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Museum of Vertebrate Zoology, Berkeley, California, July 12, 1937.

BIRD LIFE IN NEVADA WITH REFERENCE TO MODIFICATIONS IN STRUCTURE AND BEHAVIOR

By JEAN M. LINSDALE

No doubt many readers of the *Condor* have traveled across the state of Nevada, either by way of a transcontinental railroad line or by one of the main automobile highways. Whatever the route, I suspect that the most vivid impression was of barrenness and desolation. Indeed, the comment I have heard most often, when bird life in Nevada was mentioned, has been that "no birds live there." Sometimes, I have been told by persons who had lived for a long time in the state that only one or two kinds of birds lived in their neighborhood. Even naturalists have remarked that they considered Nevada a place characterized by absence of animal life and especially of birds. It is little wonder that, although more than eighty persons have done some bird work in the state, scarcely anyone has resided there for long who observed birds in serious fashion.

My first bird trip to Nevada was made about ten years ago, and since then I have returned many times and have paid much attention to the problems of bird life pertinent to that region. This remains one of the last large areas in the country the avifauna of which is little known. Most compilers of state lists of birds are able to invite special interest for their state on account of the "abundance and variety" of its bird life. No such claim can be made for Nevada; the chief interest in its bird life results from the sparseness of population. It is a population composed of relatively few species, considering the large size of the area. This very circumstance makes this to me a place of exceptional interest for bird study. The scattered representatives of most of the species make it impossible to predict where in the state any given kind of bird will occur. A bird cannot be considered as present in any locality without actually finding it there. The same kind of uncertainty applies to the seasonal status of each kind of bird.

In discussing the bird life in Nevada I intend to consider only a few general topics. These are the physical characteristics of the area which in some way affect the avifauna, some of the ways in which birds have responded structurally to the geographic conditions there, and the more striking responses they have made in behavior to the desert environment of the Great Basin.

Nevada ranks sixth among the states in size; it is seven-tenths as large as California. Of its seventy million acres, barely four million are in farms and fewer than five hundred thousand are under irrigation. The area considered forest is approximately five million acres, but not much of this is covered with timber, and everywhere the trees are scattered. In general, this state is a high plateau, 4000 to 6000 feet above sea level. At the southern tip it drops abruptly down to the Colorado River which leaves the boundary at about 500 feet altitude. On the plateau are many mountain ranges, some of them 100 miles long and 9000 to 11,000 feet high. Several peaks are around 13,000 feet high. The ridges are nearly parallel and mostly run north and south. They are sharp and narrow, being separated by narrow, level-floored valleys. The only large east and west valley in the state is the one through which the Humboldt River flows. North of this the mountainous area is broken by many low passes and it constitutes the divide between the Humboldt and the branches of the Snake River.

Nearly all the rivers in the state empty into lakes which have no outlets, or they lose their water by absorption and evaporation as they spread out over the floors of the valleys. Many of the valleys are closed drainage systems with no stream channels and are so inclosed by mountains that they would hold large lakes before overflowing. They characteristically have playa lakes in their centers in years of extra rainfall or snow.

A consideration of climate is important in any distributional study of birds. The most striking climatic features of Nevada are its bright sunshine, small annual rainfall in the valleys and deserts, heavy snowfall in the higher mountains, dryness and purity of the air, and exceptionally great diurnal ranges in temperature. Reno, at 4500 feet, has temperature near the average, with an annual mean of 50 degrees. In summer, maximum temperatures near 100 degrees occur at many places, especially in the south. Lowest winter temperatures are in the northeast. The temperature goes below zero everywhere except in the extreme south.

The length of the growing season varies greatly, but it averages from seven to eight months in the extreme south and from two to five months in most other localities. In the north, frost may occur in any month of the year, but the last killing one usually comes about June 1. The first killing frost in autumn usually occurs in the first half of September in the north and northeastern parts of the state, but not until November in the south.

Average annual precipitation for the Nevada section is 9.02 inches. The wettest year (1906) had an average for all the stations of 15.87 inches; the driest (1928), 4.87 inches. January has the greatest precipitation, and August the least. The eastern slope of the Sierra Nevada receives the greatest annual precipitation, and the lowest part of the plateau area, just east of the Sierra and southward to the edge of Death Valley, receives the least. The number of days per year with 0.01 inch or more of precipitation varies from 14 at Clay City, southern Nye County, to 67 at Tahoe. At Marlette Lake the annual snowfall is 255 inches while at Logandale, Clark County, it is less than one inch. Evaporation at Clay City, on the eastern edge of Death Valley, averages more than 11 feet of water per year.

