Climatic Effects on the Seasonality of California's Avifaunas

by Gerald V. Tangren

SOME BIRD POPULATIONS have developed migration as an adaptation to seasonal changes, and as an alternative to other strategies when, presumably, the risks encountered by migrating to a more favorable area are less than the risks that would be encountered by remaining in one area all year. The availability of food and nesting sites, predators, competitors, and climatic severity and variability all contribute to determining the risks involved in not migrating. Consequently, because it is the sum result of the constituent species' strategies, an avifauna's seasonal change with the migration of its members should reflect the seasonal changes in the avian-perceived environment. Climate directly influences these seasonal changes and, therefore, also the associated avifaunal change.

Several studies show ways seasonality influences the size of the migratory component of avian communities. MacArthur (1959) proposes that the number of Neotropical migrants breeding in different North American habitats depends upon the corresponding size of the predictable spring and summer increase of resources from winter levels. Several tropical studies (Tramer 1974c, Willis 1966, Leck 1972) suggest that these same birds on their wintering grounds are using resources not exploitable by resident tropical species, but only by this seasonal component of the avifauna. Tramer (1974b) describes how snow cover eliminates ground feeding niches in colder North American regions during winter and forces many birds to withdraw. Bock and Lepthien (1974) also hypothesize that winter severity controls the number of wintering species: where more favorable conditions exist higher resource productivity supports more species with narrower niches.

The state of California, because it varies climatically from hot deserts to high mountains and cool ocean coasts, provides an opportunity to investigate within a limited geographic area the seasonal changes resulting from migration in local avifaunas. Furthermore, data are present in sufficient quantity for California in the form of Christmas Bird Counts from *Audubon Field Notes* and *American Birds* and of U.S. Fish and Wildlife roadside Breeding Bird Surveys. There are several problems with using these counts (see Tramer 1974a and Bock and Lepthien 1974 for the Christmas Bird Counts and Aldrich and Robbins 1970 for the Breeding Bird Surveys), but their quantity makes these censuses optimal for composing a comprehensive picture of the relationships between the migratory component of avifaunas from different regions of California and the climate of these regions.

Methods

THE SIZE of the migratory component is calculated for each Christmas Bird Count area and for each roadside Breeding Bird Survey route as the percent of migrant species present in the total number of recorded landbird species. This yields wintering migrant percentages for the Christmas Bird Counts and breeding migrant percentages for the Breeding Bird Surveys. Defined as *breeding migrants*, rather than as *residents*, are those species that are either absent in winter or are present in only very low numbers compared to the breeding season *Wintering migrant species* are those species usually not nesting in the area. This breeding migrant criterion departs from other studies in which only species that winter primarily

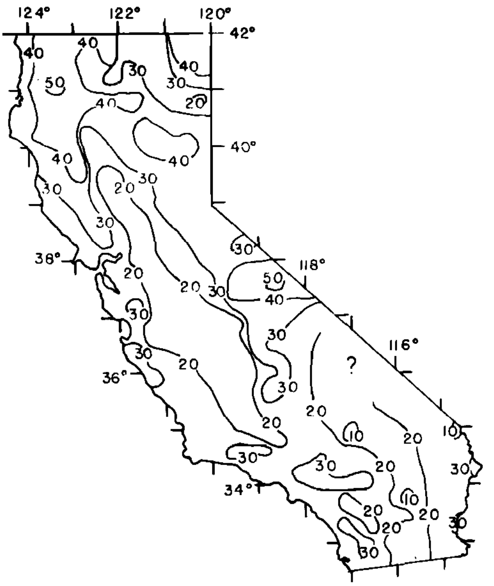

Figure 1. Distribution of breeding migrant species on California roadside Breeding Bird Surveys expressed as the per cent of the total number of landbird species. The question mark indicates the lack of sufficient information to draw the isoclines along the southeastern border.

in the Neotropic (MacArthur 1959) or south of southern California (Stewart 1972) are considered breeding migrants, but my criterion more closely compares with the wintering migrant definition. I base the species classifications primarily upon my field experience in California, but also upon information from Hoffmann (1932) and McCaskie and DeBenedictus (1965) and upon comparisons between proximate Christmas Bird Census areas and Roadside Survey routes. Most species are readily assignable, but in a very few cases the decisions are almost arbitrary.

Some partially migratory species, such as the House Wren (*Troglodytes aedon*), cause incongruities in the classifications; the wren I classify as a resident for Christmas Bird Censuses but as a breeding migrant for Roadside Surveys. Other inconsistencies are caused by species with some resident and some migratory populations, such as the White-crowned Sparrow (*Zonotricha leucophrys*), or by censused areas that by their altitudinal range include both breeding and wintering habitat for altitudinal migrants. I exclude as waterbirds on each census all birds on the American Ornithologists' Union (1957) list in order up to and including the Anseriformes and the Osprey (*Pandion haliaetus*), the Gruiformes, the Charadriformes, and the Belted Kingfisher (*Megaceryle alcyon*).

