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ANALYSIS OF GEOGRAPHIC VARIATION IN THE TOWNSEND'S WARBLER

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ABSTRACT.—The hypothesis that there are no morphologically separable populations of Townsend's Warblers (*Dendroica townsendi*) was tested by analysis of male and female specimens. Two populations of Townsend's Warblers were identified: (1) those wintering in Mexico/Central America; and (2) those wintering in California/Oregon. Principal component and discriminant function analyses identified wing length as the most useful variable for separating the wintering groups. Identification of breeding areas of wintering birds by wing length was complicated by feather wear. It appears, however, that the shorter-winged birds wintering in California/Oregon breed in the Queen Charlotte Islands, and the longer-winged birds wintering in Mexico/Central America breed throughout the remainder of the species' range. Although formal designations of subspecies of the Townsend's Warbler must await further clarification of breeding areas, I conclude that populations of this species can be distinguished with sufficient accuracy to satisfy reasonably rigorous subspecies criteria.

Many species of wood warblers (Emberizidae: Parulinae) of western North America seem likely to have resulted from radiation of eastern species (Mengel 1964, Hubbard 1969). One such group of species has been labeled the "*Dendroica virens* complex" (Mengel 1964, Mayr and Short 1970)—the four western members of the group may have evolved from one or more colonizations of a precursor of the Black-throated Green Warbler. Although the Black-throated Green Warbler has two recognized subspecies, all western members of the complex are presently considered monotypic (AOU 1957). Not all authorities, however, have fully agreed on this latter classification. Oberholser (1930) recognized two subspecies of the Black-throated Gray Warbler (*D. nigrescens*): the northern, nominate form based on J. K. Townsend's type published in 1837, and a southern one for which the name *Sylvia halseii* Giraud 1841 was already available. With some emendation of ranges this treatment was followed by Paynter (1968; where Oberholser is incorrectly cited as 1934). In addition, Grinnell (1905) recognized two morphologically distinct populations of the Townsend's Warbler (*D. townsendi*), but stopped short of naming a subspecies. Indeed, my study was suggested by Grinnell's note and was designed to test the hypothesis that no readily identifiable morphological groups of Townsend's Warblers exist.

METHODS

Museum specimens of adult male and female Townsend's Warblers were measured with vernier calipers for the morphological characters given in Table 1; methods used to measure these characters were given by Morrison (1982). Specimens were available from the two primary wintering areas of the Townsend's Warbler—California/Oregon and southern Mexico/Central America (primarily from Sinaloa, Nuevo Leon, and Tamaulipas south to Guatemala and Honduras); the species does not usually winter *between* these two areas (Phillips 1951, AOU 1957). To avoid the possibility of migrants on their way to southern Mexico/Central America being included in the California/Oregon sample of wintering birds, only specimens collected after early October were included in the latter sample. Migrant and breeding individuals were available from throughout the western North American range of the Townsend's Warbler (AOU 1957). Morphological data (standardized) were subjected to principal component analysis (PCA) using the Biomedical Computer Programs (Dixon

TABLE 1. Morphological measurements (mm) of male and female Townsend's Warblers wintering in southern Mexico/Central America (Group 1) and California/Oregon (Group 2), and for all specimens analyzed (Group 3), which includes breeding and migrating birds.

