data. In the next section application of the method, as imperfect as it is, delivers results that do not violate the intuition of observers who have personal experience with discriminability of objects on the basis of their surface properties. Not all the empirical findings are trivial; the results discussed in the following sections reveal contrast differences that one might not have expected without the use of color-space analysis.

CALCULATION OF A COLOR-SPACE FOR WOOD-WARBLERS

Ambient irradiance.—The properties of light that irradiates a surface affect perception of that surface. The following data describe the effect on perception of variation in time of year and amount of vegetation between the source and the irradiated surface. Variables such as latitude, time of day, and extent of cloud cover were held constant.

Northern temperate forests were divided into: (1) coniferous forest, (2) broadleaf forest, (3) clearing. Coniferous and broadleaf forests were subdivided into young forests, with trees 10 m tall or less; two-layered forests, with a canopy above 10 m and a layer of foliage below 10 m; and one-layered forests, with a canopy above 10 m and no understory.

Measurements were taken during June 1973 and May 1974 at Lake Itasca, Minnesota. The young broadleaf forest contained Quaking Aspen (*Populus tremuloides*), Paper Birch (*Betula papyrifera*), and Red Maple (*Acer rubrum*). The two-layered broadleaf forest contained the above species and Red Oak (*Quercus rubra*). The one-layered broadleaf forest was an almost pure stand of Quaking Aspen. The young coniferous forest was a pure stand of Jack Pine (*Pinus banksiana*). The canopy in the two-layered coniferous forest contained White Pine (*P. strobus*) and White Spruce (*Picea glauca*); the understory was Balsam Fir (*Abies balsamea*). The one-layered coniferous forest was a pure stand of Red Pine (*P. resinosa*).

Spectral measurements were taken across the visible spectrum from 400 nm (750 THz) to 750 nm (428.6 THz) at 25 nm intervals with an ISCO model SR battery-powered spectroradiometer that was cosine-corrected according to Lambert's Law. Measurements were taken only under clear sky and only between 0945 and 1400 Central Daylight Time (C.D.T.). On all measurements the spectroradiometer was held vertically with the sensor 1.7 m above the ground and pointing toward the sky. The sensor was in the shadow of a tree trunk except in the clearing where the sensor was in direct sunlight.

Data recorded in the field were corrected for factory instrument calibration factors and reduced by computer. The basic results are expressed as spectral power flux densities ($\mu\text{W cm}^{-2} \text{THz}^{-1}$), hereafter referred to as a "power-density function." Each spectrum was integrated by Riemann sums to provide the total power flux called irradiance ($\mu\text{W cm}^{-2}$) over the 428.6 to 750 THz range. The computer program used the 1931 C.I.E. distribution coefficients (Weast 1976) to calculate the chromaticity coordinates of the ambient illumination. Illuminance also was calculated by computer (in lux) from the 1924 C.I.E. photopic luminosity curve

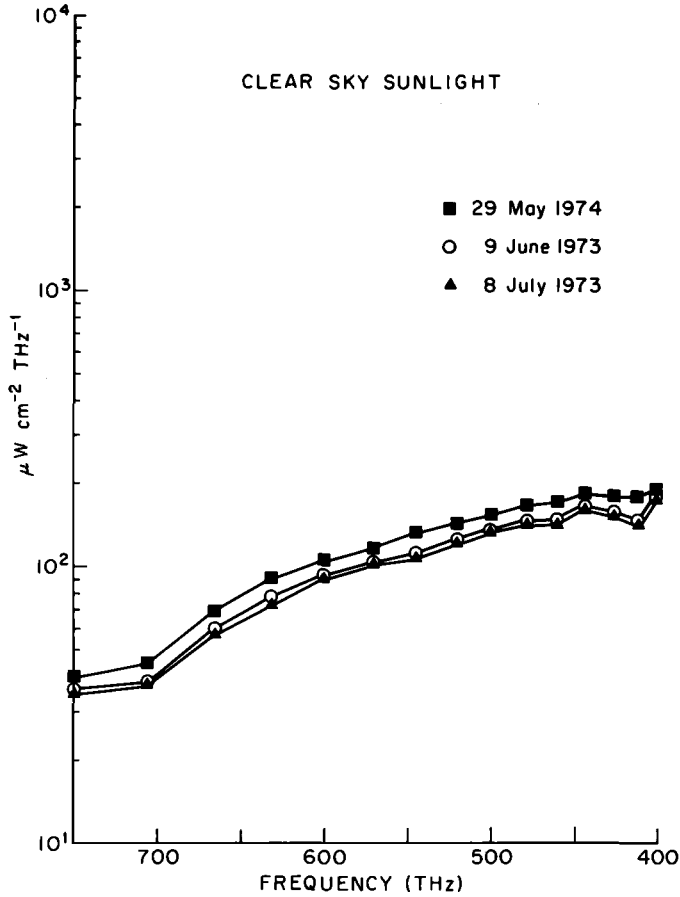


FIGURE 35. The spectral composition of sunlight shown as a power-density function of spectral position. All measurements were taken between 1330 and 1400 C.D.T. under clear skies at Lake Itasca, Minnesota.

(Weast 1976). The calculation of illuminance was based on the use of the “standard observer” curve, and thus expresses the approximate brightness of light to the human eye. For vertebrates such as birds that have spectral sensitivities similar to those of the human eye, illuminance more closely approximates brightness than the physical irradiance values. For animals such as insects whose spectral sensitivities are shifted away from the red end of the spectrum into the ultraviolet, neither illuminance nor irradiance provides an estimate of the apparent brightness of the ambient light.

The power-density function of direct sunlight measured in a clearing is shown in Figure 35 for May, June, and July. The only variable is time of year; the power-density function decreases very slightly as the season progresses. Both irradiance and illuminance were slightly lower on 9 June 1973 than on 29 May 1974 (Table 20). In all other respects the functions (Fig. 35) were identical. The power-density function is lowest in violet and highest in red, with an almost linear increase in between.

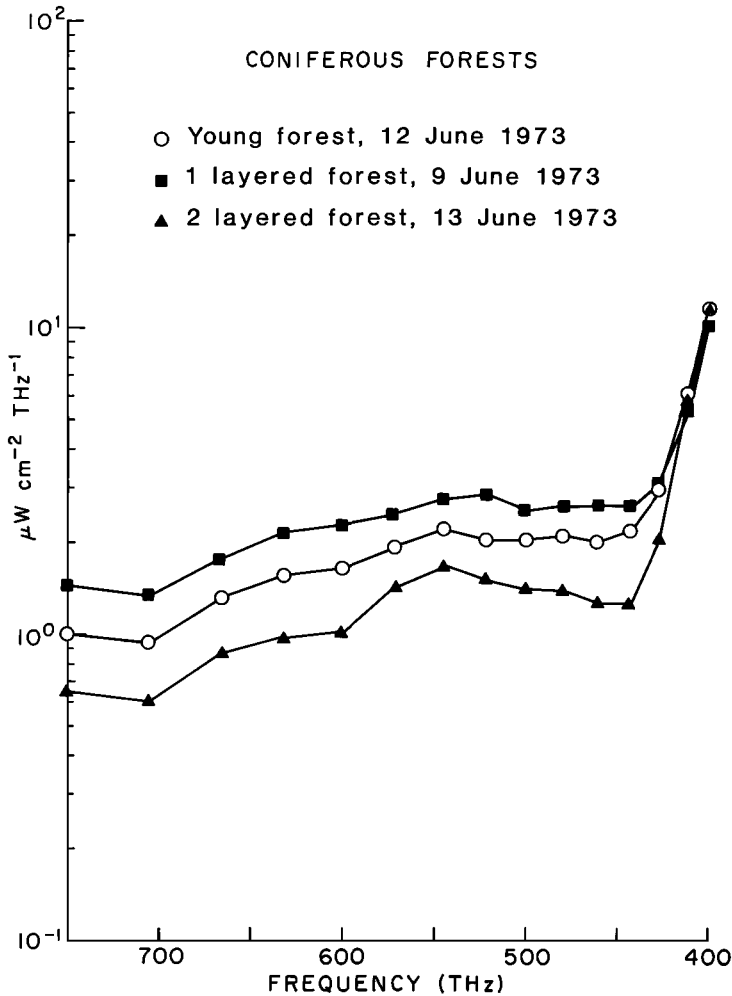


FIGURE 36. A comparison of spectral irradiances beneath the canopy in one-layered, two-layered, and young coniferous forests. Measurements were taken between 0945 and 1200 C.D.T. in June 1973 at Lake Itasca, Minnesota, and are expressed as a power density function of spectral position.

The power-density function measured in coniferous forests (Fig. 36) is lowest at the violet end of the spectrum (750 THz) and increases toward the red end of the spectrum (428.6 THz). The power-density functions of the different habitats converge in the red end of the spectrum where there is a dramatic increase between 444 THz and 400 THz. The rapid rise in the power-density function is not seen in measurement of unobstructed sunlight (Fig. 35). Irradiance and illuminance are highest in the one-layered forest and lowest in the two-layered forest (Table 20), but irradiance and illuminance in the three coniferous forest-types is one to two orders of magnitude less than in direct sunlight.

The power-density functions of broadleaf forests measured in June (Fig. 37) show a pronounced peak at 456 THz, a peak not present in coniferous forests (Fig. 36) and also absent in direct sunlight (Fig. 35). As in coniferous forests,

TABLE 20
IRRADIANCE AND ILLUMINANCE OF DIRECT SUNLIGHT MEASURED IN A CLEARING
AND OF TRANSMITTED AND REFLECTED SUNLIGHT MEASURED IN SIX DIFFERENT
FOREST TYPES AT DIFFERENT TIMES OF YEAR

Habitat	Irradiance ($\mu\text{W cm}^{-2}$)	Illuminance (lux)
Clearing		
29 May 1974	4.0×10^4	9.3×10^4
9 June 1973	3.5×10^4	8.2×10^4
Coniferous forest		
Young, 12 June 1973	7.3×10^2	1.4×10^3
Two-layered, 13 June 1973	5.4×10^2	1.0×10^3
One-layered, 9 June 1973	8.8×10^2	1.8×10^3
Broadleaf forest		
Young, 29 May 1974	4.1×10^3	8.8×10^3
Young, 12 June 1973	1.2×10^3	2.1×10^3
Two-layered, 29 May 1974	2.8×10^3	6.1×10^3
Two-layered, 12 June 1973	8.4×10^2	1.5×10^3
One-layered, 13 June 1973	1.4×10^3	2.7×10^3

power-density rapidly increases between 444 THz and 400 THz. Irradiance and illuminance are highest in the one-layered forest and lowest in the two-layered forest (Table 20). The same relationship was observed in coniferous forests. Irradiance and illuminance tend to be higher in broadleaf forests than in coniferous forests (Table 20), but are still about an order of magnitude less than direct sunlight.

The power-density functions of young and two-layered broadleaf forests before the leaves emerge in early June show no peak (Fig. 38) and, therefore, resemble the power-density function in direct sunlight (Fig. 35) and in coniferous forests (Fig. 36). Irradiance and illuminance values are three to four times greater before the leaves emerge than after emergence (Table 20).

