LARGE-BILLED INSECTIVOROUS BIRDS:
A PRECIPITOUS DIVERSITY GRADIENT

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Most hypotheses proposed to account for a latitudinal species-diversity gradient in a particular taxon (e.g., the "time" hypothesis and the "predation" hypothesis, after Pianka 1966) can operate independently of any geographic difference in the abundances of the resources partitioned by the taxon. (For theoretical reviews, see Klopfer 1959; MacArthur 1964, 1969; Whittaker 1965, 1969; Pianka, op. cit.; MacArthur and Wilson 1967; Slobodkin and Sanders 1969; Orians 1969.) An important class of hypotheses, however, postulates that some resource or set of resources, marginal in one area, is increased in abundance in a second area so as to allow more species of a certain kind to evolve and/or persist (MacArthur's category 4, 1969). Implicit in such an hypothesis, of course, is the assumption that at or below some level, productivity limits, or is proportional to, species diversity. To detect such an effect, often a useful procedure is to subdivide the given taxon into groups of species, each largely dependent on a particular kind of resource, and then to look for differences between groups in the steepness of their individual diversity gradients.

In this study I have followed such a procedure in an analysis of the insectivorous birds of North and Middle America, a group which shows a marked diversity gradient on a macrogeographic scale. Some of the results have been alluded to previously (Moreau 1966; Orians 1969), but are here quantitatively documented for the first time. The material below should be considered supplementary to the more extensive data and conclusions of Orians' (1969) study.

Excluding families whose members mostly probe or excavate for their prey [Picidae (woodpeckers), Sittidae (nuthatches), Dendrocolaptidae (woodhewers), and Certhidae (creepers)], there are ca. 121 breeding bird species found in the transcontinental belt of North America (42–44° N) whose food is estimated to consist entirely or primarily (≥ 70 per cent) of arthropods. In contrast, there are ca. 225 such species, somewhat less than twice as many, in the belt 8–10° N traversing Central America, despite the fact that the area of the tropical belt is only about one-seventh that of

the temperate. The species may be plotted according to the number whose bill lengths fall into each of several size categories. When this is done (fig. 1), a striking difference appears: bill lengths of tropical species are distributed over a much greater range than are those of temperate species (about a 40 per cent extension). Furthermore, the bulk of the tropical species falls over considerably higher values (median, about 16.0 mm) than does that of the temperate species (median, about 11.8 mm). Indeed, below 14 mm, temperate species are slightly more numerous than tropical ones; it is *entirely* above this value that the great increase from 42–44° N to 8–10° N in tropical insectivorous bird species diversity takes place.

Before speculating on the causes of this pattern, the possibility must be considered that it is merely a consequence of the coarseness of the aereal transects. That is, perhaps if we were to examine areas of several hundred acres, we would find much the same distributions of bills at all latitudes. This would imply that the geographic ranges of large-billed insectivorous birds are relatively smaller than the ranges of small-billed insectivorous birds in the tropics than at higher latitudes. In other words, when moving from one small area to another, faunal turnover for large-billed species would be relatively greater in the tropics, thus transmuting the phenomenon to be explained.

