

STUDIES ON THE PHYTO-VERTICAL DISTRIBUTION  
OF BIRDS.

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BY DISTRIBUTION is meant the natural geographical range of a species or any other taxonomic group of organisms. The concept of distribution carries with it the implication of parallelism to the surface of the earth. There is, however, another well recognized plane of distribution of animals which is vertical to the surface of the earth. The term *vertical distribution* has become recognized as designating altitudinal distribution over areas of the magnitude of life zones with reference to distance from sea level. Students of bird life have found during comparatively recent years that there is a definite vertical distribution of birds in the vegetation. In order to distinguish this local vertical distribution from the more inclusive zoogeographical term, it is here proposed that the term, *phyto-vertical distribution*, designate the local vertical distribution of birds in any vegetational formation with reference to distance from the topographical floor, i. e. the ground.

It has not been until recently that ecologists have recognized a vertical habitat gradation in the vegetation. Several authors have given some attention to the vegetational levels at which the various types of animals live. The outstanding studies in this field are those of W. C. Allee (*Distribution of Animals in a Tropical Rain Forest with Relation to Environmental Factors, Ecology, 1926*) and A. A. Allen (*Book of Bird Life, 1930*).

Dr. Allee gives the following zones as a classification of the levels to be found in the tropical jungle of the rain-forest type.

- “1. The air above the forest.
2. Tree tops above the main forest roof, 125 or more feet high.
3. Upper forest canopy, 75–100 feet high.
4. Lower tree tops (second story or mid-forest) 40–60 feet high.
5. Small trees, 20–30 feet high.
6. Higher shrubs, 10 feet high.
7. Forest floor.
8. Subterranean.”

Dr. Allee does not discuss all the strata given in his classification, nor does he give any criteria for placing the animals into their corresponding zones. Furthermore, he does not take up the mammals or birds. Dr. Allee's classification is a purely botanical one.

Dr. A. A. Allen gives a general classification of bird habitats in wooded areas as follows.

“Birds of the Woodland and Woodland Borders.

- (a) Ground-nesting birds
- (b) Birds of the undergrowth and low bushes.
- (c) Birds of the higher bushes and lower branches.
- (d) Birds of the higher branches and tree tops.
- (e) Birds that nest in holes."

Dr. Allen arranges only birds of the woodland and woodland borders in a phyto-vertical distribution. The criterion for the first and last subdivisions seems to be the nesting site of birds, but the author gives no criteria for the placement of birds in the other zones. Obviously the criteria of that author depend on no single activity of bird behavior.

Dr. R. B. Cowles (1933, unpublished paper) discusses the vegetational habitats of the South African Thorn Bush area in the following way.

"It will be noted that the main vegetational areas are: Bush, Scattered Bush, Edge of Bush, including marginal areas of both types, Shrubby areas, Grass, and Marsh." This of course, is not a vertical classification, but a horizontal one. Dr. Cowles continues below, "There is considerable vertical movement but the birds in the lower areas are seemingly more closely related to their habitat than the tree top forms, and the ground cover forms are still more restricted." The idea of phyto-vertical distribution is presented here with the three zones; "tree top," "intermediate," and "ground cover," given as levels in the vegetation. However, no criterion is given for the relegation of birds to the plant formation.

In our studies in the chaparral it has been found necessary to recognize definite zones, based on the various levels of the vegetation, and to select one or more activities of bird behavior which could be used as indicators of the affinity of a given species to a given zone.

There are three fundamental activities of bird behavior which might serve as criteria for placing them in their corresponding zones; (1) the height at which they feed, (2) the altitude of the nesting site, and (3) the elevation of the place where they would commonly fly for refuge when pursued by an enemy.

The place where a bird feeds is very variable, depending on the quantity and quality of food available in a given place. Feeding is not always an activity that will take place in any definite zone. We may dismiss this criterion as being too variable for our purposes. In fact, zoogeographical literature and observations in animal behavior indicate that spatial changes in the location of the available food supply tend more than any other factor to cause animals to leave their normal habitats and range out into others, (i. e. the sporadic migrations of birds, lemmings, locusts, etc.).

