# THE SIERRA MADREAN ELEMENT OF THE AVIFAUNA OF THE CAPE DISTRICT, BAJA CALIFORNIA

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The Cape district, or terminal third of the peninsula of Baja California, has long been recognized as an area especially rich in endemic species and subspecies of birds. The district, as defined by Nelson (1921:plate 31), includes that portion of Baja California lying south of a line, arching sharply to the north, from Santa Rosalía on the Gulf coast at latitude 27° 20' N to Santo Domingo Point on the Pacific coast at latitude 26° 19' N. Grinnell (1928:7) listed 46 species and subspecies of birds endemic to this region. Of these, 43 were considered by him to have arrived "from the north, . . . over continuous land, rather than from across the Gulf to the eastward." The invasions of the Cape presumably occurred "by way of its basal territory, from California, Arizona, and Sonora." The hypothesis of northern (meaning not trans-Gulf) origin of most of the vertebrates endemic to the Cape district has also been expressed by Nelson (1921) and by Johnston (1924). In a later statement, Grinnell (1928:12) concludes that of all the areas of differentiation in Baja California, "it can be said that the Cape district appears to have acted most potently with respect to bird life, ..." (italics mine). The idea is implied by Grinnell that there has been a marked differentiation in the Cape district of pioneer ancestral stocks, and that because of this differentiation, the avifauna of that region now includes an unusually large number of endemic forms.

However, Oberholser (1919:211) pointed out that the distinctive Brown Towhee of the Cape district (Pipilo fuscus albigula), a form connected by a series of intergrading populations with the Brown Towhees of the Pacific coast of California, actually resembles P. f. mesoleucus of Arizona, New Mexico, and northwestern México more than it does the coastal races to the north, although mesoleucus on the one hand, and the Brown Towhees of California and Baja California on the other, are geographically isolated. Davis (1951:98) suggested that, rather than being a strongly differentiated endemic of the Cape district, albigula was actually a non-differentiate, a form which, far from being very distinct from the ancestral stock which pioneered in the Cape district, might actually be rather similar to it. According to this viewpoint, it is the Brown Towhees of the Pacific coast that have diverged farthest from the original stock, leaving the towhee of the Cape district a relatively little differentiated relict contrasting sharply with them. It is the intent of this paper to consider the variational trends exhibited by the endemic species and subspecies of birds that occur, at least in part, in the mountains of the Cape district, and to test the "strong differentiate" versus "weak differentiate" hypothesis for this group.

There is no fossil evidence from Baja California to indicate the history of the flora of that region. However, the mountains of the Cape district support a vegetation that contains a Sierra Madrean woodland element evidently derived from the Madro-Tertiary flora. As Axelrod (1958) points out, the occurrence in Miocene floras of southern California of fossil equivalents of modern woodland species of the Cape highlands, together with fossil equivalents of living species typifying the Californian flora, and fossil equivalents of recent species now occurring in the Sierra Madrean woodland in the interior southwestern United States and adjacent México, indicates that the Lagunan woodland of the Cape district is a segregate of the Madro-Tertiary flora. The presence in the Cape highlands of modern plant species of definite Madro-Tertiary affinities suggests that, after reaching the Pacific coast, the Madro-Tertiary flora, moving northwestward from northern México in the Miocene, spread down the entire peninsula of Baja California

and was replaced subsequently over most of the terminal two-thirds of the peninsula by the very rich desert flora found there today; the Sierra Madrean woodland element of the Madro-Tertiary flora persisted only in northwestern Baja California and in the highlands of the Cape district. This element, once widespread, probably provided the avenue of dispersal for Acorn Woodpeckers, Robins, White-breasted Nuthatches, and the other upland species found in the Cape highlands today. In many instances, these species are isolated from the nearest population of the same species or genus by a great expanse of unfavorable desert habitat. Since the Madro-Tertiary flora presumably originated in northern México, it seems likely that the avian species associated today with the remnants of the Sierra Madrean woodland element in the Cape district actually followed this flora from northern México to the Pacific coast and thence south down the length of the peninsula to the Cape. Although various authors have stressed the fact that most of the vertebrate fauna in Baja California probably came from the north rather than across the Gulf of California, the birds presently associated with the Sierra Madrean woodland element seem especially favorable for consideration, as there is some historical evidence that suggests that these birds not only came from "the north," but more specifically from northern México. The history of the Madro-Tertiary flora and the apparent correlation between the past movements of this flora and the present distribution of the Brown Towhee have been discussed by Davis (1951:96-98) and exemplify the kind of past population movements presumed typical for most of the species of birds found in the Cape highlands today.

