ADAPTIVE VARIATION IN THE GENUS *VIREO*

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ONE aspect of a recently completed study (Hamilton, 1958MS) of species relationships in the genus *Vireo* was an analysis of intraspecific variation of certain external characters. The objective of this paper is to present the patterns of variation exhibited by those members of this genus having wide distributions in North and Middle America, and to comment on some possible explanations for the adaptive meanings of such patterns. A secondary purpose is an examination of the possibility that interspecific competition has been operative in furthering the ecological separation of two closely related, sympatric species, the Solitary and Yellow-throated vireos (*V. solitarius* and *V. flavifrons*).

There is an important need for more studies of intraspecific variation in several species of an avian genus rather than in single species alone; we need to know the extent and degree of conformity to ecogeographical rules in species of various genera in order to obtain a valid concept of the phenomena of parallel evolution and adaptation in response to environmental gradients. To reach this understanding, more comparative studies of variation within groups having both similar and different distributional patterns will be needed. Snow's (1954*a*; 1954*b*) analysis of variation in external morphology and habitat preferences within the species of *Parus* has shown how much information concerning the process of adaptation may be gained from such a comparative study. There are few other adequate studies of variation within avian genera, exceptions being the examinations by Miller (1941) and Pitelka (1951) of the genera *Junco* and *Aphelocoma.*

All too often, studies of character variation in relation to change in environment have stressed examples in agreement with the standard ecogeographical rules, and have failed to examine the exceptions which, as Mayr (1956:106) has recently emphasized, should receive more attention. Concerning this point, Salomonsen's (1955) study of migration and variation in some Old World species that previously were thought to represent inexplicable reversals of Bergmann's rule, and Moreau's (1957) analysis of climatic variation in the African populations of the *Zosterops* complex are two examples of studies that have demonstrated patterns of adaptations under different climatic or ecological conditions. Such studies provide convincing evidence of an adaptive significance for intraspecific variation.

Throughout this study, I have tried, where appropriate, to compare the genus *Vireo* with another continental, oscine genus, *Parus*, whose ecological and climatic adaptations in the Palearctic have been studied. There are, however, several basic differences in the general ecology of the species of

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these two genera that do not permit the assumption of common mechanisms of adaptation applicable to both. Most species of *Vireo* (excluding endemic, insular forms in the Caribbean) are migratory or partially migratory and have discontinuous distributions in both temperate and tropical regions of the New World; as many as five species may be sympatric (although separated by habitats) during the breeding season, yet co-occupancy of the same habitat is almost unknown. The Old World members of *Parus* are resident or partially migratory species having continuous or discontinuous distributions primarily in the temperate regions of the Palearctic. In this group, co-occupancy of the same habitat appears well developed among the sympatric species during the breeding season; Snow (1954*a*:19) states that four or five species may occur together within the same habitat. Thus, with different ecological and ethological environments, dissimilar patterns of variation are not unexpected for the two genera.

In general for the species of *Vireo*, most of the characters studied showed clinal variation, but not necessarily in accordance with the accepted climatic or ecogeographical rules. Variation in body size (as indicated by wing length), bill length and tail length were exceptions. Bergmann's rule—that within one species individual body size tends to be larger in colder regions than in warmer regions—was found unsatisfactory for explanation of the variation patterns of the members of the genus. For example, in the Solitary Vireo (*V. solitarius*) the northern populations are migratory (Fig. 1) and have their winter quarters in Middle America (north to central Mexico), a region where resident or partially migratory populations may have either larger *or* smaller wing lengths than their northern counterparts.

Before continuing, I would like to point out that my conclusions, reported in this paper, on the adaptive significance of variation in body size within the species of *Vireo* and some other New World species *do not invalidate* Bergmann's rule. Rather, I interpret my findings to represent alternative possibilities: First, other selective forces (e.g., selective action of certain attributes of the summer environment—high temperatures and/or various humidities) may mask, modify, or interact with the selective action of cold temperature. Second, the winter temperatures to which the various populations of the species concerned are exposed may be above the "threshold" below which cold temperature would exercise a selective action. This second alternative would also permit the action or concurrent actions of other selective forces.

METHODS

Wing length measurements were taken (to nearest 1.0 mm.) from wrist to tip of longest primary with wing flattened. Bill length (culmen) was measured from the nasal-frontal hinge with calipers (to nearest 0.5 mm.). Tail lengths were taken with calipers measuring (to nearest 0.5 mm.) the distance from the base of the middle rectrices to their distal tips. Measurements from specimens showing worn or damaged feather tips were not included in the variation data presented in this paper. In determining the "breeding population samples" from which the measurements were taken, I tried to secure 10 or more male specimens collected during or immediately prior to the breeding

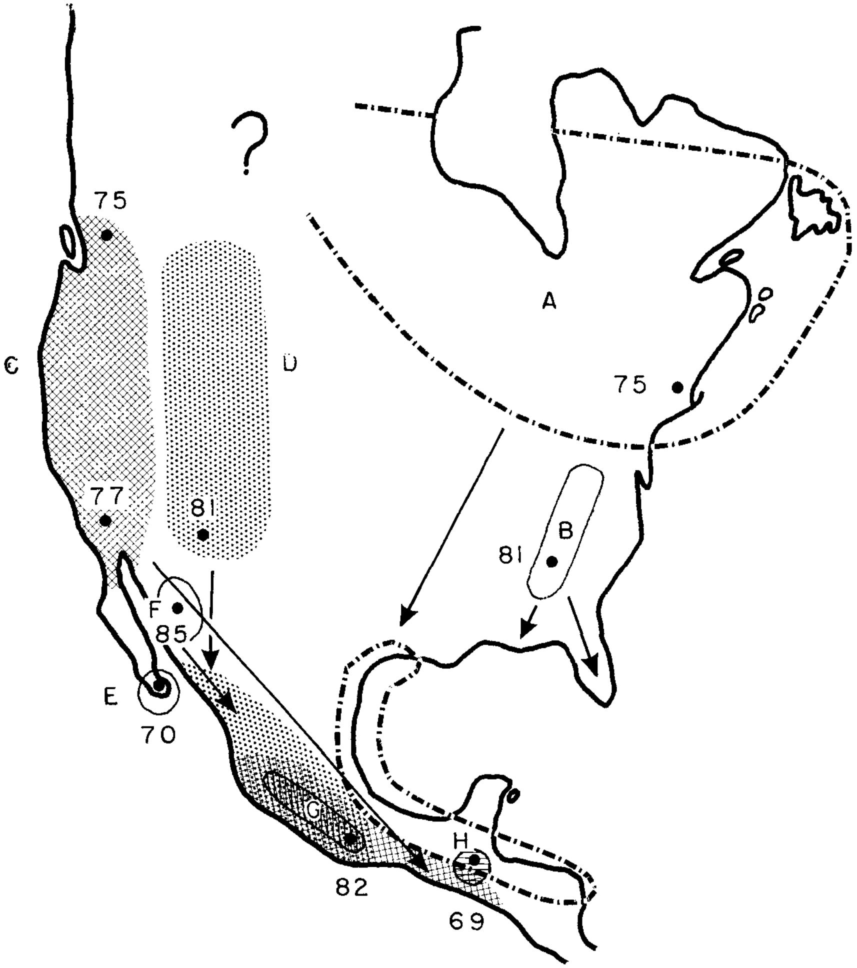

Fig. 1. Geographic variation in wing length within *Vireo solitarius* showing the breeding and wintering quarters of the various segments or populations. Arrows lead from breeding to wintering quarters; areas without arrows represent resident segments or populations. Black dots indicate geographic locations of breeding populations with mean wing lengths given to nearest 1.0 mm. (see Table 2). Segments: A, *solitarius*; B, *alticola*; C, *cassinii;* D, *plumbeus*; E, *lucasanus*; F, *pinicolus*; G, *repetens*; and H, *montanus.*

season in or about the same locality or region. Because of a slight sex difference in size, only male specimens were included. Measurements of differences between lengths of primary feathers (utilized in determining the "wing-tip index" values presented in Table 6) were taken to the nearest 1.0 mm.

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SPECIES GROUPS WITHIN THE GENUS

Vireos are nine- or ten-primaried oscines which glean insects from foliage. The genus is restricted to temperate and tropical America with nearly all of the species occurring in North and Middle America. There are no species endemic to South America, although members of wide-ranging, polytypic species or superspecies occur there. Endemic and divergent representatives are found in the Greater Antilles. Members of the genus show virtually no evidence of sexual dimorphism in color. At least for the breeding season, monogamous pair formation is characteristic for all species. The habitat for the genus is primarily broadleaved vegetation, but the various species may be designated as being either thicket foragers or arboreal foragers.

The various species or superspecies may be divided (Hamilton, 1958MS) into the following species groups based on morphological and ecological characters:

Subgenus *Vireo*
(eye-rings and wing-bars present)

griseus group
(thicket foragers)

Species	*Breeding distribution*
V. griseus. White-eyed Vireo. (includes *V. pallens*, *V. crassirostris*, *V. gundlachii*, *V. modestus*, and *V. caribaeus.*)	Eastern United States, both coastal lowlands of Middle America, Bermuda, and various islands of the West Indies.
V. carmioli. Yellow-winged Vireo.	Mountains of Costa Rica and western Panama.
V. bairdi. Cozumel Vireo.	Cozumel Island off Quintana Roo.

V. osburni. Osburn's Vireo.	Blue Mountains of Jamaica.
V. nanus. Lawrence's Vireo.	Hispaniola and Gonave Island.
V. latimeri. Latimer's Vireo.	Puerto Rico.
V. bellii. Bell's Vireo.	Lowlands of southwestern United States, east to Mississippi Valley, and south to northern Mexico.
V. vicinior. Gray Vireo.	Arid lowlands of southwestern United States and northern Mexico.
V. nelsoni. Dwarf Vireo.	Southwestern Mexico (Michoacan, Guanajuato, and Oaxaca).

solitarius group
(arboreal foragers)

V. solitarius. Solitary Vireo.	Forested North America south through montane Mexico to highlands of Honduras.
V. flavifrons. Yellow-throated Vireo.	Broadleaved forests of eastern North America.
V. atricapillus. Black-capped Vireo.	Southwestern Kansas south through Oklahoma and west-central Texas to central Coahuila.
V. huttoni. Hutton's Vireo.	Southwestern British Columbia south through western United States (east to the Rocky Mountains and western Texas) to Mexico and Guatemala.

Subgenus *Vireosylva*
(eye-rings and wing-bars absent)

gilvus group
(arboreal foragers)

V. gilvus. Warbling Vireo. (includes *V. leucophrys.*)	Broadleaved forests (montane) of North, Middle, and South America.
V. philadelphicus. Philadelphia Vireo.	Eastern North America.

olivaceus group
(arboreal foragers)

V. olivaceus. Red-eyed Vireo. (includes *V. flavoviridis* and South American forms.)	Broadleaved forests (lowlands) of North, Middle, and South America; absent from southwestern United States and western Mexico.
V. altiloquus. Black-whiskered Vireo. (includes *V. magister.*)	Florida Keys and islands of the Caribbean (includes several coastal areas and islands of Yucatan, Quintana Roo, British Honduras, and Honduras).
V. hypochryseus. Golden Vireo.	Lowlands and foothills of western and southwestern Mexico.

Of these species, *V. griseus*, *V. solitarius*, *V. huttoni*, *V. gilvus*, and *V. olivaceus* are of wide distribution and demonstrate pronounced geographic variation. The remaining species of *Vireo* are either monotypic or polytypic species with relatively restricted distributions, and exhibit little or no ecogeographical variation.

Compared to presumably related oscine genera (e.g., the "coerebid" complex of honeycreepers or the *Dendroica* group of wood-warblers), the species of *Vireo* show little divergence in terms of habitat preferences, coloration, or modifications of the external morphology. With exception of two specialized species (*V. osburni* and *V. nanus*) endemic to islands in the Caribbean, the vireos appear to have uniform bill structures and essentially similar feeding adaptations.

The vireos are all fairly similar in appearance, being mostly yellow-greenish species characterized by the presence or absence of eye-rings, eye-stripes, and wing-bars. These are some of the morphological characters that taxonomists have used to determine the species and their relations to each other. The adaptive values of these characters are not clear, but presumably they may represent species recognition characters aiding individuals in finding conspecific mates. If this is true, a larger array of differences in such characters (ethological isolating mechanisms) might be expected when sympatric species exist in close proximity to one another; this might be especially important if the breeding and foraging positions of the different species overlap within a common habitat during the breeding season. Theoretically, there would be available, in different genera or groups of related species, alternative possibilities or "avenues" for obtaining (in response to natural selection) ecological and ethological compatibility for sympatric relationships.

