FREQUENCY OF OCCURRENCE OF BIRDS IN YOSEMITE VALLEY, CALIFORNIA

BASED ON RECORDS BY MR. AND MRS. CHARLES W. MICHAEL

WITH TWO GRAPHS

By JEAN M. LINSDALE

The problems involved in the determination of populations of birds deserve the serious attention of all field naturalists. Discussions of this subject doubtless will be profitable for a long time. Such studies provide basic material for, or contribute to, so many phases of natural history that it is surprising that so little attention has been devoted to them in the past. Reference is often made to the inadequacy of the commonly accepted usages for expressing the relative abundance of animals. The insufficiency of our knowledge of animal populations is made obvious whenever an attempt is made to determine actual numbers of individuals present on any given area.

Possibly the most difficult of these problems is the determination of actual numbers of a given species or group of species. With the exception of a very few kinds this seems to be practically impossible to accomplish for birds—even when limited, small areas are concerned. In practice, census counts of birds are estimations of approximate numbers and are reliable mainly in proportion to the knowledge and acumen of the observer who makes them. Capabilities of field naturalists vary so greatly that it is impossible to get more than the most generalized results from comparing census counts made by more than one observer.

My own enquiries into the question of determination of numbers of birds suggest that in view of the limitations of method as now known it is more profitable to try to determine the relative frequency of occurrence of birds for a given region than to try to make counts of all the individuals present. An adaptation of a method used by botanists in population studies of plants, which helps in expressing the relative frequency of occurrence in birds, has been given briefly in outline (Condor, xxx, 1928, pp. 180-184).

Raunkiaer derived what he called the Law of Frequence from eleven different pieces of botanical work carried on by himself and others in different parts of Europe. In nearly all such surveys it is learned that there are many more species of low frequence than of high frequence. A curve expressing the numbers in the different classes of frequence has two peaks, a high one expressing the least frequence, and a lower one expressing the greatest frequence. If the species of frequences of respectively 1-20 per cent, 21-40 per cent, 41-60 per cent, 61-80 per cent, and 81-100 per cent are grouped into classes designated as A, B, C, D, and E, the law of frequence might be expressed $A>B>C>$, equal to, or $<D<E$ (Kenoyer, Ecology, VIII, 1927, p. 343).

This application to birds rests upon the primary assumption that in the area studied the number of days of observation of a bird species will reflect the extent of area occupied and the total number of individuals present, or, that over a reasonable number of days the more numerous species will be observed more often than the less numerous ones. It is recognized that several factors are at work to decrease the reliableness of such computations. For example, nocturnal birds will naturally rank lower than diurnal ones present in equal numbers. Small birds of retiring habits will be slighted in comparison with large birds of obtrusive habits. Varying weather conditions will be reflected in numbers of birds observed, and daily differences in the route or the distribution of attention of the observer are sure to influence the records.

It must be kept in mind that the perfection of environmental adaptation of a species is not always parallel to or reflected in its observed frequency of occurrence. Caution must be taken not to expect these simple indices to show too much about the avian population of an area. By recognizing their limitations we are in better position to make use of them in studying the true characters of a bird population.

In spite of the effects of all these detracting influences I feel confident that they are compensated for when the conditions outlined in this and my previous report are attended to. These involve among other requirements:

1. Selection of an area of appropriate size—such that one day's observation may be expected to indicate fairly the bird species present—and with definite limits.
2. Keeping records by a method sufficiently simple that analyses can be made without waste of effort.
3. Maintaining observation over a period of time sufficient to give adequate representation to the various kinds of birds. The optimum number of days for such a survey remains to be determined.

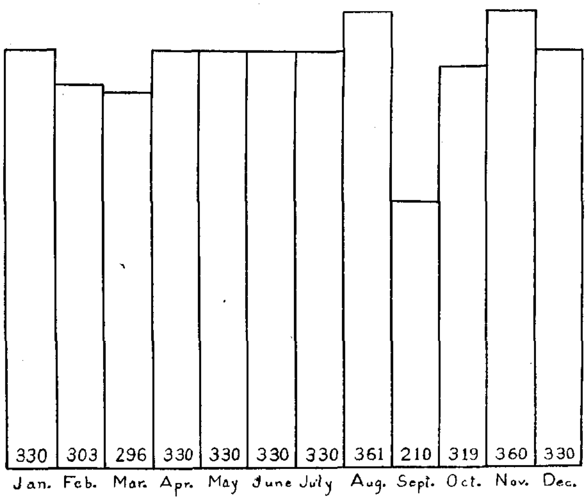

Fig. 24. CHART SHOWING DISTRIBUTION OF FIELD DAYS BY MONTHS.