The prevailing winds are from the south, southwest, and west. Wind velocities are generally light, and severe wind storms occur only at rare intervals. In the average year there are 193 clear days, 87 partly cloudy days, and 85 cloudy days. At Reno the average percentage of possible sunshine is 74.

I recite all these facts concerning Nevada, not for any interest they may arouse in themselves, but because I believe they are important among the circumstances which determine what set of bird species will inhabit the area, which govern to some extent the structural characters of those birds, and which influence profoundly the habits and behavior of the birds. The search for the manner of these responses by the birds to their surroundings accounts for my interest in the bird life in Nevada.

Within this large district, extending five hundred miles between 35 degrees and 42 degrees north latitude and more than three hundred miles between 114 degrees and 120 degrees west longitude, we find enough bird problems to hold our attention for a long time. Although some progress has been made in cataloging the kinds which occur there and in mapping records of their occurrence, scarcely a start has been made in interpretation of their responses to the conditions I have just outlined.

A general review of the avifauna of Nevada shows approximately 340 species and subspecies that may be considered as members of the Recent avifauna of the state. Of these I have examined skins of 315 kinds—24 per cent as many as are in the 1931 check-list of the American Ornithologists' Union. Of the remaining 25 kinds some have been collected, but for the most part they are known from the state on the basis of sight records. A list of kinds whose status is hypothetical includes 14 birds. Of the birds in the main list there are 276 full species, or 37 per cent as many as are included in the A. O. U. Check-list.

When the whole list is analyzed on a basis of seasonal occurrence, it can be divided approximately into the following proportions: Permanently resident, 42 per cent; summer resident, 30 per cent; winter visitant, 12 per cent; transient, 9 per cent; accidental or irregular, 5 per cent; extinct, 1 per cent. The species in the last group are the California condor and the sharp-tailed grouse. These percentages can be only approximate on account of the meager information concerning many of the species.

Within the state of Nevada thirty-seven bird species change sufficiently in structural characters to be represented by more than one recognizable breeding race. In some of these only two such geographical races have been distinguished; in a few at least three are present; one has four. This group of species includes seven non-passerine and thirty passerine kinds. The non-passerine ones are: dusky grouse, screech owl, great horned owl, red-breasted sapsucker, Williamson sapsucker, hairy woodpecker, and downy woodpecker. All these are characterized by discontinuous distribution. In each there is decrease in size toward the south and the largest individuals are in the northeast corner of the state where also white coloration is conspicuous in the plumage.

The rest of the geographically variable species are all in the single order, Passeriformes. They are therefore fairly closely related. They are all small birds and are generally represented in collections by extensive material. Hence they may be considered in the present analysis with considerable assurance and on basis of a large amount of factual detail. Special effort has been made to procure skins to represent all parts of the state and at seasons when they would be most significant.

The following paragraphs summarize the geographic variations detected in Nevada specimens of these variable passerine species.

Horned lark: numerous in valleys; three races; darkest in northwest part of state; palest toward the east.

Crested jay: sparse on a few mountains in extreme western, eastern and southern parts of state; three races; no intergradation in this area; southern and eastern races paler.

California jay: present on most of the mountain ranges; two races; larger and grayer toward east; large bill in northwest.

Mountain chickadee: resident in the mountains; two races; race in northwestern part darker and smaller.

Gray titmouse: present on many juniper-piñon-covered mountains; two races; large bill in northwest; gray toward east.

White-breasted nuthatch: resident on many mountain ranges; two races; extremely long slender bill over most of state; short stubby bill in extreme east.

Pigmy nuthatch: scarce, on a few mountain ranges; two races; southern one paler and grayer.

Brown creeper: present on a few mountain ranges; three races; increase of gray coloration toward east and south.

Bewick wren: scarce, but widespread in state; two races; grayer and larger toward southeast.

Long-billed marsh wren: numerous in marshy places; two races; Colorado River race darker than one on plateau.

Hermit thrush: common on higher mountains; three races; larger and grayer toward east.

Olive-backed thrush: present in larger mountain ranges; two races; grayer toward east.

Western bluebird: scarce in eastern and western sections; two races; western race with blue on back, eastern with back wholly chestnut.