In the present analysis, consideration is given to those endemics of the Cape district listed by Grinnell (1928) which occur, at least in part, in the Laguna and Victoria mountains. In addition, the Warbling Vireo of the Cape district (*Vireo gilvus victoriae*), described by Sibley (1940), is also considered.

#### ANALYSIS OF THE AVIFAUNA

Species with Mexican mainland affinities.—Of the 17 species and subspecies considered in this paper, 11 appear to have their closest relationships with related forms in México and the southwestern United States east of the Colorado River rather than with related forms on the Pacific coast of California. These are as follows:

Columba fasciata vioscae. Band-tailed Pigeon. The distribution of this form is restricted to the mountains of the Cape district, in which it is a common breeding bird (Grinnell, 1928:104). Friedmann, Griscom, and Moore (1950:115) list it as resident in the oak belt of the Cape district, at times descending into the foothills. Brodkorb (1943:19) recognized three races of Columba fasciata, exclusive of vioscae, which he did not consider. These are monilis, a large, dark race ranging from British Columbia to northern Baja California; fasciata, paler than monilis and with a shorter wing, ranging from the Rocky Mountains south to Guatemala; and letonai, the smallest of the three races, intermediate in coloration between monilis and fasciata, and resident in the mountains of Honduras, El Salvador, and Nicaragua. There is thus a cline of decreasing wing length from northwest to southeast. In wing length, vioscae is similar to fasciata. In color, it is the palest of all races. This is especially noticeable ventrally, as the posterior underparts of vioscae are less washed with color and are more whitish. There is some individual variation in this character, however, and in some specimens of vioscae the ventral wash of color extends as far posteriorly as in other races. The population of the Cape district is further characterized by the virtual loss of the dusky band across the middle of the tail; this band is distinct in the other races. Of the three mainland races, vioscae is most similar to fasciata in size and color, and it differs sharply from the large, dark race monilis to the north.

Otus asio xantusi. Screech Owl. According to Grinnell (1928:116), xantusi is a "common resident in the Cape district.... Apparently occurs from the coastal lowlands (Arid Tropical life-zone) up to the tops of the Victoria Mountains." This form is thus not restricted to the Sierra Madrean woodland element of the vegetation of the Cape district. Of the 21 specimens of xantusi in the Museum of

Vertebrate Zoology (exclusive of nestlings), only one was collected in the mountains; the remaining 20 were collected at or below the 800-foot level. This suggests that xantusi is more common in the lowlands of the Cape district than in the mountains. Nevertheless, it is included here because it has been recorded from the mountains as well. Moore and Peters (1939:42) stated that xantusi was "nearest to sinaloensis" of southern Sonora and northwestern Sinaloa. Miller and Miller (1951:175) were of the opinion that the close affinity of xantusi and sinaloensis suggested by Moore and Peters "may be misleading," and they believed that xantusi is closer in most features to yumanensis of the lower Colorado River and the Colorado Desert. Otus asio quercinus, which ranges from central northern California south to latitude 31°N in northwestern Baja California, is a far darker form than xantusi; cardonensis, which ranges from about latitude 31°N south to latitude 29°N in Baja California, is darker than either yumanensis to its north or xantusi to its south. The relationships of xantusi are clearly with the races yumanensis, cineraceus, which ranges from southern Nevada and southern Utah south to central Sonora, and sinaloensis. It seems likely that xantusi has retained certain features of an ancestral population which reached the Cape district from northwestern México via the southwestern United States, probably following the Arid Subtropical Scrub complex which existed as a border vegetation to the Sierra Madrean woodland element of the Madro-Tertiary flora (Axelrod, 1950).

Hylocharis xantusii. Xantus Hummingbird. This well-marked form is a "common resident in the Cape district, where found from sea level to the tops of the highest mountains, though breeding most numerously, perhaps, in the mountains. . . .," and it occurs "sparsely or locally, as far as latitude 29°" (Grinnell, 1928:134). Although H. xantusii is a very distinct form and probably represents a valid species mainly confined to the Cape district, its affinities are obviously with the White-eared Hummingbird. H. leucotis, which ranges from southern Arizona south to El Salvador, Honduras, and Nicaragua and is confined as a breeding species to highland regions. Xantusii and leucotis were at one time segregated in the genus Basilinna. Although now considered members of the genus Hylocharis, they are still retained in the subgenus Basilinna (American Ornithologists' Union, 1957:307), and they differ from the other members of the genus Hylocharis in their possession of a white postocular streak and a black or dusky auricular stripe. There is no doubt that xantusii is a well-marked differentiate of the Cape district, but it is obvious from its similarity to leucotis that it has been derived from that form. Grinnell (1928:7) stated that H. xantusii was one of three species in the avifauna of the Cape district that most probably colonized that area directly from the Mexican mainland to the east. However, it seems even more probable that the population ancestral to xantusii may have pioneered from the Mexican mainland via the Sierra Madrean woodland element of the Madro-Tertiary flora, rather than from across the Gulf of California. The fact that xantusii is found today in arid tropical vegetation as well as in the vegetation of the highlands does not necessarily mean that the population originally colonizing the Cape region came directly from the east. If the ecologic requirements of the presumed ancestor, leucotis, have been at all constant through time, a direct colonization from the east would have entailed an invasion by a highland form, well removed from the coast, across the lowlands west of the Sierra Madre Occidental and across the Gulf of California before reaching the highlands of the Cape where it would find suitable habitat. If leucotis were today a bird that ranged, at least in part, into the arid tropical vegetation of the Mexican mainland, there would be more reason to assume a direct trans-Gulf invasion of the Cape district by this form. It seems much more likely that the pioneer "Basilinna" stock reached the Cape via the Sierra Madrean woodland element.