In this respect, it is interesting to compare the habitat distributions of the species of *Parus* that are sympatric in the Old World with those of the sympatric species of *Vireo*, since both groups consist of insect-feeding species which forage in foliage. For sympatric species of *Parus* in the western Palearctic, *habitat co-occupancy* (sympatric species occurring together within the same habitat during the breeding season) is well developed, with the species concerned having different—but overlapping—feeding niches (see Gibb, 1954), having different coloration patterns, and belonging to different species groups or subgenera (as delimited by Snow, 1954*b*:566–567). However, morphologically similar species, such as the Willow Tit (*P. montanus*) and the Marsh Tit (*P. palustris*), both members of the *Poecile* species group, when sympatric in Europe normally are separated by habitat (Snow, 1954*b*: 579). In the Balkans (Serbia), a third member of the *Poecile* species group, the Somber Tit (*P. lugubris*) occurs in sympatry with these two species; all three related species are markedly separated from one another by their restriction to different habitats (Matvejev, 1950:177–180). Consequently, it would appear that differences in species recognition characters of the external morphology of some species (e.g., *P. major*, *P. caeruleus*, *P. ater*; each belonging to a different species group or subgenus) are associated in some unknown manner with the development of habitat co-occupancy as a type of sympatric relationship. For species of *Parus* that have been studied, Hinde (1952:190) concludes that there are "few essential differences" in behavior between different species. Thus, for members of this genus occupying the same habitat, it would seem that selection has favored (along with the necessary adjustments in feeding ecology) traits of behavior which promote disregard of nonconspecific individuals.

In contrast to the general pattern for *Parus* cited above, the sympatric species of *Vireo* show *habitat separation* (sympatric species occurring during the breeding season in different or separate habitats or in different, stratal subdivisions of a habitat), somewhat similar to that of the members of the *Poecile* species group of *Parus.* Habitat separation for sympatric species of *Vireo* may be of two types: First, utilization of distinct habitats ("spatial separation") with no lateral overlap except for limited possibilities along the boundaries of contiguous habitats (e.g., sympatric populations of *V. bellii, V. vicinior, V. solitarius,* and *V. huttoni* in the San Bernardino Mountains of southern California; see Grinnell and Swarth, 1913:292). Second, a "stratal separation" of habitat(s) within a plant association (e.g., *V. olivaceus* foraging and nesting in the canopy with *V. griseus* occupying the shrub layer of the same broadleaved, riparian woodlands in the eastern United States; see Hoiberg, 1954:369).

For sympatric species of *Vireo,* this "stratal" type of habitat separation (which may result sometimes in overlap of foraging positions) nearly always occurs between members of different subgenera (i.e., one species having eye-rings and wing-bars while the other lacks such morphological characters). In addition to the example of *V. griseus* and *V. olivaceus* cited above, *V. solitarius* and *V. gilvus* in the western United States seem to have overlapping (regularly?) foraging positions in broadleaved, riparian areas. In southeastern Arizona, Marshall (1957:62) finds that *V. huttoni* (a member of the *solitarius* species group) may occur with these two species in riparian areas. However, *V. huttoni* is normally restricted to oak woodlands with continuous canopy, and, in the western United States, this habitat is usually separate from (but often contiguous to) the habitats of other species of *Vireo* (see Grinnell and Swarth, 1913:292). Of the sympatric species of *Vireo,* the two that appear to coexist within a habitat (habitat co-occupancy) during the breeding season are *V. olivaceus* (arboreal forager) and *V. flavifrons* (arboreal, but strictly crown-layer forager), each belonging to a separate subgenus. My examination of the breeding-bird censuses from eastern and southeastern United States reported in *Audubon Field Notes* during the past seven years indicates numerous occurrences of these two species on the same study tract; unfortunately, no information is available as to the foraging ecology and breeding positions of these two species in areas where they appear to occupy the same unit of habitat. The "spatial" type of habitat separation appears to be the prevalent condition between sympatric species belonging to the same species group or subgenus (e.g., *V. bellii* and *V. vicinior* in southwestern United States, and *V. gilvus* and *V. philadelphicus* in northeastern United States). Generalizations such as these indicate that a certain divergence in relationship (as suggested by the presence or absence of eye-rings and wing-bars) as well as a difference in foraging positions is manifested (or necessary?) when species of *Vireo* exist in close proximity to one another.

It would seem, then, that within the genus *Vireo* selection has operated for occupation (at least during the breeding season) of separate habitats rather than for habitat co-occupancy in achieving the necessary ecological (and ethological?) compatibility required if previously isolated forms are to develop sympatry upon contact. Since this type of sympatric relationship results in each species having its breeding and feeding positions spatially separate from those of other species, the necessity for different ethological isolating mechanisms would be much reduced. Thus, it is not surprising that the members of this genus are mostly uniform, plain-colored species showing little diversity in external morphology or general ecology. Admittedly, there is a problem here of "cause or effect"; either the species of a given subgenus or species group have not diverged (in morphology and/or vocalizations?) sufficiently for habitat co-occupancy or the stringency of habitat selection (resulting in habitat separation) has eliminated or decreased selection for pronounced ethological isolating mechanisms. Nevertheless, occupation of spatially separated habitats appears to be a generalization applicable to members of both subgenera of *Vireo*, and this study can offer no information on the problem of why selection has favored habitat separation as an "avenue" for the development of sympatry in this avian group. Comparisons with the Palearctic *Parus* have been discussed above. In contrast to sympatric relationships in *Parus* and *Vireo*, it would appear, in the thrush genus *Catharus*, that selection has stressed emphasis on vocal and behavioral modifications—rather than differences in plumage coloration or spatial separation of habitats—as a possible "avenue" for obtaining ethological compatibility in sympatric situations (see Dilger, 1956*b*:347–351).

Little is known about the behavior and general ecology of the various species of *Vireo*. Lawrence (1953) reported some information on the breeding biology of *V. olivaceus*, and Pitelka and Koestner (1942) reported similarly on *V. bellii*. More information on behavior and foraging ecology would be extremely useful, and will be necessary before these generalizations on sympatry and habitat utilization in the genus *Vireo* can be accepted as more than tentative.

MIGRATION PATTERNS OF VIREOS

Since all the species of *Vireo* having wide distributions in North and Middle America are migratory (excepting the permanently resident *V. huttoni*), any attempt to correlate intraspecific variation with environmental factors must take into account the climate of the winter quarters as well as that of the breeding quarters. Salomonsen (1955) has discussed the role of migration in relation to intraspecific variation. He points out that within some migratory species the populations breeding in the northern part of the species' range have winter quarters further south than the winter quarters of conspecific populations whose breeding ranges are south of (but contiguous to) those of the northerly breeding populations; the northern populations are thus long-distance migrants and the populations breeding in the lower latitudes are short-distance migrants. A species with such a migration pattern is considered by him to have a "leap-frog" or allohiemic migration pattern. As he further states, the short-distance migrants (having winter quarters north of those of the long-distance migrants) are subjected to colder winter temperatures. From such observations he reasons—in accordance with the heat conservation principle underlying Bergmann's rule—that the populations exposed to colder winter temperatures should be larger, resulting in an apparent reversal of Bergmann's rule. His examination of ringing returns and the distribution of many European species showing reversals of Bergmann's rule have demonstrated that nearly all of these species are "leap-frog" or allohiemic migrants.

Thus, considering "competition . . . for food as the primary reason for wide dispersal in the off-season", Salomonsen (1955:10) has divided migration patterns into two major categories: (1) Synhiemy or the condition whereby the various populations of the same species coexist in a common wintering quarter; (2) Allohiemy or the condition whereby populations within a species have separate (geographically) wintering quarters. Intermediate conditions between these two categories are also recognized by him.

Considering the possible importance of the location of winter quarters on geographical variation, a study of migration within the genus *Vireo* was undertaken. Below is a tentative statement of migration patterns for some of the species of this genus that I have determined on a basis of study of literature, and the "subspecific" allocation of specimens (Mus. Comp. Zool.) taken in winter quarters:

griseus (6 to 9 races)	allohiemic (tandem pattern?)
bellii (4 races)	allohiemic (leap-frog?)
vicinior (monotypic)	synhiemic
solitarius (9 to 10 races)	allohiemic (leap-frog)
flavifrons (monotypic)	?
atricapillus (monotypic)	synhiemic

gilvus (5 to 6 races)	allohiemic (leap-frog)
philadelphicus (monotypic)	synhiemic
olivaceus (10 to 12 races)	allohiemic (leap-frog)

It can be seen from this listing that the allohiemic species are polytypic. Also, each of the allohiemic species demonstrates, in varying degrees, ecogeographical variation. The synhiemic species are monotypic, with their winter quarters unified and rather restricted (excepting *V. flavifrons*) in geographic area. This condition is the expected one, for, as Salomonsen (1955:53) suggests, allohiemic species with geographically isolated populations during the winter will have their various populations exposed to different environments and different selection pressures. Further, it must be remembered that some of these allohiemic species have discontinuous distributions; here, reduction of gene flow between various conspecific populations might facilitate adaptive divergence (viz., climatic adaptation) at the intraspecific level (see Mayr, 1954:160–163). *Vireo solitarius* and *V. gilvus* are allohiemic species consisting of mostly migratory populations; however, both have developed local, endemic populations (*lucasanus* and *victoriae* segments, respectively) resident to the Cape region of Baja California.

The suppressing action of a common winter quarters on intraspecific variation within synhiemic species is possibly illustrated by *V. atricapillus.* This species shows no variation in external morphology although the breeding range is strongly discontinuous, being restricted to isolated foothills in Coahuila, central and western Texas, southern Oklahoma, and southwestern Kansas. Moore (1938:25) has reported the winter quarters of these populations on the coast of Sinaloa. A common wintering area here helps to explain the lack of variation in a monotypic species.

Unlike the other monotypic species, *V. flavifrons* has widespread wintering quarters extending from southern Mexico south to Venezuela and Colombia. The lack of ecogeographical variation in this species does not necessarily imply a common winter quarters for the species, for specimens collected throughout the large, wintering area cannot be compared (phenotypically) with population samples collected throughout the breeding quarters in eastern North America. In a later section of this paper, I suggest that *V. flavifrons* is a "young" species with fluctuating populations and is in process of extending its breeding range. Banding returns may eventually explain the migratory pattern of the populations of *V. flavifrons.*

Geographic Variation in Size

Within the genus *Vireo*, trends of intraspecific variation in size (as indicated by variation in wing length) seem in conflict with Bergmann's rule; little evidence was found for a negative correlation between wing length and temperature. Of the wide-ranging species of this genus, sufficient material for adequate analysis was available for *V. griseus*, *V. solitarius*, *V. huttoni*, *V. gilvus*, and *V. olivaceus*. Of these species, *V. solitarius*, *V. huttoni*, and *V. gilvus* have the largest wing lengths in the approximate region of northwestern Mexico with smaller wing lengths occurring elsewhere (Tables 2, 3, 4). *Vireo olivaceus* and *V. griseus* (excluding insular populations) demonstrate (Tables 1, 5) north to south clinal decreases in wing length; however,

TABLE 1
MEASUREMENTS[1] FOR *VIREO GRISEUS* SUPERSPECIES

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	$\frac{100\times\text{bill}}{\text{wing}}$	$\frac{100\times\text{tail}}{\text{wing}}$
1.	Southern New England (*noveboracensis*)	64.6 ± 0.6 (11:64–66)	13.6 ± 0.3 (11:13–14)	51.1 ± 1.2 (11:49–53)	21.1	79.1
2.	Virginia to New Jersey (*noveboracensis*)	63.7 ± 0.6 (12:62–64)	13.4 ± 0.4 (12:13–14.5)	50.4 ± 1.4 (12:48–53)	21.0	79.1
3.	Georgia (*noveboracensis?*)	63.5 ± 0.6 (12:62–64)	13.4 ± 0.6 (12:12.5–14.5)	49.8 ± 1.1 (12:48–52)	21.1	78.4
4.	Southern Florida and Keys (*maynardi*)	60.5 ± 1.0 (15:58–62)	15.1 ± 0.4 (15:14.5–16)	48.2 ± 1.1 (15:46–50)	25.0	79.7
5.	Bermuda (*bermudianus*)	58.8 (8:56–60)	15.0 (8:14–16)		25.5	
6.	Kansas (*noveboracensis*)	62.4 ± 0.6 (11:61–63)	13.6 ± 0.4 (11:13–14.5)	50.8 ± 0.9 (10:49–52)	21.8	81.4
7.	Tennessee (*noveboracensis*)	61.2 ± 0.4 (11:61–63)	14.4 ± 0.4 (11:14–15)	48.8 ± 0.9 (11:47–50)	23.5	79.7
8.	Louisiana (*griseus*)	61.3 ± 0.6 (13:60–62)	14.6 ± 0.6 (12:13.5–15)	49.0 ± 1.0 (13:47–50)	23.8	79.9
9.	Brownsville area, Texas (*micrus*)	58.1 (7:57–59)	12.4 (7:12–13)	47.4 (7:46–48)	21.3	81.6
10.	San Luis Potosi (*micrus*)	59.7 ± 0.5 (10:59–61)	13.9 ± 0.7 (10:13–15)	49.1 ± 1.3 (10:47–52)	23.3	82.2
11.	Yucatan and British Honduras (*semiflavus?*)	57.4 ± 1.6 (16:54–59)	14.1 ± 0.9 (16:12.5–15)	47.6 ± 1.3 (16:45–49)	24.6	82.9
12.	Lowlands of Costa Rica (*pallens?*)	55.6 (7:55–56)	14.2 (7:13.5–14.5)	46.4 (7:45–47)	25.5	83.5
13.	Bahama Islands (*crassirostris*)	64.9 ± 2.1 (12:62–70)	15.9 ± 0.6 (12:15–70)		25.3	
14.	Tortuga Island (*tortugae*)	63.7 ± 1.3 (11:61–66)	15.6 ± 0.4 (11:15–16)	50.7 ± 1.3 (10:49–54)	24.5	79.6
15.	Cuba (*gundlachii*)	56.0 ± 1.0 (12:55–58)	15.1 ± 0.5 (12:14–16)	51.3 ± 0.9 (12:50–53)	27.0	91.6
16.	Jamaica (*modestus*)	58.6 (7:57–60)	12.6 (7:11.5–13)		21.5	
17.	Old Providence Island (*approximans*)	61.4 (5:60–63)	15.6 (5:15–17)		25.4	
18.	Cozumel Island (*V. bairdi*)	62.1 (9:60–64)	15.3 (9:15–16)	52.6 (9:50–56)	24.6	84.7
19.	Highlands of Costa Rica (*V. carmioli*)	66.4 (9:64–69)	12.4 (8:12–13)	46.6 (8:45–50)	18.7	70.2
20.	Porto Rico (*V. latimeri*)	65.3 (7:63–67)	13.6 (7:13–14.5)	59.5 (6:58–62)	20.8	91.1

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[1] For Tables 1–5, measurements cited as follows: mean to nearest 0.1 mm. plus or minus standard deviation to nearest 0.1 mm. (number of sample: range of sample). Standard deviation not calculated for samples of fewer than ten individuals.

the northern breeding populations of these two species migrate, respectively, to South America and Middle America. The northern breeding populations of *V. solitarius* and *V. gilvus* also migrate to the lower latitudes (Middle America) for the off-season. Populations of *V. huttoni* are resident in evergreen–oak habitats throughout the western United States and Mexico.