I plotted the points that represent the ambient illumination in different habitats on a chromaticity diagram (Fig. 39) using the "x" and "y" chromaticity coordinates computed from the power-density spectra of the habitats. The approximate range of wavelengths that appear "green" to the human eye is from about 491 to 575 nm (shaded region, Fig. 39). Therefore, all forest habitats have greenish light with respect to equal-energy white. The points representing direct sunlight lie along the yellow-green boundary. The point that represents illumination in a young broadleaf forest before the leaves emerge also lies on the yellow-green boundary, but the illumination in a two-layered broadleaf forest before the leaves emerge is similar to the illumination in coniferous forests. All the points lie close to equal energy white light; that is, light in all the forest types and unfiltered sunlight is poorly saturated.

The light in forests is much less bright (lower illuminance), more green, and more saturated than direct sunlight. The peak in the green region of the power-density function in broadleaf forests probably represents transmission and reflection of light by the leaves of broadleaf trees. Transmission through the needles of conifers is probably negligible and reflection from needles is probably less than from leaves. The greater transmission through the leaves of broadleaf trees may

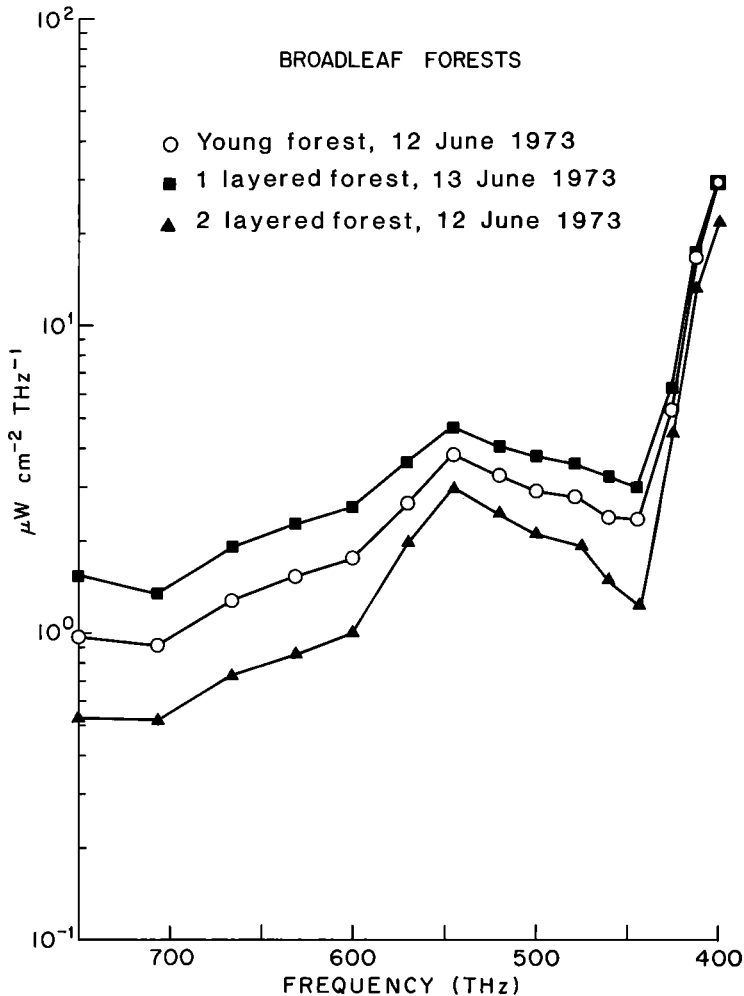


FIGURE 37. A comparison of spectral irradiances beneath the canopy in one-layered, two-layered, and young broadleaf forests. Measurements were taken between 1100 and 1400 C.D.T. in June 1973 at Lake Itasca, Minnesota, and are expressed as a power-density function of spectral position.

also account for the greater saturation of the green light in broadleaf forests. Leaf-emergence in broadleaf forests reduces brightness (illuminance) and increases saturation of the green forest light.

The effects on ambient illumination are small and based on relatively few measurements, but coincide with the effects described by Hailman (1979) for southeastern and western pine forests and southeastern broadleaf forests. The data suggest small, but consistent, habitat-correlated differences in ambient irradiance, differences that could affect the reflectance spectrum of optical signals (Fig. 32) such as crown patches, tailspots, or wingbars. Differences in ambient illumination are incorporated in the calculation of contrast-distance, and the data presented in this section emphasize the importance of the ambient illumination in the calculation of contrast.

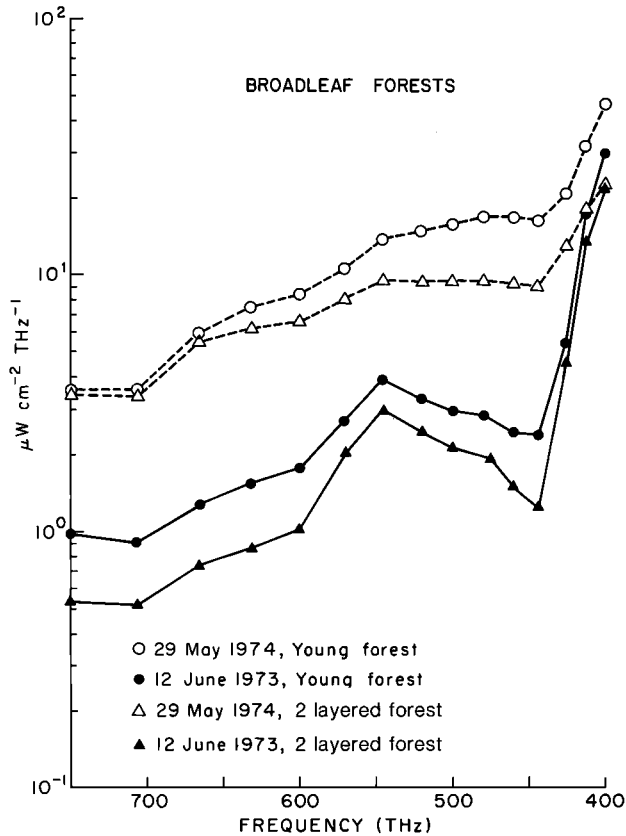


FIGURE 38. A comparison of the spectral irradiances beneath the canopy in two-layered and young broadleaf forests in May 1974 and June 1973. Measurements were taken between 1000 and 1400 C.D.T. at Lake Itasca, Minnesota, and are expressed as a power-density function of spectral position.

Sample color-space.—The contrast-distances between coniferous needles and broadleaf leaves and the feather colors of wood-warblers under clear sky illumination (9 June 1973) are small (Fig. 40). Yellow-green, brown, gray, black, and chestnut feather colors plot very close to leaf colors (Fig. 40); hence, they have a small contrast-distance and provide concealing coloration. White, yellow, and orange feather colors plot far from the leaf colors (Fig. 40); hence, they have a large contrast-distance and should be highly visible. These results are certainly consistent with qualitative judgments of the visibility of differently colored wood-warblers in the field.

PREDICTED COLOR OF TAILSPOTS AND WINGBARS

The preceding section demonstrates that irradiance characteristics differ in different habitats. Differences in relative luminance, purity, and dominant wavelength affect the contrast-distance between feather colors and the background of green leaves of different species of trees. In this section the contrast-distance is calculated for the differently colored tailspots and wingbars of wood-warblers under specified conditions.

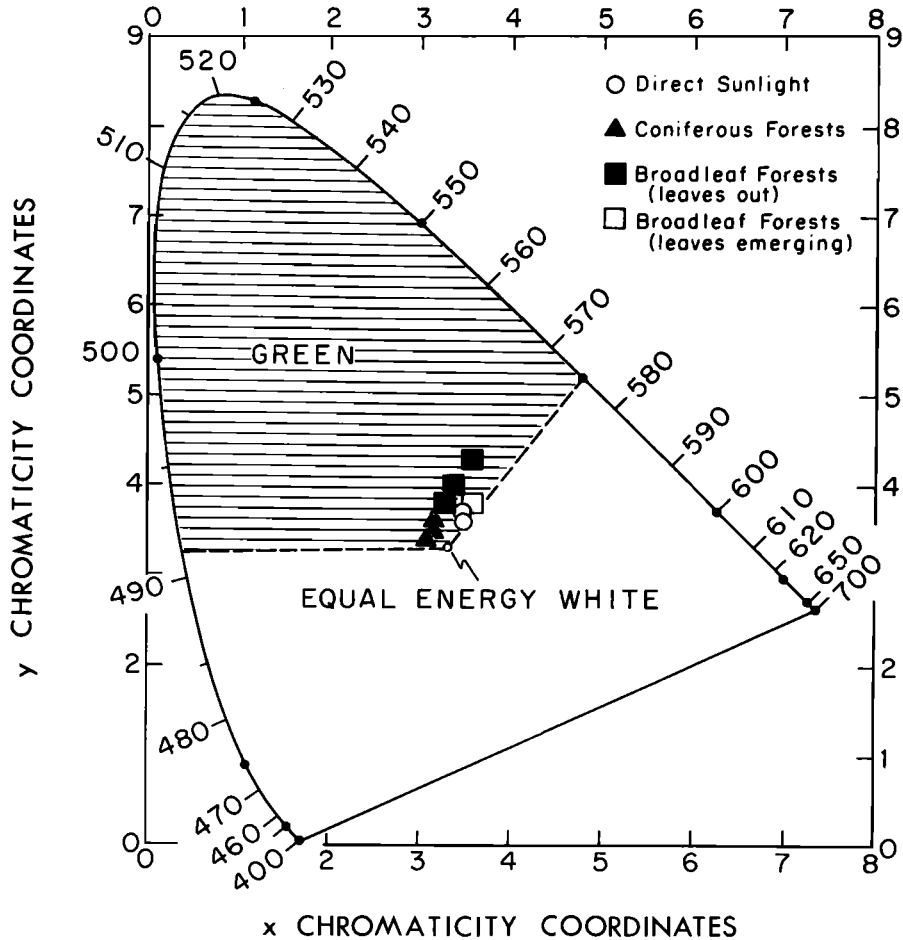


FIGURE 39. C.I.E. chromaticity diagram with points representing the illumination in six forested habitats and in direct sunlight.

The tailspots and wingbars of wood-warblers create optical signals (Chap. 6). Therefore, their coloration has evolved for maximum visibility which, in terms of the color-space, means the maximum contrast-distance between the color of the tailspots or wingbars and the color of the background.

Tailspots and wingbars are revealed in flight at which time their contrast appears to be primarily with the habitat. Because I am unable to equate internal (with surrounding body) and external (with habitat) contrast, and because external contrast appears to be more important in this case, the following analysis is based exclusively on the contrast-distance between color of the tailspots or wingbars and the color of the habitat.