The data on nesting sites has been secured from the literature (Dawson, *Birds of California*, 1923; Wheelock, *Birds of California*, 1920; Hoffmann, *Birds of the Pacific States*, 1927). The site at which a bird places its

nest may be a good indicator of the place at which that species attains greatest security from predators. For this reason the nesting site may be considered a good indicator of the habitat of that species. The level in the vegetational formation which a bird selects as place of refuge may also be considered an indicator of the specific ecological niche of that bird. One element is common to both these criteria—Safety; safety on the one hand for its offspring, exemplified by the choice of the nesting site; and safety on the other hand for itself, exemplified by our criterion of the refuge site.

The area in which the observations here recorded (Table I) were made lies around the campus of the University of California at Los Angeles. The vegetation of this area is typical chaparral; dense brush on the sides and tops of the hills, and low trees and high bushes in the canyon bottoms. This canyon bottom vegetation is composed mainly of willow (*Salix*), live oak (*Quercus*), and sycamore (*Platanus*). The hillside vegetation consists of low bushes such as chamise (*Adenostoma*), wild lilac (*Ceanothus*), sumac (*Rhus*), and many other annuals and perennials. Much of the natural vegetation of the region has been disturbed; however, there is still enough present so that the birds of the original vegetation are still abundant. The least molested parts of the campus are three stream beds and their adjoining areas. Two of these streams continually carry water, while the third, running along the east side of the campus, is characteristically dry. The stream bed on the northwest corner of the campus is characterized by a thick growth of willows, 8 to 10 feet high, and interspersed throughout the district are live oaks and sycamores. The other stream is located on the west boundary of the campus. It was overgrown by thickets of willow near the water, but on the adjoining hillsides the low bush type of vegetation dominates. At the south end of this stream there was a small marsh, with a growth of cattails. This whole interesting ecologic formation has now been destroyed. The canyon that is situated on the east side of the campus is characteristically dry and is covered by the low bush, brushy type of chaparral. A great part of the area is covered with grasses, wild oats (*Avena*), and brome (*Bromus*), with other secondary succession plants. There are also a few areas which have been planted to non-native ornamentals.

We have divided the above vegetational formation into the following phyto-vertical zones:

- A. Ground Zone.—Not exceeding one foot above the ground nor five feet below it.
- B. Low Bush Zone.—One to five feet in altitude.
- C. High Bush Zone.—Five to fifteen feet in altitude.
- D. Low Tree Zone.—Fifteen to forty-five feet high.
- E. Aërial Zone.—Above the substratum, in the air.

There is no high tree zone in this area, the highest trees are the sycamores which reach a height of forty-five feet in this vicinity. The lower branches of the trees and high bushes when overlapping were regarded as being in the zone to whatever altitude they corresponded in terms of feet. For instance, some of the lower branches of the sycamores are in the high bush zone, and similarly there occurs overlapping between high and low bushes, and between the low bush and the ground zone.

The procedure followed in making the observations consisted in one's walking as quietly as possible through the various districts of the area, taking notes as to the zones into which the birds would fly upon the approach of the observer, and if possible to startle a bird by coming up to it unobserved. The ideal method, of course, is to watch to what level a bird will fly when pursued by a Hawk or other enemy. Every opportunity to observe birds under such circumstances was taken.

## RESULTS.

TABLE I.

