AN ECOLOGIC ANALYSIS OF THREE CALIFORNIA AVIFAUNAS

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One facet of ecology is the study of the adaptations and adjustments which exist between animals and the environmental conditions surrounding them. Studies of such adjustments are made in the laboratory by placing an animal under a particular set of conditions and measuring its response when a condition is changed. Similar studies of adaptation can be made in the field on either a single species or an entire fauna. Here, variation in environmental conditions may be studied in two ways: one may remain in a single area centering attention on adjustments made by animals to the seasonal changes in the environment, or one may study several areas at the same season each having different environmental conditions and compare the responses of the animals.

To make such field studies of adaptation in birds, one requires a method of analyzing the composition of an avifauna which applies at all seasons of the year (this rules out analyses based on some aspect of breeding behavior) and which will permit comparison between avifaunas having differing species composition. The feeding habits and the foods taken provide a basis for such an analysis. The method of analysis described in this paper, while technically original, is derived from similar systems and concepts used by many workers. Particular acknowledgement should be made to the writings of Colquhoun and Morley (1943), Moreau (1948), and Smith (1951), and to the teachings of Loye Miller.

The analysis is performed by sorting the members of an avifauna into four major groups based on the feeding station within the habitat where they feed. In order of increasing height off the earth, these are: "ground"; "timber," a term used to include the trunks and larger branches of the trees and shrubs; "foliage," used to include both the leaves and the twigs supporting the leaves; and "air." For purposes of simplicity no distinction is made between feeding stations in shrubs and in trees, nor is any effort made to distinguish between strata of different height within a forest. Additions of this sort are possible where the community structure is complex enough to make them desirable.

Following this initial breakdown, further fractionation is made within three of the groups based on either the type of food taken or the method of foraging. Within the "ground" group the birds are assorted into "seeds," "insects," and "predator" categories. Where a species falls into the food categories depends on which type of item forms a major part (over 50 per cent) of its diet. The compilation of Martin, Zim, and Nelson (1951) was used as an authoritative source on percentage composition of diet in most instances. Since the diet of many species changes with the seasons, the classification of such species must be correspondingly changed. The "timber" group is divided into "searching" and "drilling" birds based on the method of obtaining food, since nearly all birds in this group feed largely on insects, sapsuckers being an exception. The "foliage" birds are divided into three categories: "seed," a term applying not only to birds which feed on nuts and seeds while still on the tree but also to those feeding on buds, ovaries of flowers, and other semi-woody substances; "insects," which applies to birds which feed on insects and also to those taking berries; and "nectar," which includes birds feeding on flower nectar regardless of how they obtain it. The "air" group is not subdivided since all such birds feed on insects. This system classifies the avifauna into nine categories (fig. 1).

The size of each of the nine categories within an avifauna may be registered in two ways. The species present in each category may be counted or the actual number of

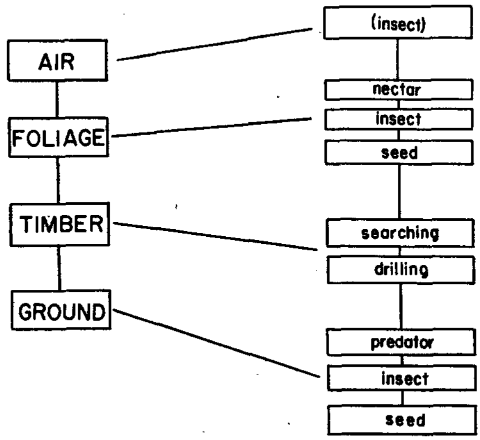

Fig. 1. Diagram of the feeding groups on the left and the nine categories into which they are divided on the right.

individuals, or index thereof, may be determined. Of these two alternatives the latter is somewhat better, as it gives a more accurate representation of the actual avian biomass within each category, but such information is difficult to gather. Both these methods are shown in the analysis for the Yosemite area (fig. 3).

Graphic presentation of the size of each group and subdivision is made by a series of nine bars placed horizontally on a vertical axis and grouped into the four major feeding stations. The width of the bar represents the numerical size of the group. The height of the bar is merely such that the resulting "tree" is properly proportioned. When analysis of the changes in the composition of an avifauna throughout the yearly cycle is made, one such diagram is prepared for the avifauna present in each month. Examination of the feeding habits of the species present must be made for each month and reclassification made for those birds which change their feeding habits with seasonal change in the environment. The resulting series of twelve diagrams forms an "avifaunal spectrum" of the area. When analysis of several areas is to be made for the same time of year, one or several such diagrams for each area are prepared, depending on the length of the season under consideration.

Additional comparison with climatic or other environmental conditions may be obtained by graphing the range of such conditions for each month under the avifaunal diagram. Parallels between changes in environmental conditions and avifauna are thus exposed. If such a complete diagraming is made and is to be compared with another spectrum plus climatic graphs from another region, it is essential that the same scale be used in all diagrams.

Similar diagrams were used during the past year to present to students the avifaunas (breeding birds) of ecologic formations in California as determined by Miller (1951). The birds listed by Miller as "1" and "2" for a formation were used as being those species characteristic of the formation. The species were sorted into the nine categories previously described and were diagrammed with all the "1" species to the left of the vertical axis and all "2" species to the right. The resulting diagrams are highly concentrated summaries of the avifaunas—abstractions upon an abstraction, so to speak.

The three locations used in the present analysis are: Boca Spring, Nevada County, California, visited in 1949, 1950, and 1951 by the author while obtaining birds for experimental work; Yosemite Valley, California, for which were available the data sum-