A flying wood-warbler is seen against a variety of backgrounds as it flies past different types of vegetation. Reflectance spectra were measured for fresh leaves collected near the photometric laboratory in Madison, Wisconsin. Included were leaves or needles of the American Elm (*Ulmus americana*), Basswood (*Tilia americana*), Bur Oak (*Quercus macrocarpa*), Paper Birch, Red Maple, White Pine,

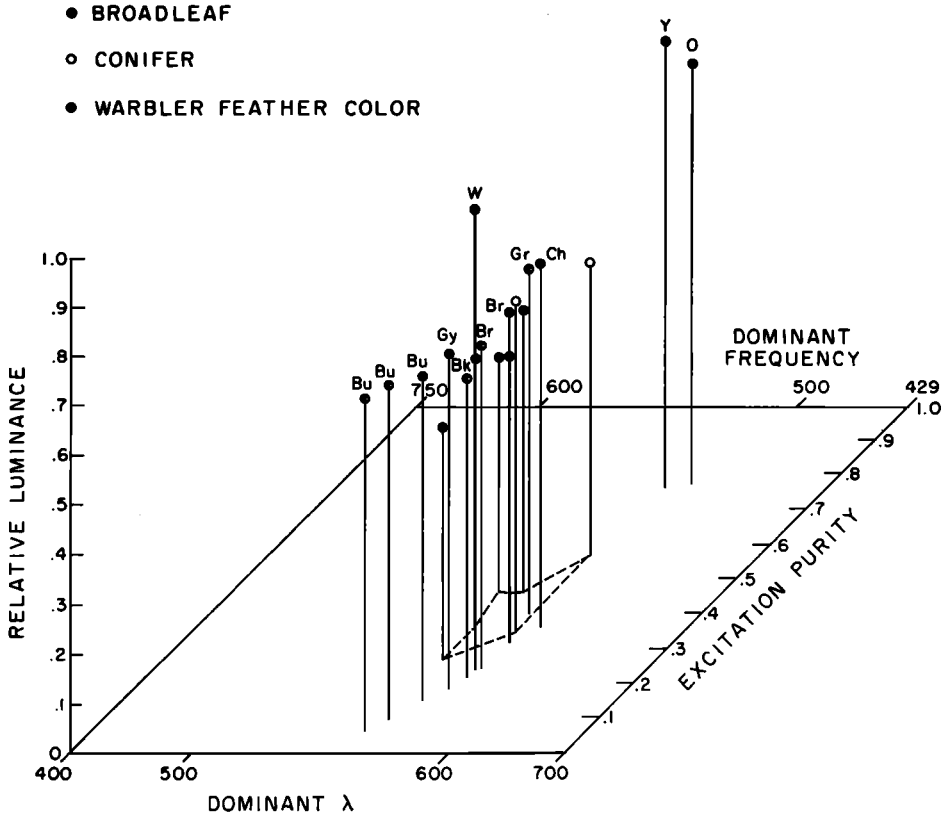


FIGURE 40. A sample color-space in which all colors are viewed in clear sky sunlight. The equally-weighted scales of the three perceptual parameters are indicated. The vertical projection of the points onto the base of the cube is shown to help locate the points in space and define their coordinates of dominant wavelength and excitation purity. The length of the projection line expresses relative luminance. The polygon on the base of the cube connects the dominant frequency and excitation purity coordinates of leaf-green in five species of broadleaf trees and two conifers. All other points represent feather colors (see Fig. 2, Table 1). Those colors that plot near the leaf colors will appear inconspicuous whereas those such as yellow, white, and orange, that plot far from the leaf colors will appear conspicuous.

and White Spruce. Of these the Paper Birch, Bur Oak, and Red Maple commonly occur in broadleaf habitats of wood-warblers breeding at Itasca, Minnesota, where display behavior was studied. Lacking more complete data on the leaf composition of the forests of Itasca, Minnesota, I assumed that leaves of these three broadleaf species were equally abundant and calculated contrast-distance, C , between the feather's color and the color of birch, maple, and oak leaves as:

$$C_{br}^{bs} = 0.33(C_b^{bs} + C_m^{bs} + C_o^{bs}) \quad 7.5$$

where C is the contrast-distance of the color against birch, b , maple, m , or oak, o , leaves. The contrast-distance is calculated in the shade, bs , of a broadleaf forest, br .

The spectral irradiance of sunlit patches within a forest is identical to that in the open (Hailman 1979) and distinctly different from irradiance within forest

shade (Fig. 36 vs 37, 38). A wood-warbler in flight in a broadleaf or coniferous forest flies through sunlight and shade. The contrast-distance of a wood-warbler viewed in sunlight, s , against a background of birch, maple, and oak leaves is:

$$C_{br}^s = 0.33(C_b^s + C_m^s + C_o^s) \quad 7.6$$

Because the wood-warbler is in sunlight half the time and shade half the time, its mean contrast-distance, MC , in a broadleaf forest is half the sum of equations 7.5 and 7.6:

$$MC_{br} = 0.5(C_{br}^{bs} + C_{br}^s) \quad 7.7$$

White pine and white spruce are abundant in the coniferous forests of Itasca, Minnesota. In conifer shade the contrast-distance between feather colors and a coniferous background c is:

$$C_c^{cs} = 0.5(C_p^{cs} + C_s^{cs}) \quad 7.8$$

where C is the contrast-distance between feather colors and pine needles, p , or spruce needles, s , as viewed in coniferous shade, cs .

When viewed in sunlight, s , the calculation is similar:

$$C_c^s = 0.5(C_p^s + C_s^s) \quad 7.9$$

The mean contrast-distance in a coniferous forest is half the sum of equations 7.8 and 7.9:

$$MC_c = 0.5(C_c^{cs} + C_c^s) \quad 7.10$$

Based on equations 7.7 and 7.10 white has the maximum contrast-distance from foliage in all forest types (Table 21). Yellow and orange have their maximum contrast-distance against broadleaf leaves and particularly in young broadleaf forests during leaf-emergence, a time when territorial and courtship displays are most frequent. Because tailspots and wingbars create optical displays, maximum contrast is important to their function. Therefore, *prediction 7.1*: white should be the most common color of tailspots and wingbars; *prediction 7.2*: yellow and orange, if they occur, are most common among wood-warblers in broadleaf forests and least common among wood-warblers in coniferous forests.

OBSERVED COLOR OF TAILSPOTS AND WINGBARS

The observed frequencies of white, yellow, and orange tailspots and wingbars (Tables 2 and 3) were tested against the null hypothesis of equal frequencies, using the chi-square Goodness of Fit (Roscoe 1975) to assess significance. Sexes were tested separately.

Habitat preference is based on the number of observations of territorial males and their mates. Observations of migrants were excluded. After identifying a wood-warbler, I waited 10 sec and recorded the species of tree in which it was perched or the dominant species of the canopy if the wood-warbler's perch was in the understory. Species are compared by their probability of occurrence in broadleaf and coniferous forests.

American Redstarts and Yellow Warblers are the only species with colored tailspots among the species that were studied. The distribution of observations of each species in broadleaf and coniferous forest was tested against the null

TABLE 21
 CONTRAST-DISTANCE OF WHITE, YELLOW, AND ORANGE FEATHERS FROM BIRCH,
 MAPLE, AND OAK LEAVES IN A BROADLEAF FOREST AND FROM PINE AND SPRUCE
 NEEDLES IN A CONIFEROUS FOREST

Feather color	Broadleaf		
	Young ¹	2-layered ¹	1-layered
White	0.61/0.62	0.61/0.60	0.61
Yellow	0.59/0.57	0.58/0.56	0.58
Orange	0.49/0.46	0.49/0.45	0.48
Coniferous			
White	0.59	0.59	0.59
Yellow	0.55	0.55	0.56
Orange	0.45	0.45	0.46

¹ 29 May 1974; 12 June 1973.

hypothesis of equal distribution of observations, using the chi-square Goodness of Fit to assess significance. Older male redstarts were tested separately from first-year males and females because of differences in the color of tailspots. Several species had yellow or orange wingbars. Habitat preferences were compared in wood-warblers with colored vs white wingbars using the Mann-Whitney *U*-test (Roscoe 1975).

Among wood-warblers with tailspots, white is significantly more common (*prediction 7.1*) than yellow or orange among males ($\chi^2 = 84.8$, d.f. = 2, $P < 0.001$, Table 2) and females ($\chi^2 = 78.9$, d.f. = 2, $P < 0.001$, Table 3). In other avian families (e.g., Turdidae, "Fringillidae") white is equally dominant among species that display with the tail (Hinde 1955, 1956; Andrew 1957; Hailman 1958; Balph 1977). Species with white tailspots occur in both coniferous and broadleaf habitats (Table 22, *prediction 7.1*). Adult male redstarts occur significantly more frequently in broadleaf forests (*prediction 7.2*; $\chi^2 = 49.8$, d.f. = 1, $P < 0.001$; Tables 22 and 23) than in coniferous forests. The trend is similar among Yellow Warblers (*prediction 7.2*; $\chi^2 = 13.7$, d.f. = 1, $P < 0.001$; Tables 22 and 23). Although similar (Table 23), the trend among young male and female redstarts is not significant ($\chi^2 = 1.6$, d.f. = 1, $0.25 > P > 0.10$). The lack of significance may result from the small sample size. However, adult males have priority access to territories (Morse 1973; Howe 1974; Procter-Gray and Holmes 1981) and young males may occupy habitats less favorable to their optical signalling.

Among wood-warblers with wingbars, white is significantly more common (*prediction 7.1*) than yellow or orange among males ($\chi^2 = 22.5$, d.f. = 2, $P < 0.001$, Table 2) and females ($\chi^2 = 98.7$, d.f. = 2, $P < 0.001$, Table 3). Species with yellow or orange wingbars occur more often in broadleaf habitats (*prediction 7.2*, $U = 1$, $P < 0.01$, Table 22) than in coniferous habitats. Problems of internal versus external contrast and undefined backgrounds render analysis of other color patches too speculative until we know more about when and how such patches are displayed, illuminance during their display, and the location of observers.

CONCLUSIONS REGARDING COLOR-CONTRAST

Irradiance outside forests is high (Fig. 35) and nearly white (Fig. 39). In such bright habitats (e.g., prairies, tops of trees) dark birds (e.g., Lark Bunting, *Cal-*

TABLE 22
PREFERRED HABITAT OF SPECIES WITH DIFFERENTLY COLORED TAILSPOTS AND
WINGBARS

Species	Probability of occurrence in coniferous forests	Probability of occurrence in broadleaf forests	Tailspot color	Wingbar color
Chestnut-sided	0.12	0.88	white	yellow
Am. Redstart ♂	0.16	0.84	orange	orange
Golden-winged	0.20	0.80	white	yellow
Yellow	0.22	0.78	yellow	yellow
Black-and-white	0.23	0.77	white	white
Am. Redstart ♀	0.30	0.70	yellow	yellow
Northern Parula	0.41	0.59	white	white
Black-thr. Green	0.55	0.45	white	white
Yellow-rumped	0.55	0.45	white	white
Bay-breasted	0.70	0.30	white	white
Blackburnian	0.70	0.30	white	white
Magnolia	0.82	0.18	white	white
Pine	0.94	0.06	white	white

mospiza melanocorys, Indigo Bunting, *Passerina cyanea*) can achieve high contrast. The low irradiance and increased saturation within forests (Fig. 36, 37) selects for white or yellow optical signals (Table 21). Differences in the irradiance of different habitats (Fig. 39) may be an important factor in the evolution of differently colored optical signals. However, a more precise statement of the evolutionary importance of habitat-correlated differences in irradiance awaits measurement of additional habitats under more varied conditions (see Hailman 1979).

