Brant—t'lick—t'lick—t'lick—high key, sharp, not too fast at beginning, but ending in a quick roll.

White-fronted—tad-lick—tad-lick—tad-lick—lick—lick—lick (idem)
Snow Goose—cwaw—caw-qua—cwaw—repeated
"China Goose" or Ross Goose—calls like Brant—t'lick—t'lick—t'lick

In 1907 the Chamberlain tract comprising 5,000 acres of the Suisun marsh was sold for \$20.00 per acre, or a total of \$100,000.00, to Frank Maskey et al., and all of the clubs were closed. It so happened that two of the three purchasers did not get a chance to fire a shot. Charley Fair was killed in July, 1907, in an automobile accident, and Joe Harvey died of pneumonia in September of the same year. After their deaths, the tract was divided up again, and four of the men who were members of the Ibis Club for the 1906 season (McAllister, Babcock, Eells and Otis) became members of the Cordelia Shooting Club.

Benicia, California, August 1, 1937.

BIOTIC ASSOCIATIONS AND LIFE-ZONES IN RELATION TO THE PLEISTOCENE BIRDS OF CALIFORNIA

By ALDEN H. MILLER

Life-zones in California are today fairly well recognized distributional divisions into which land plants and animals may be grouped. The zonal classification of a biota is inevitably subject to criticism because each organic species presents a separate problem in distribution; each responds to the numerous physical and biotic factors in different manner so that a given aggregation of species can not be bounded by any single factor or even simple group of factors of the environment. For this reason associations of plants and animals within broad zonal categories rightly receive attention as more precisely classifying the requirements and environment of species. Ultimately it is the ecologic niche, with all that that term implies in the way of significant life associates, which classifies the species biotically to the finest degree.

These familiar concepts of distribution constitute an absorbing problem when an attempt is made to apply them to conditions in the past. Our curiosity concerning the appearance of the country in former ages is one of the main reasons for study of the fossil record.

How is it feasible to piece together information bearing on this problem from fossils? The line of reasoning is as follows: (1) If in a fossil fauna the same species as live today occur, they must have required similar environmental conditions; (2) these species may have had associates that were the same, or that were similarly adapted, to those they now have; if they were known to have had a few associates like the present ones, we can assume that conditions were closely similar; (3) several associational groups along with indicator species point to a life-zone of a particular type; these also suggest the type of climate.

Several portrayals of conditions in the vicinities of the Rancho La Brea, McKittrick, and Carpinteria asphalt deposits have been offered. The excuse for another rendition of the picture of these most important Pleistocene localities is not any new method of approach, but only that more evidence has accumulated which needs to be fitted into our knowledge of the whole situation. Also, the comparison of the three faunas has not been fully developed.

Rather belatedly in the history of research on the asphalt deposits are complete studies of land birds of smaller types, and of the plants. These two elements of the biota, more than other elements thus far studied, reflect the precise environmental conditions.

They should be relied upon extensively, as should also the small rodents, were they better known.

A fundamental consideration in using modern species as indicative of past conditions is the question of constancy of habitat preference. Have species been as conservative in changing their environmental requirements as they have been in altering their structure? I am inclined to believe they have, since in general, outside of purely historical phases of their anatomy, their structure in large measure reflects their environment and mode of life. Both structure and instinct for a certain environment at least are hereditary. However, one must always be on guard in assuming identity of environmental niche for a species in the past and in the present. Much weight must be given to the degree of importance and to the flexibility of the environmental adjustments in the bird or the plant as it is known today. One could not believe that the Wren-tit of the Carpinteria was without some form of brush in which it might dwell. But the Red-winged Blackbird might have occurred even if water, which it normally seeks, were not present.

There is certain good evidence that animal and plant associations and the special requirements of modern species were similar in the Pleistocene. In the McKittrick, Mason (MS) finds a saltbush, Atriplex polycarpa, such as now abounds in the western San Joaquin Valley. Today this is the habitat of the Sage Sparrow in this area. Among the McKittrick bird fossils are several bones indistinguishable from those of modern Sage Sparrows. The association appears to be an old one. In the Rancho La Brea are remains of many live-oak trees. In the oak trees were Lewis Woodpeckers. At Carpinteria there were Monterey and Bishop pines; associated with these were Pigmy Nuthatches, today rigidly adherent to identical forests at sea-level in central California. One is impressed by this evidence for constancy in association and environment.