Variable	Group 1		Group 2		Group 3	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
MALES	$n = 30$		$n = 27$		$n = 207$	
Primary 9 length (P9)	66.0	1.18	63.9	0.85*	65.2	1.35
P8	66.9	1.23	64.8	0.87*	66.1	1.34
P7	66.9	1.22	64.8	0.83*	66.1	1.33
P6	65.8	1.20	63.5	0.72*	64.9	1.37
P5	60.1	1.11	58.2	0.58*	59.5	1.24
P4	56.5	0.97	54.8	0.53*	56.0	1.18
P3	54.2	0.88	52.6	0.51*	53.7	1.17
Tail length	51.6	1.39	50.6	1.11*	51.3	1.51
Tarsus length	17.4	0.43	17.5	0.40	17.6	0.47
Bill length	6.8	0.19	7.0	0.16*	6.9	0.23
Bill width	2.7	0.09	2.8	0.12*	2.8	0.13
Bill depth	2.9	0.12	3.0	0.11	3.0	0.14
Hallux length	4.8	0.29	4.9	0.21	4.9	0.28
Claw length	4.7	0.14	4.9	0.15*	4.8	0.19
FEMALES	$n = 16$		$n = 10$		$n = 75$	
P9	62.2	1.04	60.6	1.03*	61.4	1.29
P8	63.1	0.94	61.7	1.07*	62.4	1.22
P7	63.0	0.95	61.8	1.11*	62.4	1.20
P6	61.7	1.54	60.6	0.89*	61.1	1.33
P5	57.0	1.11	55.6	1.07*	56.3	1.19
P4	53.9	0.93	52.4	0.97*	53.0	2.36
P3	51.8	0.87	50.4	0.88*	51.3	1.04
Tail length	49.8	1.69	48.8	1.04	49.4	1.40
Tarsus length	17.3	0.30	17.3	0.58	17.3	0.41
Bill length	6.9	0.20	6.9	0.19	6.9	0.24
Bill width	2.7	0.08	2.8	0.10	2.8	0.10
Bill depth	3.0	0.13	3.0	0.11	3.0	0.13
Hallux length	4.8	0.19	4.9	0.29	4.8	0.23
Claw length	4.8	0.17	4.9	0.15	4.7	0.20

* $P < 0.05$; t-test (Group 1 versus Group 2).

and Brown 1979). With PCA, one need not a priori assume that different groups (i.e., subspecies) are present in the sample (Neff and Smith 1979). Data falling into definable groups were then analyzed by two-group discriminant function analysis (DFA) with direct inclusion of variables using the Statistical Package for the Social Sciences (Klecka 1975). The DFA commenced with a test of the null hypothesis of equality of within-group variance-covariance matrices (Cooley and Lohnes 1971:224). The a posteriori probability of an individual's assignment to one of the a priori groups was then calculated (i.e., classification analysis). Only one member of any highly ($r > 0.7$) intercorrelated group of variables was included in DFA (Williams 1981). Log transformations of data did not substantially alter results.

RESULTS

The first component derived from principal component analysis of male and female morphological data accounted for most of the variation among individuals; the first component was identified as a function of wing length for both sexes (Table 2). The second component for males and the third for females accounted for a lower percentage of the variation; these were associated with bill shape. Finally, the third component for males and the second for females again accounted for little of the total variation; they were identified as functions of leg structure.

Plotting data for wintering individuals on the first two principal component axes tended to sort out two overlapping groups of male (Fig. 1) and female (Fig. 2) Townsend's Warblers—these groups correspond to individuals wintering in (1) southern Mexico and Central America; and (2) California and Oregon. Birds wintering in southern latitudes had longer wings, but smaller bills and legs, than their northern counterparts (see also Table 1).

Identification of the breeding grounds for the two groups of wintering individuals was complicated by differential feather wear sustained during migration and on breeding grounds among individuals within each population. That is, breeding birds collected at the same location and date often differed markedly in amount of wear of primaries; wing tips were often damaged or broken, thus precluding

TABLE 2. Principal component analysis (varimax rotation) of morphological measurements of male ($n = 207$) and female ($n = 75$) Townsend's Warblers. See Table 1 and text for description of variables.

Variable	Component I	II	III
MALES			
P9	0.913	0.031	−0.004
P8	0.941	0.033	0.055
P7	0.940	0.039	0.059
P6	0.954	0.014	0.042
P5	0.895	−0.081	0.006
P4	0.912	−0.101	−0.017
P3	0.876	−0.109	−0.017
Tail length	0.601	0.264	−0.143
Tarsus length	0.084	0.622	−0.104
Bill length	0.142	−0.031	0.554
Bill width	−0.052	−0.019	0.794
Bill depth	−0.144	0.334	0.620
Hallux length	−0.060	0.747	0.211
Claw length	−0.019	0.695	0.065
Percent variation	45.2	13.1	8.7
Cumulative percent variaton	45.2	58.3	67.0
FEMALES			
P9	0.887	−0.192	0.112
P8	0.922	−0.104	0.102
P7	0.914	−0.107	0.102
P6	0.898	0.073	0.072
P5	0.901	0.051	−0.132
P4	0.268	0.143	−0.345
P3	0.852	−0.001	−0.195
Tail length	0.384	−0.014	−0.206
Tarsus length	0.250	0.126	−0.045
Bill length	0.102	0.419	0.542
Bill width	−0.016	0.798	0.078
Bill depth	−0.171	0.792	0.035
Hallux length	−0.075	−0.152	0.731
Claw length	0.104	0.311	0.687
Percent variation	37.8	14.0	9.7
Cumulative percent variation	37.8	51.8	61.5