PER CENT OF MIGRANT SPECIES is used as a measure of migrant composition because the errors introduced by the census methods affect it least. The number and ability of observers affect the detected number of migratory species and individuals because a better observer or greater number of observers conceivably increases the total numbers. Also, because each censused area encloses a mixture of habitats, the per cent of migratory individuals is biased toward the value of the one or several habitats preponderant in the area. A tendency for the rarer species to be migrants does cause an

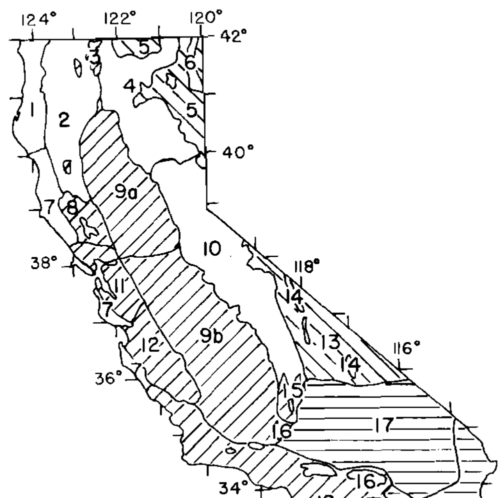

Figure 2. The California breeding avifaunal districts from Miller (1951). Districts crossed by horizontal lines are Sonoran districts, crossed by lines sloping down left Californian districts, sloping right Great Basin, and not crossed Boreal. The districts are 1) Northern Coast, 2) Trinity, 3) Shasta Valley, 4) Cascade, 5) Modoc, 6) Warner, 7) Central Coast, 8) Clear Lake, 9) Great Valley, a) Sacramento Valley, b) San Joaquin Valley, 10) Sierra Nevada, 11) San Francisco, 12) San Benito, 13) Inyo, 14) Great Basin Mountains, 15) Upper Kern, 16) San Bernardino, 17) Mojave, 18) San Diego, 19) San Diegan Mountains, 20) Colorado.

error in the calculated per cent of migratory species, but this error is usually minor. A total of 54 Christmas Bird Counts from winter 1971–72, plus 30 from 1955–74 to increase coverage, and a total of 151 roadside surveys from 1973 are analyzed here.

To investigate correlations between climate and the breeding and wintering migrant percentages, I match 40 Christmas Bird Counts and 44 roadside surveys with 49 weather stations (from Durrenberger 1965) within close proximity in distance and altitude to the censused areas or routes. Climatic variables used are mean June high temperature, mean December high temperature, mean total June precipitation, mean total December precipitation, and mean total annual precipitation All statistical comparisons are made using the .05 significance level. That is, there are only five chances out of 100 that the relationships found could be due to peculiarities of my sample, rather than being representative of the populations under study.

Results

FIGURE 1 MAPS THE BREEDING migrant percentages found on the California roadside Breeding Bird Surveys. This pattern can be compared with the pattern of the breeding avifaunal districts of California (Figure 2) outlined by Miller (1951). The higher percentages of migrants are in coniferous forest districts (Boreal districts), in the Great Basin districts, in the northern end of the Sacramento Valley, and along the Colorado River, with the highest percentage (fifty) in both the Trinity and Mono districts. Areas with extensive riparian habitat, such as the northern Sacramento Valley where remnants of the once extensive Great Valley riparian exist (Gaines 1974) and the Colorado River floodplain, apparently contain higher breeding migrant percentages than do adjacent areas. Water may also be a factor in the Great Basin where the variation in migrant breeding percentages is greater than in the remainder of California. The lower percentages of breeding migrants are in the remainder of the Great Valley and in the Colorado River floodplain, Mojave, and San Diego (inland only) districts, with the lowest percentages along the deserts' western edges

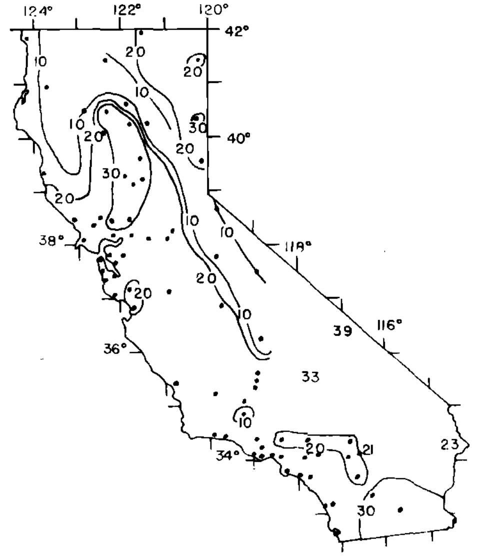

Figure 3. Distribution of wintering migrant species on California Christmas Bird Counts expressed as the per cent of the total number of landbird species An insufficient number of counts is available to draw continuous isoclines. Each censused area is indicated by a point with the exception of four southeastern censuses represented by the actual percentage value. Values for censuses of much of the southwestern two-thirds are between twenty and thirty per cent.