Similar habitats have qualitatively similar spectral irradiances regardless of latitude (compare Figs. 36, 37 to Hailman's 1979:figs. 73-75), a finding that may account for widespread similarities of color (Bailey 1978; but see Willson and von Neumann 1972) and pattern (Burt and Gatz 1982) among birds occupying similar habitats. Despite the similar color of optical signals among tropical and temperate birds, sexual dimorphism and dorsal contrast are more common among temperate species than tropical species (Bailey 1978). The trend probably reflects the need for rapid sexual identification and territorial establishment (Hamilton 1961; Hamilton and Barth 1962), rather than differences in spectral irradiance.

Background is important for its perceived color (Fig. 40) and for its pattern of

TABLE 23
PREFERRED HABITAT OF SPECIES WITH ORANGE OR YELLOW TAILSPOTS

Species	Number of observations in		Probability distribution is random
	Broadleaf forest	Coniferous forest	
Yellow	23	9	<0.001
Am. Redstart			
Adult ♂	92	18	<0.001
1st yr. ♂, ♀	7	3	0.25 > P > 0.10

color. Hailman's (1979) quantification of the spectral radiance of optical backgrounds represents a pioneering effort that must be greatly expanded. A need also exists for detailed ethological study. Few of the many studies of male courtship document the position from which the female or rival watches (but see Hamilton 1965); thus, the background is unspecified. Endler (1978, 1980, 1984) has shown that evolution of animal color patterns is influenced by the color pattern of the background, but that evolutionary direction depends on the balance between sexual selection and predation.

The color-space is based on many assumptions necessitated by lack of knowledge, which provide an outline for future research into the evolution of optical signals. The model cannot deal with nonspectral purples nor with exceptionally luminous backgrounds such as the ocean and the sky (see discussion in Hailman 1977a, 1979). Furthermore, treatment of color as dominant frequency, a physical measure, rather than hue, a perceptual measure, is a serious drawback to the suggested color-space. Hailman (1979) has suggested a color-space based on the Ostwald color system and shaped like two cones base to base. Hailman's color-space is unquantified, but would arrange hues, including non-spectral purples, around the equator of the double-ended cone. Billmeyer and Saltzman (1966) offer additional untried possibilities for perceptual color-spaces. The best shape for a color-space is conjectural, but the need is evident. Such a system, if perfected, would allow accurate prediction of display colors based on those points within the color-space that plot farthest from those of the relevant backgrounds and of cryptic colors based on those points that plot closest to the relevant backgrounds.

CHAPTER 8

AN INTEGRATIVE APPROACH

"I'm afraid we have been a little too sure that the Stoat turns white to make itself invisible against its background of snow, in accordance with the theory of protective coloration. . . . Theoretically, the Ptarmigan believes that what is creeping up on it is a piece of snow, and the Ermine is after something it can't see but wants to eat. Who do they think they're fooling, anyway? Just a few old professors?"

(Cuppy 1941:112-113)

A brief, integrative review is now presented for the hypotheses discussed in the preceding chapters. These hypotheses account for some aspects of color and color pattern of wood-warblers (Table 24) and provide some insights into the diversity and interaction of selective pressures acting on animal coloration.

COLOR AND COLOR PATTERNS IN WOOD-WARBLERS: A SUMMARY

Unfeathered surfaces.—The upper mandible of wood-warblers is consistently dark. Such coloration would reduce reflectance that might interfere with vision (Table 24). Furthermore light-billed species forage in shade where illuminance and reflectance are minimized. Although dark coloration maximizes absorption of solar radiation and equilibrium temperature, the arrival and departure sequences of species and their winter distribution are not correlated with differences in color of the upper mandible as would be expected if the dark color had a thermo-regulatory function. The mandibles account for less than 10 percent of the body's heat loss (Deighton and Hutchinson 1940; Veghte and Herreid 1965; Hill et al. 1980) which may explain the lack of correlation. The closed bill is not used in display, although the open mouth is turned toward the rival in the threat display of the American Redstart (Ficken 1962). The dark, melanic layer could shield internal cells from ultraviolet radiation (Porter 1967, 1975; Porter and Norris 1969). However, Willow Flycatchers with artificially increased reflectance from their upper mandibles moved to shade to forage (Burt 1984). Because the ultraviolet shield was not altered, the observed behavioral change argues against radiation shielding as a primary function of mandibular color. The result is consistent with the need to reduce reflectance that interferes with vision.

The legs of wood-warblers vary from dark to light. Physiological studies (Deighton and Hutchinson 1940; Veghte and Herreid 1965; Baudinette et al. 1976; Chappell 1980a) have shown that up to 56 percent of a resting bird's heat loss is through the legs. Wood-warblers tend to withdraw the legs into the belly feathers as potential convective heat loss increases, a behavioral result consistent with the legs being an important heat sink. The thermo-regulatory importance of leg color (Table 24) is suggested by the fact that species with dark legs, which maintain a higher equilibrium temperature than light legs, migrate north earlier, migrate south later, and winter farther north than light-legged species. The legs apparently are not used for display, and most wood-warblers have black or brownish legs that are not visible at a distance. However, the orange legs of the Blackpoll Warbler

TABLE 24
EVALUATION OF HYPOTHESES¹

Body regions	Hypotheses					
	Abrasion resistance	Energy flow	Reflectance into eyes	Patterns for continuous communication	Minimize conspicuousness	Maximize conspicuousness
Crown	+	0	na	na	+	0
Face (eyebrow stripe, eye-ring, eyeline, whisker)	0	0	-	0	0	0
Upper mandible	-	-	+	na	0	0
Lower mandible	-	-	na	na	0	0
Neck (nape, collar, throat)	+	0	na	na	+	+
Dorsum (back, rump, upper tail coverts)	+	0	na	na	+	-
Tail	+	na	na	na	+	0
Tailspots	+	na	na	+	-	+
Venter (breast, belly, under tail coverts)	+	0	na	na	-	+
Flank	0	0	na	na	0	0
Remiges	+	na	na	na	0	0
Wingbar	+	0	na	+	-	+
Legs	na	+	na	na	0	0

¹ Six hypotheses have been discussed. They correctly predict (+) coloration on some regions of the wood-warblers' body and incorrectly predict (-) coloration in other regions. In many cases the hypothesis applies, but knowledge is insufficient to evaluate predictions (0); in other cases the particular hypothesis is not applicable (na).

and the lemon yellow legs of the Canada Warbler may be optical signals. No studies address this possibility. The other hypotheses discussed are not applicable to the legs whose color appears to be a significant factor in the wood-warbler's behavioral and thermal energetics.

Feathered surfaces.—Facial coloration and its pattern remain largely unexplained (Table 24). The eyeline is significantly darker than expected which may be an adaptation to reduce reflectance that interferes with vision (Rohwer et al. 1983). The feathers of the face, however, create a matte finish that scatters light thereby reducing reflectance and the need for light absorbing colors. Colors that hide the eye from potential prey may account for the dark facial coloration of some wood-warblers, but for most species the complex facial patterns remain unexplained. The face may be the most intricately patterned, most brightly colored, and least understood area of birds.

Melanic feathers resist abrasion significantly better than nonmelanic feathers. The rapid, occasionally turbulent airflow over the dorsum, remiges, and rectrices of flying birds exposes these areas to potentially intense abrasion from airborne particles and suggests that coloration of these regions is an adaptation to minimize abrasion. Exposure to ultraviolet radiation increases the sensitivity of feathers to abrasion (Bergman 1982). However, the darkest feathers are least affected, again emphasizing the selection for heavily melanic feathers on the dorsum where both ultraviolet radiation and abrasion are factors. Green, brown, and gray are the least conspicuous feather colors when viewed against a broadleaf or coniferous canopy. Hence, selection for crypsis may be another factor in dorsal coloration. Furthermore, countershading, which reduces the appearance of three dimensionality, would select for dark dorsal and light ventral coloration. Coloration of the dorsum

may result from four or more different selection pressures (Table 24). Energy balance is probably not a factor in plumage coloration since selection of a favorable microhabitat and ptiloerection can drastically alter the insulating properties of the plumage (Walsberg 1983).

Few hypotheses apply to the remiges and rectrices (Table 24), but color of both areas is accurately predicted by the need for abrasion resistance. Wingbars and tailspots create optical signals and their white or yellow colors maximize contrast with either broadleaf or coniferous foliage, the backgrounds against which the signals are usually seen. Placement of the tailspots where they are completely or partially covered when not displayed maintains crypsis among birds that are not signalling, and the sudden display of color enhances the conspicuousness of the signal. Tailspots are located on the lateral-most rectrices where they can be flashed by fanning the tail and hidden by closing the tail. If sudden, temporary conspicuousness combined with crypsis at other times were the only selective force acting on tailspots any position on the lateral rectrices would do, but abrasion of non-melanic barbs is a problem, thus the tailspots must be located away from the distal tip and lateral edge of the feather, the two areas most subject to abrasion by rapidly moving, turbulent air. The need for a contrasting, flashable signal dictates the existence, color, and general position of the tailspots, whereas abrasion resistance dictates the details of the spots' position on the lateral rectrices. Tailspots provide an excellent example of the way in which several hypotheses combine to define color and pattern precisely.

The throat and venter are prominent during many displays of wood-warblers (Ficken and Ficken 1962b) which probably accounts for their conspicuous white or yellow color. Nonetheless little is known about the location of observers during displays; hence, the background of the throat or venter is unspecified. We cannot predict the particular colors and patterns that will be most conspicuous. A further complication is the contrast among markings (internal contrast) on the throat or venter versus contrast of these markings with the background (external contrast). At present too little is known to predict color and pattern of the throat and venter accurately.

CONCLUDING REMARKS

Only a few of the many hypotheses that account for the colors of animals have been discussed. With these hypotheses I have stressed the need for a quantitative, predictive approach to the study of animal coloration.

I recognize that not all selective pressures can be quantified. I have avoided identity hypotheses (e.g., sexual selection [Darwin 1871], status signalling [Rohwer 1975, 1982; Rohwer and Rohwer 1978]) because they are unquantifiable. Despite my bias, identity hypotheses are vitally important, but, to take just one example, sexual selection alone cannot account for brightly colored males. Sexual selection may favor males with conspicuous optical signals, but what constitutes a conspicuous signal? What is its color? What is its pattern? Only recently have these quantitative questions begun to receive attention (Hailman 1977a, 1979; Endler 1978, 1980, 1984). The example also illustrates the complementary nature of many hypotheses. Sexual selection accounts for the need for bright colors whereas habitat constraints determine which colors appear bright. Tailspots provide another

example of how several selection pressures complement each other to define precisely the pattern and color of markings.