analysis of many specimens. It was thus difficult to objectively assign breeding individuals to one of the two wintering groups based on principal component analysis. Therefore, I applied discriminant function analysis using the two groups of wintering individuals, with non-wintering individuals included as "unknowns" in the analysis. Because the lengths of all primaries were intercorrelated, only the longest (i.e., eighth) was included in the DFA. Although discriminant function analysis forces an unknown into one of the a priori groups, the technique eliminates much of the observer's bias.

The discriminant function (DFA) showed a significant separation between the two wintering groups of male Townsend's Warblers; the two groups had similar variance-covariance matrices (Table 3). The standardized discriminant function coefficients indicated that length of the eighth primary and claw length were the

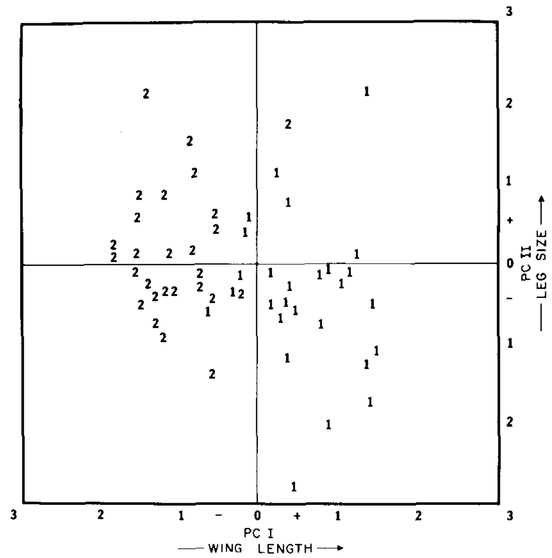

FIGURE 1. Plot of individuals derived from principal component analysis of morphological measurements of male Townsend's Warblers collected during winter in (1) southern Mexico/Central America and (2) California/Oregon.

variables best separating the groups; all other coefficients were less than ±0.40. The DFA for separation of wintering females was fair but not significant ($P > 0.05$); the two groups had similar variance-covariance matrices (Table 3). The standardized discriminant function coefficients were all below ±0.40 except for length of the eighth primary; wing length thus best separated the two groups.

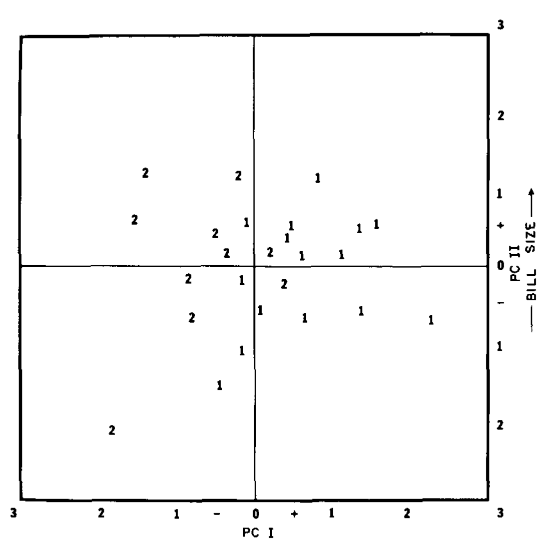

FIGURE 2. Plot of individuals derived from principal component analysis of morphological measurements of female Townsend's Warblers collected during winter in (1) southern Mexico/Central America and (2) California/Oregon.

TABLE 3. Two-group discriminant function analysis of morphological measurements of Townsend's Warblers wintering in southern Mexico/Central America and California/Oregon. Sample sizes and a description of variables included in the analysis are given in Table 1 and the text.