One possible way to check for this is to compare geographic ranges. However, because of the possibility of patchiness over the total range, I shall use a different test, that of comparing avifaunas of small areas with regard to bill lengths. Nine tropical and 24 temperate censuses were examined. Of the many possible temperate censuses, I selected those associated with well-known ecological studies (Kendeigh 1946, 1948; Odum 1950; Salt 1957). The tropical censuses include five Panamanian areas from the MacArthur et al. (1966) study of tropical bird species diversity, plus four Mexican censuses published by the Audubon Society (Davis and Morony 1953a, b; Davis 1955; Davis and Davis 1957). The majority of the temperate areas censused fall
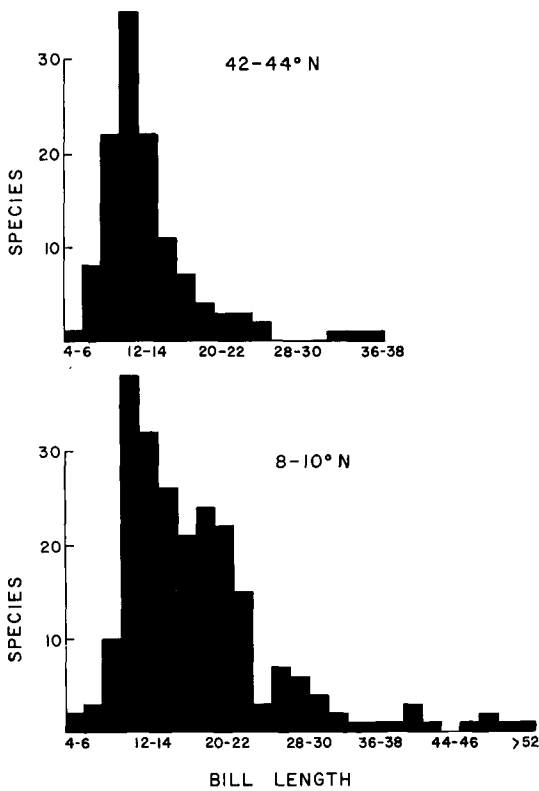
FIGURE 1. Distributions of bill lengths (mm) for insectivorous (70 per cent or more arthropod food) species of birds breeding in a tropical (8–10° N) and a temperate (42–44° N) latitudinal transect. Measurement used is "exposed culmen." All birds in the following families whose diets could be classified as insectivorous are included: Fringillidae, Paridae, Icteridae, Parulidae, Tyrannidae, Apodidae, Hirundinidae, Caprimulgidae, Cuculidae, Strigidae, Cotingidae, Formicariidae, Furnariidae, Mimidae, Corvidae, Turdidae, Bucconidae, Galbulidae, Momotidae, Troglodytidae, Laniidae, Sylviidae, Motacillidae, Vireolaniidae, Cyclarhidae, Chaemaeidae, Rhinocryptidae, Thraupidae, and Vireonidae. Information on diet was taken from Salvin and Godman (1879–1904), Judd (1901), Beal (1907, 1910), Carriker (1910), Bryant (1914), Bent, and sources therein (1919–1968), Hallinan (1924), McAtee (1926), Van Tyne (1929, 1935), Dickey and van Rossem (1938), Skutch (1944a, b, 1945, 1946, 1954a, b, 1958, 1960, 1962a, b, 1963, 1964, 1965, 1966, 1967), Wagner (1944), Pough (1949), Martin et al. (1951), Gross (1952), Craighead and Craighead (1956), Van Tyne and Berger (1959), and Slud (1964). Diets of temperate species are classified according to data from spring and summer months. Each category spans a 2-mm increase in bill length. Data on bill length were gathered from Ridgway and Friedmann (1901–1950) or were measured from specimens at the Museum of Comparative Zoology, Harvard University.

within 42–44° N; those of MacArthur et al. fall within 8–10° N. Table 1 lists for each census: the number of insectivorous species, the median bill length of the distribution of species' bills (counting each species once as in fig. 1), and the median bill length of the distribution of species' bills, each species being weighted by its abundance. The medians by species for all but one temperate census fall below all those for the tropical censuses. The exceptional temperate area—grassland—has a larger median than only one tropical area—the upland cloud forest. The medians by individuals show a slightly less complete separation. That for the cloud forest is smaller than those for almost half the temperate samples, and that for the temperate grassland is larger than those for three tropical samples. The tendency, however, is still highly significant ($P < 0.001$ by the Mann-Whitney U-Test, Siegel 1956). Orians' (1969) Costa Rican data, though not quantitatively analyzed for bill length distributions, seem to contrast in the same way with temperate areas, as he points out. We may conclude that the direction of the difference certainy holds over fairly small areas. It is still possible, of course, that microhabitat differences restrict the species of these small areas in such a way that in still smaller areas, large- and small-billed forms occur in the same proportion regardless of latitude. However, the upper limit of bill length for most of the tropical censuses was a good bit higher than that for most of the temperate ones.