	Nesting Site	Refuge Site	Times Studied	Variations
<b>Lophortyx c. californica.</b>				
VALLEY QUAIL . . . . .	Ground	Ground	73	1
<b>Zenaidura macroura marginella.</b>				
WESTERN MOURNING DOVE . . . . .	High bush	Low tree	42	0
<b>Cathartes aura septentrionalis.</b>				
TURKEY VULTURE . . . . .	Cliffs	Aerial	40	0
<b>Accipiter cooperi.</b> COOPER'S HAWK . . . . .	High tree	Aerial	8	0
<b>Buteo borealis calurus.</b> WESTERN				
RED-TAILED HAWK . . . . .	High tree	Aerial	9	0
<b>Falco s. sparverius.</b> AMERICAN				
SPARROW HAWK . . . . .	High tree	Low tree	57	0
<b>Speotyto cunicularia hypugea.</b>				
BURROWING OWL . . . . .	Underground	Ground	15	0
<b>Geococcyx californianus.</b> ROAD-				
RUNNER . . . . .	Ground	Ground	18	0
<b>Balanosphyra formicivorous bairdi.</b>				
CALIFORNIA WOODPECKER . . . . .	Low tree	Low tree	42	0
<b>Colaptes cafer collaris.</b> RED-SHAFTED				
FLICKER . . . . .	Low tree	Low tree	24	2
<b>Sayornis nigricans.</b> BLACK PHOEBE . . . . .	High bush	Low bush	45	12
<b>Otocoris alpestris actia.</b> CALIFORNIA				
HORNED LARK . . . . .	Ground	Ground	30	0
<b>Aphelocoma c. californica.</b>				
CALIFORNIA JAY . . . . .	High bush	High bush	51	8

TABLE I—Continued.

	Nesting Site	Refuge Site	Time Studied	Variations
<b>Molothrus ater obscurus.</b> DWARF COWBIRD.....	Low bush (Parasite)	Low bush	19	0
<b>Agelaius phoeniceus.</b> RED-WINGED BLACKBIRD.....	Low bush	Low bush	20	0
<b>Sturnella neglecta.</b> WESTERN MEADOWLARK.....	Ground	Ground	81	5
<b>Carpodacus mexicanus frontalis.</b> CALIFORNIA LINNET (House Finch)....	Variable	High bush	76	24
<b>Spinus tristis salicamans.</b> WILLOW GOLDFINCH.....	High bush	High bush	15	0
<b>Spinus psaltria hesperophilus.</b> GREEN-BACKED GOLDFINCH.....	High bush	High bush	22	5
<b>Zonotrichia l. leucophrys.</b> WHITE- CROWNED SPARROW.....	Low bush	Ground	29	6
<b>Zonotrichia coronata.</b> GOLDEN- CROWNED SPARROW.....	—	Low bush	6	0
<b>Melospiza melodia.</b> SONG SPARROW....	Low bush	Low bush	83	13
<b>Passerella iliaca.</b> FOX SPARROW.....	Ground	Ground	65	8
<b>Pipilo crissalis senicula.</b> ANTHONY'S BROWN TOWHEE.....	Low bush	Low bush	54	16
<b>Petrochelidon l. lunifrons.</b> CLIFF SWALLOW.....	Cliffs	Aerial	35	0
<b>Lanius ludovicianus gambeli.</b> CALIFORNIA SHRIKE.....	High bush	High bush	22	0
<b>Dendroica aestiva brewsteri.</b> CALIFORNIA YELLOW WARBLER.....	High bush	High bush	18	0
<b>Dendroica a. auduboni.</b> AUDUBON'S WARBLER.....	High bush	High bush	40	8
<b>Geothlypis trichas occidentalis.</b> TULE YELLOWTHROAT.....	High bush	High bush	18	4
<b>Mimus polyglottos leucopterus.</b> WESTERN MOCKINGBIRD.....	High bush	High bush	78	18
<b>Toxostoma r. redivivum.</b> CALIFORNIA THRASHER.....	Low bush	Low bush	16	0
<b>Telmatodytes palustris paludicola.</b> TULE WREN.....	Low bush	Low bush	13	0
<b>Psaltriparus m. minimus.</b> COAST BUSH-TIT.....	High bush	High bush	32	5
<b>Chamaea fasciata henshawi.</b> PALLID WREN-TIT.....	Low bush	Low bush	36	5
<b>Polioptila caerulea amoenissima.</b> WESTERN GNATCATCHER.....	Low bush	Low bush	26	0
<b>Oxyechus v. vociferus.</b> KILLDEER.....	Ground	Aerial	30	0

A total of thirty-six species were under observation; some for the whole period of study, and some for a part of the time. The time it was under observation depended on the status of the particular species in our locality. According to the refuge criterion, of these thirty-six species, seven have been relegated to the ground zone, ten to the low bush zone, ten to the high bush zone, four to the low tree zone, and five to the aërial zone. The column captioned *Variations* in our table indicates the number of times at which a species failed to choose the zone selected by that species the majority of times observed. The bird that was most variable in its choice of a refuge zone was the Linnet (*Carpodacus mexicanus frontalis*). The ratio of its variation was approximately 1 to 3.