Balanosphyra formicivora angustifrons. Acorn Woodpecker. This form is a "common resident in the oak belt on the mountains of the Cape district" (Grinnell, 1928:124). The races of the Acorn Woodpecker may be divided into two general groups. In the first, the breast band is virtually solid black, with very little white spotting and streaking posteriorly. This group includes bairdi, which ranges from Oregon to southern California, and martirensis, of northwestern Baja California. In the second group, the breast band is noticeably broken by white spots and streaks. Included in this group are angustifrons of the Cape district; formicivora, ranging from Arizona, New Mexico, and Texas south to the Isthmus of Tehuantepec, México; albeola, ranging from southeastern México to British Honduras; and lineata, which occurs from Chiapas to northern Nicaragua. Angustifrons thus appears to have closer affinities with the Acorn Woodpeckers of México and Central America than with the Pacific coastal populations to its north. In several characters, this race is distinct from all others.

The frontal band in angustifrons is by far the narrowest, the throat band is more intensely yellow, and this color continues up the cheeks and into the frontal band, which is yellow as opposed to white in other races. In female angustifrons, the red crown patch is markedly longer than broad anteroposteriorly, in contrast to other races. The nearest approach to angustifrons in this character is found in formicivora in the southern part of its range, and in lineata (albeola not seen). Despite these distinctive characters, angustifrons has its basic affinities with that section of the species which is characterized by an interrupted breast band, and it diverges from the populations of the Pacific coast and northern Baja California in this character.

Sitta carolinensis lagunae. White-breasted Nuthatch. This race is a "rather uncommon resident in the higher mountains of the Cape district" (Grinnell, 1928:221). In size, lagunae is noticeably smaller than alexandrae of the Sierra San Pedro Mártir of northern Baja California. There is a cline of increasing size in nuthatches from north to south along the Pacific coast (Hawbecker, 1948:30-32), culminating in alexandrae. Between the latter and lagunae there is a noticeable decrease in size. In color, lagunae is noticeably darker than either alexandrae or aculeata to the north. It corresponds most closely to the dark races nelsoni, umbrosa, and mexicana, which range from the Rocky Mountains of Montana south through the Sierra Madre Occidental to the central plateau of México. Grinnell (1926:408) noted that "in certain respects (shape of bill, color of sides and flanks) lagunae resembles nelsoni and mexicana [including umbrosa] of the Rocky Mountain region of the United States and Mexico, rather than alexandrae and aculeata of the Pacific Coast region to the northwest."

Vireo huttoni cognatus. Hutton Vireo. Cognatus is a "common resident locally in the mountains of the Cape district proper" (Grinnell, 1928:195). In the general pallor of its coloration, this race differs sharply from typical huttoni, which ranges from British Columbia south to northwestern Baja California. It differs similarly from V. h. mexicanus of the central plateau and Sierra Madre del Sur of México, and from V. h. carolinae, which ranges from extreme southern Texas south to northeastern México. The obvious similarity of cognatus is to the pale race stephensi, which ranges from southeastern Arizona and southwestern New Mexico south in México to Nayarit and Zacatecas. Dorsally, cognatus is similar to stephensi, and ventrally it is even paler than that form. Cognatus and stephensi are sharply differentiated from all other races of Vireo huttoni in their pale coloration; cognatus is another endemic of the Cape district that diverges strongly from the populations to its northwest and resembles most closely the populations of northwestern México.

