# AN ANALYSIS OF WINTER BIRD-POPULATION STUDIES

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BEGINNING in 1948, *Audubon Field Notes* has published a series of winter bird-population studies, at first under the editorship of Robert E. Stewart, and more recently Haven Kolb. Altogether, 506 studies have appeared in the 17 years. Apparently no one, heretofore, has had the temerity to make an analysis, but in thoughtful editorial comments, Kolb pointed out that Pacific Coast populations are more dense; and Stewart that more mesic habitats have higher densities.

The method of winter population studies should be explained briefly. The area studied is from 15 to 100 acres, although forest plots studied are nearly all between 20 and 60 acres. (Personally, I find that 20–30 acres is the best size for a forest area census by a lone observer.) At least 6 times during the winter a count is made in which all birds seen or heard on the area in a day are recorded and an average is taken. The counts are converted to a density of birds per 100 acres. Of course, a few census workers have very properly counted elongated habitats or edges in a linear fashion, as birds per mile.

My analysis here includes only forests (248 studies) and grasslands (25 studies), and edges have been omitted as far as possible. Many forest areas included, however, contain several species which are "edge species" in the sense of Kendeigh (1944) because of the edge effect of windfalls, small creeks and the like. I compared the very few counts from desert, marsh, and other

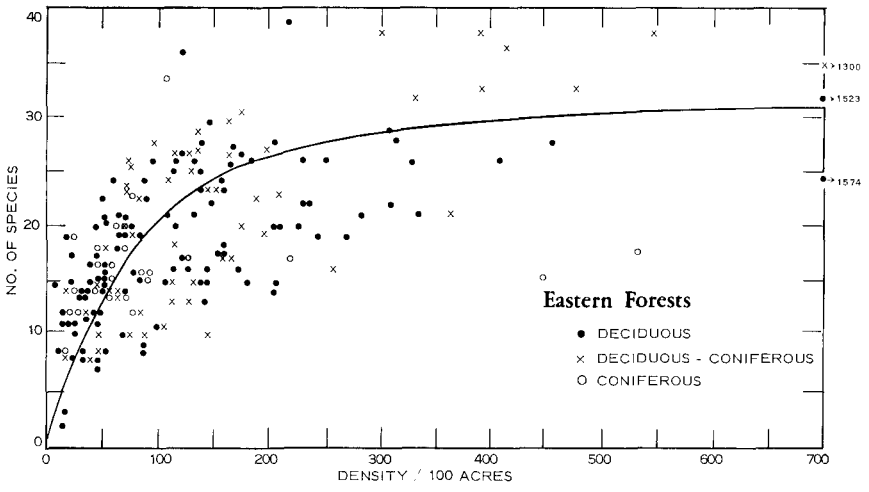


FIG. 1. Eastern Forests.