Vireo solitarius.—In this species (see Fig. 1 and Table 2), the resident populations (*notius* and *montanus* segments) occurring in British Honduras and Guatemala, respectively, have the smallest wing lengths of all the widely distributed populations of the species. The largest wing lengths are found in breeding populations from the foothills and mountains of northwestern (*pinicolus* segment) and central (*repetens* segment) Mexico; populations of the former segment apparently move south during the winter to central Mexico in the general region of the resident populations of the latter segment. Breeding populations with wing lengths intermediate between the extremes cited above occur in Baja California (*lucasanus* segment) and in temperate North America (*cassinii, plumbeus, solitarius,* and *alticola* segments). Since most of the migratory populations breeding in North America have winter quarters extending approximately from central and eastern Mexico to the Guatemala–Nicaragua area, they are thus subjected to about the same winter temperatures as the resident populations of that region. According to Bergmann's rule, populations exposed to colder winter temperatures should have larger wing lengths than those having warmer winter quarters; the wing lengths and winter quarters of the populations of segments *solitarius* and *alticola* in eastern North America indicate an allohiemic migration pattern for the two segments which may be interpreted (Salomonsen, 1955:44) as a manifestation of Bergmann's rule. The populations of *V.*

TABLE 2

MEASUREMENTS FOR *VIREO SOLITARIUS*

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	New England (*solitarius*)	75.1 ± 0.9 (30:73–77)	13.4 ± 0.4 (27:12–14)	53.6 ± 1.0 (30:52–56)	17.8	71.4
2.	Central Virginia (*alticola*)	79.2 ± 0.7 (24:78–81)	14.4 ± 0.3 (20:13.5–15)	55.9 ± 1.0 (24:54–57)	18.2	70.6
3.	Western North Carolina and South Carolina (*alticola*)	81.2 ± 1.1 (22:80–84)	15.6 ± 0.5 (22:14–16)	55.9 ± 1.0 (22:57–62)	19.2	74.0
4.	Southern British Columbia (*cassinii*)	74.6 ± 1.2 (12:72–76)	14.9 ± 0.7 (12:13.5–16)	54.4 ± 0.9 (12:53–56)	20.0	72.9
5.	Central and southern California (*cassinii*)	76.9 ± 1.5 (14:73–78)	15.1 ± 0.4 (21:14.5–16)	55.3 ± 1.0 (20:53–57)	19.6	71.9
6.	Cape region of Baja California (*lucasanus*)	70.1 ± 1.7 (12:66–72)	15.2 ± 0.4 (29:14–16)	52.1 ± 1.1 (29:50–54)	21.7	74.3
7.	Colorado (*plumbeus*)	77.2 ± 0.6 (11:76–78)	14.8 ± 0.4 (11:14–15.5)	54.9 ± 0.9 (11:53–56)	19.2	71.1
8.	Southeastern Arizona (*plumbeus*)	81.3 ± 1.0 (21:79–83)	15.0 ± 0.6 (21:14.5–16.5)	58.0 ± 1.3 (21:56–60)	18.5	71.3
9.	Sonora (*pinicolus*)	84.7 ± 1.1 (12:83–87)	15.2 ± 0.3 (12:14–16)	62.2 ± 1.0 (12:60–63)	17.9	73.4
10.	Guerrero (*repetens*)	82.4 (7:80–83)	15.9 (7:14–16)	58.7 (7:55–59)	19.3	71.2
11.	Guatemala (*montanus*)	68.5 (4:66, 69, 69, 70)	13, 13	50, 50, 51	19.9	

gilvus have a pattern of geographic variation in wing length (Table 4) similar to that of *V. solitarius.*

Vireo huttoni.—A striking departure from Bergmann's rule is the variation in wing length (Table 3) within *V. huttoni,* the only nonmigratory species of North and Middle American distribution. The largest wing lengths in this species are characteristic of populations (*stephensi* segment) restricted to forested areas of northwestern Mexico; the smallest wing lengths are from populations (*huttoni* segment) resident to southern British Columbia. Intermediate wing lengths are from populations of western United States (*huttoni* segment), northern and northeastern Mexico (*carolinae* segment), central and southern Mexico (*mexicanus* segment), and Guatemala (*vulcani* segment). Here, it is interesting to examine (Table 3) the distributions of all the populations or segments with smaller wing lengths than the *stephensi* segment; these populations with

TABLE 3

MEASUREMENTS FOR *VIREO HUTTONI*[1]

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	Southern British Columbia and Washington (*huttoni*) (3500 ft., 36 F.)	62.8 ± 0.9 (14:61–64)	12.2 ± 0.4 (12:12–13.5)	48.2 ± 0.9 (14:47–50)	19.4	76.8
2.	Oregon and northern California (*huttoni*) (4000 ft., 40 F.)	63.5 ± 0.8 (23:62–65)	12.8 ± 0.5 (19:11.5–13.5)	49.5 ± 1.6 (23:47–53)	20.2	78.0
3.	Central California (*huttoni*) (4200 ft., 44 F.)	63.9 ± 0.9 (16:62–65)	12.6 ± 0.4 (15:11.5–13)	50.7 ± 1.1 (16:49–53)	19.7	79.3
4.	Southern California (*huttoni*) (5500 ft., 46 F.)	65.7 ± 0.9 (11:64–68)	12.8 ± 0.5 (11:11.5–13.5)	50.9 ± 1.3 (11:49–53)	19.5	77.5
5.	Cape region of Baja California (*cognatus*) (4000 ft., 55 F.)	66.8 ± 1.1 (15:66–70)	13.4 ± 0.6 (28:12–14.5)	51.5 ± 1.2 (31:48–53)	20.1	77.1
6.	Arizona (*stephensi*) (6200 ft., 45 F.)	66.5 ± 1.1 (16:65–68)	12.9 ± 0.5 (16:12.5–14)	51.7 ± 1.0 (16:50–53)	19.4	77.7
7.	Chisos Mts. in western Texas (*carolinae*)	66.1 (7:63–68)	13.1 (7:12.5–13)	52.1 (7:50–54)	19.8	78.8
8.	Sierra del Carmen, Coahuila (*carolinae*) (7000 ft., 51 F.)	65.6 (9:64–68)[2]	12.9 (9:12–14)	51.4 (9:49–52)	19.7	78.4
9.	Sonora (*stephensi*) (5000 ft., 55 F.)	68.7 ± 1.0 (10:67–70)	13.1 ± 0.3 (10:13–14)	55.5 ± 1.0 (10:54–57)	19.1	80.8
10.	San Luis Potosi (*carolinae?*) (5700 ft., 59 F.)	67.3 ± 1.1 (18:65–69)	12.8 ± 0.4 (18:12–13.5)	52.8 ± 0.8 (18:51–54)	19.0	78.5
11.	Morelos and Federal District (*mexicanus*) (6000 ft., 54 F.)	66.6 ± 1.2 (14:64–68)	13.1 ± 0.6 (12:12.5–14.5)	53.8 ± 0.8 (14:52–55)	19.7	80.8
12.	Southern Mexico (*mexicanus*) (7000 ft., 63 F.)	66.3 (8:65–68)	13.2 (8:13–14)	51.4 (8:49–52)	19.9	77.5
13.	Guatemala (*vulcani*) (5000 ft., 65 F.)	63, 64, 65	12, 12, 12.5	45, 48, 48		

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[1] For this species, altitude (accurate to nearest 500 ft.?) and mean temperature (°F.) of coldest month have been estimated and are included here.

[2] Chord measurement.

smaller wing lengths occur in relatively more humid regions to the north, east, and south of northwestern Mexico.

Vireo olivaceus.—Throughout the extensive breeding distribution (roughly, temperate and tropical America) of this polytypic species, there is a north-to-south clinal decrease in wing length of continental populations (New England, 83 mm.; Panama, 79 mm.; Brazil, 67 mm.; see Table 5). The North American populations (*olivaceus* segment) have winter quarters in the Amazon Basin. The Middle American populations (*flavoviridis* and [?] *hypoleucus* segments) have winter quarters extending from Panama to the Amazon Basin. In the region of the Amazon Basin and Matto Grosso, there are resident populations (see Zimmer's discussion, 1941:4–9) which, to my knowledge, have the smallest wing lengths of all the populations of this species. In this species, superficially in agreement with Bergmann's rule, the variation in wing length becomes inconsistent with the rule upon consideration of the location of the winter quarters; many of the populations breeding in Middle America (*flavoviridis* segment) have winter quarters in Panama whereas the North American populations (*olivaceus* segment) with larger wing lengths are "wintering" in the Amazon Basin during the summer of that hemisphere; however, temperature differences at these low latitudes should be of negligible effect. Until more is known about the location of the winter quarters of the populations of this species, all that can be concluded about geographic variation in wing length is that a north-to-south cline for decreased wing length exists when populations from only the breeding quarters are compared. It is possible that the northern breeding populations have an increased wing length as an adaptation for long (and fast?) migration to South America. Variation in wing length (Table 5) within *V. griseus* is similar to *V. olivaceus* in showing (for continental populations) a decrease in wing length from eastern North America south to Panama; in this species, likewise, the pattern of variation becomes difficult to interpret upon consideration of migration and location of winter quarters.

Correlations with climatic gradients.—All attempts to find a negative correlation between temperature and size (Bergmann's rule) within the various species of *Vireo* failed. Several measures of yearly fluctuations in temperature were considered: mean temperature of coldest month, mean temperature of three coldest months, and "lowest recorded temperature." However, the absence of adequate meteorological data for the localities of population samples from Middle America prevented a serious analysis of this possible relationship. Having resident populations distributed over a wide geographic region (southern British Columbia and western United States south through Mexico to the Guatemala area), *Vireo huttoni* is the one species whose various populations are exposed, consistently, to a gradient of decreasing winter temperature from south to north. There appears to be no relationship in this species (see Fig. 2) between wing length and temperature.

Moreau (1957), by use of partial correlation analysis, has presented evidence for a positive correlation between wing length and altitude (independent of effect of temperature) for the African populations of the *Zosterops* complex. My data for intraspecific variation in the species of *Vireo* fail to indicate the presence of such a phenomenon. Of the several species, the resident

V. huttoni could possibly be tested by partial correlation analysis. The scatter diagram (Fig. 3) for wing length and altitude comparisons within *V. huttoni* indicates no relationship between the two variables; however, I lack sufficient data to test the point statistically.

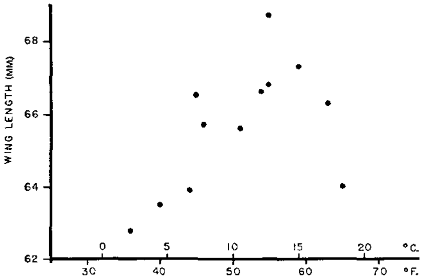

Fig. 2. Variation in wing length in relation to mean temperature of coldest month for 12 populations of the resident *Vireo huttoni* (see Table 3). Note the apparent absence of correlation between wing length (as an index to body size) and cold temperature.

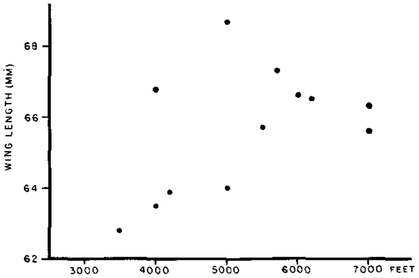

Fig. 3. Variation in wing length in relation to altitude for 12 populations of the resident *Vireo huttoni* (see Table 3). Note the lack of positive correlation between wing length and altitude.