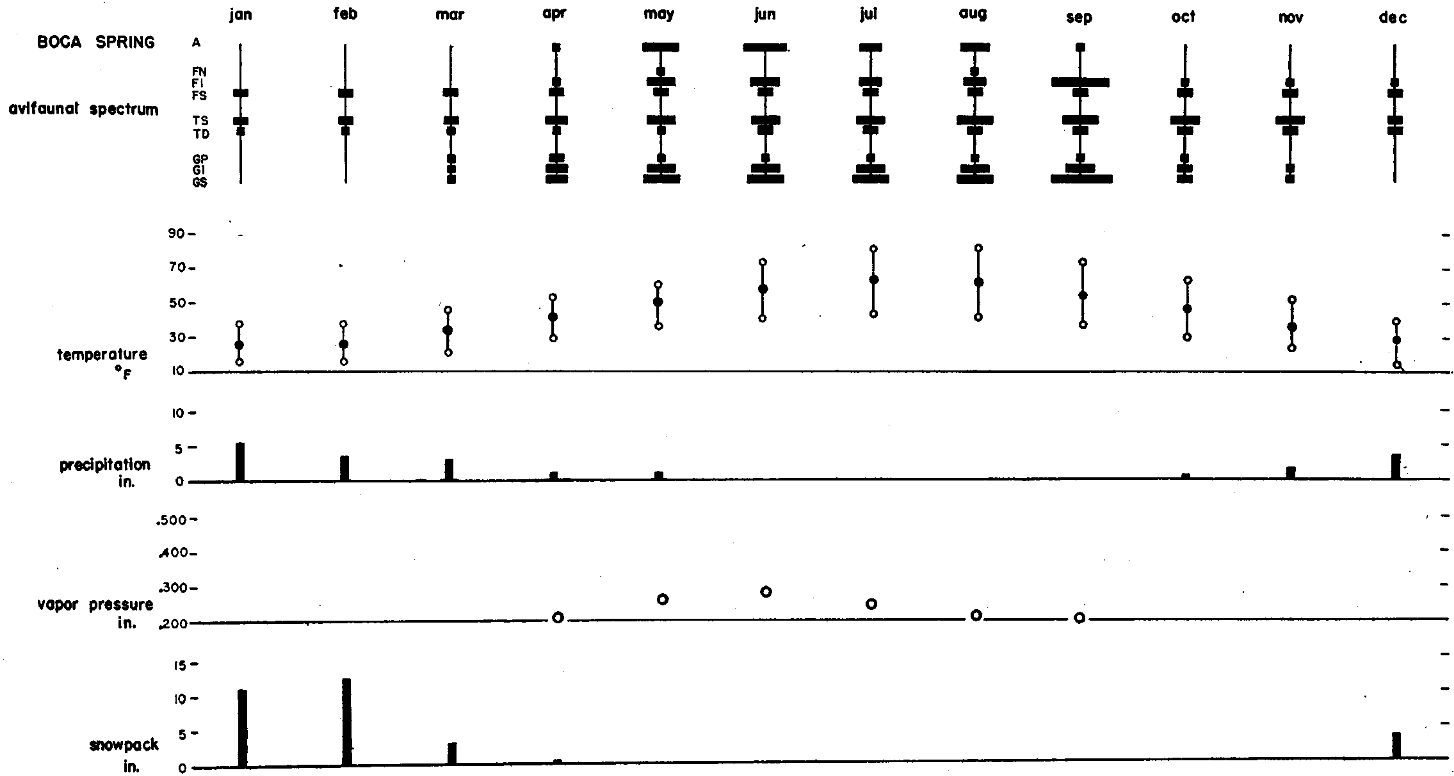

Fig. 2. Avifaunal spectrum and climate diagrams for Boca Spring, Nevada County, California.

marized by Linsdale (1932) from the notes of Mr. and Mrs. Charles W. Michael for the years 1920 to 1931; and Glen Oaks canyon on the outskirts of Glendale, California, visited frequently by the author between 1936 and 1942 in company with William G. Webb and Vincent S. Yoder.

BOCA SPRING, NEVADA COUNTY

Boca Spring is a permanent spring 8½ miles northeast of Truckee at an elevation of 6000 feet on the east slope of the central Sierra Nevada of California. The area studied consists of a meadow approximately one hundred yards long watered by the spring and the xeric pine forest surrounding the meadow. The forest is made up of three vegetational strata. The tree layer is composed of second growth *Pinus jeffreyi,* thirty to sixty feet high, and spaced evenly about ten to thirty yards apart. The shrub layer consists of bushes of three species, *Artemisia tridentata, Purshia tridentata,* and *Wyethia mollis,* spaced two to six feet apart. Between these bushes grows a sparse cover of grasses, *Bromus tectorum, Poa secunda,* and *Sitanion hystrix,* and forbs not identified. This vegetation represents that of an ecotone between the pine forests of higher elevations and the *Artemisia* covered sagebrush desert of lower elevations. The meadow vegetation consists of a great variety of grasses, sedges, and rushes, some of which are *Juncus balticus, J. nevadensis, J. effuses, Carex kelloggii, C. nebraskensis,* and *Mimulus guttatus.* In the running water coursing through the meadow are *Lemna* sp. and *Montia* sp. The entire area studied slopes toward the west.

Climatically Boca Spring is dry, having an annual total precipitation of 21 inches, about half to one-third that of the same elevation on the west slope of the Sierra. Summer temperatures are warm in the daytime, with cool nights and frost possible at practically any time of the year. Snowfall is moderate, being about half that at the same elevation on the Sierran west slope. Winter temperatures tend to be lower, both day and night than on the west slope.

Although no detailed studies of soil were made, the soil appears to be shallow and of poor quality. Rocky outcrops are common over the area, and in eroded ruts in the roads a rocky substrate, composed of boulders ranging from an inch in diameter upward, is revealed only a few inches below the surface. The soil within the meadow is rich and at least a foot deep in the deepest portions. It is, however, saturated with water a greater part of the growing season, and it is frozen solid the rest of the year.

In the fall, birds apparently migrating south along the east slope of the Sierra Nevada pass through Boca Spring, and for a few weeks they swell the avifauna both in total number and in species composition. Winter populations are small and widely scattered. The avifauna increases through the spring to the full size of the breeding population in early summer and drops off in later summer due, it is suspected, to an up-mountain migration of postbreeding birds to the forests and meadows of the Sierran crest where the vegetation is still lush at that season (fig. 2).

Except for November, January, and February, trips were made to this area monthly, usually for three days. Careful surveys and notes were made of the avifauna on each trip. Composition of the bird life of those months when the area was not visited was derived from generalized reports on the bird life of the central Sierra Nevada at those seasons and by interpolation from data obtained in adjacent months.

YOSEMITE VALLEY, YOSEMITE NATIONAL PARK

Yosemite Valley has been visited by so many people and accounts and photographs published so frequently, that a detailed description of it is unnecessary. Accounts of the flora may be found in Hall and Hall (1912). The valley lies in a glacier-carved gouge