With other species the situation is different. If one knew the California Condor only from its distribution in the last fifteen years, he might conclude the species required a semi-arid mountainous country. Condors are, however, represented in Pleistocene deposits in northern California and in Florida, as also at several intervening stations in the Great Basin and Rocky Mountain states. In historic times they occurred in Oregon, the San Francisco Bay region and in other areas of diverse type. For one reason or another a withdrawal from certain zones and associations has taken place. Obviously this species is a poor zonal indicator, past or present.

Not long ago I chanced upon the unmistakable bones of a Pileated Woodpecker (Ceophloeus pileatus) in the La Brea. This startling occurrence would suggest a substantial coniferous forest in the area, a situation at variance with botanical evidence and with the remainder of the animal associates such as horned larks, meadowlarks, magpies and shrikes. Something does not fit, and obviously the Pileated Woodpecker is the one that is out of step with the whole company. But here are some considerations: in the last century in California (see Grinnell, Pac. Coast Avif. no. 11, 1915, p. 81) there were reported occurrences of this woodpecker at Mount Diablo and at Hollister, San Benito County, both sparsely timbered, essentially Upper Sonoran regions, Is not the Pileated Woodpecker a species that is retreating from areas of marginal habitat to regions of denser timber? Also, the rarity of the bird in the pits must be taken into account. A fossil ordinarily indicates a species of at least moderate abundance because the chances of entombment of rare species are slight. But in the La Brea such a wealth of material is accumulated that we can, as with living birds, think of species either as of normal occurrence or as strays or vagrants. Certainly the Pileated Woodpecker and the Saw-whet Owl might be classed as the latter. Hildegarde Howard (Condor, vol. 32, 1930, pp. 81-88) has shown the importance of relative abundance in a fossil fauna of this kind in determining the biotic associations and the conditions of deposition.

I propose now to consider the smaller land birds of the three asphalt accumulations that have some bearing on past ecological conditions. In the Carpinteria (Miller, A. H., Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 21, 1932, pp. 169–194) the following species occur which are absent in the La Brea and McKittrick deposits: Pigmy Nuthatch, Sitta pygmaea (3 specimens); Red-breasted Nuthatch, Sitta canadensis (1); Wren-tit, Chamaea fasciata (2); Pine Siskin, Spinus pinus (1); Red Crossbill, Loxia curvirostra (2); and Fox Sparrow, Passerella iliaca (1). This group, especially those small perishable species that are represented by more than one individual, fairly well indicates a phase of the biotic environment peculiar to this one of the three asphalt tombs. This phase is the Monterey pine forest with its characteristic underbrush. In addition to the conifers of the forest, there was manzanita (Arctostaphylos) in abundance (Chaney and Mason, Carnegie Inst. Wash., Publ. 415, 1933, pp. 45-79) which doubtless served for cover for the Wren-tits. Meadowlarks were scarce; horned larks and shrikes were absent. The quail were California Quail, not Mountain Quail, which situation compares favorably with that in the coastal Transition forest today. Brown Towhees (Pipilo fuscus) and California Jays (Aphelocoma californica) both indicate the proximity, or intermixture, of Upper Sonoran. This is emphasized by the relative abundance of Cyanocitta and Aphelocoma which occur in the ratio of 2 to 11. Everyone who has considered the problem agrees that the Carpinteria represents a Transition, or near-Transition, Monterey forest such as now is found on Point Pinos, Monterey County. This closed-cone pine forest association is characteristic of the fog belt and now occurs in only slightly modified form in restricted areas on the coastal slopes west of the main coastal fault lines and on some of the coastal islands as far south as Cedros Island, Lower California (Mason, Carnegie Inst. Wash., Publ. 415, 1934, pp. 81-179).