Statistic or characteristic	Male	Female
Eigenvalue	2.125	0.719
Canonical correlation	0.825	0.647
Wilks' lambda	0.320	0.582
Chi-square	58.103	11.381
df	8	8
Significance	<0.001	0.181
Box's M	41.939	68.523
df	36, 9935.8	36, 1557.6
Significance	0.50	0.21
Standardized discriminant function coefficients		
P8	0.876	0.927
Tail length	0.106	0.198
Tarsus length	0.158	−0.285
Bill length	−0.472	0.013
Bill width	0.027	−0.027
Bill depth	−0.224	0.364
Hallux length	0.261	−0.209
Claw length	−0.613	−0.246

The classification of wintering males based on the two-group discriminant analysis was good, with about 95% of each group correctly identified as wintering in either southern Mexico/Central America or California/Oregon. The classification of wintering females was fair, with about 88% of the southern Mexico/Central America group and 73% of the California/Oregon group correctly classified. The results of classification analysis for each non-wintering individual are summarized by geographic region (Table 4). Male and female birds wintering south of the United States apparently breed throughout the interior western United States. Classification of male birds wintering in California and Oregon was about equally divided between those collected in the Queen Charlotte and Vancouver islands. No other group of males had over 30% of its individuals classified with birds wintering in California/Oregon. All female specimens collected on the Queen Charlotte and Vancouver islands, except for one, were identified with birds wintering in southern latitudes. Specimens collected along coastal Alaska opposite the Queen Charlotte Islands were clearly identified with birds wintering in southern latitudes. A large series of specimens collected during April and May in California were apparently birds migrating north from southern wintering grounds (see also Grinnell 1905). Unfortunately, I could seldom determine if a specimen had been breeding near, or migrating through, the collection site: Townsend's Warblers apparently begin to establish territories during late April and May while other individuals are migrating through the same area (pers. observ.).

Clinal variation in morphological characters of males was analyzed by correlating each measurement with the latitude or longitude of collection from presumed breeding birds. All correlations were low and nonsignificant ($r^2 < 0.05$; $P > 0.05$). Sample sizes were insufficient for analysis of clinal variation in female specimens.

DISCUSSION

Results of this study show that two identifiable populations of Townsend's Warblers can be distinguished with sufficient accuracy to meet "accepted" subspecies criteria (see Rand 1948, Amadon 1949, Rand and Traylor 1950). Opinions differ, however, as to what constitutes a subspecies and whether or how they

TABLE 4. Classification analysis of nonwintering Townsend's Warblers (included as unknowns) resulting from two-group discriminant function analysis of morphological measurements of birds wintering in southern Mexico/Central America (Group 1) and California/Oregon (Group 2).[a]

	No. and percent classified in group			
	Male		Female	
Location	Group 1	Group 2	Group 1	Group 2
April/May, California	13 (76.5)	4 (23.5)	11 (78.6)	3 (21.4)
Cascades (Oregon, Washington, Alberta)	6 (85.7)	1 (14.3)	—[b]	—
Rocky Mountains	16 (69.6)	7 (30.4)	4 (80.0)	1 (20.0)
Northeast Oregon	5 (71.4)	2 (28.6)	—	—
Okanogan (Washington/British Columbia)	14 (77.8)	4 (22.2)	4 (80.0)	1 (20.0)
Sitkan region (Alaska)	15 (83.3)	3 (16.7)	3 (75.0)	1 (25.0)
Queen Charlotte Islands	4 (36.4)	7 (63.6)	1 (16.7)	5 (83.3)
Vancouver Island	6 (46.2)	7 (53.8)	0 (0.0)	5 (100.0)

[a] Values = number of individuals (with percent in parentheses).
[b] Indicates insufficient sample size.