Vireo gilvus victoriae. Warbling Vireo. The Warbling Vireo is a "fairly common breeding species in the higher parts of the Cape region. . . ." (Grinnell, 1928:194). The winter range of this form is unknown (Pac. Coast Avif. No. 33, 1957:231). Although Grinnell recognized the possibility that the Warbling Vireo of the Cape district might represent a distinct race, this was not described until 1940 (Sibley, 1940:255). In his description of victoriae, Sibley noted that the brownish dorsal coloration of this race established it as a member of the integrating series connecting the northern "gilvus" group of vireos with the brownish "amauronotus" group of eastern and southeastern México. In comparing breeding specimens of victoriae with similar specimens of swainsonii of the western United States exclusive of the Great Basin, leucopolius of the Great Basin, and brewsteri of the Sierra Madre Occidental south to Nayarit, it is apparent that swainsonii is separable from the other races on the basis of its olive-green coloration dorsally. Color differences among the other races are not striking, possibly because of the worn nature of the available material. However, as Sibley pointed out, leucopolius is definitely a gray form. Victoriae is closest to brewsteri in dorsal coloration, both being more brownish than either swainsonii or leucopolius. The relationships of victoriae thus appear to be with brewsteri; victoriae is distinguishable from that race, however, on the basis of wing, tail, and bill measurements.

Pipilo erythrophthalmus magnirostris. Rufous-sided Towhee. This race is a "common resident of the mountainous portions of the Cape district" (Grinnell, 1928:181). The western races of Pipilo erythrophthalmus fall into two main groups. The races of the Pacific coast (exclusive of the island race clementae) are of a generally dark coloration. These populations range from British Columbia south to northwestern Baja California. The populations ranging eastward from interior California through the Great Basin, Rocky Mountains, and northern Great Plains, and south to the central plateau of México, are noticeably paler, with more olive or gray in the dorsal coloration. The affinities of magnirostris are clearly with this second group; the population of the Cape district is strongly

differentiated from *umbraticola* of northwestern Baja California, an obvious member of the Pacific coastal group of races. The western interior and Mexican races of *P. erythrophthalmus* are so variable in color that it would be speculative to point to any particular race as having especially close affinities with *magnirostris*. Yet it is obvious that the relationships of the latter are with the races to the northeast and east, and not with the populations of the Pacific coast.

Pipilo fuscus albigula. Brown Towhee. Albigula is a "common resident, locally, in the Cape district, where occurring chiefly in brushy parts of the Lower Sonoran and Arid Tropical life-zones" (Grinnell, 1928:182). Davis (1951:15) noted that specimens of albigula from the Cape highlands are rare in collections whereas specimens taken at lower elevations are abundant. This race is considered here because it does range up into the mountains, even though its center of abundance seems to be in the lowlands. The resemblance of albigula to the Brown Towhees of northwestern México and the southwestern United States east of the Colorado River has been mentioned previously. The situation is discussed in greater detail by Davis (op. cit.: 43-45 and 94-98).

Aimophila ruficeps sororia. Rufous-crowned Sparrow. This form is stated by Grinnell (1928:174) to be a "common resident locally in the mountains of the Cape district." Sororia differs considerably from the nearest population to the northwest, canescens, which ranges from southwestern California to northwestern Baja California. In the general pallor of its coloration and in the much greater development of ventral white sororia is much more nearly similar to scottii of Arizona, New Mexico, northeastern Sonora, and northwestern Chihuahua, and to simulans, which ranges in México from southern Sonora to Nayarit and from southern Chihuahua south through Durango and Zacatecas to Guanajuato. Van Rossem (1934:487), in his description of simulans, stated that this form is "almost exactly similar in coloration and size to Aimophila ruficeps sororia of Lower California," from which it could be differentiated on the basis of smaller bill size. The affinities of sororia are clearly with the populations to its northeast and east, and not with the populations of the Pacific coast to its north.

Junco bairdi. Baird Junco. This species is a resident of the Victoria Mountains at higher elevations (Grinnell, 1928:170). As stated by Miller (1941:220), "Its affinities are not with the [dark-eyed] juncos of northern Lower California, but with the yellow-eyed forms of Mexico and Guatemala." Bairdi shows resemblance in some characters to Junco alticola of southeastern Chiapas and southwestern Guatemala, in others it resembles J. fulvescens of interior Chiapas, and in still others it resembles J. phaeonotus, which is resident from southeastern Arizona and southwestern New Mexico south to southern México. "Speaking broadly, it is a pale, dwarfed representative of the Central American juncos" (op. cit.:221). After making detailed comparisons between bairdi and the other species of the "Rassenkreis Junco phaeonotus," Miller concludes that it is "problematical that affinities of bairdi are all with J. phaeonotus, although the resemblance still seems closer to that species than to alticola and fulvescens" (op. cit.:225). He was of the opinion (op. cit.:226) that the colonization of the Cape district by the stock ancestral to bairdi was from the south or east, but not by way of any land connection between the Mexican mainland and the peninsula of Baja California. At the present time, bairdi is one of only a few juncos "that breed under zonal conditions lower than Transition. . . . The nature of the region [which it occupies] compares most closely, as far as Junco-inhabited regions are concerned, with the Upper Sonoran oak belt of Arizona, which adjoins the habitat of [Junco phaeonotus] palliatus in the Transition Zone and which at times is invaded by that race" (op. cit.:225). It seems likely that Junco bairdi is another form of Mexican origin that followed the Madro-Tertiary flora from México to the Cape district and has retained a number of features which characterized the original pioneering population.