One striking fact which became clear in the course of the study was the location of the populations with the largest wing lengths within the species, *V. solitarius*, *V. huttoni*, and *V. gilvus*. Within each the largest mean wing lengths are from the plateaus and mountains of northwestern Mexico (Sonora), a region relatively more arid than any other within the distribution of each of these species. It became evident that the one feature of the environment of the breeding distributions that was related or correlated (in three species of *Vireo* at least) with the clinal variation in wing length was "humidity" or "aridity." In brief, wing length (presumably an indication of body size) was smaller in humid regions and larger in arid regions (for intraspecific comparisons only). In *V. olivaceus*, it is difficult to explain the observed variation in these terms; however, the populations with the smallest wing lengths are resident in the warm, moist regions of the Amazon Basin. And within *V. griseus* (considering continental populations only) the populations with the smallest wing length (*pallens* segment) are resident in the humid, coastal lowlands of Costa Rica. I have tentatively designated this observation as an "aridity effect" which means, simply, that within wide-ranging species of temperate and tropical distribution there may be a tendency for individuals of populations occurring in hot, arid regions to have greater wing lengths than individuals in hot, humid regions. This observation is not new, for

Ripley (1950:361) and Salomonsen (1955:44–46) have noted or presented evidence suggesting that populations of arid regions may be characterized by larger individuals.

"Aridity effect" or "latitude effect."—I have suggested above that the intraspecific increase in wing length of *Vireo* populations occurring in Sonora, Mexico, may represent a positive response in body size to the "aridity" or low humidity of that region. Readily, a similarity appears between this "aridity effect" and the "latitude effect" as described by Snow (1954*a*) for intraspecific variation in some species of *Parus*. In both genera, the populations with larger wing lengths occur in foothills or mountains of lower latitudes. For both genera, these regions (both approximately 30°N) are in climatically arid areas of northwestern Mexico and northwestern Africa, respectively. However, it must be remembered that both in *Parus* (see Snow, 1952:489–490) and in *Vireo* (see Marshall, 1957:106–107) these populations under consideration occur in the forested elevations of the highlands.

Discussing the relationship between wing length and temperature within the species of *Parus* showing the "latitude effect," Snow (1954*a*:20–21) states "With the same winter temperatures, wing-length tends to be greater at lower latitudes than it is at higher latitudes." Such a relationship with winter temperature is not true for the genus *Vireo*. First, the populations of *V. solitarius* and *V. gilvus* breeding in northwestern Mexico move south during the winter to central and southern Mexico. Second, the *V. huttoni* populations resident in northwestern Mexico (Sonora) are exposed to milder winter temperatures than the populations resident to southern British Columbia.

Snow's interpretation of the latitude effect stresses the importance of feeding ecology with the short day for food gathering during winter in the higher latitudes (Scandinavia) being a critical factor limiting body size. Could this interpretation apply to the species of *Vireo*? It would seem that this is not the case since most populations of *V. solitarius* and *V. gilvus* (and other *Vireo* species) breeding in high latitudes migrate to tropical or subtropical Middle America for the off season. Also, the resident populations of *V. huttoni* extend north only as far as southern British Columbia (50°N)—to about the latitude of southern England or central Europe.

Presence of an Aridity Effect in other New World Species

One value of studying variation and relationships among the species of a genus is the possibility of finding additional parallels or new expressions of evolutionary phenomena which may be characteristic of other genera. This is especially true for comparative studies of intraspecific variation. Considering the well-known parallelism of climatic adaptation at the intraspecific level, the possibility of finding similar "aridity effects" within species of other avian genera should be considered in that this may represent a modification or suspension of Bergmann's rule.

For this purpose, I have tried to examine (from the literature and with specimens) some wide-ranging North American species with populations occurring (as annual or summer residents) in northwestern Mexico or southwestern United States:

Dryobates pubescens. Downy Woodpecker.—My measurements (mean wing length to nearest 1.0 mm. for males only [number in sample: range of sample]) indicate that the greatest wing lengths in this resident species are from southwestern United States: New Mexico, 104 (7:103–106); Colorado, 104 (8:102–105); British Columbia, 98 (9:97–100); Alberta to Manitoba, 99 (12:97–100); Michigan, 95 (8:93–96); Newfoundland, 95 (9: 93–97); New England, 95 (11:93–97); Virginia, 93 (12:92–96); and Florida, 90 (13: 88–91). As in some other North American species, the smaller individuals occur in the southeastern United States.

Sitta carolinensis. White-breasted Nuthatch.—Hawbecker's (1948) study of variation in populations of this resident species in the western United States demonstrates a north-to-south cline for increased wing length (Arizona populations, 90 mm.). My measurements for the eastern United States are: Georgia, 88 (10:87–90) and Florida, 86 (12:84–87).

Lanius ludovicianus. Loggerhead Shrike.—Miller's (1931) investigation of this species reveals that the populations with the longest wings (102 mm.) are resident to the arid lowlands of northwestern Mexico (Sonora) and those with the shortest wings (97 mm.) are resident to southeastern United States (mostly lowlands). Populations in other regions (including southern Mexico) have intermediate wing lengths.

Richmondena cardinalis. Cardinal.—The greatest wing lengths in this resident species are also from northwestern Mexico (Sonora lowlands). My measurements: Sonora (Guaymas area), 98 (15:95–100); Texas (Edwards Plateau), 94 (10:92–96); Kansas, 94 (8:92–95); eastern Texas and northern Louisiana, 93 (14:89–94); Florida, 89 (10: 87–90); San Luis Potosi, 88 (10:87–90); and Guerrero, 85 (8:83–87).

Salomonsen (1955:44–46) is aware of this tendency for increased wing length in populations of southwestern United States and northern Mexico. Discussing "leap-frog" migration in the Summer Tanager (*Piranga rubra*), he states that the populations (*cooperi* segment) breeding in the southwestern United States are larger than their counterparts (*rubra* segment) breeding in the eastern United States. He also discusses a comparable example for the variation in the Blue Grosbeak (*Guiraca caerulea*), and suggests that the Song Sparrow (*Melospiza melodia goldmani*) and the Red-winged Blackbird (*Agelaius phoeniceus sonoriensis*) are examples of "increased wing lengths in Mexican forms, . . ."

It is my belief that these examples cited as evidence for an "aridity effect" for some North America bird species represent parallel adaptations to the general low humidity and high summer temperatures (as these conditions may affect selective action on general body size) of northwestern Mexico and the southwestern United States. Whether similar "effects" will be found in species of large distributions (extending throughout diverse climatic regions) restricted to other continents remains to be determined. Since adaptation may represent interactions or conflicts between various selective forces, this "aridity effect" need not hold true for all North American species with comparable distributions. Miller (1931:104) has made the plausible suggestion that increased wing length in *Lanius ludovicianus* is characteristic of populations inhabiting open land or regions of widely spread vegetation. Pitelka (1951:366) concludes the same for the larger, inland races (*superciliosa* and *immanis* segments) in comparing the "*californica*" group of races of the Scrub Jay (*Aphelocoma coerulescens*). It is noteworthy that Pitelka found the smallest wing lengths from the populations of this species resident to Florida. Finally, I find little evidence for the presence of Bergmann's rule, *per se*, within New World species.

ADAPTIVE SIGNIFICANCE OF INTRASPECIFIC VARIATION IN SIZE

In the previous sections, I have tried to emphasize the relationship between wing length and environmental conditions among the populations within the species of *Vireo* and some other Nearctic species. Examples have been cited from both resident and migratory species. Within migratory species, consideration of geographic location of winter quarters indicates still a relationship between wing length and change in environment. This "aridity effect" represents, as other ecogeographical rules, no more than a correlation between a

TABLE 4

MEASUREMENTS FOR *VIREO GILVUS*

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	Massachusetts (*gilvus*)	72.4 ± 0.8 (19:71–74)	14.8 ± 0.5 (19:14–16)	51.4 ± 1.1 (19:49–53)	20.4	71.0
2.	North-central United States (*gilvus*)	69.9 ± 0.8 (15:68–71)	14.7 ± 0.6 (13:13.5–16)	50.1 ± 1.1 (15:48–52)	21.0	71.7
3.	Tennessee (*gilvus*)	71.3 ± 0.6 (10:70–72)	14.3 ± 0.3 (10:14–15)	50.1 ± 1.0 (10:48–51)	20.1	70.3
4.	Southern British Columbia (*swainsonii*)	67.6 ± 0.6 (13:66–68)	13.8 ± 0.4 (12:12.5–14)	50.6 ± 0.5 (13:49–51)	20.4	74.9
5.	Oregon (*swainsonii*)	67.8 ± 0.7 (19:67–70)	13.9 ± 0.4 (22:12.5–14)	52.6 ± 0.8 (22:51–54)	20.5	77.6
6.	Central California (*swainsonii*)	68.5 ± 0.9 (10:66–69)	14.3 ± 0.5 (10:13.5–15)	52.5 ± 1.3 (10:51–55)	20.9	76.6
7.	Southern California (*swainsonii*)	69.1 ± 1.1 (16:66–71)	14.1 ± 0.4 (22:13.5–15)	52.2 ± 1.0 (22:50–54)	20.4	75.5
8.	Cape region of Baja California (*victoriae*)	66.7 ± 1.2 (14:65–69)	15.1 ± 0.5 (24:14–16)	51.6 ± 1.2 (24:49–53)	22.5	77.4
9.	Arizona (*swainsonii*)	72.4 (8:70–74)	15.0 (8:14–16)	51.5 (8:49–53)	20.7	71.1
10.	Sonora (*brewsteri*)	73.4 ± 0.9 (11:72–75)	15.1 ± 0.5 (11:14–16.5)	54.4 ± 1.0 (11:52–55)	20.6	74.1
11.	San Luis Potosi (*eleanorae?*)	70.0 ± 1.1 (15:68–72)	14.8 ± 0.4 (15:14–15.5)	49.2 ± 1.0 (15:48–51)	21.1	70.3

character (here, wing length and, presumably, body size) and a changing environment (see Mayr, 1956:105). Since these intraspecific variations are orderly rather than random, selection forces—through unknown mechanisms—must be responsible for the clinal geographic changes.

Scholander (1955) has criticized the "physiological meaning" of the climatic or ecogeographical rules (for homeotherms, in general) by pointing out (p. 22) that variation in insulation is a more efficient method for controlling the loss of heat to the environment than shifts in surface/volume ratios. And his evidence indicates this. However, if change in body insulation (occurring between the peripheral tissues and the environment) were the only selective mechanism involved, we would expect similar body size for individuals from widely separated localities within the species' range, other conditions being equal. The fact remains that there are numerous cases of intra-

TABLE 5

MEASUREMENTS FOR THE *VIREO OLIVACEUS* SUPERSPECIES

No.	Locality and name of segment	Wing mm.	Bill mm.	Tail mm.	100×bill / wing	100×tail / wing
1.	Southern British Columbia (*olivaceus*)	82.0 ± 1.1 (13:80–84)	17.1 ± 0.4 (13:16.5–18)	57.4 ± 0.5 (13:56–58)	20.9	70.0
2.	Montana (*olivaceus*)	81.7 ± 0.9 (10:80–83)	17.1 ± 0.4 (10:16.5–18)	57.6 ± 1.2 (10:55–59)	20.9	70.5
3.	Massachusetts (*olivaceus*)	82.5 ± 0.8 (22:81–84)	16.9 ± 0.5 (22:16–18)	56.6 ± 0.8 (22:55–59)	20.5	68.6
4.	Virginia (*olivaceus*)	81.4 ± 0.9 (16:80–83)	17.1 ± 0.5 (16:16–18)	56.2 ± 0.9 (16:55–58)	21.0	56.2
5.	North Carolina (*olivaceus*)	81.5 ± 0.5 (13:80–83)	17.1 ± 0.3 (13:16.5–17.5)	56.7 ± 1.1 (13:54–58)	20.9	69.8
6.	Tennessee (*olivaceus*)	81.2 ± 0.6 (14:80–83)	18.4 ± 0.5 (14:17–19)	56.1 ± 1.3 (14:53–58)	22.7	69.3
7.	Northeastern Mexico (*flavoviridis*)	81.1 ± 0.6 (12:80–82)	18.8 ± 0.4 (12:18–19.5)	56.3 ± 1.1 (12:55–59)	23.2	69.4
8.	Southern Mexico (*flavoviridis*)	77.9 ± 1.5 (12:75–81)	18.4 ± 0.4 (12:17.5–19)	55.4 ± 1.2 (12:53–57)	23.6	71.1
9.	Guatemala and British Honduras (*flavoviridis*)	79.4 ± 1.3 (14:76–81)	18.1 ± 0.4 (12:17–19)	55.3 ± 0.5 (14:54–56)	22.8	69.6
10.	Panama (*flavoviridis*)	78.6 (7:78–80)	18.4 (7:18–19)	—	23.4	—
11.	Brazil (*solimoensis*?)	67.2 ± 0.9 (10:65–68)	15.7 ± 0.5 (10:15–17)	54.6 ± 1.0 (10:53–56)	23.4	81.3
12.	Florida Keys (*V. altiloquus barbatulus*)	80.5 (8:78–82)	18.5 (8:18–19)	—	24.2	—
13.	Bahama Islands (*V. a. barbatulus*)	80.3 (8:78–82)	19.5 (8:18–20)	—	24.3	—
14.	Grand Cayman Island (*V. a. magister*)	74.6 (5:73–76)	18.0 (5: 18)	—	24.1	—
15.	Hispaniola (*V. a. altiloquus*)	83.0 (8:82–84)	21.4 (8:20.5–22.5)	—	25.8	—
16.	St. Kitts Island (*V. a. barbadensis*)	80.9 (8:78–82)	20.0 (8:19–21)	63.2 (8:62–65)	24.7	78.1

specific gradients for wing length within bird species. How is this to be explained? The next six paragraphs in this section are speculative, and are presented with the hope of stimulating interest concerning the adaptive significance of intraspecific variation:

1. The channels for heat dissipation available to the bird body are convection, conduction, radiation, and evaporation (vaporization). Salt (1952:128) points out that the first two channels are of little or decreased importance (in passerine species, at least), leaving radiation and evaporation as the two primary channels for heat dissipation. Wallgren (1954:65) finds that evaporation represents a larger percentage (at least 40 per cent at 30°C.) of the total heat loss at higher temperatures in two species of *Emberiza*; this is expected since radiation is proportional to the temperature gradient between the body and surrounding environment. Thus, for birds a certain component of the total heat dissipation may be attributed to thermal properties of internal surface tissues (for vaporization) as well as external tissues (for radiation).