Throughout the preceding chapters hypotheses have been based on physical and chemical principles in an attempt to answer the question "What are the best colors or patterns for this animal?" This is the "evolutiono-engineering approach" (Tracy 1979a). Its advantage lies in revealing the principles on which particular adaptations are based, but it has the disadvantage of ignoring evolutionary history. Selection is constrained by variability. Regardless of its engineering advantages, a particular color or color pattern cannot evolve unless the color or pattern is within the species' natural variability. Thus species may lack a predicted color (e.g., light colored legs of the Common Yellowthroat, an early migrant), because genetic variability has not included the "best" color or pattern. A second evolutionary problem arises when related species share a trait that may result from common ancestry or convergent or parallel evolution. These evolutionary problems have not been emphasized, in part, because I wished to emphasize the deductive power of the "evolutiono-engineering approach," and, in part, because evolutionary historical problems have not been severe.

All preceding analyses assume that color and its pattern are adaptive, but color and color pattern may result from pleiotropisms, pharmacology (e.g., humans turning blue in cold water), or chance. They may also be adaptive, but species' differences may only represent alternative solutions to the same design problem. Although non-adaptive explanations cannot be dismissed, the match between predicted and observed colors suggests that the adaptive models developed in the preceding chapters deal with significant selective pressures. Color and color pattern are highly variable traits (Dwight 1900; Roberts 1936; Oberholser 1974; Rappole 1983), and a varied, integrative approach to the study of color is important (contra Baker and Parker 1979). As hypotheses that account for color become increasingly precise, we will be better able to understand the relative importance and interaction of physical, social, and historical factors that have determined the colors and color patterns of animals.

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APPENDIX I

SCIENTIFIC AND COMMON NAMES OF WOOD-WARBLEDERS

Listed below are the scientific and common names of all wood-warblers included in this study. The classification follows that suggested by Lowery and Monroe (1968), Parkes (1978), and the American Ornithologists' Union Check-list (1983). Species are listed alphabetically within genera following the suggestion of Moreau (1962). Common names are from Skutch (1954), Griscom and Sprunt (1957), Meyer de Schauensee (1970), and the AOU Check-list. The most recent reference is followed when disagreements arise, except where noted.

<i>Vermivora bachmanii</i>	Bachman's Warbler
<i>V. celata</i>	Orange-crowned Warbler
<i>V. chrysoptera</i>	Golden-winged Warbler
<i>V. crissalis</i>	Colima Warbler
<i>V. luciae</i>	Lucy's Warbler
<i>V. peregrina</i>	Tennessee Warbler
<i>V. pinus</i>	Blue-winged Warbler
<i>V. ruficapilla</i>	Nashville Warbler
<i>V. virginiae</i>	Virginia's Warbler
<i>Parula americana</i>	Northern Parula
<i>P. pitiayumi</i>	Tropical Parula
<i>P. superciliosa</i>	Crescent-chested Warbler
<i>P. gutturalis</i>	Flame-throated Warbler
<i>Dendroica adelaidae</i>	Adelaide's Warbler
<i>D. caerulescens</i>	Black-throated Blue Warbler
<i>D. castanea</i>	Bay-breasted Warbler
<i>D. cerulea</i>	Cerulean Warbler
<i>D. chrysoparia</i>	Golden-cheeked Warbler
<i>D. coronata</i>	Yellow-rumped Warbler
<i>D. discolor</i>	Prairie Warbler
<i>D. dominica</i>	Yellow-throated Warbler
<i>D. fusca</i>	Blackburnian Warbler
<i>D. graciae</i>	Grace's Warbler
<i>D. kirtlandii</i>	Kirtland's Warbler
<i>D. magnolia</i>	Magnolia Warbler
<i>D. nigrescens</i>	Black-throated Gray Warbler
<i>D. occidentalis</i>	Hermit Warbler
<i>D. palmarum</i>	Palm Warbler
<i>D. pensylvanica</i>	Chestnut-sided Warbler
<i>D. petechia</i>	Yellow Warbler

<i>D. pharetra</i>	Arrow-headed Warbler
<i>D. pinus</i>	Pine Warbler
<i>D. pityophila</i>	Olive-capped Warbler
<i>D. plumbea</i>	Plumbeous Warbler
<i>D. striata</i>	Blackpoll Warbler
<i>D. tigrina</i>	Cape May Warbler
<i>D. townsendi</i>	Townsend's Warbler
<i>D. virens</i>	Black-throated Green Warbler
<i>D. vitellina</i>	Vitelline Warbler
<i>Catharopeza bishopi</i>	Whistling Warbler
<i>Mniotilta varia</i>	Black-and-white Warbler
<i>Setophaga ruticilla</i>	American Redstart
<i>Protonotaria citrea</i>	Prothonotary Warbler
<i>Helmitheros vermivorus</i>	Worm-eating Warbler
<i>Limnothlypis swainsonii</i>	Swainson's Warbler
<i>Seiurus aurocapillus</i>	Ovenbird
<i>S. motacilla</i>	Louisiana Waterthrush
<i>S. noveboracensis</i>	Northern Waterthrush
<i>Oporornis agilis</i>	Connecticut Warbler
<i>O. formosus</i>	Kentucky Warbler
<i>O. philadelphia</i>	Mourning Warbler
<i>O. tolmiei</i>	MacGillivray's Warbler
<i>Geothlypis aequinoctialis</i>	Masked Yellowthroat
<i>G. beldingi</i>	Belding's Yellowthroat
<i>G. flavovelata</i>	Altamira Yellowthroat
<i>G. nelsoni</i>	Hooded Yellowthroat
<i>G. poliocephala</i>	Gray-crowned Yellowthroat
<i>G. rostrata</i>	Bahama Yellowthroat
<i>G. semiflava</i>	Olive-crowned Yellowthroat
<i>G. speciosa</i>	Black-polled Yellowthroat
<i>G. trichas</i>	Common Yellowthroat
<i>Microligea palustris</i>	Green-tailed Ground Warbler
<i>Teretistris fernandinae</i>	Yellow-headed Warbler
<i>T. forsi</i>	Oriente Warbler

<i>Leucopeza semperi</i>	Semper's Warbler
<i>Wilsonia canadensis</i>	Canada Warbler
<i>W. citrina</i>	Hooded Warbler
<i>W. pusilla</i>	Wilson's Warbler
<i>Cardellina rubrifrons</i>	Red-faced Warbler
<i>Ergaticus ruber</i>	Red Warbler
<i>E. versicolor</i>	Pink-headed Warbler
<i>Myioborus albifrons</i>	White-fronted Redstart
<i>M. bruniceps</i>	Brown-capped Redstart
<i>M. cardonai</i>	Saffron-breasted Redstart
<i>M. melanocephalus</i>	Spectacled Redstart
<i>M. miniatus</i>	Slate-throated Redstart
<i>M. ornatus</i>	Golden-fronted Redstart
<i>M. pariae</i>	Yellow-faced Redstart
<i>M. pictus</i>	Painted Redstart
<i>M. torquatus</i>	Collared Redstart
<i>Euthlypis lachrymosa</i>	Fan-tailed Warbler
<i>Basileuterus basilicus</i>	Santa Marta Warbler
<i>B. belli</i>	Golden-browed Warbler
<i>B. bivittata</i>	Two-banded Warbler
<i>B. chrysogaster</i>	Golden-bellied Warbler
<i>B. cinereicollis</i>	Gray-throated Warbler
<i>B. conspicillatus</i>	—
<i>B. coronatus</i>	Russet-crowned Warbler
<i>B. culicivorus</i>	Golden-crowned Warbler
<i>B. flaveolus</i>	Flavescent Warbler
<i>B. fraseri</i>	Gray-and-gold Warbler
<i>B. griseiceps</i>	Gray-headed Warbler
<i>B. hypoleucus</i>	White-bellied Warbler
<i>B. leucoblepharus</i>	White-browed Warbler
<i>B. luteoviridis</i>	Citrine Warbler
<i>B. melanogenys</i>	Black-cheeked Warbler
<i>B. nigrocristatus</i>	Black-crested Warbler
<i>B. rufifrons</i>	Rufous-capped Warbler
<i>B. signatus</i>	Pale-legged Warbler
<i>B. tristriatus</i>	Three-striped Warbler

<i>Phaeothlypis fulvicauda</i>	Buff-rumped Warbler
<i>P. rivularis</i>	River Warbler
<i>Granatellus pelzelni</i>	Rose-breasted Chat
<i>G. sallaei</i>	Gray-throated Chat
<i>G. venustus</i>	Red-breasted Chat
<i>Xenoligea montana</i>	White-winged Warbler
<i>Peucedramus taeniatus</i>	Olive Warbler
<i>Conirostrum albifrons</i> ¹	Capped Conebill
<i>C. bicolor</i>	Bicolored Conebill
<i>C. cinereum</i>	Cinereous Conebill
<i>C. ferrugineiventre</i>	White-browed Conebill
<i>C. leucogenys</i>	White-eared Conebill
<i>C. rufum</i>	Rufus-browed Conebill
<i>C. sitticolor</i>	Blue-backed Conebill
<i>C. speciosum</i>	Chestnut-vented Conebill

¹ Following Lowery and Monroe (1968) I have retained *Conirostrum* among Parulinae despite its uncertain taxonomic status (AOU 1983).

APPENDIX II-1

RELATIVE AREAS OF BODY REGIONS

Body regions	Proportion of total body surface
Crown	0.03
Nape	0.05
Back	0.12
Rump	0.06
Upper tail coverts	0.06
Tail	0.10
Tailspots	0.02
Eyebrow stripe	0.01
Neck	0.03
Eyeline	0.01
Eye-ring	0.01
Whisker	0.01
Throat	0.03
Breast	0.07
Belly	0.10
Flank	0.06
Under tail coverts (crissum)	0.06
Wing	0.15
Wingbar	<u>0.02</u>
Total	<u>1.00</u>

APPENDIX II-2

PROPORTIONS OF NON-MELANIC PLUMAGE

Oceanic species (37) and species of the Arabian desert (30) grouped by proportion of non-melanic plumage (feathers that contain no melanin) and listed alphabetically by scientific name.

0.0–0.09 Non-melanic Plumage

Oceanic species.—*Anous stolidus*, *A. tenuirostris*, *Catharacta skua*, *Diomedea nigripes*, *Fregata andrewsi*, *F. aquila*, *Fulmarus glacialis*, *Halocyptena microsoma*, *Macronectes giganteus*, *Nesofregatta fuliginosa*, *Stercorarius longicaudus*, *S. parasiticus*, *S. pomarinus*.

Desert species.—*Alectoris graeca*, *Ammomanes deserti*, *A. phoenicurus*, *Anthus campestris*, *Corvus corax*, *Oenanthe isabellina*, *O. xanthopyrna*, *Onychognathus tristranii*, *Pterocles coronatus*, *P. senegallus*, *Rhodopechys githaginea*.

0.10–0.19 Non-melanic Plumage

Oceanic species.—*Stercorarius longicaudus*, *S. pomarinus*.

Desert species.—*Ammoperdix heyi*, *Calandrella rufescens*, *Oenanthe moesta*, *Petronia petronia*.

0.20–0.29 Non-melanic Plumage

Oceanic species.—*Garrodia nereis*.