Loggerhead shrike: frequent in valleys and flats; two races; birds near Colorado River differ from those on plateau in being larger and grayer.

Bell vireo: restricted to small areas on Colorado River and Ash Meadows; two races; Colorado River birds more greenish and smaller.

Blue-headed vireo: present on mountains in western and eastern sections; two races; eastern birds grayer.

Orange-crowned warbler: present on several mountain ranges; two races; eastern birds with larger size and duller coloration.

Yellow warbler: frequent in vegetation bordering streams; three races; larger size and heavier streaks toward east.

Audubon warbler: common on the timbered mountains; two races; larger size and more extensively black toward east.

Yellow-throat: frequent in marshy areas; two races, one on plateau grayer and one in southern part of state greener, brighter, coloration more distinct and bill larger.

Pileolated warbler: present on several mountain ranges; two races; larger and duller toward east.

Red-winged blackbird: numerous in marshy places over whole state; three races; long slender bill toward northwest and south; heavy, short bill in east; female paler toward east and south.

Cowbird: frequent in the valleys; two races; larger on the plateau, with longer and more slender bill, female paler; Colorado River race small, with stubby bill, and female darker.

Blue grosbeak: scarce near Colorado River and part way north in the state; two races; Colorado River birds have larger bills.

Crossbill: irregular on higher mountain ranges; two races; larger and paler toward east.

Spotted towhee: common in lower parts of mountains; two races; heaviest bill in northwest corner; longer wing and tail and paler coloration toward east.

Sage sparrow: numerous in valleys and flats; two races; smaller and grayer toward southwest.

Junco: common on many mountain ranges; three races; grayer toward east; no intergradation with Sierran race, unless on Charleston Mountains.

Fox sparrow: common on several mountain ranges; four races; largest bill toward west, brown toward north, grayest and smallest at south.

Song sparrow: common along streams; three races; large bill toward northwest, grayer toward east, Colorado River birds extemely pale.

When these items are analyzed, it becomes evident that several general principles are involved in them. In the first place many of these variable species are ones which are not uniformly common across the area. Sometimes the populations are separated by hundreds of miles of uninhabited territory. The breaks in range, however, coincide with observed changes in structure. This change from one discernible race to another takes place repeatedly, but not always, in certain narrow belts of territory. Some such districts in Nevada may be designated as follows:

(1) The eastern base of Sierra Nevada, which marks the eastern limit of many species and races.
(2) The boundaries of the old Lahontan Lake basin, which coincide closely with ranges of some geographic races of birds.
(3) The high mountain ranges in the northeastern and eastern parts of the state, which mark the western limits of certain Rocky Mountain species and races.
(4) The southern margin of the high plateau, which probably is more generally a boundary to ranges of species than of geographic races.
(5) The immediate vicinity of the Colorado River, which is inhabited by several distinctive species and races.
(6) The northeastern extension of the Mohave Desert, which extends over the western boundary of the state, and which brings in at least three races of birds.

The structural characters most often concerned in the geographic changes noted are the bill, which usually becomes shorter and stubbier toward the east and smaller toward the south; the wings and tail, which generally are longer toward the east; and general coloration, which becomes paler and distinctly grayer toward the east, and sometimes brighter and darker in the vicinity of the Colorado River.

The recurrence of the same sort of change in many species seems to indicate that the environment is effective in causing the change in some way additional to the single factor of isolation. Some observations support the view that some of these changes in structure have adaptive value. It seems likely that lengthened wing and grayness of coloration, at least, may be explained on this basis.

In taking up the problem of the responses birds make in behavior to this desert environment I shall refer to the results of a study made in the region of the Toyabe Mountains, a high mountain range in central Nevada which with the adjacent valleys contains habitats representative of much of the Great Basin. The efforts of five persons on 321 days in this area between 1930 and 1933, provided a large accumulation of field notes, photographs, plant specimens, and about 2500 specimens of vertebrates. Emphasis was given to the study of species as units in the whole fauna, and especially to the responses of each kind of animal to its environment and to other animals. In all, 215 kinds of vertebrates were studied, including 3 amphibians, 13 reptiles, 152 birds, and 47 mammals. Most attention was given to the birds.