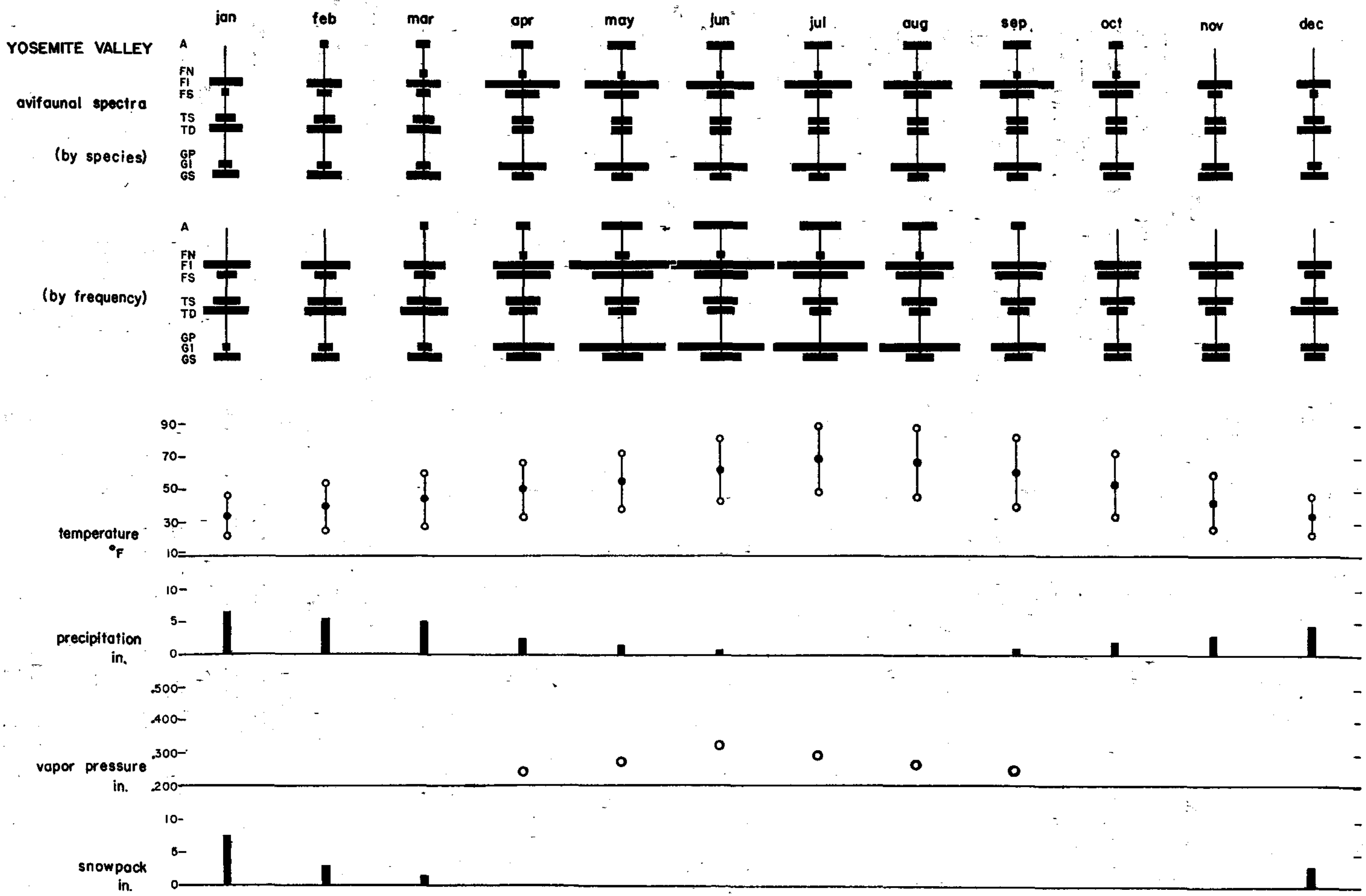

Fig. 3. Avifaunal spectra and climate diagrams for Yosemite Valley, California.

in the west slope of the Sierra Nevada at an elevation of 4000 feet, walled by cliffs and peaks of elevations from 6000 to 9000 feet. The Merced River traverses this valley from east to west.

The flora varies from an open coniferous forest composed of yellow pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga taxifolia*), incense cedar (*Libocedrus decurrens*), white fir (*Abies concolor*), and black oak (*Quercus kelloggii*) through moist meadows to streamside associations of willows (*Salix* sp.), black cottonwood (*Populus fremontii*), dogwood (*Cornus nuttallii*), and alder (*Alnus rhombifolia*). Golden-cup oak (*Quercus chrysolepis*) is found on the talus slopes along the margins of the narrow valley.

The region has a moderate climate. Days become hot in midsummer, but night temperatures are cool. Winter temperatures are moderately cold, with a light snowfall, which, however, varies widely from one year to the next. The total precipitation averages 33 inches a year. Probably the weather within the valley, bounded as it is on all sides by high walls, is not characteristic of other places on the west slope of the Sierra at the same elevation.

The species composition of the avifauna, by months, was plotted (fig. 3, upper series of diagrams) from the list presented by Linsdale (*op. cit.*, table 1). The diagrams by frequency for each month were made by totaling the frequency values for the month in question for all species of one category. This sum was divided by 50 to the nearest whole number and the quotient used to determine the length of the bar in the diagram (fig. 3, lower series of diagrams). The number 50 was chosen arbitrarily so as to produce horizontal bars within the same value ranges as in the species diagrams.

GLEN OAKS CANYON, GLENDALE, LOS ANGELES COUNTY

Glen Oaks Canyon lies at the eastern edge of the city of Glendale in the coastal chaparral belt of southern California. At the time the data used here were collected it was relatively unaffected by human activities except those of hikers and occasional naturalists. Some small check dams three to six feet high were once installed to retard runoff. To insure that there would be some runoff to retard, the undergrowth had been cleared from the walls of the canyon, but at the time of the visits this had all grown back, the dams had silted in and were almost hidden in leaf mold. The canyon, running from north to south, drained several square miles of chaparral-covered hillside. Water ran in the bottom in a small rivulet during practically the entire year, and it reached creek proportions, four to ten feet wide, during severe rains. At its mouth the canyon opened to form a sandy wash although the water drained into the ground before reaching this spot during most of the year.

Vegetation in the sandy mouth of the canyon consisted of a scattered tree canopy of live oak (*Quercus agrifolia*) and California sycamore (*Platanus racemosa*). There was an interrupted shrub layer of *Ribes speciosum, Stachys bullata, Nicotiana glauca, Solanum douglasii,* and *Sambucus coerulea*. The ground was covered each spring by a growth of annual grasses which gave way during the summer to scattered composites such as *Senecio vulgaris*.

Upstream from its mouth the canyon narrowed and become steep walled. The tree layer made a continuous canopy of sycamore and live oaks, mostly the latter, now changed in habit from a wide-crowned form into tall slender trees carrying leaves only on the upper branches. There were, in addition, cottonwoods (*Populus fremontii*) and laurel (*Umbellularia californica*) growing along the bottom of the canyon. The understory consisted of poison oak (*Rhus diversiloba*), *Rubus vitifolia,* ferns, *Equisetum,* and numerous annual forbs and grasses. Much of the ground surface carried no lower vegetation, but a layer of leaves and leaf mold covered the decomposing granite soil.