Desert species.—*Burhinus oedichnemus*, *Calandrella cinerea*, *Alaemon alaudipes*, *Chlamydotis undulata*, *Eremophila alpestris*, *Oenanthe leucopyga*, *Ramphocoris clot-bey*, *Scotocerca inquieta*.

0.30–0.39 Non-melanic Plumage

Oceanic species.—*Diomedea irrorata*, *Macronectes giganteus*, *Nesofregatta fuliginosa*, *Stercorarius parasiticus*, *Thalassoica antarctica*.

Desert species.—*Athene noctua*, *Bubo bubo*, *Melanocorypha calandra*, *Oenanthe deserti*, *O. lugens*, *O. monacha*, *Sylvia nana*.

0.40–0.49 Non-melanic Plumage

Oceanic species.—*Diomedea bulleri*, *D. cauta*, *D. chrysostoma*, *Fulmarus glacialis*, *F. glacialoides*, *Phalaropus fulicaria*, *P. lobatus*, *Sterna fuscata*.

0.50–0.59 Non-melanic Plumage

Oceanic species.—*Diomedea chlororhynchus*, *D. immutabilis*, *D. melanophrys*, *Phalaropus tricolor*.

0.60–0.69 Non-melanic Plumage

Oceanic species.—*Diomedea exulans*, *Rhodostethia rosea*.

0.70–0.79 Non-melanic Plumage

Oceanic species.—*Diomedea albatrus*, *Xema sabini*.

0.80–0.89 Non-melanic Plumage

Oceanic species.—*Diomedea epomophora*.

0.90–1.00 Non-melanic Plumage

Oceanic species.—*Gygis alba*, *Pagodroma nivea*, *Pagophila eburnea*.

APPENDIX III

SYSTEMÉ INTERNATIONALE (SI) UNITS USED IN THE TEXT AND THE FOLLOWING APPENDICES

Radiant energy can be measured from different reference points, in units based on physical quantities (radiometry), or in units based on human perception (photometry). The following list refers only to measures used in the text and following appendices. More complete discussions are available in Preisendorfer (1976), Hailman (1977b), and Gates (1980); Sustare (1979) provides a clear summary of the measures and their interrelationships.

Quantity	SI unit	Abbreviation
<i>Radiometric units</i>		
Radiant flux	Watts	W
Irradiance (Flux density at the receiving surface)	Watts per square meter	W m ⁻²
Radiance (Flux density emitted from a surface)	Watts per steradian per square meter	W st ⁻¹ m ⁻²
<i>Photometric units</i>		
Luminous flux	Lumens	lm
Illuminance (Flux density at the receiving surface)	Lumens per square meter, Lux	lm m ⁻² , lx
Luminance (Flux density emitted from a surface, brightness)	Candelas per square meter	cd m ⁻²

APPENDIX IV

DETAILS OF ENERGY BALANCE IN THE LEGS OF WOOD-WARBLED

LIST OF SYMBOLS

The algebraic symbols used in Appendix IV and Chapter 4 coincide with those of Bligh and Johnson (1973) insofar as possible. Where needed, additional symbols are drawn from Gates (1980) and Mugaas and King (1981).

- A = surface area (cm^2): A_n = area perpendicular to direction of heat flow; A_p = projected surface area perpendicular to the solar beam; A_t = total surface area
 C = convective heat transfer (μW or $\mu\text{W cm}^{-2}$)
 c = convection constant ($4.32 \times 10^2 \text{ J cm}^{-2} \text{ }^\circ\text{K}^{-1}$)
 d = characteristic dimension of wood-warblers' legs (cm)
 E = evaporative heat transfer (μW or $\mu\text{W cm}^{-2}$)
 F = radiation view factor (dimensionless); F_g = view factor to the ground; F_s = view factor to the sky; F_t = total view factor
 h_c = convective heat transfer coefficient ($\mu\text{W cm}^{-2} \text{ }^\circ\text{K}^{-1}$)
 K = conductive heat transfer (μW or $\mu\text{W cm}^{-2}$)
 k = thermal conductivity ($\mu\text{W cm}^{-2} \text{ }^\circ\text{K}^{-1}$)
 L = longwave (thermal) irradiance (μW or $\mu\text{W cm}^{-2}$): L_a = absorbed; L_r = radiated
 l = length of wood-warbler's legs (cm)
 M = metabolic free energy production (μW or $\mu\text{W cm}^{-2}$)
 R = thermal resistance ($^\circ\text{K cm}^2 \mu\text{W}^{-1}$): R_b = thermal resistance of bone; R_s = thermal resistance of skin
 S = shortwave (solar) irradiance (μW or $\mu\text{W cm}^{-2}$): S_a = absorbed; S_p = direct; S_r = reflected; S_s = scattered
 St = stored body heat (μW or $\mu\text{W cm}^{-2}$)
 T = temperature ($^\circ\text{K}$): T_a = air temperature; T_c = core temperature; T_g = ground temperature; T_r = radiant surface temperature; T_s = sky temperature
 u = wind speed (cm sec^{-1})
 α = mean absorptivity (dimensionless): α_s = absorptivity to shortwave (solar) radiation; α_L = absorptivity to longwave (thermal) radiation; α_λ = absorptivity at wavelength λ .
 ϵ = emissivity (dimensionless): ϵ_g = emissivity of the ground; ϵ_l = emissivity of the legs of wood-warblers; ϵ_s = emissivity of the sky
 θ = angle between the direct solar beam and the long axis of the leg (radians)
 ρ = mean reflectance (dimensionless): ρ_g = reflectance from the ground; ρ_λ = reflectance at wavelength λ
 σ = Stephan-Boltzmann constant ($5.67 \times 10^{-6} \mu\text{W cm}^{-2} \text{ }^\circ\text{K}^{-4}$)
 τ_λ = transmittance at wavelength λ

GENERAL STATEMENT OF ENERGY BALANCE

Equation 4.1 is a general statement of steady state energy balance:

$$S_a + L_a + M = L_r \pm C \pm K + E \pm St \quad 4.1$$

Here each term in equation 4.1 is restated in variables that are measurable and apply specifically to the legs of wood-warblers. Rewriting proceeds from left to right. Each term is specified before advancing to the next term. When all terms have been specified, the equation is reassembled. The derivation assumes that the legs are at rest in the sunlight.

ABSORBED SUNLIGHT

Legs in sunlight are irradiated from direct sunlight, sunlight scattered (Rayleigh and Mie scattering) and reflected by the atmosphere, and sunlight reflected from objects in the habitat. Absorption depends on the leg's mean absorptivity to shortwave (solar) radiation, α_s , a spectral integral that depends on atmospheric conditions that alter the solar spectrum. Despite the necessity of specifying atmospheric conditions, the mean absorptivity is a single dimensionless number that represents the percentage of incident solar energy absorbed by a colored surface under specified conditions. Comparisons of ab-

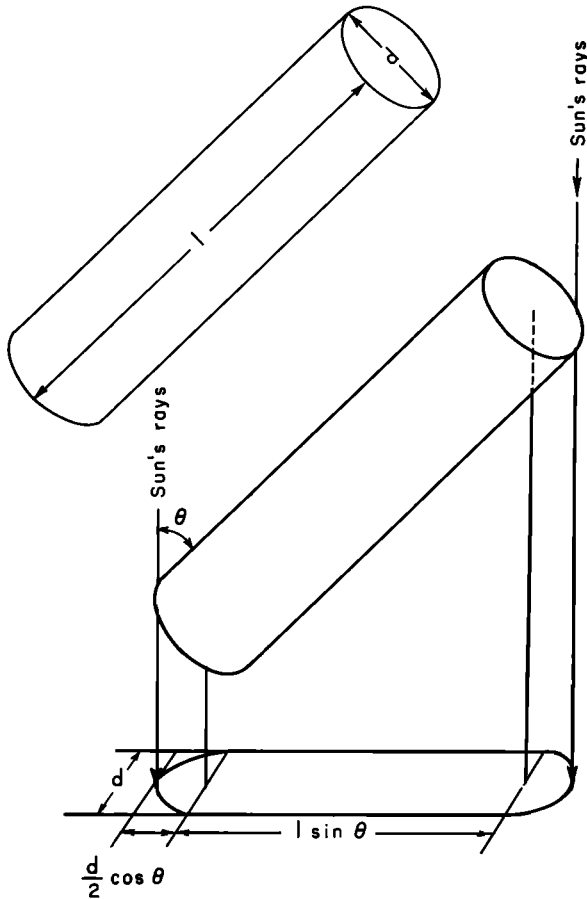


FIGURE 41. Calculation of the silhouette area of a cylinder.

sorption spectra are more readily summarized by comparison of the mean absorptivities than by comparison of the absorption spectra themselves. Furthermore the energy-balance equations of Gates (1962, 1963, 1965a, 1965b, 1970, 1980), Porter and Gates (1969) and Mugaas and King (1981) are based on the mean absorptivity to solar (shortwave) radiation. Other factors that affect total absorption, for example surface area, are best sorted out by treating absorption of direct, S_{ap} , scattered, S_{as} , and reflected, S_{ar} , sunlight as separate terms whose sum is the absorbed solar energy, S_a (Porter and Gates 1969):

$$S_a = S_{ap} + S_{as} + S_{ar} \quad \text{IV.1}$$

Absorbed direct sunlight.—The energy absorbed from direct sunlight (μW) is calculated from the following expression (Lowry 1969):

$$S_{ap} = \alpha_p A_p S_p \quad \text{IV.2}$$

where A_p is the projected surface area (cm^2) perpendicular to the solar beam (silhouette area), and S_p is the irradiance of the incident direct sunlight ($\mu\text{W cm}^{-2}$). In shade S_p is zero. The mean absorptivity of wood-warblers' legs can be measured spectrophotometrically from specimens, and the irradiance of direct sunlight can be measured spectroradiometrically in habitats frequented by the birds, but silhouette area varies with the orientation of the leg relative to the sun.

Assuming the leg to be cylindrical, its silhouette is a rectangle whose area is:

$$A_p = dl \sin \theta \quad \text{IV.3}$$

where d is the diameter of the leg (cm), l is the length of the leg (cm), and θ is the angle between the solar beam and the long axis of the leg (Fig. 41). In theory the ends of the silhouette are half ellipses formed by the ends of the cylinder (Fig. 41). In practice the bird's body is at one end of the cylinder and the toes at the other end. Therefore, no half elliptical shadows are cast. Because the toes are small compared to the legs, they are omitted from the energy balance model of the legs.

For reasons made clear in the following sections, equation IV.3 is expressed in terms of the total surface area of the leg, A_t . The total surface area is:

$$A_t = \pi dl$$

The silhouette area (equation IV.3) may now be rewritten in terms of the total area:

$$\begin{aligned} A_p &= dl \sin \theta A_t / \pi dl \\ A_p &= \sin \theta A_t / \pi \end{aligned} \quad \text{IV.4}$$

Calculation of the absorbed direct sunlight (IV.2) can now be rewritten by substituting equation IV.4 for A_p :

$$S_{ap} = \alpha_s \sin \theta A_t S_p / \pi \quad \text{IV.5}$$

The advantage of equation IV.5 over equation IV.2 is that all variables are measurable.