A point may be raised as to the reason for going to a remote locality to study processes which take place wherever vertebrates occur. The explanation lies in the circumstance that in the high desert mountain ranges of the central Great Basin many of the environmental conditions which are suspected of affecting these animals are present in apparently extreme form. In such severe surroundings it was anticipated that more examples of environmental control of vertebrates could be observed in a short time than in a more equable region. More species and individuals here probably are living near their limits of toleration as regards one or more of their environmental influents than in other regions in the United States.

Factors which influence the distribution of vertebrates must be of the same kinds which affect the daily routine of behavior of the individuals. If an animal is enabled by its structure (including the equipment involved in its sensory behavior) to cope with its

surroundings and survive, it is likely to be able to live wherever similar surroundings exist. Species doubtless tend to extend their ranges until they reach places where the individuals can no longer accommodate themselves to the environmental conditions. This does not imply necessarily that the same kind of factor is responsible for range delimitation everywhere along the border of an animal's range. It does seem obvious, though, that the factors which delimit ranges of species must be of the same kind as determine local habitats.

If the line of reasoning suggested above is valid, then one profitable means of learning the nature of the factors effective in habitat restriction and range delimitation is to study the behavior of individuals and to pay attention to details of responses of the animals to their surroundings. Useful facts to be sought are examples of individual actions which show some connection with the environment. The observations must concern wild animals in their natural surroundings.

A major cause for confusion in attempts to analyze the environmental relations of birds may be the failure to distinguish between internal and external factors concerned in these relations. It may be impossible to separate completely these two kinds of influences and to evaluate them in the whole question of habitat behavior. But the problem would be simplified if consistent effort were made to learn the reasons for restriction in habitats by studying both the organism and its objective surroundings. It must be remembered that every individual reacts to a given set of surroundings in its own peculiar way and that the reactions of members of a species resemble one another in manner comparable to the resemblance of external features of structure. Hence it is practicable to combine items dealing with members of a single species, but not of distantly related ones.

As regards internal factors, it may be better to formulate a series of reasonable assumptions, for purposes of field analysis, than to engage in practically endless tests (measurements) of physiological and psychological activity. For example, we may accept it as demonstrated that birds have remarkably well developed powers of vision, without being able to determine with exactness many qualities of those powers. Many details have been discovered in connection with the units concerned in the physiological behavior of certain types of birds. These furnish clues as to what we may expect to learn of the physiology of other birds and of the possible relations between physiological conditions, behavior, and the external environment.

These internal factors involve the genetic history of the race and even of the individual insofar as this determines: (1) sensory responses to stimuli of vision, audition, and orientation; (2) hormonal rhythms and responses in the pituitary, gonads, and thyroid; and (3) behavior patterns involved in the nervous system.

The external factors which seem worthy of attention are mainly of two sorts—physical, having to do with topography, climate, weather, light, vegetation, and water; biotic, mainly those of food and competition with animals of other kinds or of the same kind.

Birds of the Great Basin possess certain characteristics of behavior and structural adaptation to this particular environment, which seem to distinguish them from birds, even of the same species, in other parts of the United States. Among these the following seem sufficiently prominent to deserve emphasis and to merit special study by anyone who has opportunity to watch birds in this region. In some instances these general statements are hypothetical and must remain so until more substantial evidence is available to test them.

A high proportion of the birds here is migratory, obviously on account of the severity of the winter climate. Although I have indicated that 42 per cent of the species in

the state are permanently resident, the figure is much smaller when any restricted district on the plateau is considered. Of all the categories of seasonal occurrence the one including the greatest number of individuals for any such district is that of summer residents. Stated another way, most of the birds in an area like the Toyabe region are the ones which live there during the summer. This group is larger than even the transient one. Many species which do not leave the region move to milder parts of it to escape storms.

Adult protective coloration is exemplified by a high proportion of the species, and appears to be correlated with scarcity of plant cover. The lack of an adequate screen of plants for concealment necessitates resemblance between the color of plumage and the background if the birds are not to be conspicuous. The general grayish cast throughout the whole habitat in the Great Basin extends to living as well as to other material there. Even the plants usually appear more gray than green. Most of the bird species, at least in terrestrial habitats, of the Great Basin are plainly colored. Many of these have been changed still more toward gray in this region. A large population of carnivorous species is on hand and constantly patrolling the ground, thus automatically maintaining this relationship.

Long range vision is acute, probably directly the result of scattering distribution of individuals and lack of screen of plants. On many occasions it was demonstrated that these birds of the desert are alert to see objects at great distances. The small birds need extra time to seek hiding places if discovered by predators, and all the birds require sharp vision to detect other members of the same species or to find food. These things are not only far separated over the desert, but the atmosphere is generally so clear as to permit their detection at a great distance.