In the McKittrick the following species appear in the pit that has a representative dry-land fauna: Bendire Thrasher (Toxostoma bendirei), Cliff Swallow (Petrochelidon albifrons), House Finch (Carpodacus mexicanus), Cactus Wren (Heleodytes, sp.), and Sage Sparrow (Amphispiza belli). These appear in neither of the other two locations, although the House Finch probably will be found with further study of the Rancho La Brea. Amphispiza belli is especially characteristic of the McKittrick area today. Other common land birds that contribute to the zonal-associational picture are Horned Lark (Otocoris alpestris), Sage Thrasher (Oreoscoptes montanus), Loggerhead Shrike (Lanius ludovicianus), California Quail (Lophortyx californica), and Burrowing Owl (Speotyto cunicularia).

The environment would appear to have been similar to that there now, except for local topography, were it not for the presence of several California Jays (Aphelocoma californica). These do not occur at McKittrick now, but are found some distance above and westward in the arid coast ranges. Mason (MS), however, finds remains of pinyon pines, indicative of a suitable plant association for this jay. A single magpie (Pica), possibly a straggler, is present. The pinyon forest does not now extend much north and west of Mount Pinos in southern Kern County. It would appear, then, that this particular arid interior, Upper Sonoran association extended farther north, and to lesser elevations, in the past. Proximity of such an environment to the pits might explain the occurrence of jays; the immediate environs still could have been as truly Lower Sonoran as at present. Certainly the majority of the land fauna indicates an atriplex belt as strictly Lower Sonoran in aspect as that there today.

The remains of thrashers identified as *bendirei*, rather than the expected *lecontei*, afford an interesting item of distribution. Bendire Thrashers are now largely confined to the regions east of the Colorado River, but one small breeding colony has been found (Pierce, Condor, vol. 23, 1921, p. 34) near Victorville, on the Mohave desert, San Ber-

nardino County. The species is notoriously spotted in its distribution in Arizona, especially along its northern limits. A closer faunal relation of the Mohave desert and the Kern Basin in the Pleistocene might easily have brought the Bendire Thrasher this far north, as also the Cactus Wren, if it was the same as the living species. Cactus Wrens are not found in the San Joaquin Valley at present. On the basis of Recent distribution of the Leconte Thrasher, Grinnell (Condor, vol. 35, 1933, p. 113) has pointed to the likelihood of former connections of the Lower Sonoran regions of the Mohave and San Joaquin areas, most probably by way of Walker Pass and the Kern River Valley. The Leconte Thrashers may well have been in the vicinity of McKittrick in the Pleistocene without having become entrapped.

Another unusual occurrence in the McKittrick is a small raven, indistinguishable from the White-necked Raven (*Corvus cryptoleucus*). Although now a desert species, it was less restricted in the past. It also occurred rarely in the Rancho La Brea. A notable absentee is the crow which so readily became entrapped in the other asphalt pools. Surely if it had been present in the area, it would appear as a fossil. Ravens are abundant. Crows are today absent from the arid western San Joaquin Valley, except in the river bottoms.

In summary, McKittrick and Carpinteria on opposite sides of the coast range were even more strongly contrasted zonally than now, the Carpinteria distinctly more humid with a Transition forest, the McKittrick possibly with closer approach spatially to Upper Sonoran than at present, but yet with arid, desert aspect no less extreme than that of today. The lake that provided conditions for the water-bird fauna is to be compared with the Recent desert lakes of this region.

What does the Rancho La Brea represent, an extension of the Monterey biotic province southward, a true San Diegan District environment, or one of distinctly tropical nature? I have mentioned the anomalous occurrence of a Pileated Woodpecker, and there are other rarities like the chickadee, Saw-whet Owl and Steller Jay. But the majority of the abundant species pertain to the Upper Sonoran-San Diegan fauna. Yellow-billed Magpie (*Pica nuttallii*), Western Meadowlark (*Sturnella neglecta*), California Quail (*Lophortyx californica*), California Jay (*Aphelocoma californica*), California Thrasher (*Toxostoma redivivum*), and Loggerhead Shrike (*Lanius ludovicianus*) are well-represented species of significance in this connection. Meadowlarks are much more abundant than in the McKittrick; Horned Larks are less abundant. Sage Thrashers are rare, but are common in the McKittrick. Pine-forest associates are almost absent. Significantly, we find in pit 10 (the Recent pit) an absence, or near absence, of oakforest dependents (*Pica* and *Aphelocoma*), and an increased percentage of *Sturnella*.