Absorbed skylight.—The following equation is for calculation of the energy absorbed (μW) from sunlight that has been scattered and reflected by the sky (Lowry 1969; Mugaas and King 1981):

$$S_{as} = \alpha_s F_s A_t S_s \quad \text{IV.6}$$

The irradiance of skylight (sunlight scattered and reflected by the sky), S_s , incident on the legs ($\mu\text{W cm}^{-2}$) can be calculated from measurements of extraterrestrial irradiance, atmospheric pressure, and particle- and moisture-content of the atmosphere (Liu and Jordan 1960; McCullough and Porter 1971; Gates 1980). The radiation view factor to the sky, F_s , is the percentage of surface area that sees the sky. Half of the cylindrical leg sees the sky. Substituting for the view factor, equation IV.6 can be written as:

$$S_{as} = 0.5 \alpha_s A_t S_s \quad \text{IV.7}$$

Absorbed reflected sunlight.—The energy absorbed (μW) from sunlight reflected by the ground is calculated from (Porter and Gates 1969; Gates 1980; Mugaas and King 1981):

$$S_{ar} = \alpha_s F_g A_t \rho_g (S_p + S_s) \quad \text{IV.8}$$

The irradiance of the reflected sunlight incident on a warbler's legs ($\mu\text{W cm}^{-2}$) is the sum of the direct, S_p , and scattered, S_s , sunlight that strikes the ground and is reflected, where ρ_g is the percentage of incident solar radiation reflected from the ground. The percentage of the leg's total area, A_t , that sees the ground is its radiation view factor to the ground, and for a cylindrical leg F_g is one half. Substituting for the view factor equation IV.8 becomes:

$$S_{ar} = 0.5 \alpha_s A_t \rho_g (S_p + S_s) \quad \text{IV.9}$$

Absorbed sunlight: reassembly.—The sum of equations IV.5, IV.7, and IV.9 is the total absorbed sunlight:

$$S_a = \alpha_s A_t [\sin \theta S_p / \pi + 0.5 S_s + 0.5 \rho_g (S_p + S_s)] \quad \text{IV.10}$$

ABSORBED THERMAL ENERGY

All parts of the environment emit thermal (longwave) radiation, but because the temperature of the sky is significantly below that of the rest of the habitat, I separated absorption of thermal radiation from the habitat and from the sky. Absorbed thermal energy (μW) is calculated from the equation (Calder and King 1974):

$$L_a = \alpha_L \epsilon_g F_g A_t \sigma T_g^4 + \alpha_L \epsilon_s F_s A_t \sigma T_s^4 \quad \text{IV.11}$$

where α_L is the mean longwave (thermal) absorptivity, ϵ_g is the emissivity of the ground, and ϵ_s the emissivity of the sky. The radiation view factor to the ground, F_g , or the sky, F_s , is the percent of the total surface area that receives radiation. The Stephan-Boltzmann constant, σ , is $5.67 \times 10^{-6} \mu\text{W cm}^{-2} \text{ } ^\circ\text{K}^{-4}$. The temperature of the habitat is T_g , the temperature of the sky is T_s , and both are measured in $^\circ\text{K}$.

The wavelength of thermal radiation exceeds 4000 nm (Gates 1965a; Tracy 1979b). Longwave radiation is almost completely absorbed by biological tissue regardless of color (Gates 1963; Birkebak 1966), hence

$$\alpha_L = 1 \quad \text{IV.12}$$

Emissivity is the amount of energy emitted by a material expressed as a fraction of the amount of energy at the same wavelength emitted by a black body at the same temperature (Lowry 1969). Thermal radiation emitted by the sky was not measured. However, Swinbank (1963) developed an empirical equation that relates the equivalent black body temperature to the temperature measured on a Stevenson screen 200 cm above the ground. The sky temperature calculated from Swinbank's formula is a fictitious temperature that considers the sky a black body radiator (emissivity of 1) to give the value for the total infrared sky radiation (Porter et al. 1973). The emissivity of the ground depends on its composition, but is always close to one (Gates and Tantraporn 1952; Geiger 1957; Gates 1963; van Wijk 1963; Buettner and Kern 1965).

$$\epsilon_g = \epsilon_s = 1 \quad \text{IV.13}$$

Half of a cylindrical leg views the sky and half views the ground, therefore the respective view factors are:

$$F_g = F_s = 0.5 \quad \text{IV.14}$$

On clear days the radiant temperature of the sky is about 20°K below the temperature of the air (Swinbank 1963):

$$T_s = T_a - 20 \quad \text{IV.15}$$

Substituting equations IV.12 through IV.15 into equation IV.11 and collecting terms gives the following equation for absorbed thermal energy:

$$L_a = 2.84 \times 10^{-6} A_i [T_g^4 + (T_a - 20)^4] \quad \text{IV.16}$$

METABOLISM

Metabolism is another source of energy (equation 4.1). Because little living tissue is found in the tarsometatarsus and phalanges (Berger 1968, 1969), the metabolic heat generated in these areas is negligible. Blood could carry metabolic heat from the body into the legs. However, metabolic heat carried into unfeathered legs is rapidly lost at air temperatures below body temperature (Johansen and Millard 1973; Murrish and Guard 1976; Hill et al. 1980). Such loss may be vital to preventing a rise in body temperature when air temperature and insolation are high (Steen and Steen 1965; Johansen and Millard 1973; Murrish and Guard 1976; Lustick et al. 1979), but may be a serious handicap when air temperature is low (Chappell 1980a; Hill et al. 1980). However, in many if not all birds heat flow to the legs can be minimized by heat exchange between the arterial blood flowing to the legs and venous blood flowing from the legs (Irving and Krog 1955; Scholander 1957; Kahl 1963; Ederstrom and Brumleve 1964). Reduction in the blood flow to the legs and hence in the heat flow from the body also occurs (Baudinette et al. 1976). Therefore under moderate to cold air temperatures metabolic heat generated in wood-warblers' legs and metabolic heat entering the legs from the body are negligible and metabolism can be dropped from the equation.

RADIATIVE ENERGY LOSS

Energy is lost from the legs through radiation (μW) according to the equation (Gates 1980):

$$L_r = \epsilon_l F_l A_l \sigma T_l^4$$

Where ϵ_l is the emissivity of the legs, F_l is the total radiation view factor, and T_l is the temperature of the radiating surface (°K); the other terms were explained earlier.

Biological tissue has a thermal emissivity of approximately one (Hammel 1956; Monteith 1973), with the sole exception of a South American iguanid lizard, *Liolaemus multiformis* (Pearson 1977; Tracy 1979b). The total view factor is the fraction of the surface area that radiates to the environment. A surface with pockets has a view factor relative to the total area that is less than one. Although cylindrical legs of wood-warblers have no pockets, they radiate at each other. The legs are about 1.5 mm in diameter (see Fig. 24) and 1 cm apart. Therefore each leg occupies about 0.02 of the others' view and the total view factor is approximately 0.98.

Wood-warblers' tarsometatarsi lack feathers, which means that the temperature of the radiating surface is the skin temperature. The temperature difference between the core of the legs and the skin, ΔT_{r-c} , is proportional to the natural logarithm of the ratio of the thermal resistance of skin, T_s , to the thermal resistance of bone, r_b (Chao 1969).

$$\Delta T_{r-c} \propto \ln r_s/r_b$$

The thermal resistance of bone and skin are almost identical (Büttner 1936; Kirkland 1967); hence, the ratio r_s/r_b is one. The natural logarithm of one is zero, so the surface and core temperatures of the wood-warbler's leg are the same.

These simplifications lead to the following expression for energy radiated from the legs:

$$L_r = 5.56 \times 10^{-6} A_r T_c^4 \quad \text{IV.17}$$

CONVECTIVE ENERGY LOSS

Convective energy exchange (μW) is expressed in the relationship (Gates 1962):

$$C = h_c A_s (T_r - T_a) \quad \text{IV.18}$$

where h_c is the convective energy transfer coefficient.

Energy is lost by convection whenever the temperature of the adjacent air (T_a) is below the legs' surface temperature (T_r). The adjacent air is the boundary layer, and its thickness determines the rate of energy exchange. Increasing the wind speed decreases the thickness of the boundary layer and increases convective energy exchange. Increasing the diameter of the leg increases the thickness of the boundary layer and decreases convective energy exchange. The convection coefficient, h_c , expresses the relationship of wind speed to diameter (Kreith 1973; Gates 1980):

$$h_c = c(u/d)^{0.5} \quad \text{IV.19}$$

where u is wind speed (cm sec^{-1}), d is diameter of the leg (cm), and k is a constant such that h_c has units $\mu\text{W cm}^{-2} \text{K}^{-1}$. Gates (1962) found that c is $4.32 \times 10^2 \text{ J cm}^{-2} \text{K}^{-1}$ for a smooth cylinder with its long axis perpendicular to the direction of wind flow. I assume that the legs of wood-warblers conform to those conditions. Such conditions need not mean that the legs are parallel to the sun's rays, a condition that would place them in the body's shadow. When the sun is low in the sky, the light and wind would approach from the same angle.

Robinson et al. (1976) calculated that convective heat loss was proportional to $u^{0.5}$, a relationship empirically verified among birds (Gessaman 1972; Robinson et al. 1976; Chappell 1980a). However, the relationship may not apply generally. Among mammals convective heat loss appears to be more nearly proportional to u (Heller 1972), but see Chappell (1980b).

The surface temperature of the legs (T_r) is equal to the core temperature of the legs (T_c) as shown above. Substituting equation IV.19 for h_c in equation IV.18 gives the following equation for convective energy exchange:

$$C = 4.32 \times 10^2 [u/d^{0.5} A_s (T_c - T_a)] \quad \text{IV.20}$$

CONDUCTIVE ENERGY LOSS

At temperatures below the wood-warbler's body temperature most substrates that the legs touch conduct heat away from the body according to Fourier's equation (Condon 1967; Calder and King 1974):

$$K = k A_h dT/dx$$

where K is the conductive heat transfer (μW), k is the thermal conductivity ($\mu\text{W cm}^{-1} \text{K}^{-1}$), A_h is the area perpendicular to the heat flow (cm^2) and dT/dx is the variation in temperature ($^\circ\text{K}$) with distance in the x -direction (cm). Conductivity and area are measurable, but temperature variation with distance cannot be measured for substrates in the wood-warbler's environment; therefore, energy loss by conduction is not calculable.

If convective energy loss is neglected, the estimated energy loss from the legs is low. The less energy the wood-warbler loses to the environment, the colder the temperature it can tolerate. Neglecting conduction leads to the conclusion that the leg is more tolerant of cold than is actually the case. If the error is similar in all wood-warblers, comparison of energy balance in the legs of different species is unaffected. At environmental temperatures close to the wood-warbler's body temperature, conduc-

tive energy loss is negligible and environmental temperatures never greatly exceed a wood-warbler's body temperature, 40°C (Baldwin and Kendeigh 1932; Udvardy 1953). Conductive energy loss is not considered in calculations of energy balance in the legs of wood-warblers.