One explanation of figure 1 is that tropical insectivorous avifaunas may contain a greater number of pokers and probers than do temperate ones, possibly associated with a greater complexity of vegetation surface, especially epiphytical. By excluding woodpeckers, creepers, woodhewers, and nuthatches from this analysis, we have reduced considerably any such possible effect, but we have not, of course, eliminated it: certain antbirds, wrens, and others do often use their long bills to probe. Comparative geographic information on the feeding habits of birds is not in so standardized a form that we can rigorously examine this possibility. However, we can look at families common to tropical and temperate latitudes whose species are primarily insectivorous and differ markedly in their manner of obtaining prey. Figure 2 shows, for eight bird families, bill length histograms for tropical and temperate transects across those latitudes used in figure 1. Species from the top four families primarily obtain their prey aerially, whereas those from the bottom four more often probe or glean. In all but the Hirundinidae, the tropical group has longer-billed representatives than does the temperate group. In two of the four aerial-feeding groups, but in all of the other groups, the median is greater for tropical than for temperate faunas. Interpreting the data liberally,

TABLE 1. Avifaunal properties of censuses from small tropical and temperate areas.

Vegetation and locality	No. species	Median bill length (mm)[a]	
		Species	Individuals
Temperate censuses			
North Carolina[b]			
Mesic shrubland, hemlock sere	3	10.4	10.0
Intermediate hemlock-hardwood	14	11.6	11.4
Virgin hemlock	13	11.4	9.9
Xeric shrubland, oak-chestnut sere	4	10.6	9.6
Intermediate deciduous forest	9	11.7	11.7
Mature climax	11	11.7	11.7
Michigan[c]			
Grassland	4	14.3	14.3
Aspen-red maple	12	13.3	12.7
Pine-aspen	11	11.7	11.7
Cedar-aspen	18	11.4	11.4
Cedar-balsam	19	10.2	9.9
Beech-maple-pine	18	11.5	11.7
Northeast[d]			
Mixed shrubs and small trees (N. Y.)	22	11.9	11.4
Beech-maple-hemlock (N. Y.)	14	11.6	11.7
Hemlock-beech (N. Y.)	15	11.4	9.9
Pine-hemlock hardwoods (Vt.)	20	11.1	10.7
White-red spruce (Me.)	13	9.8	9.7
Spruce-fir (Ontario)	17	9.9	9.6
Wyoming[e]			
Lodgepole pine	3	10.6	10.6
Lodgepole-spruce-fir	5	10.5	10.5
Spruce-fir	8	11.9	10.6
Willow-sedge swamp	8	12.8	11.4
Scrub-meadow	6	11.9	11.4
Flatland-aspen	9	12.4	6.3
Tropical censuses			
Panamá[f]			
Mature forest	21	16.0	13.4
Second growth	17	18.1	17.4
High savanna	3	19.4	17.0
Low savanna	5	15.4	15.4
Mangrove	5	14.5	14.0
México[g]			
Tropical rainforest (Veracruz)	41	15.8	15.8
Tropical prairie (Veracruz)	37	17.5	14.5
Upland tropical forest (Chiapas)	25	18.9	17.5
Cloud forest (Chiapas)	14	14.2	11.0

[a] Measurement used is "exposed culmen." Note that in all tropical and all but two temperate censuses the median for individuals is less than that for species. This implies that small-billed species are relatively more numerous in a given small plot. Because small-billed species are usually small-bodied, the result parallels that obtained for insects (Schoener and Janzen 1968): the mean for size-abundance curves by species is greater than that by individuals. It is also to be expected from the smaller home range or territory size of smaller insectivorous birds (Schoener 1968b).
[b] Odum (1950).
[c] Kendeigh (1946).
[d] Kendeigh (1948).
[e] Salt (1957).
[f] MacArthur et al. (1966) as reproduced in MacArthur and Wilson (1967).
[g] Davis and Morony (1953a, b), Davis (1955), and Davis and Davis (1957).

there may be some indication that this hypothesized effect plays a part, but it at present seems insufficient. Incidentally, the fact that differences within widespread families are not so extreme as the total difference depicted in figure 1 leads one to suppose that much of the latter is due to families largely restricted to one or the other area, a supposition which is in fact correct (see Orians 1969, and below).