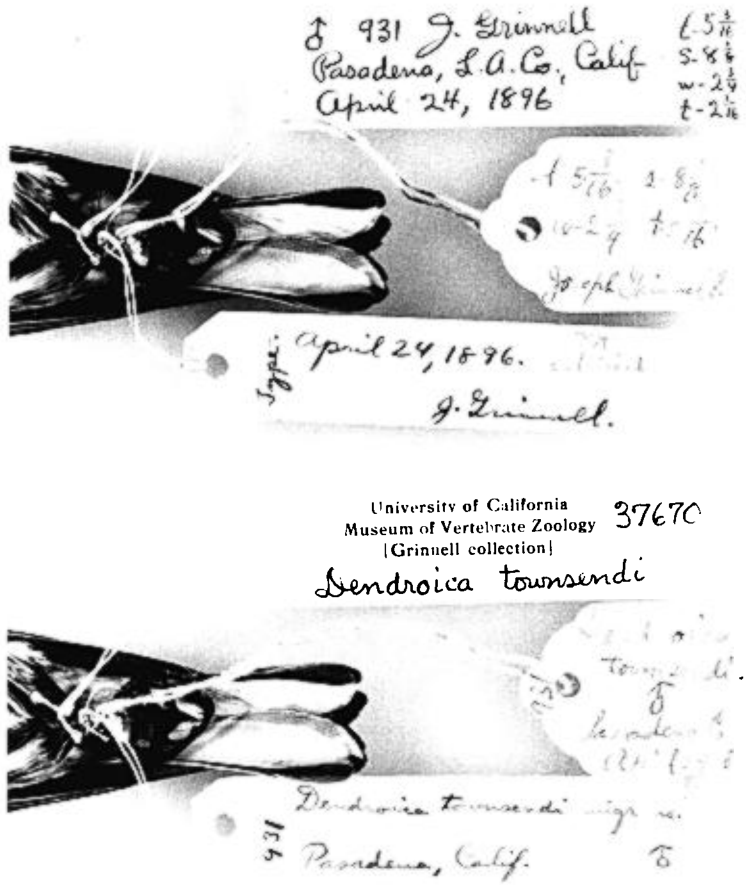

FIGURE 3. Photographs of labels for male Townsend's Warbler, which was apparently suggested by Joseph Grinnell as a suitable type of the long-winged population of this species; an official designation of this bird as a type was never published and no such designation is made in this paper.

should even be recognized and defined (e.g., see "Commentary" by various authors, Auk 99:593–615; 1982). Wing length best separated populations of males and females. Although separation of the two populations was nearly complete for wintering birds, identification of breeding grounds was complicated by feather wear and the difficulty in separating breeding and migrating birds. The absolute difference in bill and leg (which includes toe and claw size) dimensions between populations was too small to be useful, in a practical sense, in identifying breeding localities. Variations in morphology were not the result of purely clinal trends in characters. Grinnell (1905) previously identified these same two groups of wintering birds (using males only) and likewise showed the Mexican and Central American wintering populations to have longer wings and smaller bill dimensions than their northern counterparts. Although Grinnell did not analyze breeding populations, he suggested that birds wintering in southern latitudes breed throughout most of the interior western United States, and birds wintering in California and Oregon breed along coastal Alaska (Sitkan district). My results differ from this in part. I found that birds wintering in the United States breed on the Queen Charlotte Islands and possibly Vancouver Island. As did Grinnell (1905), I found that the birds wintering south of the United States breed throughout the remainder of the species range (see AOU 1957). Remember that specimens from the Sitkan district of Alaska were classified with birds wintering in southern latitudes. My conclusions on specific breeding localities must be tempered by variations in measurements of non-wintering birds caused by feather wear. If additional specimens of early-fall fresh-plumaged birds were collected before migration, they would help to circumvent the problem of feather wear. The possibility of introgression between mainland and island breeding birds, especially on Vancouver Island, must be assessed. It appears, nevertheless, that two subspecies of the Townsend's Warbler exist. As did Grinnell (1905), I will refrain from formally naming these subspecies until additional *known* breeding specimens can be collected.

Although he never published his findings, Joseph Grinnell apparently suggested a type specimen for the population of "long-winged" Townsend's Warblers that he identified as wintering in southern Mexico and Central America. This specimen was found during the course of this study (Fig. 3). Grinnell footnoted his 1905 description of variation in the Townsend's Warbler as follows: "Anti-splitters please take note that I have here pointed out a subspecies without burdening it with a name." In the event that a subspecies should in the future be formally named, I suggest that Grinnell's name for this population be used, although it may be appropriate to select another type specimen.

Regardless of the formal designation of subspecies in the Townsend's Warbler, the existence of two widely separated wintering grounds occupied by individuals with differing morphologies must be assessed in an ecological context. Migration distance is said to be related to wing length (see review by Hamilton 1961; but see Keast 1980), and the Townsend's Warbler fits this premise. The difference in wing, bill, and leg morphology may be related to the foraging substrates, foods, and climatic conditions encountered by these populations on breeding or wintering grounds (e.g., see Banks 1964; Bock 1966; Power 1969, 1970; James 1970; Rothstein 1973; Greenberg 1981). The selection pressures exerted by the winter environment may be important in determining the non-wintering behavior of these populations (e.g., see Salomonsen 1955, Fretwell 1972). Development of a comprehensive model accounting for colonization and possible isolation of populations of the Townsend's Warbler is beyond the scope of this paper. Note, nevertheless, that the Queen Charlotte Islands were probably forested refugia during the Pleistocene (Heusser 1960); such refugia may have supported isolated populations of the ancestor of the Townsend's Warbler during colonization of western environs (Mengel 1964). Subspecies of other birds endemic to the Queen Charlotte Islands have been described (e.g., Steller's Jay, *Cyanocitta stelleri carlottae*; Pine Grosbeak, *Pinicola enucleator carlottae*; AOU 1957).