EVAPORATIVE ENERGY LOSS

Conversion of a liquid to a gas (evaporation) requires energy (heat of evaporation), so that many animals have evolved methods of evaporative cooling, such as panting, anointing the body with saliva, or sweating from specialized glands. The legs of wood-warblers have neither respiratory organs nor sweat glands. Storks and vultures defecate on their legs, thus increasing energy loss through evaporation (Kahl 1963; Hatch 1970), but this behavior is unknown in wood-warblers. The legs of wood-warblers become wet during rainstorms, on mornings when dew is heavy, and after bathing; on such occasions evaporation can occur. If energy lost by evaporation, E' , is expressed as energy lost per unit area ($\mu\text{W cm}^{-2}$), then evaporative energy loss from the legs is:

$$E = E'A, \quad \text{IV.21}$$

where E is evaporative energy loss (μW).

STORED ENERGY

Because of the legs' lack of insulation, negligible thermal resistance (see above), large surface area, and small volume, they are unable to store heat. Hence the storage term is neglected.

ENERGY BALANCE: REASSEMBLY

Energy-flow in the legs of wood-warblers is stated in general terms in equation 4.1:

$$S_a + L_a + M = L_r \pm C \pm K + E \pm St \quad 4.1$$

The survey of terms in the above equation is complete and the more precisely stated terms can be reassembled to make some algebraic simplifications. The reassembled equation can then be used to study the thermal and behavioral energetics of differently colored legs of wood-warblers.

Substituting the more precisely stated expressions determined in the preceding sections yields the following statement of steady-state energy balance in the legs of wood-warblers:

$$\begin{aligned} \alpha_s A_t [\sin \theta S_p / \pi + 0.5 S_s + 0.5 \rho_g (S_p + S_s)] + 2.84 \times 10^{-6} A_t [T_g^4 + (T_a - 20)^4] \\ = 5.56 \times 10^{-6} A_t T_c^4 + 4.32 \times 10^2 (u/d)^{0.5} A_t (T_c - T_a) + E'A_t \end{aligned}$$

All terms contain the total area (A_t), which may be cancelled to yield:

$$\begin{aligned} \alpha_s [\sin \theta S_p / \pi + 0.5 S_s + 0.5 \rho_g (S_p + S_s)] + 2.84 \times 10^{-6} [T_g^4 + (T_a - 20)^4] \\ = 5.56 \times 10^{-6} T_c^4 + 4.32 \times 10^2 (u/d)^{0.5} (T_c - T_a) + E' \end{aligned} \quad \text{IV.22}$$

APPENDIX V

CORRELATIONS WITH ARRIVAL, DEPARTURE, AND
DECEMBER DISTRIBUTION OF WOOD-WARBLERS

Species are listed in Appendices V-1-V-5 by their mean earliest arrival dates in the spring at Madison, Wisconsin, and Itasca, Minnesota; their mean latest departure dates in the autumn at Madison; and the northern limit of their December distribution across North America. Weights are the mean weights of adult males captured at the Powdermill observatory (Clench and Leberman 1978). Arrival sequences are compared to spring weights. Departure sequence and December distribution are compared to autumnal weights.

APPENDIX V-1

SPRING ARRIVAL SEQUENCE AT MADISON, WISCONSIN, 1971-1975

Species	Mean minimum temperature (°C) on date of arrival	Spring weight (g)	Munsell color value of legs			
			Dark	Light	Lighter	Lightest
Yellow-rumped	0.6	13.4	2			
Pine	2.8	14.2 ¹	2			
Orange-crowned	3.3	9.8	2			
Palm	3.3	10.3	2			
Northern Waterthrush	3.9	16.7		4		
Black-and-white	3.9	10.7	2			
Nashville	4.4	8.2	2			
Yellow	4.4	10.2		4		
Black-throated Green	4.4	8.9	2			
Common Yellowthroat	4.4	9.4			6	
Blue-winged	4.4	8.2	2			
Blackburnian	4.4	10.7	2			
Prothonotary	4.4	12.9	2			
Ovenbird	4.4	18.6			6	
Tennessee	5.0	10.2	2			
Northern Parula	5.0	8.1		4		
Golden-winged	5.5	9.0	2			
Blackpoll	5.5	13.0			6	
Cape May	5.5	11.2	2			
Magnolia	5.5	8.9	2			
American Redstart	5.5	8.3	2			
Bay-breasted	5.5	13.4	2			
Cerulean	5.5	9.4	2			
Chestnut-sided	5.5	9.9	2			
Wilson's	6.1	7.6			6	
Canada	6.1	10.6				8
Connecticut	6.6	16.5			6	
Kentucky	7.2	13.5				8
Black-throated Blue	7.2	9.9		4		
Mourning	7.2	12.9			6	

¹ Only weights of birds caught in October were available.

APPENDIX V-2
 SPRING ARRIVAL SEQUENCE AT ITASCA, MINNESOTA, 1973, 1974

Species	Mean minimum temperature (°C) on date of arrival	Spring weight (g)	Munsell color value of legs			
			Dark	Light	Lighter	Lightest
Yellow-rumped	3.3	13.4	2			
Pine	3.3	14.2 ¹	2			
Palm	3.3	10.3	2			
Nashville	3.9	8.2	2			
Black-and-white	3.9	10.7	2			
Ovenbird	3.9	18.6			6	
Cape May	3.9	11.2	2			
Yellow	3.9	10.2		4		
American Redstart	4.4	8.3	2			
Magnolia	4.4	8.9	2			
Black-throated Green	4.4	8.9	2			
Orange-crowned	4.4	9.8	2			
Wilson's	5.0	7.6			6	
Northern Parula	5.0	8.1		4		
Chestnut-sided	5.0	9.9	2			
Blackburnian	5.0	10.7	2			
Common Yellowthroat	5.0	9.4			6	
Golden-winged	5.6	9.0	2			
Blackpoll	5.6	13.0			6	
Tennessee	5.6	10.2	2			
Northern Waterthrush	6.1	16.7		4		
Connecticut	6.1	16.5			6	
Bay-breasted	6.1	13.4	2			
Mourning	6.7	12.9			6	
Canada	7.2	10.6				8

¹ Only weights of birds caught in October were available.

APPENDIX V-3
AUTUMN DEPARTURE SEQUENCE FROM MADISON, WISCONSIN, 1971-1974

Species	Mean minimum temperature (°C) on date of departure	Autumnal weight (g)	Munsell color value of legs			
			Dark	Light	Lighter	Lightest
Yellow-rumped	-4.4	14.3	2			
Orange-crowned	2.8	9.4	2			
Nashville	4.4	8.9	2			
Palm	4.4	10.9	2			
Black-throated Green	4.4	9.8	2			
Tennessee	5.0	9.2	2			
Magnolia	5.5	9.6	2			
Ovenbird	5.5	22.4			6	
Common Yellowthroat	6.1	12.1			6	
Black-and-white	6.1	11.9	2			
Chestnut-sided	6.7	9.7	2			
American Redstart	6.7	8.2	2			
Blackpoll	6.7	13.3			6	
Bay-breasted	7.2	13.7	2			
Northern Parula	7.2	8.4		4		
Black-throated Blue	7.7	10.3		4		
Northern Waterthrush	7.7	19.0		4		
Cape May	8.9	13.2	2			
Golden-winged	9.4	9.1	2			
Blackburnian	10.0	10.4	2			
Wilson's	10.6	8.5			6	
Canada	11.1	10.6				8
Yellow	12.8	10.6		4		

APPENDIX V-4
DECEMBER DISTRIBUTION IN NORTH AMERICA, 1947-1973

Species	Temperature (°C) at northern limit of December range	Autumnal weight (g)	Munsell color value of legs			
			Dark	Light	Lighter	Lightest
Yellow-rumped	2.8	14.3	2			
Palm	8.3	10.9	2			
Townsend's	8.5	9.8 ¹	2			
Pine	8.8	14.2	2			
Common Yellowthroat	9.6	12.1			6	
Orange-crowned	11.4	9.4	2			
Black-throated Gray	11.8	9.8 ¹	2			
Wilson's	14.1	8.5			6	
Yellow-throated	14.4	- ²	2			
Black-throated Green	15.0	9.8	2			
Black-and-white	15.3	11.9	2			
Nashville	16.4	8.9	2			
Yellow	17.0	10.6		4		
Prairie	17.2	8.7	2			
Tropical Parula	17.2	8.4 ³		4		
Ovenbird	17.7	22.4			6	
Northern Parula	18.3	8.4		4		
American Redstart	19.2	8.2	2			
Northern Waterthrush	19.2	19.0		4		
Black-throated Blue	19.4	10.3		4		

¹ Weight unavailable, but assumed to be the same as the congeneric Black-throated Green Warbler (Mengel 1964).

² Weight unavailable, species deleted from correlation by weight.

³ Weight unavailable, but assumed to be the same as the congeneric Northern Parula.

APPENDIX V-5
CORRELATION OF WEIGHT AND THE COLOR OF WOOD-WARBLERS' LEGS

Species	Spring weight (g)	Munsell color value of legs			
		Dark	Light	Lighter	Lightest
Wilson's	7.6			6	
Northern Parula	8.1		4		
Nashville	8.2	2			
Blue-winged	8.2	2			
American Redstart	8.3	2			
Black-throated Green	8.9	2			
Magnolia	8.9	2			
Golden-winged	9.0	2			
Common Yellowthroat	9.4			6	
Cerulean	9.4	2			
Orange-crowned	9.8	2			
Chestnut-sided	9.9	2			
Black-throated Blue	9.9		4		
Tennessee	10.2	2			
Yellow	10.2		4		
Palm	10.3	2			
Canada	10.6				8
Black-and-white	10.7	2			
Blackburnian	10.7	2			
Cape May	11.2	2			
Prothonotary	12.9	2			
Mourning	12.9			6	
Blackpoll	13.0			6	
Yellow-rumped	13.4	2			
Bay-breasted	13.4	2			
Kentucky	13.5				8
Pine	14.2	2			
Connecticut	16.5			6	
Northern Waterthrush	16.7		4		
Ovenbird	18.6			6	

APPENDIX VI
CORRELATION BETWEEN MUNSELL COLOR VALUE OF THE UPPER MANDIBLE AND
PERCENT OF FORAGING TIME SPENT IN SUNLIGHT

Species	Percent of foraging time spent in sun- light	Munsell color value of the upper mandible			
		Dark	Light	Lighter	Lightest
Palm	55	1			
Yellow	46	1			
Yellow-rumped	33	1			
Wilson's	31	1			
Tennessee	31	1			
Mourning	27	1			
Pine	19	1			
Blackpoll	18		2		
Cape May	18	1			
American Redstart	14	1			
Orange-crowned	14		2		
Black-throated Green	12	1			
Blackburnian	11	1			
Nashville	11	1			
Common Yellowthroat	8	1			
Bay-breasted	7	1			
Northern Parula	4	1			
Black-and-white	4	1			
Bay-breasted	3		2		
Magnolia	3	1			
Chestnut-sided	2	1			
Golden-winged	0	1			
Black-throated Blue	0	1			
Canada	0			3	
Northern Waterthrush	0			3	
Ovenbird	0				4

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