Species with Pacific coastal affinities.—The next group of Cape district endemics to be considered includes forms which clearly have their affinities with related forms found today on the Pacific coast to the northwest. This group includes three species, as follows:

Aphelocoma coerulescens hypoleuca. Scrub Jay. Hypoleuca ranges "from the mangrove swamps and arid tropical vegetation along the coast up into the woodlands of the Sierra de la Laguna" (Pitelka, 1951:247). The Scrub Jays of the Cape district are thus distributed widely beyond the limits of the Sierra Madrean flora of the highlands. The species occupies not only the Cape district and the northwestern part of the peninsula, but the central part as well, from Yubay and Santa Rosalía Bay south at least to Loreto (latitude 26°N) and the west side of the Sierra de la Giganta. "In no other part of its relatively large area of distribution does A. coerulescens occur over so wide a range of environments

as in the Cape region" (op. cit.:247). The affinities of hypoleuca, and of cactophila of the middle part of the peninsula, are clearly with the populations of the Pacific coast.

Psaltriparus minimus grindae. Common Bushtit. This race of the bushtit is a "common resident on the mountains of the Cape district" (Grinnell, 1928:224). The species limits of P. minimus are somewhat uncertain at the present time. Some taxonomists consider minimus as including the Blackeared Bushtit, P. melanotis, which ranges from southern New Mexico and western Texas south to Guatemala, and others consider minimus and melanotis as separate species. Considering the bushtits of North America and México solely on a population basis, and ignoring the formal taxonomic treatment of the minimus and melanotis groups, it is evident that the bushtits of the Cape district have no affinity with the black-eared "melanotis" populations of México. The minimus group, which ranges from British Columbia and the Great Basin region south to the Cape district, northern Sonora, southern New Mexico, and western and central Texas, can be divided into two well-marked sub-groups; in one, the pileum is gray, concolor with the dorsum, and in the other the pileum is brown, contrasting sharply with the gray dorsum. The first group occupies the Great Basin region, and the second is distributed along the Pacific coast. Grindae clearly belongs to the second group, and its affinities are obviously with the populations to the northwest.

Vireo solitarius lucasanus. Solitary Vireo. This form is a "common resident in the Cape district proper, occurring in the breeding season chiefly at the higher altitudes" (Grinnell, 1928:195). Lucasanus differs considerably from the races plumbeus, pinicolus, and repetens, which range from Idaho, Wyoming, Montana, and South Dakota south to southern México. The affinities of lucasanus are clearly with cassinii of the Pacific coast; indeed, the intensity of yellow on the sides and flanks of lucasanus approaches the coloration of typical solitarius of the northeastern United States and Canada. It seems probable that lucasanus was derived from an ancestral stock which invaded the peninsula of Baja California directly from the northwest.

Strong differentiates of the Cape district.—The last group of species to be considered includes endemic forms which appear to be strong differentiates of the Cape region. These forms cannot be said to have particularly close affinities with other populations either to the northwest, northeast, or east. This group includes three species, as follows:

Glaucidium gnoma hoskinsii. Pygmy Owl. This form is a "fairly common resident, chiefly on the mountains . . ., in the Cape district; occurs also north nearly to latitude 27°" (Grinnell, 1928:118). It is not confined to the Sierra Madrean woodland element of the highlands; it also ranges down into the desert vegetation at lower altitudes. The limited material available to me gives no idea of the range of color variation in this form. Hoskinsii is short-winged, and in this character it approaches both grinnelli of the Pacific coast and gnoma, which ranges from southern Arizona and Nuevo León south through the Mexican highlands to Chiapas. In color, hoskinsii is far paler than grinnelli. It differs from gnoma, and from californicum of interior California and the Great Basin and Rocky Mountain ranges, in the paler, browner, less blackish striping of the underparts. Its affinities remain obscure in the absence of more adequate material, and it seems possible that hoskinsii may be a well-marked differentiate of the Cape district.