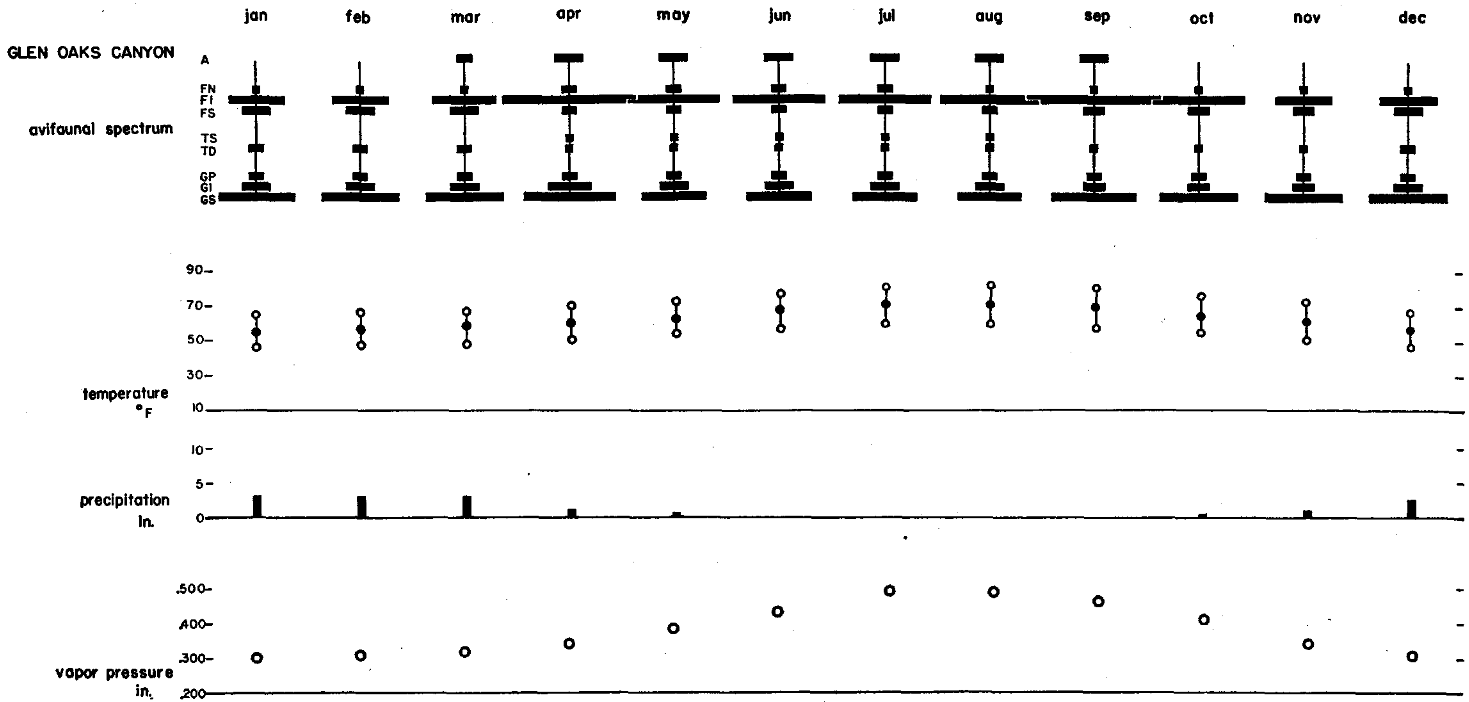

Fig. 4. Avifaunal spectrum and climate diagrams for Glen Oaks Canyon, Los Angeles County, California.

The adjacent hills were covered with coastal chaparral with all its usual elements such as *Adenostoma, Artemisia, Rhus, Rhamnus, Ceonothus,* and *Salvia.*

The climate is typical of coastal southern California. Winters are moderately warm, frosts being few and absent in some winters; summers are warm to hot; and the diurnal range from night to daytime temperatures is small at all seasons. The vapor pressure of water in the air is moderate in winter and high in late summer, but rainfall is light, with 15 inches annual average, and subject to considerable annual variation.

The avifauna of Glen Oaks canyon is made of three elements: a resident population, a summer visitant population, and a winter visitant population. These are of approximately the same size so that there is no dramatic change in the number of birds present at any one period although the species composition changes with the seasons. The summer population is somewhat higher than at other times of year (fig. 4).

Notes on the avifauna were kept through several years of frequent but irregular visiting. During 1941 an intensive study of the biota was conducted with surveys of the bird population being made on bi-weekly visits throughout the year.

DISCUSSION

Feeding is used as the basis for this study method because it is considered to be of major importance in the lives of birds and most other avian activities are subject to modification or variation as necessary to meet food demands successfully. Kendeigh (1949) and Siebert (1949) demonstrated that response to winter temperatures is governed by food intake ability. Lack (1950), Skutch (1950), Moreau (1950), and Voous (1950) report that breeding seasons of birds in various parts of the world are closely correlated with the appearance of abundant food. Furthermore, the breeding season is not the same for feeders of all types in a given area, but birds appear to breed in the most favorable feeding season often despite unfavorable climatic conditions. Errington (1941) and Cade (1952) correlate density of a species of birds with the available food in addition to other factors such as cover and roosting places. Moreau (1950) reports that breeding may be prevented or interrupted by a failure of the food supply. Lack (1947) concludes that clutch size in various species of birds is genetically determined in relation to the food available for feeding young during the breeding season. Kendeigh and Baldwin (1937) suggest, from work by Kleiber and Dougherty (1934), that unfavorable combinations of climate and a depressing influence thereof upon food intake may result in a lack of egg production in house wrens (*Troglodytes aëdon*).

It is self evident that the distribution of specialized feeders such as woodpeckers, crossbills, and hummingbirds is determined by feeding sites and food in addition to other factors such as climate and nesting sites. In other species, food considerations probably are equally significant, although less obvious without detailed study. In a study of three finches of the genus *Carpodacus* (Salt, 1952) it appeared that interaction of climatic conditions and feeding were of major importance in regulating the summer distribution of all three species, but particularly *C. purpureus* and *C. cassinii.*

A classification of birds by feeding habits shows a similarity to familial classification. Within certain families, such as the Tyrannidae, Sittidae, and Troglodytidae, feeding behavior is fairly constant, and a classification according to family is equivalent to one according to food habits. In other families, however, such as the Falconidae, Picidae, and Fringillidae, birds of diverse feeding and ecologic type are brought together taxonomically but such a grouping does not apply ecologically. Furthermore, if faunal classification were made on the basis of family groups the opportunity for comparing avifaunas from widely separated land masses would be lost. If one used such a system he would be unable, for instance, to compare the birds of the open savanna of central

Africa and its large numbers of ploceids with the avifauna of the savannas in California where no birds of this family occur except the introduced English Sparrow.

Habitat selection, the strictly psychological response by birds to the aspect of vegetation, appears to operate strongly only during the breeding season, and for this reason it will not serve as a basis for codification of ecologic preferences throughout the year. Biomes, life-zones, and biotic provinces, the major ecologic units currently used for ecologic classification, are too wide in their scope to provide any but a gross correlation between birds and their environments. Studies of bird fauna in successional stages of a particular biome provide excellent correlation between avian occurrence and vegetational characteristics but do not allow comparison between avifaunas of different geographic regions.