All of these areas with lower percentages are characterized by grassland or shrub habitats

FIGURE 3 ILLUSTRATES the pattern of the wintering migrant percentages found on California Christmas Bird Counts. The higher percentages of wintering migrants are in the Sacramento Valley and at Mojave, Colorado, and Great Basin desert localities. This distribution compares with the distribution of total wintering individuals on Christmas Bird Counts in North America where the Great Valley and northern Great Basin contain the highest values (Bock and Lepthien 1974). The lowest percentages of wintering migrants are confined to mountain areas, with moderately low percentages along the North Coast and in scattered areas of the Central Coast.

In a comparison, the breeding pattern is somewhat opposite to the wintering pattern Those districts with large migratory components in summer (primarily Boreal districts) tend to have small components in winter, in contrast to districts with large components in winter (Sonoran districts and the Great

Valley) and small components in summer. Exceptions are in localities with extensive fresh water in the more xeric regions (Sacramento Valley, Great Basin, and Colorado Desert), containing relatively high percentages in both seasons, and, except for the Great Valley, in most of the California districts, containing moderate values of both breeding and wintering migrants.

The Boreal districts experience cool summers, usually cold winters, and moderately high precipitation. The Great Valley and southeastern deserts, by contrast, are characterized by high summer temperatures, cool-to-warm winter temperatures, and low-to-moderate precipitation. It is hypothesized that the pattern of seasonal change, or of migrant composition, in California's avifaunas is related to climate. The data show that areas with high per cents of breeding migrants tend to have low June and December temperatures and high precipitation. That is, the breeding migrant percentage is inversely correlated with the mean high temperatures and is positively correlated with the mean total precipitations.

The data also show that areas with high per cents of wintering migrants tend to have high June and December temperatures and low precipitation. In other words, the wintering migrant percentage is positively correlated with the mean high temperatures and is inversely correlated with the mean total precipitation.

Table 1 presents the correlation coefficients.[1]

The correlation coefficients, although most are significant (*i.e.*, statistically reliable), are small, indicating that climate does not explain all or even most of the variation in the percentages. In addition to variation from inherent problems of the censuses, natural factors other than climate, such as fresh water abundance, differences in plant forms affecting seed and insect supply (MacArthur 1959), and human disruption of habitat, also contribute to the variation.

[1] A statistical measure that shows how closely two variables are related. The range of possible values for a correlation coefficient is from −1 to +1. A value of −1 indicates perfect negative (or inverse), correlation. A value of +1 indicates perfect positive correlation. A value of zero indicates no correlation between the two variables.

Table 1. Correlations between the migrant percentages and the climatic variables.

Variables	BM	WM	JH	DH	JP	DP	AP
Breeding migrant %	1.00	−.36	−.37	−.40	.46	.31	32
Wintering migrant %		1.00	.42	.40	−.23[a]	−.32	− 34
Mean June high temp.			1.00	.26[a]	−.36	−.57	− 56
Mean Dec. high temp.				1.00	−.51	−.30	− 36
Mean total June precip.					1.00	.65	76
Mean total Dec. precip.						1.00	98
Mean total annual precip.							1 00

[a] Not significant at the .05 level. All other values are significant

Further statistical analysis supported the pattern suggested in comparing Figures 1–3 Namely, those areas with higher temperatures during both winter and summer (the Great Valley and southeastern deserts) tend to have lower breeding migrant percentages and higher wintering migrant percentages, relative to those areas with low temperatures (the northern coast and high mountains) which tend to have high breeding migrant percentages and low wintering migrant percentages

Also, more complex statistical analysis suggests that in regions with larger migrant percentages in both seasons there are larger amounts of June rainfall usually coupled with mild winters (such as in the northern Sacramento Valley). Areas with small totals of migrants have low amounts of June precipitation and relatively more severe winters (such as in some southern California mountains). The factor that apparently most heavily affects the total migrant percentages; the existence of extensive riparian habitat, is not, however, represented in the climatic data.