Contopus sordidulus peninsulae. Western Wood Pewee. This flycatcher is a "common summer resident on the Sierra de la Laguna, in the Cape district" (Grinnell, 1928:140). Peninsulae is a pale, short-winged, short-tailed, long-billed race. It is distinct from other populations of Contopus sordidulus, and it may represent a form which has diverged considerably from its ancestral stock. Any statements regarding the affinities of this form are purely speculative.

Turdus migratorius confinis. Robin. This form is treated as a full species by most taxonomists. I follow Hellmayr (1934:354, footnote), who considered it "merely an excessively pale race of the Robin." It is a "common resident in the mountains of the Cape district" (Grinnell, 1928:233). In appearance, confinis is so pale as to differ strikingly from all other races of Turdus migratorius. It obviously represents a well-marked differentiate of the Cape district.

#### DISCUSSION

Of the 17 endemics which occur, at least in part, in the Cape highlands, only three appear to be so distinctive that they may be regarded as having lost all obvious evidence of their relationship to particular modern populations of the same species. The remaining

14 forms, although they may have developed distinctive characters, presumably under conditions of isolation in the Cape district, have retained certain features which suggest that they have been derived from ancestral stocks which are found today either on the Pacific coast or in México and the southwestern United States east of the Colorado River. Of these 14, only three show any features which suggest a relationship to forms present today on the Pacific coast. The available evidence, then, suggests strongly that most of the highland endemics of the Cape district colonized that region from the mainland of México and the adjacent inland United States. When one considers the habits of the species concerned, it does not seem likely that such sedentary forms as Rufous-sided and Brown towhees, Rufous-crowned Sparrows, Acorn Woodpeckers, Screech Owls, and others, would have invaded the Cape region by an overwater, or even island-hopping route from the Mexican mainland. It seems more likely that these species reached the Cape either by a direct land connection from the Mexican mainland or by an overland route from northern México through the adjacent southwestern United States to the base of the peninsula, and thence south to the Cape region.

The present evidence suggests that the Gulf of California and the peninsula of Baja California were blocked out in essentially their present form by early Pliocene (Anderson, 1950:1). Any trans-Gulf colonization of the Cape region, that is, by a direct land connection to the east, would have had to occur by late Miocene at the latest. Such an overland invasion is made improbable in that only two of the 46 endemics of the Cape region listed by Grinnell (1928:7) can be thought of as being of west coast Mexican tropical origin. These are the Groove-billed Ani (Crotophaga sulcirostris pallidula), which also breeds in southern Sonora and may not be a Cape region endemic (van Rossem, 1938:91), and the "Mangrove Warbler" (Dendroica petechia castaneiceps). Had invasion of the Cape occurred via a land connection to the east, we would expect to find a greater number of Mexican west coast tropical species in the Cape region today, as suitable habitat for such forms existed as a border element to the Lagunan woodland by Miocene time. As Axelrod (1958) notes, arid subtropic scrub genera such as Acacia, Bursera, Cardiospermum, Condalia, Dodonaea, Erythea, Ficus, Karwinskia, Lysiloma, Morus, Passiflora, and Pithecolobium regularly occur with fossil representatives of the Lagunan woodland in the Miocene and Pliocene floras of southern California, and a number of these genera are prominent components of the lowland vegetation of the west coast of México today, from Sonora and Sinaloa south. The only alternative hypothesis is that a number of Mexican west coast avian species did invade the peninsula of Baja California via a direct land connection, but that they have subsequently disappeared, a hypothesis for which there is no evidence at present.

The pattern of variation found in 11 of the 17 endemics considered here is one in which a relationship is indicated between the populations of the Cape highlands and populations to the northeast and east. Between these apparently related groups there intrudes a series of populations in northwestern Baja California; these populations are evidently related to forms found on the Pacific coast to the northwest. This suggests that the pioneering populations which had invaded the Pacific coast began to diverge morphologically, probably as the generalized Madro-Tertiary flora in the Pacific coastal region became segregated into modern communities such as pine-oak woodland, chaparral, and desert scrub. In the Cape region, at least, the Sierra Madrean woodland element of the Madro-Tertiary flora has retained many of its original features. As Axelrod (1950, 1958) has pointed out, such modern representatives of the Sierra Madrean woodland in the Cape region as Arbutus peninsularis, Ilex brandegeana, Populus brandegeei, and Quercus brandegei are represented by fossil equivalents in the Miocene of California and in the Pliocene of California and Nevada. Certain species found in the Cape highlands