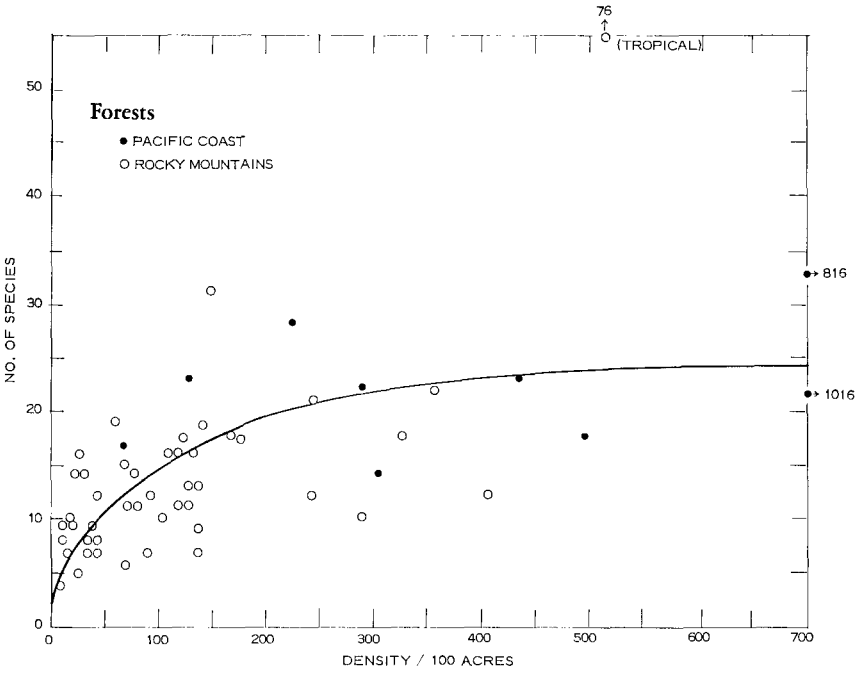


FIG. 2. Forests.

major natural habitats without reaching any conclusions worth mentioning. I lumped several areas of fairly dense woodland in with forest in crude fashion.

*First* I plotted species number against density, or species/density ratio (Fig. 1). Clearly, the data from eastern coniferous forests, eastern deciduous forests, and eastern mixed coniferous-deciduous forests approximate a parabola, with the higher values of the mixed forests (mostly southern pine mixed with oaks or gums) tending to higher species number than the other two habitats. In western forests a similar relationship appears, although the data from the Pacific Coast are scanty, with low values lacking (Fig. 2). A single count from tropical woodland is very high in species number.

In his analysis of breeding bird census data, Udvardy (1957) plotted similar curves. His tropical data described a steep straight line. I conclude, with Udvardy, that bird density in temperate forests and woodlands is dependent upon the number of niches and the number of species at hand to settle there. In tropical woodland, density is proportional to the number of species present, presumably reflecting a greater number of niches present and filled. The only thing surprising about this is that the winter data so closely support breeding figures.

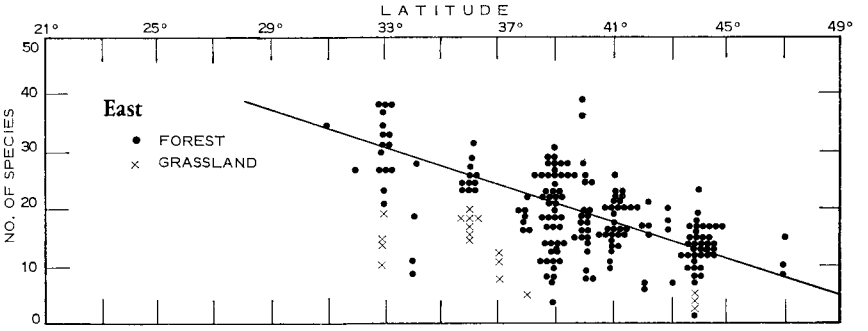


FIG. 3. East.

Grassland data are consistent with the above generalizations, but are too few to bear scrutiny.

*Second*, I plotted species number against the terrestrial latitude of the point where the census was made. In Figure 3, censuses from eastern deciduous forests appear as solid dots and censuses from various types of artificial grasslands in eastern United States (airfields, pastures, etc.) as crosses. The former approximate a straight line, with a regression of 1.6 species per degree of latitude northward. The grassland data would appear most consistent with an almost parallel, but lower, line to that of the forest data.

In the western Cordillera, or Rocky Mountain—Sierra Madre Occidental axis, Figure 4 shows forests as dots and grasslands (mostly prairie) as crosses again. The relationship is about the same—grassland parallel to, but lower