2. Concerning the role of evaporation in avian heat loss, it is interesting to examine the work of Bartholomew and Dawson (1953) on respiratory water loss in some birds of arid habitats in the southwestern United States. They find an inverse relationship between mean water loss per unit of body weight and mean body weight in comparing different species of various body sizes; they state (p. 165) "Why smaller birds should lose relatively more water in respiration than larger birds is not known, but it presumably relates to the higher metabolic rates of the former." These observations might be interpreted to indicate that a larger body size is advantageous in hot, arid environments to prevent desiccation via evaporation.

3. In a hot, humid environment, the bird body has the problem of adequate heat dissipation in that the high temperatures necessitate loss of heat by vaporization. Since the inspired air already has a relatively high actual vapor pressure, the body may have difficulty in expiring sufficient respiratory moisture. Selection for a decreased body size here with the relatively increased lung surface might facilitate heat dissipation.

4. In cold or cooler climates, the primary channel for heat loss in birds is presumably radiation. Since basal heat production appears to be the same in tropical as well as arctic forms, change in degree of insulation or change in surface/volume ratios are two possible avenues open to selection. The studies of Scholander and his co-workers (1950) would indicate that the former is more important, at least for comparisons between species. However, the majority of their data for variation in body insulation is from mammals; whether the channels for heat dissipation are the same and of equal importance for mammals *and* birds under similar environmental conditions is not clear. Snow's (1954*a*:20) analysis of variation in wing length in relation to cold temperature among the populations of *Parus major* indicates a clear trend for increased body size with colder winter temperatures that must have some adaptive significance. A study (if feasible!) of geographic variation in body insulation and heat production within a wide-ranging, resident species of bird is badly needed.

5. The phenomenon of altitudinal variation in wing length and body size within bird species should be mentioned. Moreau (1957) has presented statistical evidence for a direct relation between altitude and wing length in African populations of the *Zosterops* complex. He suggests (p. 331) that a larger wing surface (hence larger wing length) in the higher altitudes is associated with reduced air pressure. I would like to suggest that the populations in the lower altitudes are exposed to hotter, more humid climates (in terms of smaller saturation deficits for inspired air) and selection has operated for smaller-sized individuals in the lower altitudes.

6. The scheme for avian intraspecific variation in wing length (as an index to general body size) presented thus far finds—relative to body size in cooler or temperate regions—larger body sizes in the hot, dry regions and smaller body sizes in hot, humid regions. It would be naive to expect this proposed scheme to appear within all species of birds or to appear in comparisons between species restricted to different climates. Discussing such ideas for the variation in the genus *Parus*, Snow (1954*a*:23) states "Obviously at this higher systematic level the different ecological demands are of paramount importance, so that the climatic trends are likely to have been obscured by other adaptations."

The above comments on the adaptive significance of intraspecific variation in wing length and body size in bird species are, of course, conceptual and speculative.

VARIATION IN WING SHAPE

That wing shape or configuration may reflect adaptations at the intraspecific level as well as the species level is well known (Rensch, 1934; Kipp, 1936, Meise, 1938). Summarizing his evidence for Palearctic species, Rensch (1934:310) states that within a species the northern, migratory populations may have more pointed and narrower wings than their southern, resident counterparts. And, he continues, this pointed wing may be achieved by a shortening of the tenth (outermost) primary, by a shortening of the primaries behind the wing-tip, or by a lengthening of the primaries of the anterior margin of the wing. Averill (1925:354–355) discusses the relation between the reduced outermost primary and long-distance migration, and points out the prevalence of this phenomenon in the genera *Vireo* and *Hylocichla* and in some other ten-primaried oscines of North America.

Something that should receive more attention in variation studies (see Mayr and Vaurie, 1948:23) is the possibility that migration affects wing length and conflicts or interacts with expressions of climatic adaptation in general body size (as indicated by wing length). One criticism of this study of intraspecific variation in the genus *Vireo* is the absence of a more adequate measure or index for body size (for a fuller discussion of this problem see Amadon, 1943). Because of an absence of specimen weights for most species, mean wing length of the population samples has been used as an indication of body size. While there is no doubt that a larger body is accompanied by a larger wing, it is quite possible that other factors may affect wing length. Adaptation for migration may result in a lengthening or modification of the feathers of the wing-tip thereby altering the relation between body size and wing length. Until adequate series of weights (or bone measurements) are available, such comments as these must be considered as tentative.

The genus *Vireo* is well suited for an analysis of variation in wing shape both within and between species, since it includes completely migratory species, species with both migratory and resident populations, and completely resident species.

Intraspecific variation.—Comparing (Table 6) migratory and resident populations, the observation that migratory forms have more pointed wings than resident ones appears to be general for the genus. In *V. solitarius*, the populations restricted to Guatemala and Baja California (Cape San Lucas) have less-pointed wing-tips than the northern, migratory populations; this is substantiated by the agreement of several measurements testing the point. Also,

Table 6

Variation in Shape of Wing-tip in Selected Populations of Vireos[1]

Species, locality, and migration status		Difference (expressed as per cent of wing length) between longest primary and				
		2nd	5th	6th	7th	10th
*V. flavifrons**: New England	M	14	7	16	21	34
V. solitarius:						
New England	M	9	4	12	17	34
British Columbia	M	9	3	12	19	30
North Carolina	sM	7	2	10	15	30
Southern California	sM	7	2	10	16	26
Arizona	sM	7	1	9	14	25
Sonora	sM	7	1	8	15	24
Cape of Baja California	R	7	1	7	11	23
Guatemala	R	7	0	5	11	20
*V. philadelphicus**:						
New England	M	8	15	8	17	29
V. gilvus:						
New England	M	9	0	7	14	24
Cape of Baja California	R	9	0	4.5	10	21
Sonora	sM	8	0	4	13	21
*V. olivaceus**:						
British Columbia	M	7	5	13	17	26
Panama	sM	9	3	10	15	23
Brazil	R	11	0	5	8	22
V. hypochryseus:						
Western Mexico	sM(?)	18	0	1.5	4	17
V. griseus:						
New England	M	14	0	3	10	22
Central America	R	15	0	2	4	16
Cuba	R	14	0	0	3	14
V. carmioli: Costa Rica	R	14	0	4	11	20
V. atricapillus: Texas	M	14	0	2	4	16
V. huttoni:						
British Columbia	R	18	0	1.5	6	18
California	R	17	0	2	5	19
Cape of Baja California	R	18	0	1	6	18
Morelos	R	18	0	1	6	19

* Species lacking the outermost primary.

[1] This table represents an attempt to measure geographic variation in the shape ("pointed" to "blunt") of the wing-tip within some of the species of **Vireo.** The difference between the longest primary and the designated primaries (counting from outside to inside) is expressed as per cent of the mean wing length of the sample (five or more male specimens) measured. Thus a "pointed" wing-tip will have increased percentage values. Resident species or populations are indicated by "R"; migratory forms are indicated by "M" with "sM" indicating short-distance migrants for intraspecific comparisons only.

within *V. solitarius*, intermediate values for pointed wing-tip are characteristic of populations (e.g., those breeding in Arizona) having shorter migratory distances than the northern breeding populations. Exceptional to this rule, are the populations of *V. solitarius* breeding in the southern Alleghenies (*alticola* segment) and wintering on the coastal plain of the southeastern United States; these populations have more pointed wing-tips than would be expected for populations approaching resident (see Fig. 1) status.

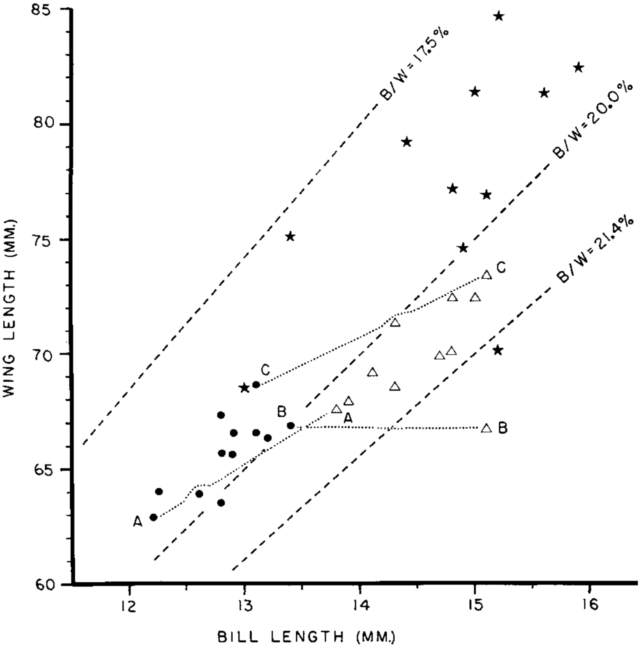

Fig. 4. Relation between wing length and bill length within *Vireo solitarius* (designated by stars), *V. gilvus* (designated by triangles), and *V. huttoni* (designated by black dots). Note the positive correlation between wing and bill length for intra- and inter-specific comparisons and the tendency for populations of *V. huttoni* and *V. gilvus* to have relatively longer bill lengths with increased wing length (see Tables 2, 3, and 4). Dashes represent lines of equal bill/wing ratios. Dotted lines connect sympatric populations of *V. huttoni* and *V. gilvus* from the same locality: A, southern British Columbia; B, Cape Region of Baja California; C, Sonora, Mexico.

Vireo griseus, *V. olivaceus*, and, less clearly, *V. gilvus* also show this intraspecific tendency for migratory populations to have more pointed wing-tips. In the species (or superspecies) *V. griseus*, the endemic, allopatric representatives resident to islands of the Caribbean have more blunted or less pointed wing-tips than the populations resident to the mainland of Central America (compare, in Table 6, wing-tip data for Cuban and Panamanian representatives of this complex). This may be due to the longer and stronger isolation of the insular forms from gene-flow as compared to mainland populations. Supporting these observations on the adaptive nature of the wing shape is the lack of variation in wing-tip in resident populations of *V. huttoni*; all these populations have (Table 6) a uniform condition in the wing-tip as shown by the consistency of four measurements.

Comparisons between species.—That migratory species have more pointed wing-tips than resident or less migratory species appears general (Table 6) for the genus and confirms the early work of Averill (1925); I have suggested elsewhere (Hamilton, 1958MS) that the loss of the functional tenth (outermost) primary might have evolved independently in each of three species groups as an adaptation for extensive migration. Comparing the nine-primaried species *V. flavifrons* and *V. philadelphicus* with their ten-primaried, sister species, respectively, *V. solitarius* and *V. gilvus*, it is seen (Table 6) that each nine-primaried species has a more pointed wing-tip than its ten-primaried sister species. Both *V. flavifrons* and *V. philadelphicus* are monotypic, completely migratory species having breeding quarters only in eastern or northeastern North America whereas *V. solitarius* and *V. gilvus* are polytypic, widespread species with breeding quarters throughout North and Middle America.

It is sometimes stated that migratory species have longer wings than resident species (see Dilger, 1956:178) with the underlying implication that a longer wing (through a lengthening of the wing-tip?) is necessary to carry a wing load twice yearly over a migration route than a wing supporting an equivalent load at a resident status. There is little indication that the migratory species of *Vireo* always have longer wings than resident species, although it is difficult to evaluate this because of the divergent effects of strong isolation on wing length in insular representatives of superspecies. *Vireo atricapillus* and *V. philadelphicus* are two completely migratory species which have shorter wing lengths in comparison to the nonmigratory populations of (say) *V. solitarius* and *V. olivaceus.* An adaptation for longer wing in response to migration could mask, as stated above, expressions of climatic adaptation of body size (as indicated by wing length). For the species of *Vireo* there is little evidence for this. Here, it is interesting to compare, for *V. solitarius*, the data of Table 6 with those of Figure 1; it will be seen that the shortest wing lengths are from resident populations of the Guatemalan region *or* the highly migratory populations of northern United States. The largest wing lengths are from populations in northwestern and central Mexico which are, respectively, short-distance migrants and resident populations. The populations of *V. gilvus* show a comparable relationship.