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RECENT PUBLICATIONS

A Guide to the Birds of Puerto Rico and the Virgin Islands.—Herbert A. Raffaele. 1983. Fondo Educativo Interamericano, San Juan. 5 p. Paper cover. $13.95. Source: Addison-Wesley Publishing Co., Inc., Jacob Way, Reading, MA 01867. This book is a field guide and more, yet no larger than a standard field guide. Its opening chapters discuss the biogeography and conservation of the Puerto Rican and Virgin Island avifaunas, giving special attention to the many endangered species. There follows a section for rapid identification of birds: forty plates (24 in color) showing all the well-documented species found on these islands accompanied by brief descriptions of the field marks on the facing pages. The illustrations have been well executed by Cindy J. House and John Wiessinger, but they do not strictly follow taxonomic order and they vary widely in the number of birds per plate. The species accounts, which occupy most of the book, treat appearance, local names, and seasonal and habitat occurrence, voice, and nesting. Vagrants and unestablished vagrants are then listed. Last, Raffaele describes seven good places to find birds in the region and provides a checklist of species keyed to those localities. Maps, index. The volume has been nicely designed and printed but its binding does not seem sturdy enough to endure heavy use. The guide is not only invaluable for resident or migrant birders in its islands, but also it can serve to identify most birds found elsewhere in the West Indies. The Spanish edition to be published next year should importantly aid in fostering local appreciation of the region's wildlife.

Wildlife and Wildlife Habitats of American Samoa: I. Environment and Ecology, II. Accounts of Flora and Fauna.—A. Binion Amerson, Jr., W. Arthur Whistler, and Terry D. Schwaner; edited by Richard C. Banks. 1982. U.S. Fish and Wildlife Service, Washington, D.C. Two parts, 119 + 151 p. Paper covers. No charge. Source: U.S.F.W.S., Region I, 500 N.E. Multnomah St., Suite 1692, Portland, OR 97232. American Samoa is a small group of atolls and volcanic islands situated about 2,900 km NNE of New Zealand. Its wildlife and natural habitats were thoroughly surveyed for the USFWS and the resulting voluminous report was abridged into the present document. The first part covers the physical environment, vegetation, terrestrial vertebrate communities, community relationships, and conservation and resource management. The second part describes the study plots, gives an annotated list of the plants, and reviews the land vertebrates. For each of the bird species there is given its Samoan name, status, a summary of observations (including those from the literature), and mention of specimens taken. Photographs, distribution maps, references, and many tables. This report, not to mention that from which it is drawn, provides valuable baseline information for assessing potential environmental impacts, identifies threatened species and habitats, and offers recommendations for management. Biologists and resource managers may find it applicable in other islands of the tropical western Pacific.

Birds of Southern California's Deep Canyon.—Wesley W. Weathers. 1983. University of California Press, Berkeley. 266 p. $35.00. Deep Canyon is located at the northwestern corner of the Coachella Valley, about 26 km southeast of Palm Springs. It descends from cool montane forest atop the Santa Rosa Mountains to the Colorado desert of the valley floor, a drop of 2,600 m in a span of only 18 km. The wide range of habitats thus encompassed support 217 species of birds (112 nesting). This book is an ecological study of the birdlife, based on the author's own fieldwork and that of many others (back to Grinnell and Swarth 1913). Nine major habitats and their avian communities are each described and analyzed. Combining data on population density with calculations of daily energy expenditure, Weathers shows the energetic impact of the species in different seasons and habitats. Following this material are the species accounts, which include general (sometimes rather elementary) natural history information as well as specific observations on status and habits in Deep Canyon. An appendix chart summarizes data on habitats and seasonal occurrence for all the species. Graphs, drawings, photographs (monochrome and color), references, index. Avian ecologists who study community dynamics in the southwestern U.S. will find much of interest in this book.