4. Limitation of recorded observations to an area of a fair degree of environmental uniformity and hence, presumably, of uniform avifaunal make-up. Value of the results for comparative purposes is largely dependent upon proper consideration of this factor.

The index numbers (percentages) show on what proportion of the whole number of days of observation each species was recorded. If a species is recorded on twenty-five out of one hundred days it seems reasonable that it would be seen close to twenty-five days in another comparable sample of one hundred days on the same area; provided seasonal and other habitat conditions are not greatly modified.

Just as the frequency index for a plant may be made large or small by changing the size of the quadrats surveyed, it seems logical to expect that the corresponding figure, determined as here suggested, for birds would vary, depending upon the unit of time used. General experience in the field indicates that the most satisfactory unit of time is one day—although it is not absolutely necessary to spend the whole of each day in the field. My impression is rather definite that in a uniform habitat area the number of species that will be discovered after the first four hours of observation in the morning will not be significant for purposes of this work. Comparison of the results obtained with those obtained and frequently reported upon in botanical surveys gives further verification to this supposition. The more uniform habitats probably require shorter periods of daily observation than the varied ones to record the species adequately.

Since the summer of 1920, Mr. and Mrs. Charles W. Michael have kept daily records of all species of birds seen by them on the floor of Yosemite Valley in Yosemite National Park, California. At the end of each month a summarized report of all observations for the preceding thirty days has been sent to the Museum of Vertebrate Zoology. Recently it occurred to me that these records would form excellent material for a test of the method now under discussion for showing relative frequency of occurrence of birds. Here were records carefully kept over a long period of time on a definitely restricted area by two persons of exceptional powers of observation. Accordingly, percentage of frequency was determined for each species for the whole period of time (August 1, 1920, to November 30, 1931) and for each of the twelve months. To obtain these percentages the total number of days each species was observed was divided by the total number of days on which observations were made. The percentages are shown in table 1 for each species which ranked above 20%. This table includes only forty out of the total of 151 species recorded, or approximately one-fourth of the whole number present.

TABLE 1.—THE FORTY SPECIES OF BIRDS FOUND MOST FREQUENTLY IN YOSEMITE VALLEY, CALIFORNIA, WITH PER CENT OF FREQUENCY FOR EACH MONTH AND FOR THE YEAR

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Blue-fronted Jay	100	100	100	100	100	100	100	100	100	100	100	98	99.8
Sierra Junco	97	100	100	100	100	100	100	98	100	100	100	96	99
Sierra Creeper	89	96	100	100	100	100	100	94	100	97	97	98	98
California Woodpecker	96	100	100	100	100	100	100	96	100	88	94	94	97
Red-shafted Flicker	89	78	98	100	100	100	100	100	100	100	98	89	96
Belted Kingfisher	80	98	92	100	100	100	100	97	86	100	92	74	89
Mountain Chickadee	63	95	99	89	80	79	85	84	96	95	82	80	86
Western Robin	52	74	97	100	100	100	100	100	100	78	61	27	80
Spurred Towhee	60	66	87	82	100	100	95	94	95	66	57	51	79
Hairy Woodpecker	62	59	66	84	85	93	86	79	74	78	73	71	76
Cañon Wren	59	71	72	82	83	60	65	76	55	81	86	90	74
Band-tailed Pigeon	27	31	53	88	100	98	100	99	97	87	45	30	71
California Purple Finch	29	41	51	88	92	100	90	43	11	20	22	25	61
Golden-crowned Kinglet	68	82	92	75	28	26	7	6	20	81	86	87	55
Red-breasted Nuthatch	39	38	60	71	74	61	44	53	66	48	89	41	52
Audubon Warbler	36	29	26	93	97	58	31	8	58	81	64	31	50
Water Ouzel	35	50	53	59	86	38	14	26	57	80	56	39	49
Ruby-crowned Kinglet	86	72	63	69	16	....	....	....	3	60	86	92	47
Chipping Sparrow	....	....	....	49	100	100	100	85	67	11	....	2	43
Brewer Blackbird	....	....	....	68	92	88	89	57	69	27	2	....	42
White-headed Woodpecker	59	62	54	64	61	63	16	16	25	33	38	53	45
Willow Woodpecker	32	15	33	51	36	53	68	56	42	25	27	34	40
Sparrow Hawk	8	13	25	53	58	43	62	60	60	27	36	14	38
Cassin Vireo	....	....	....	47	100	100	91	62	27	....	....	....	36
Black-headed Grosbeak	....	....	....	37	100	100	99	69	7	3	....	....	36
Yellow Warbler	....	....	....	12	98	100	100	91	10	....	....	....	36
White-throated Swift	....	2	29	68	99	98	70	37	57	1	....	....	35
Red-winged Blackbird	....	1	32	85	99	100	68	12	4	3	....	....	34
Wood Pewee	....	....	....	1	85	100	100	90	23	....	....	....	34
Western Bluebird	83	67	14	1	1	....	....	....	....	46	100	82	34
Western Tanager	....	....	....	5	95	100	94	69	35	....	....	....	34
Spotted Sandpiper	....	....	....	2	83	100	98	72	17	....	....	....	32
Warbling Vireo	....	....	....	47	100	100	86	18	81	....	....	....	31
Evening Grosbeak	....	1	14	32	66	63	50	69	54	12	....	....	30
Tolmie Warbler	....	....	....	7	77	100	76	65	16	....	....	....	29
Traill Flycatcher	....	....	....	....	34	100	100	86	19	1	....	....	29
Calliope Hummingbird	....	....	18	52	88	60	33	33	18	3	....	....	26
Violet-green Swallow	....	....	6	27	68	92	53	15	7	....	....	....	23
Black-throated Gray Warbler	....	....	....	52	92	56	13	19	20	2	....	....	21
Russet-backed Thrush	....	....	....	....	38	78	66	35	11	3	1	....	20