In summary of this section on variation in wing shape, it is evident for the genus *Vireo* that migratory species or populations have more pointed wing-tips than their resident equivalents. There appears for the genus no noticeable conflict between this rule and climatic adaptation of body size (as indicated by wing length) at the intraspecific level, with the possible exception of *V. olivaceus* (discussed above, p. 320). Since populations which are short-distance migrants have wing-tips intermediate in shape between those of conspecific, migratory and resident populations, it would appear that a pointed wing-tip represents an adaptation for strong migration. "Strong migration" is a vague term in need of clarification; whether a pointed wing is an adaptation for long-distance flight and support of wing load or an adaptation for rapid or more efficient flight remains uncertain. No tendencies for a longer wing associated with migration are present for comparisons between species.

VARIATION IN TAIL LENGTH

The meaning and evidence of intraspecific variation in tail length within avian species is not clear. Since the tail feathers are not vascularized or important for heat dissipation, it would be difficult to see a response to cold temperature in the manner of Allen's rule even if there were evidence for decreased tail lengths in the colder regions within species. There is virtually no evidence of this; in fact, Snow (1954*a*:23) has demonstrated for some species of *Parus* a marked tendency for populations in the coldest parts of a species' range to have relatively longer tails.

For intraspecific variation in tail length in the genus *Vireo*, there is (as expected) a positive correlation (see Figs. 5 and 7) between tail and wing length within all species for which sufficient data were available. Considering geographic patterns of variation, there is no evidence for a relatively longer or shorter tail being independently related to climatic conditions within the genus. In that most of these species are residents of or migrants to the lower latitudes, this observation might be expected. However, the resident populations of *V. huttoni* might be expected to show clinal tail length values in response to climatic changes. Indeed, the smallest tail length values of this species are from populations resident in southwestern British Columbia, but here, scatter diagram analysis (Fig. 5) reveals a positive relation with wing length for all the populations of the species. Also, for comparisons between species, the direct relation between tail and wing length is apparent.

In his study of intraspecific variation in *Junco*, Miller (1941:357) found a close and direct relationship between tail and wing length, and Vaurie's analysis (1953:465) of variation in the Muscicapini indicates the same. My examinations (by scatter diagram analysis as in Fig. 5) of tail and wing length data from some studies of intraspecific variation in North American species indicates, as expected, a positive relationship between tail and wing length; in these various species, aberrant values are from populations showing, clearly, the effect of strong isolation. Lunk's (1952:13) analysis of variation in tail/wing ratio within the Carolina Chickadee (*Parus carolinensis*) and the Black-capped Chickadee (*P. atricapillus*) clearly shows this positive relationship between the two characters and demonstrates a tendency for the populations with longer wings to have larger tail/wing ratios; this suggests that with a larger body size (as indicated by wing length) there may occur a relatively longer tail. Moreau (1955:336) finds the same increase in tail/wing ratio (relative tail length) with increase in wing length in the African *Zosterops* complex. Snow (1954*a*:23) presents data for intraspecific variation in relative tail length for three species of *Parus*, indicating a tendency (both within and between species) for increased relative tail length in the colder regions of the Palearctic. He states that a long tail is an adaptation to cold climate. He cites, however, only values for tail/wing ratios; scatter diagrams of his data for absolute tail length and wing length might show the tendency for relatively longer tails with increase in wing length.

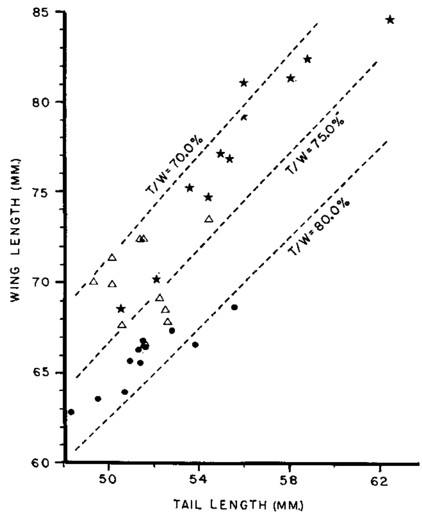

FIG. 5. Relation between wing and tail length within *V. solitarius* (designated by stars), *V. gilvus* (designated by triangles), and *V. huttoni* (designated by black dots). Note the positive relation between wing and tail (see Tables 2, 3, and 4).

This direct relationship between tail and wing length within the species of *Vireo* and other avian species is expected; with a change in body size, there is a corresponding change in tail length necessary for maintenance of body proportions and proper mobility of the organism. Also, in some cases there appears to be an allometric relation for a relatively longer tail associated with the larger body size (? in the meaning of Huxley, 1932:204–216). However, since adaptation represents a compromise between various selection forces, modifications or suspensions (such as found by Snow?) of an "allometric effect" would be expected. Thus intraspecific variation in relative tail length may be determined—in part—by variation in body size and may not represent (in lower latitudes?) the direct response of an external appendage to the selective forces of the climate.

VARIATION IN BILL LENGTH

An attempt to explain the observed variation in relative bill length (bill/wing ratio) within the species of *Vireo* in direct relation to cold temperature (Allen's rule; see Mayr, 1942:90) was not satisfactory for most species. Because migration to warmer climates for the off season is characteristic of most species or populations breeding in the high latitudes, an absence of climatic adaptation for some characters may be expected. Discussing such problems, Rensch (1952:141) has pointed out that characters changing in correlation with environmental gradients will be more pronounced in species or populations exposed to the severe winters of the higher latitudes rather than to the winters of the tropical regions. The species of *Vireo* (for which data are available) all show (see Figs. 4 and 6) the expected positive relationship between bill and wing length much the same as for tail and wing length (Fig. 5). It is not the purpose of this paper to go into a detailed discussion of variation in bill length; however, some comments on variation in relative and absolute lengths seem appropriate.

Vireo solitarius.—In this species (see Table 2), the shortest bills are found in populations resident to the Guatemalan region and from populations breeding in northern United States and migrating to Middle America for the winter. The longest bills are from populations breeding in northwestern Mexico and wintering in central Mexico. The next longest bills are from populations that winter on the coastal plain of the southeastern United States (see Fig. 1). In that these populations are probably exposed to lower winter temperatures than populations of other segments of the species (such as the resident *montanus* segment in Guatemala), a larger absolute and relative bill length here indicates a marked conflict with Allen's rule. Examining the scatter diagram (Fig. 4) for bill and wing length in this species, a direct (but not strong) relation is observed. The resident populations (*lucasanus* segment) of the Cape region of Baja California have divergent values (absolute and relative) for bill length in comparison to populations of other segments of the species.

Vireo gilvus and *V. huttoni.*—In both these species, variation in bill length (see Fig. 4 and Tables 3 and 4) is positively correlated with wing length with a tendency for the populations within each species to have relatively longer bills (larger bill/wing ratios). In examining Fig. 4, it is of interest that the population (*victoriae* segment) of *V. gilvus* from the Cape region of Baja California represents a clear departure from the pattern of variation for that species. The dotted lines in Fig. 4 connect populations from each of these two species which are taken from approximately the same locality. In each of these three examples there is a marked difference in bill and wing relation between sympatric populations of the two species. However, the populations of the two species taken from the Cape region of Baja California have approximately the same wing length (and, presumably, same body size); here, the bill lengths of the two populations are noticeably different with the population (*victoriae* segment) of *V. gilvus* showing divergence from the scatter-diagram distribution of points. The Cape of Baja California is the only locality to my knowledge where these two species are sympatric and resident throughout the year. At least for mainland areas, the habitats of *V. huttoni* (evergreen-oak) and *V. gilvus* (riparian broadleaf) are well separated, although often contiguous. Unfortunately, little is known about the habitat distribution of the vireos in this isolated region at the Cape of Baja California, and the suggestion that interspecific competition may have been responsible for the larger bill of the local population of *V. gilvus* is only speculation.

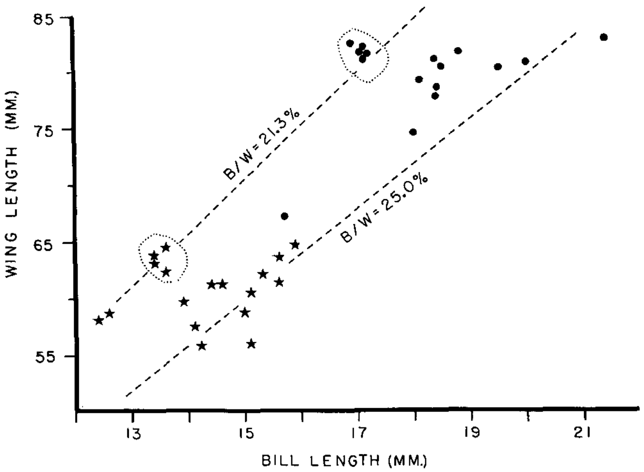

FIG. 6. Relation between wing and bill length within the semispecies *V. griseus* (first seventeen populations of Table 1 designated by stars) and the superspecies *V. olivaceus* (designated by black dots, see Table 5). Note the weak, positive correlation between wing and bill and the tendency for North American populations (enclosed by dotted lines) to have relatively smaller bill lengths.

V. griseus and *V. olivaceus.*—Scatter-diagram analysis for each of these two species or two superspecies (see Fig. 6 and Tables 1 and 5) reveals the expected (but weak) direct relation between bill and wing length except for the populations breeding in North America. The strongly isolated, insular representatives of the Caribbean area show the tendency for insular populations to have greater wing lengths and relatively longer bill lengths (see Murphy, 1938). In both species, the populations breeding in eastern and northern North America have shorter bills than would be expected for their wing lengths. Superficially, this appears as a manifestation of Allen's rule; however, these northern-breeding populations of *V. griseus* and *V. olivaceus* migrate to Central and South America, respectively, for the off season. I have no satisfactory explanation for this phenomenon. Earlier in this paper (p. 320), I discussed the unexpected (in terms of migration and climate of winter quarters) clinal increase in wing length toward the higher latitudes in *V. olivaceus.* It may be that wing length is "longer" in the higher latitudes rather than bill length is "shorter." The difficulties of interpreting appendage lengths when expressed as percentages of other appendages (such as wing length) is readily seen here (see Amadon, 1943:165).

In summary of this section, bill length is positively correlated with wing length as would be expected. Modifying this relation in *V. griseus* and *V. olivaceus* (as superspecies) is a tendency for the populations breeding in North America to have smaller relative bill lengths; since these populations are migratory, it would be difficult to interpret this condition as an action of Allen's rule. Within several species (*V. huttoni* and *V. gilvus*), there is an indication of an allometric relationship with the populations of larger wing lengths having larger relative bill lengths; the same appears to be true for comparisons between some species. For the genus *Vireo,* Allen's rule does not seem to be important as a factor in climatic adaptation.

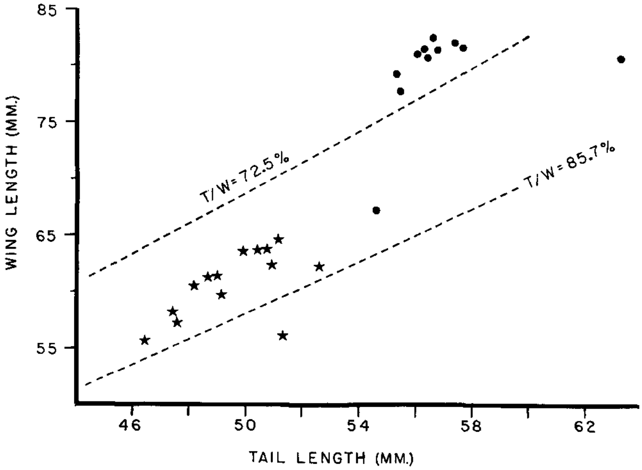

FIG. 7. Relation between wing and tail length within the semispecies *V. griseus* and the semispecies *V. olivaceus* (see Tables 1 and 5). Note the weak, positive correlation between wing and tail.

GEOGRAPHIC VARIATION IN COLOR

The characteristic pigments of vireos are melanin (gray) and lipochrome (yellow) which occur primarily in the dorsal and lateral (side and flank) feathers. An absence of pigments from the feathers of the throat and breast and/or belly and under tail coverts occurs in many species. Varying degrees of deposition of melanin and lipochrome are responsible for the coloration of the back feathers, which may vary from yellow to yellow-greenish to gray in different species. Melanin is the predominant pigment in the wing, tail, and head feathers. Species characters, such as eye-stripes, eye-rings, and wing-bars, usually are white, representing an absence of pigment, although in several species (*V. griseus* and *V. flavifrons*) the feathers of the eye-rings are yellow, showing clearly an absence of melanin in comparison to other feathers of the head.

Black coloration occurs in the crown and auricular feathers of *V. atricapillus*, a species restricted to warm, arid regions. The two species showing the most intense yellow coloration (as a character not varying geographically) are *V. carmioli* and *V. hypochryseus. Vireo carmioli* is a thicket-forager restricted to the cool, moist highlands (8,000 to 10,000 ft.) in Costa Rica and western Panama. *Vireo hypochryseus* is endemic to western and southwestern Mexico and occurs in broadleaved woodlands of the tropical deciduous vegetation zone. Brown and red pigments are rare among the species of the genus, with rufous or cinnamon coloration appearing in the feathers of *V. bairdi* on Cozumel Island.

Intraspecific variation in color. For the wide-ranging species of the genus, intensity of color or pigment deposition increases with environmental humidity in concordance with Gloger's rule. The adaptive significance of such a phenomenon is unknown. In that most *Vireo* species of North American distribution are migratory, a study of color variation in relation to humidity is hampered by a lack of knowledge of the climate of the wintering quarters of migratory populations.