The original suggestion of tropical aspect based chiefly on the presence of large raptors, many of which are now southern in distribution, is not tenable, as these forms obviously have retreated southward out of keeping with environmental changes. The suggestion that the environment corresponded to that now found somewhat to the north in the coastal oak belt was made by me (Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 19, 1929, pp. 1–22) in an earlier study, and it was thought that climatic conditions were more humid, and if anything cooler. Since Frost's (Univ. Calif. Publ. Bot., vol. 14, 1927, pp. 73–98) study of the La Brea plant remains, Mason has reviewed the evidence and points out (see Compton, Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 24, 1937, p. 88) that the flora is like that of the interior arid oak and juniper association of the Tehachapi region. This association is found in climates of moderate rainfall with low summer humidity. Similar conditions are now found in San Diego County and in Lower California close to, or on, the coast. As I now see it, the plants of La Brea and the bird associates did not require greater humidity than that characteristic of the site today,

but perhaps only slightly increased annual rainfall, at least locally, with temperatures similar or higher, and humidity probably less. A recent study of the shrews of La Brea by Compton (*loc. cit.*) shows that the desert-dwelling shrew, *Notiosorex*, is the dominant form.

To the southward on the coast the interior arid flora and the humid coastal close-coned pine forest typically are in closer proximity. This may have been true in the vicinity of Los Angeles. The La Brea was essentially the arid phase, perhaps protected from the coastal influence more than now by the Santa Monica Mountains wherein a Carpinteria-like biota may have existed. The Pleistocene peninsula extending from the Santa Monica Mountains northwestward, connecting the Santa Barbara Islands with the mainland, that Chaney and Mason postulate (loc. cit.), would have formed a protected bay to the south of it, bringing interior conditions closer to the shore line.

The only land bird that points definitely toward proximity of a coastal environment is the Northwest Crow (Corvus caurinus). This beach crow, unless it was very different in habits in the past, would not have wandered far from the shore. It had been entirely replaced by the Western Crow (Corvus brachyrhynchos hesperis) when the Recent pit containing Homo was open. But at no time was caurinus the only crow present; there were always some brachyrhynchos, while at Carpinteria, definitely on the coast, caurinus alone appears in the remains. La Brea then may have been in a marginal area with respect to the spheres of action of these two types of crow.

With respect to the northern section of the state, slightly lower zonal limits in the Shasta area are suggested by Pleistocene remains of *Dendragapus* at the 1800-foot level and by the replacement of *Aphelocoma* by *Cyanocitta* at this point where *Aphelocoma* may occur today. *Bonasa* also occurred there, which adds a humid boreal or coastal element. In Eldorado County at the 1500-foot level the presence of both *Oreortyx* and *Lophortyx* suggests marginal Transition-Upper Sonoran conditions at a point now definitely Upper Sonoran.

If we let our fancy run, and for the moment pass over the problems of time intervals within the Pleistocene, we can imagine California to have been as sharply subdivided zonally in the immediate geologic past as it is at present, with the same general distribution of zones. On the coast and in the north there was greater extension downward or southward of Transition areas, particularly a more extensive and continuous coastal pine forest. In the south, coastwise and in the interior, there was no restriction of the arid areas, but some climatic differences which favored a heavier, though arid forestation, at least locally on the coastal plane. Southern California resembled northern Lower California in abrupt contrasts, yet had certain northern components not now found in Lower California. Northern California was of more boreal aspect. The net result was a remarkable series of contrasts, especially well reflected in the biotas of Carpinteria, McKittrick and Rancho La Brea.

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