Rather than being primarily an indicator of differences in the microenvironment of the food, the longer bills of tropical species may be correlated with differences in the food itself, especially in size. That species with longer bills than those of closely related forms do, on the average, eat a greater proportion of large food items has been shown for honeycreepers (Baldwin 1953), titmice (Betts 1955),
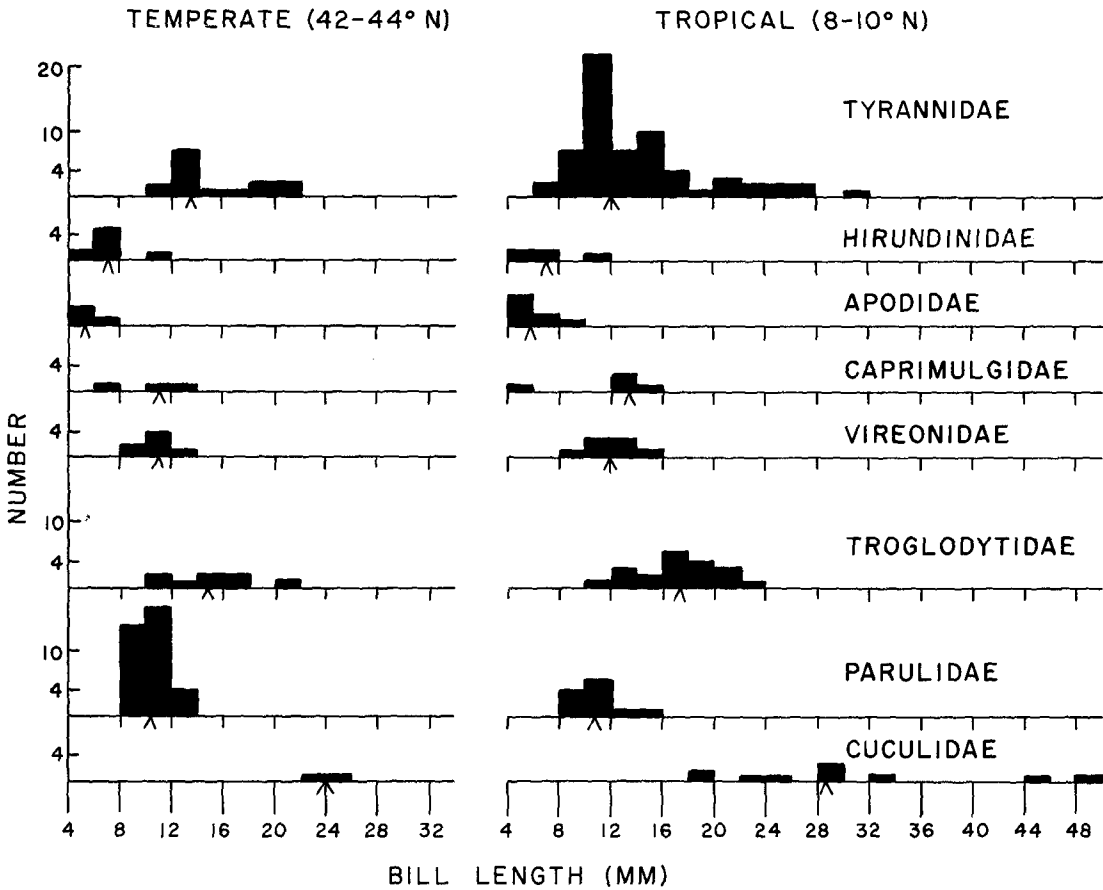
FIGURE 2.   Frequency histograms of species' bill lengths (as in fig. 1) for eight bird families with species in both tropical and temperate regions. Carat marks median bill length.

finches (Bowman 1961, Newton 1967), vireos (Root 1967), sandpipers (Holmes and Pitelka 1968), and auklets (Bédard 1969a). Experiments (Kear 1962; Hespenheide 1966; Myton and Ficken 1967) have demonstrated that some larger-billed species choose larger food more frequently and show a greater handling proficiency with such food. Exceptions to this tendency have been found among less closely related species (Root 1967; Ashmole and Ashmole 1967; Ashmole 1968), and other measurements of the bill (width, depth, cross-sectional area) have been suggested or shown to be better correlated with food size for some species (Hespenheide 1966; Johnson 1966; Newton 1967; Root 1967; Ashmole 1968). In other species, overall body size (e.g., weight) is a good predictor of relative food sizes (Lack 1946; Storer 1966; Ashmole 1968; Schoener 1968b; Bédard 1969b). However, because culmen length, width, depth, and body weight are all strongly correlated over the range of bird sizes dealt with in figure 1, it is likely that tropical and temperate avifaunas show

marked differences in the relative abundance of species which feed on large arthropods.