The nine categories used here appear to be the best choice as of this time. Further use may make changes desirable. It may be advisable to divide the "air" group into a "flying" category for the swallows and nighthawks, and a "perching" category for the flycatchers. Also, it may be more valuable to divide the birds that feed in the tree foliage from those feeding in the shrub layer. This change would require the addition of three more layers in the diagrams. For simplicity both these alternatives were rejected in this initial report; they could always be adopted if required. Basically, the choice is between a highly specific classification and a generalized one. The one here proposed is moderately generalized. Within each category the birds presumably segregate into their respective niches on the basis of size of food particles eaten, stratum within the major elevation from the ground where they feed (Colquhoun and Morley, 1943), degree of adherence to specific diet of one type, and psychological preference for a specific location. None of these subtler characteristics are revealed in this classification.

Inspection of the spectrum of a single locality for an entire year reveals that between certain months no great change in the avifauna takes place. It may prove to be convenient and to sacrifice no great degree of accuracy to group the similar months together and express their fauna by a single diagram while graphing individually those months wherein important changes take place. Thus December-January-February and June-July-August might each be expressed with a single graph and the remaining months shown individually, a reduction from twelve to eight individual figures in the spectrum.

This system of classifying field observations provides a tool for certain kinds of studies not possible with other approaches. Generalized comparisons can be made between avifaunas on an ecologic basis regardless of the taxonomic character of those avifaunas. It will permit the charting of variation in faunal structure with changes in environment due to plant succession, seasonal change, or land management manipulation. Reversing this approach, the avifauna may be regarded as a reflection of the structure and character of the environment and used to trace variation therein. Grinnell was right in regarding animals as more sensitive to the environment than any thermometer or atmometer (quoted in Allee, *et al.*, 1949:56). What apparently never occurred to him was the fact that without twenty-five years of intimate acquaintance with those animals, such as he had, you could not read this "thermometer," or if you could, you could not communicate your reading to anyone else. This type of classification also serves to throw into focus probable relationships between specific environmental conditions such as climate, vegetation, and structure and the birds living in that area.

Classifying thus, however, is a specialized approach and while exposing information of one sort it also ignores or actually conceals information of other kinds. Specific ecologic requirements of a single species are not elucidated save in a general way. Evolutionary adherence to a specific landmass or to a migrating flora is not revealed. Placing a bird in a specific food category because it eats more than 50 per cent of foods of a certain kind serves to conceal the character of the remainder of its diet. These secondary foods may be highly significant not only in governing ecologic response but also nutritionally. This is, of course, a "one factor" analysis and as such, subject to "over-implification," to coin a word.

RESULTS

Critical comparison of the spectra (figs. 2–4) for the three localities reveals many informative differences between them, not only in the presence or absence of categories at a particular season but changes of size within, and changes of proportion between, categories with the seasons. Not all these points require enumeration, but some of the more interesting merit comment.

Considering the Boca avifauna first, within the foliage group the nectar feeding birds are absent as residents and appear in the spectrum only as transients during the spring and early fall. This presumably is a reflection not of a complete lack of nectar producing flowers but of low density of them, insufficient to permit efficient harvesting of nectar by a bird confined to a limited area during the nesting period. In the ground group, winter conditions of low temperatures, especially at night, coupled with the deep snowpack serve to eliminate this stratum as a forage area during the three winter months, but ground foraging is resumed in the spring well before all the snow is melted. Ground foraging is about equally divided between insects and seeds throughout the season except in the fall when the large influx of migrant insect eaters arrives.

In the Yosemite avifauna, insect-eating birds of the foliage group are the dominant category whether listed by species or by frequency of observation of species, and more so in winter than in summer. This high winter proportion is explained by the fact that many of them at that season are actually eating berries rather than insects. Also there is an obvious rise in the foliage-insect category (by frequency) during the spring migration but not in the fall migration. In the timber group the searching birds are the constant element throughout the season. Comparison with the other diagrams reveals that such is not the case at the other two localities. In the ground group, the lack of predators is probably due to the area being a national park with a heavy human population during much of the year. It will also be noted that winter conditions in Yosemite are less effective than at Boca in modifying ground foraging, especially for the seed eaters which are practically constant both in numbers of species and frequency throughout the year.

In the avifauna of Glen Oaks both the foliage and ground groups are large. The foliage group is dominated throughout the year, but particularly in summer, by the insect eaters. There is a large influx of birds of this category to the area during both the spring and fall migrations. The seed eaters in this group feed mostly on acorns and form an important part of the foliage group only during the winter. The timber group is very poorly represented, particularly by timber searchers. Whether this is due to the characteristics of oaks and sycamores in providing foraging niches or to a different insect population is unknown. The ground foraging group is largely composed of seed eaters, more so in winter than in summer. The dry and stony ground apparently provides a poor supply of insects compared to the seed crop. This ground environment is essentially stable throughout the year, both in numbers and proportions of the three categories to one another.

The following comments are prompted by comparison of the three spectra. Boca is essentially a harsh and unproductive environment. Low winter temperatures, an appreciable snowpack, high summer temperatures, dry air, and poor soil combine to yield a limited food supply. This supply is exploited to the fullest in the summer, but supports only a meager bird life in the winter. The avifauna as here diagramed is essentially in good proportion throughout the year. Comparing the diagrams for July for all three localities will demonstrate this conclusion. Proportionality is maintained throughout the march of the seasons, the birds of all groups gradually diminishing at equal rates with the onset of winter.

The Yosemite avifauna also shows balanced proportions between groups and within each group. Major fluctuations result from changes in the population of insect eating birds. Presumably the varied avifauna results from a high variety of niches and good production of foods. This is to be expected from the moderate winter conditions, warm moist summer, and variety in the vegetation.

In the Glen Oaks area the avifauna is not well proportioned between the groups. The foliage and ground groups are much larger than the others, the air group is moderate, and the timber groups very small. Further, within the foliage and ground groups, one category is much larger than the others, particularly so in the foliage groups where the category of insect eaters is large compared to the others. This suggests either extreme conditions, or what may be another way of regarding the same circumstances, lack of variety. Weather conditions are without variety. Temperatures vary only slightly from winter to summer, and there is little spread at any season from maximum to minimum temperatures. Rainfall is slight in winter; partly compensating for the lack of summer rains is a high vapor pressure during that period producing relatively uniform conditions of moderate aridity throughout the year. Vegetation conditions also show only moderate change with the seasons. The oaks are not deciduous and many of the shrubs of the region are in leaf throughout the year. Only the grasses show a pronounced seasonal variation.

There is less difference between the localities in their air feeding birds than in any other group. The response of this group to seasonal change is nearly the same both with respect to time of arrival and departure and in numbers of species for all the three localities despite the many differences in climate and vegetation between them. Apparently birds of this feeding habit are little influenced by these two important features of the environment, which is another way of saying that in any locality there will be found about the same variation in the composition of the flying insect population.