The figures and charts derived from the bird records in Yosemite are sufficiently interesting to invite further inquiry into their significance and the bearing of the method upon the general problem of bird distribution. In the first place it should be pointed out that the results here shown are in close agreement with those obtained from similar studies of other classes of objects. That is, the Raunkiaer law applies to the distribution of many classes of objects, both animate and inanimate, in which occurrence is governed by a large number of factors. Furthermore, the results of this analysis are closely similar to those obtained in studies of frequency of birds in other localities in the United States, for example, in eastern Kansas (Linsdale, Condor, xxx, 1928, p. 180) and in northern Michigan (unpublished). The curves showing the arrangement of frequency indices for the three localities are remarkably alike.

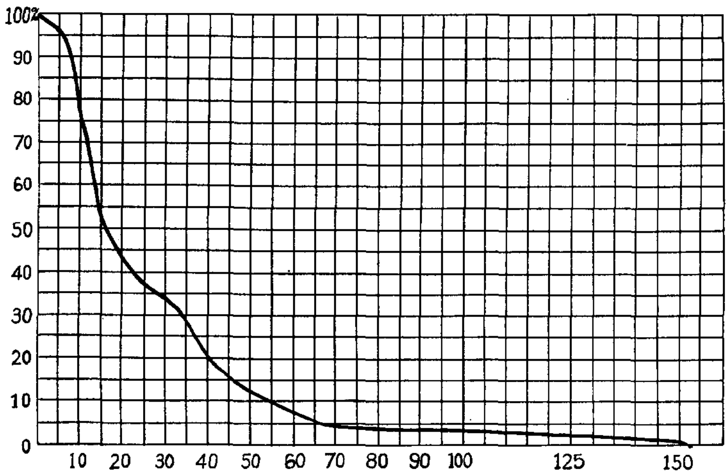

Fig. 25. GRAPH SHOWING RELATIVE FREQUENCY OF OCCURRENCE OF THE 151 SPECIES OF BIRDS THAT WERE RECORDED IN YOSEMITE VALLEY, CALIFORNIA.

Comparison of forty species of birds occuring most frequently (index more than 20%) in Yosemite Valley, California (left), and a small area in Doniphan County, Kansas (right):

1.	Blue-fronted Jay	Cardinal
2.	Sierra Junco	English Sparrow
3.	Sierra Creeper	Crow
4.	California Woodpecker	Chickadee
5.	Red-shafted Flicker	Blue Jay
6.	Belted Kingfisher	Tufted Titmouse
7.	Mountain Chickadee	Carolina Wren
8.	Western Robin	Downy Woodpecker
9.	Spurred Towhee	Mourning Dove
10.	Hairy Woodpecker	Goldfinch
11.	Cañon Wren	Robin
12.	Band-tailed Pigeon	Red-headed Woodpecker
13.	California Purple Finch	Indigo Bunting
14.	Golden-crowned Kinglet	Red-bellied Woodpecker
15.	Red-breasted Nuthatch	Red-winged Blackbird
16.	Audubon Warbler	Yellow-billed Cuckoo
17.	Water Ouzel	Chimney Swift
18.	Ruby-crowned Kinglet	Red-eyed Vireo
19.	Chipping Sparrow	Baltimore Oriole
20.	Brewer Blackbird	Western House Wren
21.	White-headed Woodpecker	Wood Thrush
22.	Willow Woodpecker	Wood Pewee
23.	Sparrow Hawk	Whip-poor-will