today, including Ilex brandegeana, Ouercus albocincta, and Rhus hartmannii, are known elsewhere only from the Sierra Madre Occidental in Sonora and Sinaloa, Further, the occurrence of members of the Cape component of the north Mexican element of the Arid Subtropical Scrub Complex together with woodland species of the Sierra Laguna component of the Sierra Madrean woodland element in the Miocene and Pliocene floras of southern California is duplicated today by the modern ecotone in southern Baja California (Axelrod, 1950). "... Arid subtropic communities probably occupied the lower, warmer levels, with woodland on bordering slopes, relations of a type which occur widely in northern Mexico, including southern Baja California, today" (Axelrod, 1958), It seems most likely that most of the avian endemics of the Cape highlands have their closest affinities with forms to their northeast and east because the habitat in which these Cape endemics occur today has become relatively little modified from the habitat with which the ancestral stocks of these species were associated in México. In northwestern Baja California, the western foothills of the Sierra Juárez and the Sierra San Pedro Mártir support a vegetation that is clearly related to the flora of southern California. As might be expected, the highland avian endemics of northwestern Baja California show clear relationships with the populations of the Pacific coast to their north. The three endemics of the Cape district which are clearly related to Pacific coastal forms. Aphelocoma coerulescens hypoleuca, Psaltriparus minimus grindae, and Vireo solitarius lucasanus, evidently colonized the Cape region at a relatively late time, after considerable divergence from the ancestral stocks pioneering on the Pacific coast had occurred.

The same type of variation is evident in other groups of animals. Thus, Hoffmeister (1951:77) stated that Peromyscus truei lagunae, the race of the piñon mouse endemic in the Laguna and Victoria mountains of the Cape district, most closely resembles P. t. gentilis. which occupies "north-central Mexico from near the United States boundary southward along the cordillera to eastern Jalisco and central Guanajuato" (op. cit.:47). "The similarity to gentilis is so marked that the question arises as to whether the populations of lagunae were not derived from the mainland of Mexico. Yet there is no evidence that the Cape and the Mexican mainland have been connected very recently geologically. Furthermore, the species P. truei does not now occur along, or near, the coast on the mainland opposite the Cape, so that there is, in addition to the width of the Gulf of California, a wide expanse of land separating the two subspecies. It seems more likely that the populations near the tip of Lower California resemble those of gentilis through parallel evolution. . . ." (op. cit.: 77, 81). An equally valid hypothesis is that lagunae has been derived from a gentilis-like ancestral population which followed the Madro-Tertiary flora from northern México to the Cape district. Parallelism implies the morphological resemblance of two separated forms because physical similarities in the habitats which they occupy have engendered similar selection pressures on each population. When the habitats involved are completely unrelated and composed of elements of obviously separate derivation, parallelism seems to be a possible explanation of the morphological resemblance between the populations concerned. But when, as in this case, the habitats involved show evidence of common origin, and indeed contain identical vegetational elements, we cannot ignore the possibility that we are dealing with animal populations of common origin, and that the historical distribution of habitat, and of the animal populations associated therewith, may provide the explanation for the morphological similarity of the separate populations concerned. As Hoffmeister (op. cit.: 81) stated: "The range of this race [P. t. lagunae] is coincidental with the local distribution of the Mexican piñon, Pinus cembroides . . . . Interestingly, the piñon of the Cape region is the same as that of the mainland of Mexico, whereas the species to the north in the San Pedro Mártir is Pinus edulis."

Although it may be impossible to document fully the historical movements of a particular flora and the animals associated with it in the absence of abundant fossil evidence, we are not justified in ignoring whatever fossil evidence is available merely because it is not complete. Although parallel evolution has often been invoked to explain the resemblances of separated populations, it is impossible to document such parallel evolution unless adequate fossil evidence is at hand to demonstrate the course of evolution in the two groups concerned. Parallelism is often invoked when the only evidence for it is the similarity of discrete populations at a given point of time. It is admissible as a possible explanation only when all other alternatives have been exhausted.

Finally, in assessing the "potency" with which the Cape district has acted on the birds of the highlands, one may say that the Cape region has acted "potently" indeed if the nature of the morphological variation in the endemics of the Cape district is ignored. In other words, if we are concerned merely with the number of recognizably distinct forms found in the Cape district, then it must be admitted that that region has been a particularly effective "center of differentiation." On the other hand, the resemblance of most of the endemics of the Cape highlands to representatives of the same, or closely related, species in the interior southwestern United States and northern México, whence the stocks ancestral to the endemics of the Cape region presumably came, suggests that in certain features the birds of the Cape highlands have diverged less from these ancestral stocks than have the representatives of these same species on the Pacific coast. From this viewpoint, the Cape region has not acted "potently" but it actually constitutes a center of relatively weak differentiation, and presumably for the reason that the habitat with which the stocks pioneering into the Cape region were associated has been relatively little altered in the Cape highlands, whereas this same earlier habitat has become much more altered on the Pacific coast.