Insectivorous birds are the most sensitive to changes in season and vegetation. The upsurge in insect eaters both in the foliage and on the ground, but not in the air, comes in the spring after the first noticeable decrease in rainfall. That is to say, these birds arrive in an area in the first dry month following the spring rains. This tendency can be seen in the spectra for all three localities. Whether there is a direct causal relation between these two events cannot be said, but it is worth noting that in the fall, when the rainfall changes gradually instead of by steps as in the spring, there is a corresponding gradual change in the insect-eating population rather than a sudden one.

In the seed-eating birds of the foliage group, the Boca population is small and constant throughout the year, the Yosemite population is highest in the summer, and the Glen Oaks population is highest in the winter. This suggests that Yosemite and Glen Oaks or similar stations are serving as summer and winter quarters for a certain portion of the seed-eating birds. Whether this actually is true or not depends on whether the decreases and increases registered represent actual departures from the areas or merely changes in food habits of birds present all year round.

The presence of a noticeable spring migration through Yosemite and a noticeable fall migration through Boca once more brings to mind the possibility of a change in the migration route up and down the Sierran axis from spring to summer. Field observations by others have also suggested this possibility, but so far no definite answer is possible without banding data.

Comparison of the three avifaunas and their changes throughout the year reveals this fact. Yosemite and Glen Oaks have a large and stable population throughout the year. This population is augmented in summer at Yosemite by the addition, largely, of insect eating birds in the air, foliage, and ground groups. In Glen Oaks the basic structure of the avifauna is even more stable .In summer there are added the insect-eating birds in the air and foliage groups and in winter the seed-eating birds in the foliage and ground groups. In both localities at least half the feeding niches are, so to speak, open for occupancy the year round. Under the conditions of climate and vegetation present in the two areas these niches will sustain the birds occupying them through the environmental stresses presented in the course of a year. The other niches are open for use during more limited portions of the winter or summer.

At Boca, on the other hand, the entire structure of the avifauna is drastically modified by the seasonal march of environmental conditions. There is only a small population of hardy species to be considered as the basic one of the area. Sooner or later, as winter conditions become more severe, practically all the niches are closed to further use by birds and they are forced to leave.

Whether the difference in pattern between Boca and the other two places is due merely to differences in elevation or is a more general distinction between the habitats of the Pacific slope and the Great Basin may be revealed by further analyses of the type here presented.

SUMMARY

A method is described for classifying the avifauna of a locality into nine categories on the basis of location of the feeding site within the strata of the vegetation and the type of food taken. A diagram of horizontal bars on a vertical axis is used to graph the results of such classification.

Yearly changes in the bird life of three Californian localities are reported and diagramed according to this system. These are: Boca Spring, Nevada County; Yosemite Valley; and Glen Oaks Canyon, Los Angeles County.

Birds of certain feeding habits, such as the air feeders, show little sensitivity to differences in environmental conditions from place to place, while other feeding types appear to be extremely sensitive, particularly those feeding on insects either in the foliage or on the ground.

Differences between these localities are revealed in the structure and proportions of their avifaunas. Presumably these differences reflect differences in vegetation structure and climate.

Both Yosemite Valley and Glen Oaks Canyon provide a sizeable proportion of niches available for use throughout the entire year, while at Boca Spring nearly all the niches are closed to use during the winter months.

AVIFAUNA OF BOCA SPRING

Species	Residence	Classification
Accipiter striatus, Sharp-shinned Hawk	Apr.	ground-predator[1]
Buteo jamaicensis, Red-tailed Hawk	Mar.–Oct.	ground-predator
Falco sparverius, Sparrow Hawk	Apr.–Sept.	ground-insect
Zenaidura macroura, Mourning Dove	Apr.–Sept.	ground-seed
Chordeiles minor, Booming Nighthawk	Aug.–Sept.	air
Phalaenoptilus nuttallii, Poor-will	May–Aug.	air
Selasphorus rufus, Rufous Hummingbird	May, Aug.	foliage-nectar
Colaptes cafer, Red-shafted Flicker	May–Oct.	ground-insect
Dendrocopos villosus, Hairy Woodpecker	All year	timber-drilling

AVIFAUNA OF BOCA SPRING *(continued)*

Species	Residence	Classification
Dendrocopos albolarvatus, White-headed Woodpecker	June–Dec.	timber-drilling
Empidonax wrightii, Wright Flycatcher	May–June	air
Empidonax griseus, Gray Flycatcher	May–Aug.	air
Contopus richardsonii, Western Wood Peewee	May–Aug.	air
Tachycineta thalassina, Violet-green Swallow	Apr.–June	air
Cyanocitta stelleri, Steller Jay	All year	foliage-seed
Nucifraga columbiana, Clark Nutcracker	Apr.–Nov.	foliage-seed
Parus gambeli, Mountain Chickadee	All year	timber-searching
Sitta carolinensis, White-breasted Nuthatch	May–Nov.	timber-searching
Sitta canadensis, Red-breasted Nuthatch	Aug.–Sept.	timber-searching
Sitta pygmaea, Pigmy Nuthatch	Apr.–Nov.	timber-searching
Certhia familiaris, Brown Creeper	All year	timber-searching
Turdus migratorius, Robin	Apr.–Sept.	ground-insect
Sialia currucoides, Mountain Bluebird	Mar.–Nov.	ground-insect
Myadestes townsendi, Townsend Solitaire	May–Dec.	foliage-insect
Regulus calendula, Ruby-crowned Kinglet	Sept.	foliage-insect
Vireo solitarius, Solitary Vireo	Sept.	foliage-insect
Vireo gilvus, Warbling Vireo	Sept.	foliage-insect
Vermivora celata, Orange-crowned Warbler	May, Sept.	foliage-insect
Dendroica auduboni, Audubon Warbler	Apr.–Sept.	foliage-insect
Dendroica occidentalis, Hermit Warbler	Sept.	foliage-insect
Wilsonia pusilla, Pileolated Warbler	May–June	foliage-insect
Piranga ludoviciana, Western Tanager	June–Sept.	foliage-insect
Carpodacus cassinii, Cassin Finch	All year	foliage-seed Dec.–Mar. ground-seed Apr.–Nov.
Chlorura chlorura, Green-tailed Towhee	May–Sept.	ground-seed
Pipilo erythrophthalmus, Spotted Towhee	Sept.	ground-seed
Junco oreganus, Oregon Junco	Mar.–Oct.	ground-seed
Spizella passerina, Chipping Sparrow	May–Sept.	ground-insect[2]
Zonotrichia leucophrys, White-crowned Sparrow	Sept.	ground-seed
Melospiza melodia, Song Sparrow	Aug.–Sept.	ground-seed

[1] A debatable classification. Many persons would classify this species as a foliage predator, but in this situation they take an important percentage of prey on the ground. Precisely what percentage cannot be determined.