Resistance to wind is effected mainly by avoiding strong winds and by possession of strong powers of flight. Even if gales are not frequent here there is often a strong wind, and the general absence of cover makes it hard for birds to avoid exposure to wind. They do seek protected places provided by bushes. One result is to strengthen the collector's impression that few birds inhabit the region. Some species which are distinctly longer-winged here than in other areas may have responded thus structurally to meet this peculiarity of a habitat distinguished by its openness. Other species which predominate in the Great Basin are ones which are strong flyers and are long-winged throughout their range. This structural modification is also advantageous in the pursuits which occur so frequently in this district.

Scattered distribution involves a high development of vocal powers to compensate for the separation of individuals. If the far separated members of a species are to hear one another, their songs and calls must be loud. Here again the characteristic species are ones possessing loud voices, and also it was observed regularly that birds in central Nevada differed in voice conspicuously from representatives of the same species in other areas, especially those nearer the Pacific Coast. And invariably voice in the Nevadan race was louder and clearer than in the Sierran or Californian one. This applied both to song and call notes.

Flight songs are noticeably frequent, probably on account of scarcity of high perches. The impression was strong, after a few seasons of field work in Nevada, that an exceptionally large proportion of the nesting species were ones in which flight song and display are conspicuous in the nesting behavior.

Resistance to heat is effected by adults mainly by avoiding it through perching in shade or off the ground. Although the air temperatures on the high plateau are not remarkably high, the clear atmosphere permits intense sunshine, and the sparse plant cover provides little protection. In the hotter parts of summer days nearly all the birds

seek to escape the intense sunshine by standing within the shadow of some plant or artificial structure. Sometimes, the birds find suitable temperatures merely by perching somewhere off the ground, but often even these places are too hot.

Nests on or near the ground are necessitated by the general limitation of the plants to low strata. Nearly every nest discovered was on the ground or so near the ground as to be easily reached by a person without climbing. Even some of the larger species which ordinarily nest high in trees commonly select low nesting sites in this area. This trait seems so firmly established that many species will take low sites when higher ones are available which resemble the normal nesting places of those birds in other regions.

Nests on the southeast sides of bushes were observed so frequently as to suggest some special significance in the circumstance. It may be connected with preference of building individuals to work in the sunshine in the early morning when the air generally is cold in this region. Or it may be partly the result of effort to escape strong wind by working in the lee of bushes. Whatever the cause, the trait was so well developed that recognition of it greatly facilitated the search for nests.

Adaptive coloration in downy young, with respect to intensity of sunlight, is shown in striking degree, and adaptive coloration of nest lining appears to parallel closely that of downy young. Young birds seem to have a narrower range of toleration of extremes of their physical surroundings than have adults. At least they are generally less able to escape unfavorable conditions than are their parents. In a series of species in the Toyabe area at least five degrees of shade are distinguished in coloration of nestling plumages (mainly down) and these are paralleled by color of the nest lining in the same species. A high positive correlation is observed between these characteristics and the kind of cover at the nest site and the general climatic ranges of the birds. Apparently those kinds of birds which nest in exposed situations, and which live in hot regions, have pale or pallid nestling plumages, and nest linings which reflect and counteract the harmful effects of sun-rays. Kinds which live in opposite conditions are dark in both these respects and thus are able to absorb and to take advantage of warmth from the sun.

The comments offered in this article are intended to summarize a series of reports dealing with materials gathered in a study of the birds of Nevada. These reports contain many facts which support statements made in this summary. They have been published as follows, by the author of the present paper.

1936. The birds of Nevada. Pac. Coast Avifauna No. 23, pp. 1–145, 1 map.

1936. Coloration of downy young birds and of nest linings. Condor, vol. 38, pp. 111–117.

1937. The natural history of magpies. Pac. Coast Avifauna No. 25, pp. 1–234, frontispiece, 20 figs. in text, 8 pls.

1938. Geographic variation in some birds in Nevada. Condor, vol. 40, pp. 36–38.

1938. Environmental responses of vertebrates in the Great Basin. Amer. Midland Nat., vol. 19, pp. 1–216, 12 figs. in text.

Museum of Vertebrate Zoology, University of California, Berkeley, September 28, 1937.