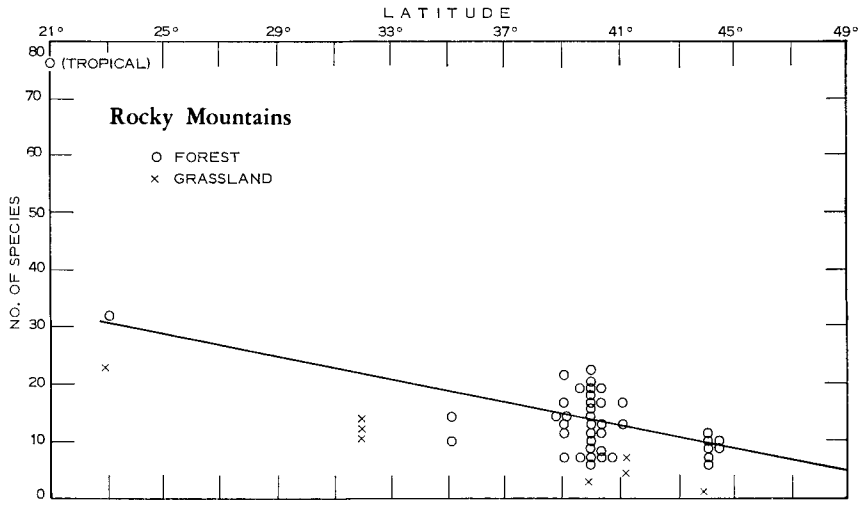


FIG. 4. Rocky Mountains.

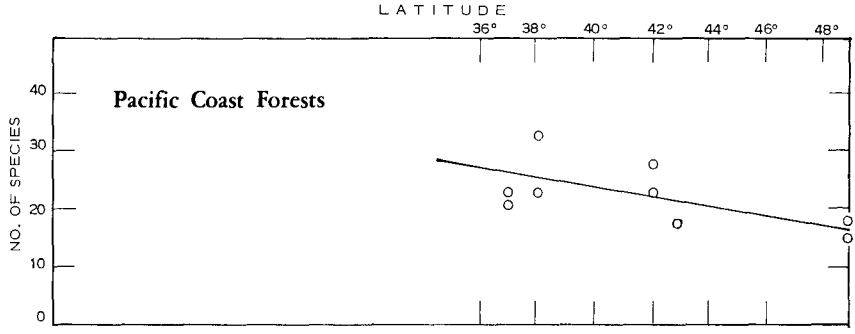


FIG. 5. Pacific Coast Forests.

than, a straight line for forest, the regression being 1 species per degree of latitude northward. A single tropical census is much too high, apparently representing an entirely different relationship.

Pacific Coast censuses (Fig. 5), representing forested localities from Santa Cruz, California, to southern British Columbia, suggest a straight line with a regression of 0.9 of a species per degree of latitude northward.

It would seem, then, reasonable to generalize that within each major temperate biome species number decreases by about 1 per degree of latitude northward.

*Third*, I plotted density against latitude. On Figure 6 are forest census data only—hollow dots from the Pacific Coast, solid dots from the East, and crosses from the Rocky Mountain—Sierra Madre Occidental axis. A curve has been drawn which approximates the Eastern data; a similar but lower curve would best represent the Rockies, and a similar but higher the Pacific Coast. Scanty grassland data (not shown) suggest the same type of relationship. In other words, density decreases northward, but at a decreasing rate as latitude increases. For the forest data, the vertices of the curves are at about 35° in the Rockies, 37° in the East, and 41° on the Pacific Coast. This suggests that long-lasting snow cover in the woods may be the limiting factor affecting density in the north and that some other factor may be limiting further south.

I am unable to derive any generalization from this relationship other than this: Different limiting factors operate on total bird densities within each major habitat north and south of about latitude 38°N. Notice that the tropical census is consistent with the others. Sorting that data into finer ecological classifications (coniferous forest, mixed deciduous-coniferous, spruce-fir, etc.) did not change the nature of the relationship, so far as I could see, and so they have not been plotted here.