#### SUMMARY

Of the 17 species and subspecies of birds endemic to the highlands of the Cape district, Baja California, 11 show morphological resemblance to modern populations of México and the southwestern United States east of the Colorado River. Only three show resemblance to populations of the Pacific coast, and only three have lost any resemblance to other modern populations.

It is suggested that the 11 forms resembling modern populations to their northeast and east colonized the Cape district from northern México, following the Madro-Tertiary flora as it spread from northern México across the southwestern United States and, presumably, down the length of the peninsula of Baja California.

The highlands of the Cape district today contain a flora which includes a prominent component of Madro-Tertiary affinities. It is concluded that the majority of the avian endemics in the Cape highlands show resemblance to Mexican populations because the vegetation of the Cape highlands has been relatively little altered since the initial invasion of the Cape district by the populations presumed ancestral to the modern endemics.

### ACKNOWLEDGMENTS

I wish to thank Dr. Charles H. Lowe, Jr., for reading the original manuscript and making a number of valuable suggestions. Dr. J. Wyatt Durham provided information on the geology of the Cape region and the Gulf of California. Specimens of *Vireo gilvus brewsteri* in the Dickey Collection were made available through the courtesy of Dr. Thomas R. Howell.

#### LITERATURE CITED

- American Ornithologists' Union
- 1957. Check-list of North American birds. Fifth Ed. (published by the Union, Baltimore, Md.). Anderson, C. A.
  - 1950. Part I. Geology of islands and neighboring land areas. In 1940 E. W. Scripps cruise to the Gulf of California. Geol. Soc. Amer., Mem. 43.
- Axelrod, D. I.
  - 1950. Classification of the Madro-Tertiary flora. Carnegie Inst. Wash. Publ. No. 590, pt. 1:1-22.
  - 1958. Evolution of the Madro-Tertiary geoflora. Bot. Rev., 24:433-509.
- Brodkorb, P.
  - 1943. Geographic variation in the band-tailed pigeon. Condor, 45:19-20.
- Davis, J.
  - 1951. Distribution and variation of the brown towhees. Univ. Calif. Publ. Zool., 52:1-120.
- Friedmann, H., Griscom, L., and Moore, R. T.
  - 1950. Distributional check-list of the birds of Mexico. Part 1. Pac. Coast Avif. No. 29:1-202.
- Grinnell, J.
  - 1926. A new race of the white-breasted nuthatch from Lower California. Univ. Calif. Publ. Zool., 21:405-410.
  - 1928. A distributional summation of the ornithology of Lower California. Univ. Calif. Publ. Zool., 32:1-300.
- Hawbecker, A. C.
  - 1948. Analysis of variation in western races of the white-breasted nuthatch. Condor, 50:26-39.
- Hellmayr, C. E.
  - 1934. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser., 13, pt. 7.
- Hoffmeister, D. F.
  - 1951. A taxonomic and evolutionary study of the piñon mouse, *Peromyscus truei*. Illinois Biol. Monog. 21, no. 4:1-104.
- Johnston, I. M.
  - 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The botany (vascular plants). Proc. Calif. Acad. Sci., ser. 4, 12:951-1218.
- Miller, A. H.
  - 1941. Speciation in the avian genus Junco. Univ. Calif. Publ. Zool., 44:173-434.
- Miller, A. H., and Miller, L.
  - 1951. Geographic variation of the screech owls of the deserts of western North America. Condor, 53:161-177.
- Moore, R. T., and Peters, J. L.
  - 1939. The genus Otus of Mexico and Central America. Auk, 56:38-56.
- Nelson, E. W.
- 1921. Lower California and its natural resources. Mem. Nat. Acad. Sci., 16:1-194.
- Oberholser, H. C.
  - 1919. Description of a new subspecies of Pipilo fuscus. Condor, 21:210-211.
- Pacific Coast Avifauna
  - 1957. Distributional check-list of the birds of Mexico. Part 2. Pac. Coast Avif. No. 33:1-436.
- Pitelka, F. A.
  - 1951. Speciation and ecologic distribution in American jays of the genus Aphelocoma. Univ. Calif. Publ. Zool., 50:195-464.
- Sibley, C. G.
- 1940. The warbling vireo of the Cape district of Lower California. Condor, 42:255-258. van Rossem, A. J.
  - 1934. Critical notes on Middle American birds. Bull. Mus. Comp. Zool., 77:387-490.
  - 1938. The groove-billed ani of Lower California and northwestern Mexico. Condor, 40:91.
- Hastings Reservation, University of California, Carmel Valley, California, October 7, 1958.