In *V. solitarius*, melanin deposition in the back, rump, and wing feathers is most intense in populations of *cassinii*, *solitarius*, *alticola*, and *montanus*, which are restricted (except southern breeding populations of *cassinii* segment) to relatively humid regions throughout the year, in comparison to the "paler" segments occurring in the interior of the continent. Of the four "dark" segments, the populations of *solitarius* and *alticola* have "bluish" crown feathers which are noticeably darker than those of *cassinii* and *montanus.*

Populations of *V. solitarius* from the Cape region of Baja California (*lucasanus* segment), southwestern United States (*plumbeus* segment), and northwestern Mexico (*pinicolus* segment) have pale colorations (light melanin depositions) and are listed here in order of decreasing darkness of the back feathers. Populations of the *pinicolus* segment are the lightest in color and are restricted to northwestern and central Mexico throughout the year, an area that is the most arid of the regions in which populations of *V. solitarius* occur. Populations of the *plumbeus* segment, although wintering south to central Mexico, breed from Wyoming through the Rocky Mountains to western Mexico; thus they are not subjected to the summer aridity of northwestern Mexico (as those of the *pinicolus* segment) or to the humidity of the Pacific coastal region (as populations of *cassinii*). Populations endemic to the Cape region of Baja California (*lucasanus* segment) are resident throughout the year, and, although restricted to a climatically arid region, occur in an area of high relative humidity (in comparison to the Mexican mainland at that latitude) due to the maritime position of the Cape (Dr. C. F. Brooks, pers. comm.). Correspondingly, these populations are slightly darker than the other two "pale" segments. Populations of *V. s. repetens* of central Mexico have not been discussed because of a lack of comparative material.

This geographic pattern of variation in melanin is generally the same for other polytypic species of *Vireo* having wide, continental distributions. *Vireo gilvus*, with a geographic distribution similar to that of *V. solitarius*, has essentially the same expression of Gloger's rule except for the populations restricted to the Cape region of Baja California (*V. g. victoriae*) which are unexpectedly lighter in coloration. *Vireo olivaceus*, *V. bellii*, and *V. griseus* show little expression of Gloger's rule for melanin variation. I am not familiar with the coloration of the *pallens* segment of the *V. griseus* complex.

Yellow pigment was found in *V. solitarius*, *V. huttoni*, and *V. gilvus* to be increased in the back and lateral feathers in populations breeding in humid regions, and decreased in intensity of deposition in the populations or segments restricted to arid regions of the interior. For continental populations of *V. olivaceus*, *V. bellii*, and *V. griseus* the same was true, although less markedly for the latter two species. In *V. solitarius*, the populations breeding in eastern North America (*solitarius* and *alticola* segments) have brighter yellow flank feathers in comparison to populations of other segments (that is, *montanus* of the Guatemalan region) occurring in humid areas.

In summary, melanin and lipochrome are the predominant pigments within the genus *Vireo*. The polytypic species with wide, continental distribution show variation in color (intensity of both pigments) in agreement with Gloger's rule. At the species level, no correlation between color and the inhabitation of a particular climate is apparent. Yellow pigment appears to be a labile character in the genus, occurring within species as an expression of Gloger's rule and occurring in different species as a species character not varying geographically. The presence or absence of pigments appears to be one method that selection has utilized for species recognition characters in the external morphology. The only evidence for coloration of species or populations blending with the habitat or environmental background is the general "greenish" hue in many species which is fairly similar to that of the foliage of the species' habitats.

INTERSPECIFIC RELATIONSHIPS

Since the results of a study of species relationships in the genus *Vireo* are being prepared for publication separately, an account of the habitat preferences and possible interspecific relations of all the species will not be presented here. However, in the course of the study it was possible to postulate in several cases the species which probably gave rise to other species also now existing. *Vireo griseus* on the mainland of eastern North and Middle America appears to be the only mainland species (other than *V. olivaceus*) which has successfully colonized the islands of the Caribbean. Some of these island representatives are still fairly similar to mainland forms both in morphology and ecology; however, on some of the islands there are "divergent" representatives (e.g., *V. osburni* and *V. nanus*). These examples demonstrate clearly that populations become isolated from the parental body of populations and undergo speciation and divergence. This speciation process may or may not result in modifications of the morphology and/or general ecology. For the species of *Vireo*, the modifications (here "modification" is used in comparison to the parental species) of morphology are of two general types: first, changes in species characters, such as emphasis or loss of coloration (change in intensity), eye-rings, and wing-bars or, second and more rarely within the genus, a change in bill structure associated with change in feeding ecology.

Among the members of the genus on the mainland of North and Middle America, there is an example of the possible origin and divergence of one species from another resulting in two species which are now sympatric; since so little information is available on the factors promoting the divergence of continental species, I am offering—in the following paragraphs—a postulated origin of *V. flavifrons* from *V. solitarius* in terms of their morphological characters, ecological relations, and geographic distributions both in breeding and wintering quarters. Part of this discussion is concerned with the hypothetical results of interspecific competition; for accounts of the meanings and evidence for competition the reader is referred to Gause (1934) and the various papers of Lack (particularly 1944).

Vireo solitarius.—This species is a ten-primaried, polytypic species having a broad breeding distribution throughout forested North and Middle America; it has a wide habitat tolerance (in comparisons with other members of this genus) with the various populations utilizing broadleaved or mixed broadleaved–conifer habitats for foraging in both crown and understory layers. All populations of the various geographic segments of this species have white eye-rings, white wing-bars, and white ventral feathers. The species demonstrates geographic variation in color in accordance with Gloger's rule with populations (*pinicolus* segment) breeding in northwestern Mexico showing almost a complete absence of yellow pigment. Populations from northeastern (*solitarius* segment) and southeastern (*alticola* segment) United States have yellow flank feathers and show, in the dorsal feathers, a marked decrease anteriorly in yellow pigment resulting in an appearance of a yellow-greenish rump blending into a grayish color for the back. The other component of the back coloration, melanin, increases anteriorly giving a "bluish" color to the crown, nape, and auricular feathers. Populations of this species from other segments (e.g., *montanus* in Guatemala) restricted to humid regions fail to show such intense yellow flank and rump feathers or dark crown feathers.

Vireo flavifrons.—This species is sympatric with the "blue-headed" populations (*solitarius* and *alticola* segments) of *V. solitarius*; in their region of geographic overlap (either in breeding or wintering quarters) these sympatric species are always separated by habitat. The breeding quarters of *V. flavifrons* are restricted to the eastern United States and southeastern Canada; in the breeding quarters, this species is strictly a crown-layer forager of deciduous, broadleaved forests. This species has a more pointed wing (Table 6) than *V. solitarius*, lacks a functional tenth (outermost) primary, and has more distant winter quarters (south to Colombia and Venezuela) than any population of *V. solitarius. Vireo flavifrons* is monotypic, the various populations showing no appreciable variation in color. Yellow pigment is restricted to the anterior half of the body with bright yellow throat and breast feathers and yellow eye-rings being characteristic of the species. In the dorsal feathers, yellow pigment increases anteriorly, presenting the appearance of a yellow-greenish head and a grayish rump; the stomach, abdomen, flank, and tail feathers have no yellow pigment.

Origin of Vireo flavifrons.—Apart from the differences stressed above, the two species (considering sympatric populations) are fairly similar in size and in expression of morphological characters, such as eye-rings, wing-bars, and bill shape; also, they are similar in that both are arboreal foragers, and Saunders (1951:165) has called attention to their similarities in song. In the systematic listings of the species of the genus, the two are always placed next to one another, and Bent (1950:285–286) has commented on their close relationship. Because of certain similarities and differences in the external morphology and in the ecology (cited below), I suggest that *V. flavifrons* is derived from *V. solitarius*, and that upon coming into contact after spatial isolation there was selection on the populations of *V. flavifrons* for restriction of foraging position to mostly crown layers of broadleaved forests (ecological isolation).

During the period of spatial isolation, the *V. flavifrons* isolate would have developed a certain genetic reorganization which was sufficient to provide effective reproductive isolation. An important point of this discussion is how much ecological and behavioral (expressed as morphological and/or vocal modifications) divergence occurred in *V. flavifrons* while in isolation; from the examples of isolated representatives of the *V. griseus* complex in the Caribbean, it is apparent that some divergence (at least in plumage coloration and/or feeding ecology) may (or may not) occur while in isolation. The yellow throat and chest of *V. flavifrons* is a unique pigment pattern for the genus, and it might well function as an ethological isolating mechanism. Several aspects of this possibility should be discussed. First, since the two species are now separated by habitat, the differences in morphology (patterns of yellow pigment) between them cannot be serving now as ethological isolating mechanisms for the prevention of hybridization or competition. This, however, does not negate the possibility that at some time in the history of *V. flavifrons* such morphological characters have effectively served as isolating mechanisms.

Second, if such a character as a yellow throat in *V. flavifrons* has acted as an isolating mechanism at some time in the past, did the acquisition of such a character occur during isolation or during early interspecific contacts with *V. solitarius* as a device (see Dobzhansky, 1940:316) for prevention of hybridization? Moore (1957:325–338) has criticized the case for development of reproductive isolating mechanisms (as characteristics of the entire species) as devices for the prevention of hybridization; he points out that selection may act for differences in the zone of overlap (but for prevention of competition rather than hybridization) and that this does not account for the occurrence of the same isolating mechanisms in populations of either species away from the zone of overlap and contact; finally, he is of the opinion (p. 337) that genetic divergence during isolation "will involve differences that will also serve as isolating mechanisms." The examples of "character displacement" cited by Brown and Wilson (1956:63) for animal species having greater differences in zones of overlap would represent, as they conclude, adaptive differences brought about by interspecific competition acting only on overlapping, sympatric populations.

As stated above, *V. flavifrons* and *V. solitarius* are now almost completely separated ecologically, and it is extremely difficult to attribute both the present ecological differences and the morphological differences (yellow throat in *V. flavifrons* and yellow flank feathers in *alticola* and *solitarius* segments of *V. solitarius*) as results of interspecific competition. However, following Moore's thesis, I have assumed that upon coming into contact with *V. solitarius*, the populations of *V. flavifrons* probably had differences in external morphology (anterior shift in yellow pigment pattern resulting in yellow throat, eye-rings, and crown feathers) which were acquired while in isolation (divergence being facilitated by the small size of range of the isolate?; see below); this anterior increase in yellow pigment then would have provided characters capable of serving as effective ethological isolating mechanisms. (If, as suggested below, these two species were not ecologically separated at the time they established contact, then there also might have occurred selection pressures favoring intensification of the plumage modifications of *V. flavifrons* which, at that time, would begin to serve as isolating mechanisms; see Sibley, 1957:187.) While similar reasoning might be stated for the development of ecological differences between these two species, I shall argue in the following paragraphs that these ecological differences should be attributed to interspecific competition (more accurately: to selection pressures for reduction of competition—see Brown and Wilson, 1956:60).

It appears that for these two species of *Vireo*, selection has ultimately resulted in a separation of habitats rather than co-occupancy of the same habitat in achieving a sympatric relationship. If interspecific competition is considered a factor in this ecological divergence, there is no need to postulate that there was a complete shift from initial habitat co-occupancy to lateral separation of habitats ("spatial habitat separation"). Since populations of both species occur in broadleaved forests in the breeding quarters, at the time of initial interspecific contact there might have been selection on populations of *V. flavifrons* for restriction of foraging positions to crown layers of the habitat (from initial contact to "stratal habitat separation"). Such a vertical, "stratal" segregation of habitats might not have been sufficient in keeping individuals of the two species ecologically separated; selection for utilization of adjacent broadleaved habitats (from "stratal" to "spatial habitat separation") would have completed the ecological (and ethological?) separation of these two species. Supporting—possibly—this argument is the observation for the entire genus, that whenever sympatric species show a "stratal" segregation of habitats, the two species are each from different subgenera (and differ by the presence or absence of eye-rings and wing-bars). As discussed above (p. 313), this indicates that differences in relationships as well as habitat and/or niche requirements are necessary before two species of *Vireo* can have overlap of their respective breeding and foraging positions.

Today there is no evidence that populations of *V. flavifrons* and *V. solitarius* ever come into contact with overlapping, breeding territories in their breeding quarters in eastern United States, and, yet, the two sympatric species may occur as local (but separated) breeders inhabiting, respectively, broadleaved woodlands and mixed broadleaved–conifer woodlands (see Todd, 1940:476–478). There is some evidence that the populations of *V. flavifrons* undergo fluctuations occasionally (E. Mayr, pers. comm.). Bent (1950:286–287) discusses the shifts in "urban" populations of this species in New England, and Thornton (1951:424) has found this species breeding on the Stockton Plateau of western Texas. *Vireo flavifrons* may be an "infant" species in the process of extending its breeding distribution.

Two other observations tend to support this postulated origin of *V. flavifrons.* First, a hybrid specimen (*V. propinquus*) with characteristics of both *V. flavifrons* and *V. solitarius* is known. I have recently examined the specimen at the U.S. National Museum and agree with Ridgway (1904:167) that the specimen is intermediate in wing structure and coloration between the two species; the noticeable intermediate characters are a very small outermost (tenth) primary, and the yellow breast feathers. The presence of a hybrid individual verifies the close relationship and relatively recent separation of the two species.