Discussion

The pattern of migrant composition in California avifaunas (Figures 1–3) and the correlation between migrant percentages and climate (Table 1) suggests that seasonal avifaunal changes are dependent on climate. Avian migration into and out of an area may very likely reflect the seasonal change in the area's potential to support birds. The simplest California example of this change is from high mountain regions, showing a large influx of breeding migrants in summer but almost no regular inward movement of migrants in winter. Populations of many species move in during the summer because with increased temperatures and the melted snow cover resource productivity and the number of feeding niches increase. But, these breeding migrants must then depart before the severe winter because with the decrease in kinds and abundance of resources, the number of niches once again becomes limited. The year 'round residents, such as woodpeckers, chickadees, kinglets, nuthatches, and finches are adapted to the winter resources (coniferous and other arboreal seeds and insects overwintering in or under bark).

The high mountains provide the simplest example because there the number of wintering migrants is almost zero, unlike other California areas where a migratory component is present in both summer and winter. The northern California coast and intermediate mountain elevations show a summer high - winter low pattern similar to high mountain regions but contain fewer breeding migrants and some wintering migrants. The lower numbers of breeding migrants may simply indicate the smaller difference between abundances of summer and winter resources. An explanation for the significant presence of wintering migrants there is however more difficult. One suggested interpretation is that although winter resources are lower than summer resources, the resources available may be different in kind, or that some resources, such as fruits and seeds, may be increased. Wintering migrants may also be utilizing resources used in summer by breeding migrants. There is no evidence, though, to indicate that some wintering migrants replace breeding migrants. Willis (1966) proposes that a year 'round resident not encountering migration risks should be able to outcompete a migrant species and replace it. Still, the impact of wintering migrants on avian communities has not been fully examined, especially in temperate regions (but see Emlen 1972 and Cody 1974).

At the other extreme from the high mountains are those areas with a low number of breeding migrants and a high number of wintering migrants, such as in the Great Valley, Colorado, and Mojave districts. Because these regions experience high summer temperatures, mild winter temperatures, and low or unpredictable summer precipitation, total resource productivity is probably actually lower in summer than in winter, opposite to most temperate zone regions. Arthropod numbers do increase from winter levels during spring in lowland California with a May peak (Verbeek 1973), but this level is not maintained into the summer. Therefore, the presence of breeding migrants in only low proportions is not unpredictable because a migrant is competing mostly with birds that are overwintering on their breeding grounds. The few breeding migrants are mostly aerial insect specialists: swallows and flycatchers. The high percentages of wintering migrants in the Great Valley and in the southeastern deserts are probably a response to the large numbers of seeds and berries present in winter, but several insectivorous species, such as the Ruby-crowned Kinglet (*Regulus calendula*) and the Yellow-rumped Warbler (*Dendroica coronata*), are also present as common wintering migrants.

The regions with moderate, but similar, migrant percentages in summer and in winter (central and southern coastal and foothill regions) appear to be intermediate cases in migrant composition and in climate between the summer high percentage - winter low and the summer low - winter high regions. Although the coastal regions usually have milder winter temperatures than the inland Great Valley, the coastal regions do not contain as high percentages of wintering migrants because more birds are resident; they are able to remain through the summer.

In summary, MacArthur's (1959) proposal that the proportion of migrants is a function of change in resource levels is generally accurate. Using climate as an indicator of environmental favorability, a pattern in California confirming MacArthur emerges along a continuum from high mountain regions through coastal regions to low inland regions. The changes in absolute resource levels, however, do not entirely account for the complete pattern because different resources, such as seeds and insects, vary independently of each other.

Areas containing riparian habitat deviate from the above continuum probably because the birds are apparently not influenced by weather as much as by conditions in riparian habitats. The high percentages of migrants present in both winter and summer may be an indication of habitat instability from flooding. A more plausible explanation would be that the resources change in kind dramatically during the annual cycle, so as to favor two different sets of birds, *e.g.*, insectivores in summer and seed eaters in winter. Further support of the second explanation would seem to be the location of the deviant areas adjacent to areas usually high in wintering migrants, but low in breeding migrants because summer weather is too severe.

ALTHOUGH SEASONAL CHANGES in California's avifaunas can be correlated with climate, this overview does not actually examine the relationship between resource changes and migrant composition. Further, the censused areas include many avian communities on which the processes that construct the large avifaunal picture are definitely operating, but on a smaller scale. Therefore, only by an examination of these processes on that smaller scale can questions posed by an examination of seasonality in California's avifaunas be answered more fully. This paper suggests several questions. 1) Is Willis' (1966) hypothesis correct that a niche in existence all year will always be occupied by a resident and not by two migrants, one in summer and one in winter? If Willis is right, 2) what is the role and impact of wintering migrants, especially in areas with lower resources in winter than in summer? 3) Why don't riparian habitats support larger resident avifaunas?

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