[2] From April through August the diet of this species is over 50 per cent insects. In September the percentage of plant food taken is over 50 per cent (see Martin, Zim, and Nelson, 1951:202)

AVIFAUNA OF YOSEMITE VALLEY

Species	Residence	Classification
Falco sparverius, Sparrow Hawk	All year	ground-insect
Actitis macularia, Spotted Sandpiper	Apr.–Sept.	ground-insect
Columba fasciata, Band-tailed Pigeon	All year	foliage-seed Apr.–Oct. ground-seed Nov.–Mar.
Aëronautes saxatalis, White-throated Swift	Feb.–Oct.	air
Stellula calliope, Calliope Hummingbird	Mar.–Oct.	foliage-nectar
Colaptes cafer, Red-shafted Flicker	All year	ground-insect Apr.–Nov. timber-drilling Dec.–Mar.
Balanosphyra formicivora, Acorn Woodpecker	All year	foliage-seed Apr.–Nov. timber-drilling Dec.–Mar.
Dendrocopos villosus, Hairy Woodpecker	All year	timber-drilling
Dendrocopos pubescens, Downy Woodpecker	All year	timber-drilling
Dendrocopos albolarvatus, White-headed Woodpecker	All year	timber-drilling
Empidonax traillii, Traill Flycatcher	May–Oct.	air
Contopus richardsonii, Western Wood Peewee	Apr.–Sept.	air
Tachycineta thalassina, Violet-green Swallow	Mar.–Sept.	air
Cyanocitta stelleri, Steller Jay	All year	foliage-seed
Parus gambeli, Mountain Chickadee	All year	timber-searching
Sitta canadensis, Red-breasted Nuthatch	All year	timber-searching

AVIFAUNA OF YOSEMITE VALLEY *(continued)*

Species	Residence	Classification
Certhia familiaris, Brown Creeper	All year	timber-searching
Catherpes mexicanus, Canyon Wren	All year	ground-insect
Turdus migratorius, Robin	All year	foliage-insect Sept.–Mar. ground-insect Apr.–Aug.
Hylocichla ustulata, Swainson Thrush	May–Nov.	ground-insect
Sialia mexicana, Mexican Bluebird	Oct.–May	foliage-insect[1]
Regulus satrapa, Golden-crowned Kinglet	All year	foliage-insect
Regulus calendula, Ruby-crowned Kinglet	Sept.–May	foliage-insect
Vireo solitarius, Solitary Vireo	Apr.–Sept.	foliage-insect
Vireo gilvus, Warbling Vireo	Apr.–Sept.	foliage-insect
Dendroica aestiva, Yellow Warbler	Apr.–Sept.	foliage-insect
Dendroica auduboni, Audubon Warbler	All year	foliage-insect
Dendroica nigrescens, Black-throated Gray Warbler	Apr.–Oct.	foliage-insect
Oporornis tolmiei, Tolmie Warbler	Apr.–Sept.	foliage-insect
Agelaius phoeniceus, Red-winged Blackbird	Feb.–Oct.	ground-seed
Euphagus cyanocephalus, Brewer Blackbird	Apr.–Nov.	ground-insect Apr.–Sept. ground-seed Oct.–Nov.
Piranga ludoviciana, Western Tanager	Apr.–Sept.	foliage-insect
Pheucticus melanocephalus, Black-headed Grosbeak	Apr.–Oct.	foliage-insect[2]
Hesperophona vespertina, Evening Grosbeak	Feb.–Oct.	foliage-seed Feb.–May, Sept.–Oct. foliage-insect June–Aug.
Carpodacus purpureus, Purple Finch	All year	foliage-seed Apr.–Oct. ground-seed Nov.–Mar.
Pipilo erythrophthalmus, Spotted Towhee	All year	ground-seed
Junco oreganus, Oregon Junco	All year	ground-seed
Spizella passerina, Chipping Sparrow	Apr.–Sept.	ground-insect[3]

[1] Mistletoe berries gathered in the trees form the major food for this species in Yosemite in winter (Grinnell and Storer, 1924:620).

[2] Classified as foliage insect since their diet consists mostly of insects and some berries (Martin, Zim, and Nelson, 1951:180).

[3] See note 2, p. 270.

AVIFAUNA OF GLEN OAKS CANYON

Species	Residence	Classification
Accipiter cooperii, Cooper Hawk	All year	ground-predator[1]
Buteo jamaicensis, Red-tailed Hawk	All year	ground-predator
Lophortyx californica, California Quail	All year	ground-seed
Columba fasciata, Band-tailed Pigeon	Dec.–Mar.	foliage-seed
Zenaidura macroura, Mourning Dove	All year	ground-seed
Otus asio, Screech Owl	All year	ground-insect
Archilochus alexandri, Black-chinned Hummingbird	Apr.–July	foliage-nectar
Calypte anna, Anna Hummingbird	All year	foliage-nectar
Colaptes cafer, Red-shafted Flicker	All year	ground-insect Mar.–Aug. timber-drilling Sept.–Feb.
Balanosphyra formicivora, Acorn Woodpecker	All year	foliage-seed Apr.–Nov. timber-drilling Dec.–Mar.
Dendrocopos nuttallii, Nuttall Woodpecker	All year	timber-drilling
Myiarchus cinerascens, Ash-throated Flycatcher	Apr.–Sept.	air
Empidonax difficilis, Western Flycatcher	Mar.–Sept.	air
Contopus richardsonii, Western Wood Pewee	Apr.–Sept.	air
Petrochelidon pyrrhonota, Cliff Swallow	Mar.–Sept.	air
Cyanocitta stelleri, Steller Jay	Dec.–Mar.	foliage-seed
Aphelocoma coerulescens, Scrub Jay	All year	foliage-seed
Parus inornatus, Plain Titmouse	All year	timber-searching Apr.–Aug. foliage-seed Sept.–Mar.
Psaltriparus minimus, Bush-tit	All year	foliage-insect
Chamaea fasciata, Wren-tit	All year	foliage-insect
Troglodytes aëdon, House Wren	Mar.–Oct.	foliage-insect