That this difference has something to do with latitudinal variations in the relative abundance or biomass of large insects is supported by what little published data exist (Schoener and Janzen 1968). We have reported relatively more small arthropods in samples from the understory of a temperate forest (ca. 42° N) during each of five months of the year than in understory samples from four tropical areas (ca. 11° N). Figure 3 illustrates the difference by plotting for sweep samples from three tropical areas and one temperate area the per cent dry weight in each of several arthropod size categories. Data are taken from Janzen and Schoener (1968) or are unpublished. The temperate sample plotted is that for June, but those from July through October contained more small arthropods. The salient feature of the graph is the extent to which the curve for the temperate sample falls below those for the tropical samples for large-arthropod sizes. These data need to be supplemented by sam-
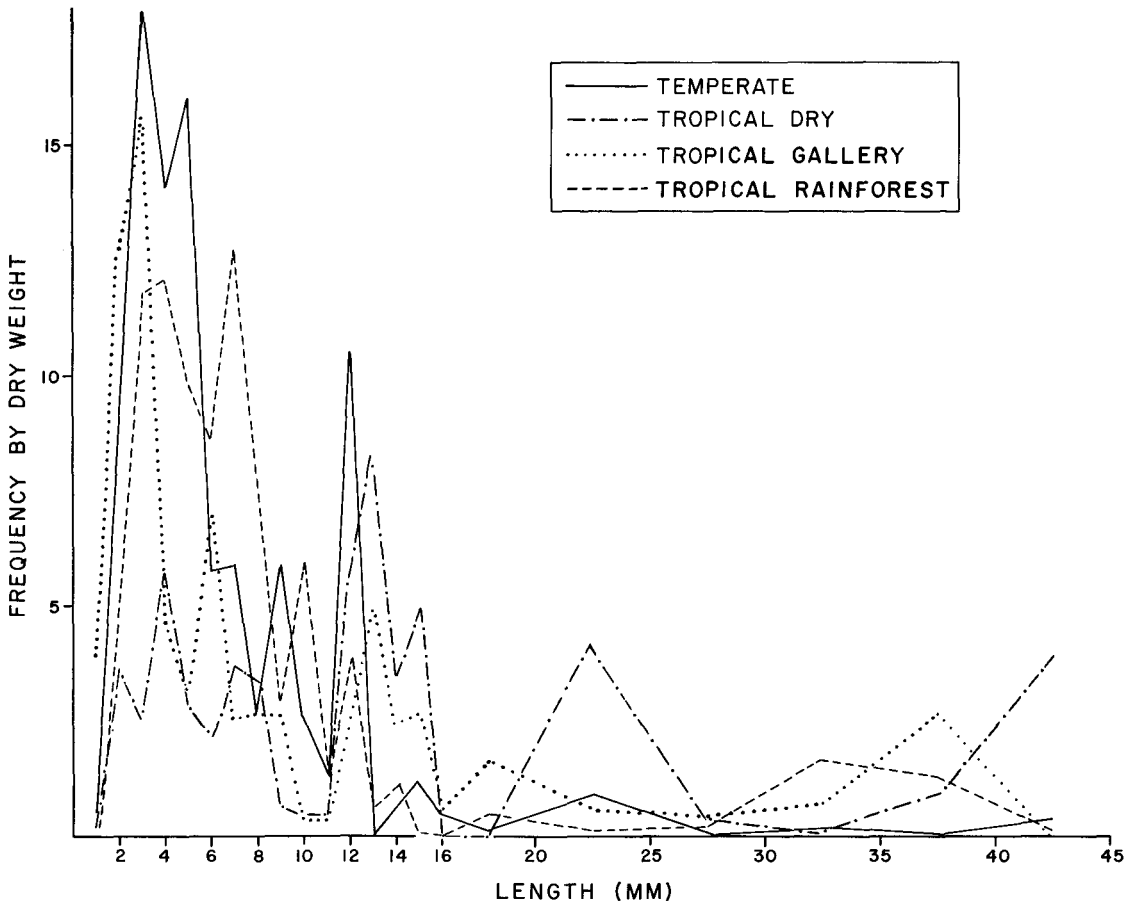
FIGURE 3. Frequency distributions of dry weight by length for arthropods from sweep samples of tropical and temperate forest understories. Total dry weights for samples in mg are: Temperate, 3444; Tropical dry, 3365; Tropical gallery, 5344; Tropical rainforest, 2661.