24. Cassin Vireo	Ruby-throated Hummingbird
25. Black-headed Grosbeak	Cowbird
26. Yellow Warbler	Bell Vireo
27. White-throated Swift	Kingbird
28. Red-winged Blackbird	Bluebird
29. Wood Pewee	Blue-gray Gnatcatcher
30. Western Bluebird	Hairy Woodpecker
31. Western Tanager	Great Blue Heron
32. Spotted Sandpiper	Barn Swallow
33. Warbling Vireo	Northern Flicker
34. Evening Grosbeak	Catbird
35. Tolmie Warbler	Turkey Vulture
36. Traill Flycatcher	Crested Flycatcher
37. Calliope Hummingbird	Rough-winged Swallow
38. Violet-green Swallow	Dickcissel
39. Black-throated Gray Warbler	Tree Swallow
40. Russet-backed Thrush	Green Heron

The 151 species of birds of Yosemite Valley are distributed in the five classes of the Raunkiaer formula as follows: 111, 20, 7, 5, 8 or in the following ratio: 73, 13, 5, 3, 5. Corresponding figures for an area surveyed in Doniphan County, Kansas, were 133, 32, 13, 6, 10 and 68, 16, 7, 3, 5. In both cases the arrangement of the formula which applies is $A>B>C>D<E$. These results agree closely with those given by Kenoyer (*op. cit.*) for analyses of frequency distribution in plant communities.

Judging from the work of various botanists (Romell, Ecology, xi, 1930, p. 591) and from observations upon the local distribution of birds it seems probable that the application of the Raunkiaer law to occurrence in birds is closely connected with the following assumptions. First, that every species is adapted to a definite set of environmental conditions; second, that the factors which influence the presence of birds in the area analyzed vary from place to place according to pure chance around a mean value; third, that it is just as probable to have species which are adapted to the rare combinations of factors as to the more common ones in the area; fourth, that over a period of time birds are likely to be observed on numbers of occasions which parallel their numbers on the area. These assumptions appear to me to be in agreement with most of the information now available concerning the distribution of birds.

From the considerations outlined above it might be concluded that one of the topics urgently requiring attention in the field-study of birds is the one having to do with the particular factors which determine or influence the presence of each kind of bird. This involves the detection and analysis of responses of individual birds to environmental factors which have to do with occurrence.

A feature of analyses of frequency of occurrence according to the Raunkiaer method which deserves emphasis is that they provide results intermediate between the two methods most frequently used but without the chief disadvantages of those methods. The almost universal custom of subjectively estimating the relative frequency of birds and assigning general terms to the various classes (abundant, common, rare) has had its limitations pointed out so often that they are well known. The opposite practice, involving elaborate procedure in census taking, is less well known and less often attempted. However, there seems to be a definite tendency on the part of workers to give too much confidence to these counts and to practicability of the procedure in obtaining them. The chief disadvantages are the great amount of time and effort required (these are needed for other kinds of observation) and the liability to error from too much dependence upon the totals which, in the case of many species, cannot be expected even to approximate the actual number.

The determination of frequency indices for birds may have significance for local studies. In the first place it makes possible the arrangement of a series of species in order of their observed frequency of occurrence. It gives a more easily understood and more nearly correct impression of relative abundance than any other practicable method known to me. In addition, possibilities are offered for the analysis of the composition of a bird population and for comparison with populations of other localities and other regions.

The results of a study such as here suggested may furnish an indication, when interpreted on the basis of the behavior of the birds, of which species deserve emphasis in studies of environmental relations. It happens that species of most frequent occurrence nearly always require thorough study, but also species of infrequent occurrence cannot be ignored in an analysis of any avifauna.

Any attempt to obtain definite first-hand knowledge of the frequency of occurrence of birds is sure to clarify any worker's concept of a bird population and its make-up. Methods of the Raunkiaer type seem to have special value for their help in giving form to our notions of bird populations. The factors concerned at any given place appear to be numerous and uneven in their effects. Development of these methods will have an important effect upon the organization of projects for the regulation of animal numbers by artificial means. They help to demonstrate that conditions which influence populations are more complex than preliminary gross studies usually indicate.

Summary.—Because of the importance of, and the difficulties encountered in, studies of bird populations, it is suggested that attention be given to methods for expressing the relative frequency of occurrence of birds. Methods of the Raunkiaer type, commonly used in studies of vegetation, may be adapted to studies of occurrence of birds when allowance is made for certain conditions peculiar to bird populations. Daily records of birds observed in Yosemite Valley over an eleven year period provide the basis for the present analysis. The results are in agreement with those obtained in surveys of plants and of birds in other regions. Possible corollaries in general natural history are sketched.

Museum of Vertebrate Zoology, Berkeley, California, March 21, 1932.