By comparison of the columns captioned *Nesting Site* and *Refuge Site* it will be seen how closely the data obtained from the literature on nesting and the data gathered by our own observations agree. If the nesting sites as given by Dawson (1923), Wheelock (1920), and Hoffmann (1927) are any indication of the zone in which a given species of bird thrives, then our data are of some value also in determining the altitude of the true habitat of the species. We find that in the chaparral the zones in which the birds place their nests follow very closely those in which they seek refuge. In some cases the nesting site is more variable as a phyto-vertical distributional indicator than the data on refuge site. For example, the nesting site of the California Jay (*Aphelocoma californica californica*) as given by Wheelock (1920), is "3 to 30 feet" from the ground. From our observations, according to the refuge site criterion, the phyto-vertical distribution of that bird is the High Bush Zone, 5 to 15 feet from the ground. Out of 51 times studied there were ten variations, or times at which the bird did not fly into the high bush zone.

The data from the literature, in many instances, could not be used as it was presented there. It was, therefore, necessary to arrange according to the zones given above. This was easily accomplished, since the authors, in the majority of cases, give the nesting altitude in feet from the ground.

We find that there are more birds in the lower zones because of the dwarfed type of vegetation existing in the area studied. Furthermore, it is much easier to place birds in the lower zones, not only because of the greater facility with which they may be observed, but because they appear more consistent in choosing their refuge zone. The nature of the heights of the vegetational components is such that the upper zones are increasingly wider than those closer to the ground. For that reason birds of the upper zones, according to the refuge criterion, have more available space for flight. For example the Bush Tit (*Psaltriparus minimus minimus*) has a distributional zone of from five to fifteen feet; while the Meadowlark (*Sturnella neglecta*) has a phyto-vertical distribution of one foot. The nesting data verify the refuge data in both these instances.

There are some birds that do not take refuge by diving into the brush or trying to hide in the vegetation, but when danger approaches they take to the air. Such birds as Swifts, Swallows, Hawks, Eagles, Sea-birds and many others that take refuge from their enemies by long continued flight, cannot be relegated to vegetational zones, but must be assigned to a zone which has no levels. This, obviously, is the Aërial Zone.

There are obviously two omnipresent zones, the ground (or water) and the air. The remaining zones are merely intergrades of these two. In some cases, as in deserts, there may be present only the ground zone, the low bush zone, and the aërial zone. In like manner in a humid transition forest the ground, high tree and aërial may be the only zones present.

The distribution of birds in this phyto-vertical scheme has been shown to be fairly definite and logical; and a bird once relegated to one zone will almost invariably be found there, if present in that locality. This, however, does not imply that the same bird will not be seen elsewhere, for in feeding, singing, or mating, the bird may range widely phyto-vertically, but when safety is required for itself or for its young, the bird seems to display a preference for a certain particular zone, which is characteristic for that species of bird. This, ecologically, may be considered to be its habitat.

#### SUMMARY.

Phyto-vertical distribution is a term used to designate the vertical distribution of birds in the local vegetation. In our studies in the chaparral, it was found necessary to delimit clear-cut zones based on the vegetational levels, and to establish criteria by which the birds could be assigned to their respective zones. The criterion used in our observations was the height of the place chosen by a bird for refuge in time of danger. We compare this to the altitude of the nesting site (our second criterion). There is a remarkable degree of agreement between the zones chosen for nesting and the zones chosen for refuge by the different species of birds.

We believe that this agreement gives us a clue to the true habitat zone of any particular species, and a basis for a phyto-vertical distribution of birds.

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