Second, Lack has consistently emphasized that as a result of interspecific competition previously isolated species will develop (or increase?) differences in ecology upon coming into contact. Among the agencies furthering ecological divergence, the geographic separation of wintering quarters would appear effective as he (1944:273, 276) has shown for sympatric species occurring (and breeding) in different habitats in England. The same appears true for sympatric populations of *V. flavifrons* and *V. solitarius.* The wintering quarters of *V. flavifrons* extend from Venezuela and Colombia north to Guatemala and southern Mexico. Populations of *V. s. alticola* winter in the lowlands of southeastern United States, and populations of *V. s. solitarius* winter from the coastal plains of southern United States south through eastern Mexico to the Guatemala–Nicaragua area. In the area of overlap of winter quarters, *V. flavifrons* occurs in the lowlands and *V. s. solitarius* is restricted to the highlands. In Guatemala, *V. flavifrons* is found in the lowlands and *V. s. solitarius* occurs in the mountains above 2,000 ft. (Griscom, 1932:317–318). In El Salvador (Dickey and van Rossem, 1938:470), *V. flavifrons* again occurs in the lowlands and *V. s. solitarius* is most abundant at 3,500 ft., but occurs as high as 8,500 ft. Away from the area of overlap of winter quarters, populations of *V. s. solitarius* winter in the lowlands of eastern Mexico. Further south in Costa Rica (where *V. s. solitarius* does not occur), populations of *V. flavifrons* winter in the mountains as well as in the lowlands (Carriker, 1910:781). I have no information on the winter habitats of *V. flavifrons* in northern South America. It would appear then that *V. flavifrons* (in its divergence from the parental *V. solitarius*) has extended its wintering quarters to be geographically separated from the parental species and that populations of the two species have an altitudinal separation of habitats in the region of overlap of winter quarters; whether interspecific competition is (or has been) a factor limiting or affecting the habitat distributions of these two species in the area of overlap of wintering quarters (as well as the geographical separation of off-season distributions) can only by suggested and remains problematic.

Finally, one problem remains to be discussed concerning the postulated origin of *V. flavifrons* from *V. solitarius.* If competition has been operative in increasing the divergence of the two species, why did most of the adaptive change necessary for ecological compatibility between the two species occur in *V. flavifrons* and not *V. solitarius*?

It is probable that the separation (during the Pleistocene?; see Rand, 1948) of the isolate *V. flavifrons* occurred somewhere in the eastern United States. Of importance here might be the magnitude or size of the geographic breeding ranges of the parental species and the isolate; at the time of separation, *V. solitarius* would still have had a wide distribution of breeding populations throughout the remaining United States and Middle America. In a discussion of the evolutionary significance of gene-flow and the peripherally isolated population, Mayr (1954:160–163) suggested that gene-flow from the interior of a species' range acts to disrupt the tendency of peripheral populations to become adapted to local environments and that peripheral isolation may permit an isolate to acquire a new gene-complex adapted to its environment without being "annually disrupted by the infiltration of alien genes and gene-combinations." His theory might be the solution to the problem presented at the beginning of this paragraph. Competition, as postulated for *V. flavifrons* and *V. solitarius*, would result in the action of natural selection on competing populations of both species. However, the competing populations of *V. solitarius* would still be recipient of gene-flow from conspecific populations (away from the area of sympatry with the isolate *V. flavifrons*) thereby diluting selective changes in the genotype for adaptive divergence. This would not be the case for the relatively smaller isolate *V. flavifrons*; these populations (all or a large component of the isolate gene pool) would be more likely to develop genotypes for modification of habitat preferences (and morphological change?) in adaptive response to the selective action of interspecific competition.

This postulated example of morphological and ecological divergence of two related species may be summarized as follows: (1) Initial isolation and development of new gene-complex in the isolate *V. flavifrons.* (2) In *V. flavifrons* while in isolation, morphological divergence which effectively serves as isolating mechanisms upon coming into contact with parental *V. solitarius.* (3) As a result of interspecific competition, restriction of habitat tolerance in *V. flavifrons.* (4) As a further ecological difference, extension of winter quarters in *V. flavifrons* for geographic (and altitudinal) separation from *V. solitarius.* (5) Correlated with No. 4, selection in *V. flavifrons* for wing modification (in response to long migration) resulting in a more pointed wing and loss of the functional tenth primary.

SUMMARY

1. The subdivisions of the genus *Vireo* are briefly discussed; apparently, selection has favored occupation of separate habitats rather than habitat co-occupancy for sympatric relationships.

2. The migration patterns of the various species are delimited according to Salomonsen's 1955 classification.

3. Trends of intraspecific variation in wing length for the genus appear to be in conflict with Bergmann's rule. *Vireo solitarius*, *V. huttoni*, and *V. gilvus* have the largest mean wing lengths in populations breeding in northwestern Mexico. *V. griseus* and *V. olivaceus* have smaller wing lengths (comparing continental populations) in the humid, tropical regions. Evidence for

similar "aridity effects" (greater wing lengths in hot, arid regions and smaller wing lengths in hot, humid regions) for variation within other New World bird species is presented.

4. Speculations are made concerning the adaptive significance of such an "aridity effect."

5. For both intra- and interspecific comparisons, migratory forms have more pointed wing-tips than resident forms.

6. Intraspecific variation in tail length is positively correlated with wing length.

7. The variation in relative bill length does not accord with Allen's rule for climatic adaptation within the genus.

8. Within the wide-ranging species of *Vireo*, variation in intensity of melanin and lipochrome supports Gloger's rule.

9. The relationship between *V. flavifrons* and *V. solitarius* is analyzed; it is suggested that some of the ecological differences between the two sympatric species may be attributed to interspecific competition.

LITERATURE CITED

AMADON, D.
1943 Bird weights as an aid in taxonomy. *Wilson Bull.*, 55:164–177.
AVERILL, C. K.
1925 The outer primary in relation to migration in the ten-primaried oscines. *Auk*, 42:353–358.
BENT, A. C.
1950 Life histories of North American wagtails, shrikes, vireos, and their allies. *U.S. Nat. Mus. Bull.* no. 197:1–411.
BARTHOLOMEW, G. A., JR., AND W. R. DAWSON
1953 Respiratory water loss in some birds of the southwestern United States. *Physiol. Zool.*, 26:162–166.
BROWN, W. L., JR., AND E. O. WILSON
1956 Character displacement. *Syst. Zool.*, 5:49–64.
CARRIKER, M. A., JR.
1910 An annotated list of the birds of Costa Rica including Cocos Island. *Ann. Carnegie Mus.*, 6(2–4):314–915.
DICKEY, D. R., AND A. J. VAN ROSSEM
1938 The birds of El Salvador. *Field Mus. Nat. Hist., Zool. Ser.*, 23:1–609.
DILGER, W. C.
1956*a* Adaptive modifications and ecological isolating mechanisms in the thrush genera *Catharus* and *Hylocichla*. *Wilson Bull.*, 68:171–199.
1956*b* Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Auk*, 73:313–353.
DOBZHANSKY, T.
1940 Speciation as a stage in evolutionary divergence. *Amer. Nat.*, 74:312–321.
GAUSE, G. F.
1934 The struggle for existence. Baltimore: Williams and Wilkins.

GIBB, J.

1954 Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis*, 96: 513–543.

GRINNELL, J., AND H. S. SWARTH

1913 An account of the birds and mammals of the San Jacinto area of southern California. *Univ. Calif. Publ. Zool.*, 10:197–406.

GRISCOM, L.

1932 The distribution of bird-life in Guatemala. *Bull. Amer. Mus. Nat. Hist.*, 64:1–439.

HAWBECKER, A. C.

1948 Analysis of variation in western races of the white-breasted nuthatch. *Condor*, 50:26–39.

HINDE, R. A.

1952 The behaviour of the great tit (*Parus major*) and some other related species. E. J. Brill, Leiden, 201 pp.

HOIBERG, A. J.

1954 Breeding-bird census; oak–pine stream bottomland. *Audubon Field Notes*, 8:369.

HUXLEY, J. S.

1932 Problems of relative growth. Dial Press, New York, 276 pp.

KIPP, F.

1936 Studien über den Vogelzug in Zussamenhand mit Flügelbau und Mauserzyklus. Mitt. Vogelwelt, 35:49–80.

LACK, D.

1944 Ecological aspects of species-formation in passerine birds. *Ibis*, 86:260–286.

LAWRENCE, L.

1953 Nesting life and behaviour of the red-eyed vireo. *Canadian Field-Nat.*, 67: 47–77.

LUNK, W. A.

1952 Notes on variation in the Carolina chickadee. *Wilson Bull.*, 64:7–21.

MARSHALL, J. T., JR.

1957 Birds of pine–oak woodland in southern Arizona and adjacent Mexico. *Pac. Coast Avif.* no. 32:1–125.

MATVEJEV, S. D.

1950 The distribution of the birds of Serbia. (in Yugoslavian) Belgrade, 362 pp.

MAYR, E.

1942 Systematics and the origin of species. Columbia Univ. Press, New York, 334 pp.

1954 Change of genetic environment and evolution. Pp. 157–180, *in* Huxley, J., Ed., Evolution as a Process. George Allen Unwin Ltd., London.

1956 Geographic character gradients and climatic adaptation. *Evolution*, 10:105–108.

MAYR, E., AND C. VAURIE

1948 Evolution in the family Dicruridae (birds). *Evolution*, 2:238–265.

MEISE, W.

1938 Über parallele geographische Variation in der Vogelwelt Ostasiens. Pp. 233–248, *in Proc. Ninth Internat. Ornith. Congr.* (Rouen).

MILLER, A. H.

1931 Systematic revision and natural history of the American shrikes (Lanius). *Univ. Calif. Publ. Zool.*, 38:11–212.

1941 Speciation in the avian genus Junco. *Univ. Calif. Publ. Zool.*, 44:173–434.

MOORE, J. A.

1957 An embryologist's view of the species concept. Pp. 325–338, *in* Mayr, E., Ed., The Species Problem. *Amer. Assoc. Adv. Sci. Publ.* no. 50.

MOORE, R. T.

1938 Unusual birds and extensions of ranges in Sonora, Sinaloa and Chihuahua, Mexico. *Condor*, 40:23–28.

MOREAU, R. E.

1957 Variation in the western Zosteropidae (Aves). *Bull. Brit. Mus. (Nat. Hist.), Zool.*, 4:311–433.

MURPHY, R. C.

1938 The need for insular exploration as illustrated by birds. *Science*, 88:533–539.

PITELKA, F. A.

1951 Speciation and ecologic distribution in American jays of the genus *Aphelcoma*. *Univ. Calif. Publ. Zool.*, 50:195–464.

PITELKA, F. A., AND E. J. KOESTNER

1942 Breeding behavior of Bell's vireo in Illinois. *Wilson Bull.*, 54:97–106.

RAND, A. L.

1948 Glaciation, an isolating factor in speciation. *Evolution*, 2:314–321.

RENSCH, B.

1934 Einwirkung des Klimas bei der Ausprägung von Vogelrassen, mit besonderer Berücksichtigung der Flügelform und der Eizahl. Pp. 285–311. *In, Proc. Eighth Internat. Ornith. Congr.* (Oxford).

1952 Klima und Artbildung. *Geol. Rundschau*, 40:137–152.

RIDGWAY, R.

1904 The birds of North and Middle America. *U.S. Nat. Mus. Bull.*, 50, pt. 3.

RIPLEY, S. D.

1950 Birds from Nepal, 1947–1949. *Jour. Bombay Nat. Hist. Soc.*, 49:355–417.

SALOMONSEN, F.

1955 The evolutionary significance of bird-migration. *Dan. Biol. Medd.*, 22(6) :1–62.

SALT, G. W.

1952 The relation of metabolism to climate and distribution in three finches of the genus *Carpodacus*. *Ecol. Monogr.*, 22:121–152.

SAUNDERS, A. A.

1951 A guide to bird songs. 2nd ed. Garden City, New York: Doubleday and Company, Inc.

SCHOLANDER, P. F.

1955 Evolution of climatic adaptation in homeotherms. *Evolution*, 9:15–26.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, AND L. IRVING

1950 Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.*, 99:259–271.

SCHOLANDER, P. F., V. WALTERS, R. HOCK, AND L. IRVING

1950 Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.*, 99:225–236.

SNOW, D. W.

1952 A contribution to the ornithology of north-west Africa. *Ibis*, 94:473–498.

1954*a* Trends in geographic variation in Palaearctic members of the genus *Parus*. *Evolution*, 8:19–28.

1954*b* The habitats of the Eurasian tits (Parus spp.). *Ibis*, 96:565–585.

THORNTON, W. A.
1951 Ecological distribution of the birds of the Stockton Plateau in northern Terrell County, Texas. *Texas Jour. Sci.*, 3:413–430.
TODD, W. E. C.
1940 Birds of western Pennsylvania. Pittsburgh: University of Pittsburgh Press.
VAURIE, C.
1953 A generic revision of flycatchers of the tribe Muscicapini. *Bull. Amer. Mus. Nat. Hist.*, 100:457–537.
WALLGREN, H.
1954 Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. *Acta Zool. Fennica*, 84:1–110.
ZIMMER, J. T.
1941 Studies of Peruvian birds. The genus *Vireo*. *Amer. Mus. Nov.*, 1127:1–20.

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY, CAMBRIDGE 38, MASSACHUSETTS, JANUARY 30, 1958