AVIFAUNA OF GLEN OAKS CANYON *(continued)*

Species	Residence	Classification
Thryomanes bewickii, Bewick Wren	All year	foliage-insect
Toxostoma redivivum, California Thrasher	All year	ground-insect
Hylocichla guttata, Hermit Thrush	Oct.–Apr.	ground-insect
Hylocichla ustulata, Swainson Thrush	Apr.–Sept.	ground-insect
Sialia mexicana, Mexican Bluebird	Dec.–Apr.	ground-insect
Polioptila caerulea, Blue-gray Gnatcatcher	All year	foliage-insect
Regulus calendula, Ruby-crowned Kinglet	Oct.–Mar.	foliage-insect
Phainopepla nitens, Phainopepla	Apr.–Sept.	foliage-insect[2]
Vireo huttoni, Hutton Vireo	All year	foliage-insect
Vireo bellii, Bell Vireo	Apr.–Sept.	foliage-insect
Vireo solitarius, Solitary Vireo	Apr., Sept.–Oct.	foliage-insect
Vireo gilvus, Warbling Vireo	Apr.–Oct.	foliage-insect
Vermivora celata, Orange-crowned Warbler	Mar., Sept.	foliage-insect
Dendroica aestiva, Yellow Warbler	Apr.–Sept.	foliage-insect
Dendroica auduboni, Audubon Warbler	Sept.–Apr.	foliage-insect
Dendroica nigrescens, Black-throated Gray Warbler	Apr., Sept.	foliage-insect
Dendroica townsendi, Townsend Warbler	Apr., Oct.	foliage-insect
Dendroica occidentalis, Hermit Warbler	Apr., Aug.	foliage-insect
Wilsonia pusilla, Pileolated Warbler	Apr.–Oct.	foliage-insect
Icterus cucullatus, Hooded Oriole	Apr.–Sept.	foliage-insect
Piranga ludoviciana, Western Tanager	Apr., Sept.	foliage-insect
Pheucticus melanocephalus, Black-headed Grosbeak	Apr.–Sept.	foliage-insect
Passerina amoena, Lazuli Bunting	Apr.–Sept.	ground-seed
Carpodacus mexicanus, House Finch	All year	ground-seed
Spinus psaltria, Arkansas Goldfinch	All year	ground-seed
Spinus lawrencei, Lawrence Goldfinch	Apr.–Sept.	ground-seed
Pipilo erythrophthalmus, Spotted Towee	All year	ground-seed
Pipilo fuscus, Brown Towhee	All year	ground-seed
Junco oreganus, Oregon Junco	Oct.–Apr.	ground-seed
Spizella passerina, Chipping Sparrow	Apr., Sept.	ground-seed (Sept.) ground-insect (April)
Zonotrichia coronata, Golden-crowned Sparrow	Sept.–Apr.	ground-seed
Zonotrichia leucophrys, White-crowned Sparrow	Sept.–Apr.	ground-seed
Passerella iliaca, Fox Sparrow	Oct.–Apr.	ground-seed
Melospiza melodia, Song Sparrow	All year	ground-seed

[1] This classification is open to debate. The exact percentage of prey taken on the ground cannot be stated.
[2] Classified thus instead of "air" on the basis of data from Martin, Zim, and Nelson (page 159) and personal observations that in this area they depend heavily on berries of *Sambucus* for food supply.

WEATHER DATA

Glen Oaks Canyon. All data are for Los Angeles from the United States Department of Agriculture Weather Bureau; see "Climatic Summaries by Sections to 1930" (Section 18). Vapor pressure data are taken from Day (1917). Vapor pressure is that for 5:00 p.m., Pacific Standard Time.

Yosemite Valley. All data are from "Climatic Summaries by Sections to 1930" (Section 17), except snowpack and vapor pressure data. Snowpack figures were derived by averaging monthly records for the years from 1937 to 1948 published by the United States Department of Commerce in "Climatological Data, Monthly Summaries, California Section." Vapor pressure figures are for South Entrance (Yosemite) Ranger Station, elevation 5120 feet, at 4:30 p.m., Pacific Standard Time, from 1938 to 1948 (data provided by Fire Weather Section of Weather Bureau at San Bruno, California).

Boca Spring. Mean temperature based on a 30-year record is for Boca from McAdie (1903). Maximum and minimum temperatures are for Truckee from "Climatic Summaries by Sections to 1930" (Section 16). Precipitation figures are for Boca, also from the Climatic Summaries. Snowpack figures are for Boca averaged from monthly records in climatological data of the United States Department of Commerce from 1937 to 1948. Vapor pressure figures are for Sierraville, elevation 5000 feet, 20 miles northwest of Boca, at 4:30 p.m., Pacific Standard Time, for the years from 1938 to 1948; these data were provided by the Fire Weather Section of the Weather Bureau at San Bruno, California.

LITERATURE CITED

Allee, W. C., Emerson, A. E., Park, O., Park, T., and Schmidt, K. P.
1949. Principles of animal ecology (Philadelphia, Pa., W. B. Saunders Co.).

Cade, T. J.
1952. The influence of food abundance on the over-wintering of pine grosbeaks at College, Alaska. Condor, 54:363.

Colquhoun, M. K., and Morley, A.
1943. Vertical zonation in woodland bird communities. Jour. Anim. Ecol., 12:75-81.

Day, P. C.
1917. Relative humidities and vapor pressures over the United States. Mo. Weather Rev. Suppl. No. 6.

Errington, P. L.
1941. An eight-winter study of central Iowa bob-whites. Wilson Bull., 53:85-102.

Grinnell, J., and Storer, T. I.
1924. Animal life in the Yosemite (Berkeley, Calif., Univ. of Calif. Press).

Hall, H. H., and Hall, C. C.
1912. A Yosemite flora (San Francisco, Calif., Paul Elder and Co.).

Kendeigh, S. C.
1949. Effect of temperature and season on energy resources of the English sparrow. Auk, 66:113-127.

Kendeigh, S. C., and Baldwin, S. P.
1937. Factors affecting yearly abundance of passerine birds. Ecol. Monog., 7:91-124.

Kleiber, M., and Dougherty, J. E.
1934. The influence of environmental temperature on the utilization of food energy in baby chicks. Jour. Gen. Physiol., 17:701-726.

Lack, D.
1947. The significance of clutch size. I and II. Ibis, 89:302-352; 90:25-45.
1950. The breeding seasons of European birds. Ibis, 92:288-316.

Linsdale, J. M.
1932. Frequency of occurrence of birds in Yosemite Valley, Calif. Condor, 34:221-226.

Martin, A. C., Zim, H. S., and Nelson, A. L.
1951. American wildlife and plants (New York, N. Y., McGraw-Hill Book Co., Inc.).

McAdie, A. G.
1903. Climatology of California. U. S. Dept. Agr., Weather Bureau, Bull. L.

Miller, A. H.
1951. An analysis of the distribution of the birds of California. Univ. Calif. Publ. Zool., 50:531-644.

Moreau, R. E.
1948. Ecological isolation in a rich tropical avifauna. Jour. Anim. Ecol., 17:113-126.
1950. The breeding seasons of African birds. 1. Land birds. Ibis, 92:223-267.

Salt, G. W.
1952. The relation of metabolism to climate and distribution in three finches of the genus *Carpodacus*. Ecol. Monog., 22:121-152.

Seibert, H. C.
1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photo-periods. Auk, 66:128-153

Skutch, A. F.
1950. The nesting seasons of Central American birds in relation to climate and food supply. Ibis, 92:185-222.

Smith, K. D.
1951. On the birds of Eritrea. Ibis, 93:201-233.

Voous, K. H.
1950. The breeding seasons of birds in Indonesia. Ibis, 92:279-287.

Department of Zoology, University of California, Davis, California, January 10, 1953.