Some theories for the origin of the migratory habit—the "Northern Ancestral Home Theory" and the "Southern Ancestral Home Theory"—need a

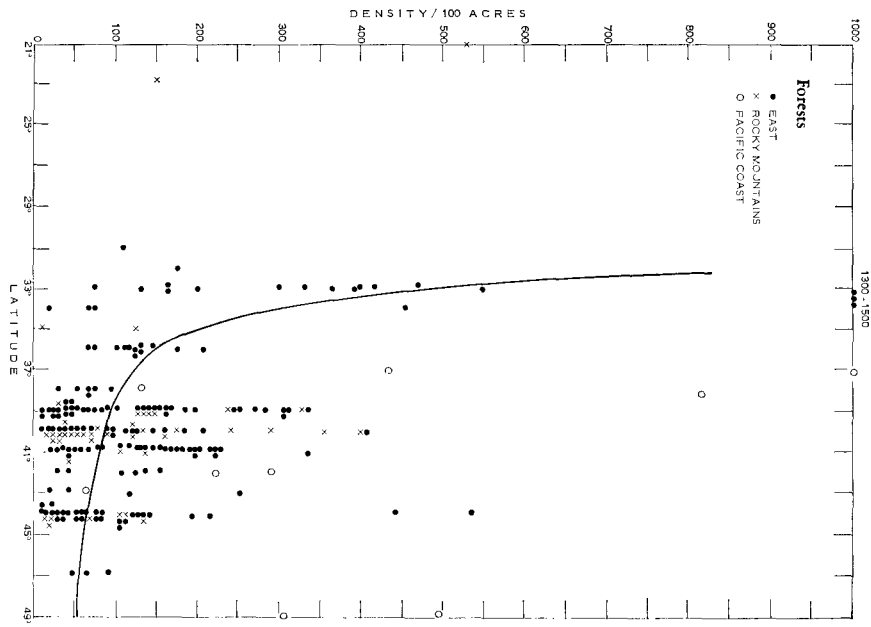


FIG. 6. Forests.

measure of the degree of crowding toward the equator in winter. For that matter, it is obvious that there is *some* equatorial crowding in Northern Hemisphere winter, because at that season many boreal birds have flown south to the tropics and few birds have flown south from the tropics into the Southern Hemisphere. Figure 6 provides a tentative measurement of the degree of southward crowding in winter.

Comparison of winter data with breeding bird censuses as reported in *Audubon Field Notes*, 1937 to 1964, is of interest (Table 1). For simplicity, the breeding bird densities, calculated on the basis of territorial males, have been doubled for comparison with these winter data which are calculated on individual birds. Breeding census data were taken from Udvardy's (1957) analysis; inspection of more recent censuses (1957–64) indicates no radical changes. In the forest censuses, species number in the mean of each major category rises by from four to seven species, winter to summer. Density rises from winter to summer in the mean of each category, also, multiplying by factors of from 1.5 to 4.4. In the grassland censuses, on the other hand, mean species number declines from winter to summer by five and density declines by almost one half.

Udvardy did not compare breeding data with latitude, but he did point

TABLE 1
SEASONAL CENSUS COMPARISON

| Area | Winter | | | Breeding | | |
|---|---|---|---|---|---|---|
| | Number of counts | Mean species number | Mean density | Number of counts | Mean species number | Mean density |
| Deciduous forest, Eastern | 187 | 19 | 148 | 130 | 23 | 600 |
| Deciduous-coniferous mixed forest, Eastern | 55 | 21 | 175 | 46 | 28 | 490 |
| Coniferous forest, Eastern | 25 | 16 | 101 | 28 | 20 | 440 |
| Coniferous forest, Rockies and Pacific Coast | 48 | 13 | 165 | 26 | 19 | 254 |
| All grasslands | 26 | 12 | 278 | 21 | 7 | 150 |

All densities are per 100 acres; breeding densities are doubled from the originals, which were expressed as territorial males only.

out that densities in tropical forests and savannas tended to be higher than in temperate forests and savannas, although not above temperate extremes. Apparently the same is true of winter densities.

Perhaps future winter population studies from tropical and from far northern localities will make these preliminary hypotheses valid and meaningful.

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