ples from many more localities and from different vegetational strata before a trend can be conclusively established. However, unless tropical insects are absolutely much less abundant than temperate ones (Data from Schoener and Janzen, 1968, show a partial trend in this direction, but must be interpreted very cautiously, since neither differences in foliage volume nor surface area per sweep were estimated.), the data are consistent with the hypothesis that tropical areas may be able to support more species of insectivorous birds in part because they contain a greater biomass of large-sized arthropods, thus extending the range of the food-size dimension over which species niches can viably be placed (Schoener 1965; MacArthur 1969). That is, were there even a rough correspondence between bill length and the mean or median prey size taken, figure 1 could be interpreted as implying that tropical insectivorous species' niches are arranged over a wider range along the food size dimension, or, at the very least, are

more evenly distributed over that dimension. Indeed, an increase in the maximum species-specific bill length often holds within single genera of insectivorous birds and is associated with greater bill differences between members of congeneric associations in tropical than in temperate areas (Schoener 1965).

As argued elsewhere (Schoener and Janzen 1968), the longer average growing season of most tropical areas should allow many insects, especially herbivorous ones, to evolve a larger size than could similar insect species in temperate areas. Moreover, the greater number of large insects or greater variance in insect size distributions was not regularly associated with an increase in insect species diversity, at least for our sweep samples from small areas, though there was, of course, a greater number of insect species in certain tropical samples. Thus an increased opportunity for niche diversification based upon increased structural diversity of resources need not be entirely dependent upon an increased species number

comprising that resource, a conclusion which has been drawn, but for birds as related to vegetation, by MacArthur and MacArthur (1961), MacArthur et al. (1966), MacArthur (1969), and Orians (1969).

A further fact suggesting an effect of arthropod size is that the smallest-billed birds of the tropical censuses reported in table 1 are those from upland cloud forest, and the largest-billed temperate birds are from grassland. Schoener and Janzen (1968) showed that samples from certain moist areas contained a greater number of small arthropods than did those from adjacent dry areas. Furthermore, as Orians (1969) suggests, a lower absolute abundance of all insects in tropical montane forest than lowland forest could preferentially eliminate the large-billed species, since their prey are relatively less abundant. Perhaps also in wet montane forests climatic restrictions on the feeding activity of insects limit their size in the same way as seasonal restrictions were hypothesized to limit their size in temperate areas; Janzen, however, has some preliminary evidence (cited in Orians 1969) against this idea.

Orians (1969) has demonstrated that a major difference between tropical and temperate avifaunas is the much greater proportion in tropical areas of species which forage primarily by hovering for stationary prey. He further pointed out that such species are often big-headed and feed on large insects. Orians suggested, much as has been argued above, that a greater absolute abundance of large insects in tropical areas would favor more species of such birds there. However, there is no necessary identity of birds which take large prey and those which hover, and indeed Orians has advanced hypotheses for the prevalence of hovering in tropical forests which are independent of the abundance of large insects. Therefore, we might expect the latitudinal increase in large-billed forms to involve both hovering and non-hovering species, since a greater availability of large insects in tropical areas should affect the diets and diversity of all kinds of insectivorous foragers. Data in figure 2 for the Cuculidae, Troglodytidae, Vireonidae, and Caprimulgidae, families whose members do not primarily hover for prey, support this idea: bills are longer for tropical species. As Orians mentions, however, many of the typically tropical families of birds (Bucconidae, Momotidae) have species that both are large-billed and hover for prey; some (e.g., Formicariidae) contributing to the trend in figure 1 are not, however, comprised of hovering species.

In conclusion, a large portion of the increase in bird species diversity in the tropics is that involving the addition of large-billed insectivorous forms, and this increase may be due to a greater availability of food along one end of a "critical" niche dimension. That an hypothesis involving increased availability of certain types of foods may be plausibly applied to diversity gradients in other kinds of birds, such as frugivorous and nectivorous species, is suggested in Orians' (1969) discussion.

ACKNOWLEDGMENTS

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