SPECIES RELATIONSHIPS AND ADAPTATIONS FOR SYMPATRY IN THE AVIAN GENUS VIREO

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INTRODUCTION

This paper reviews species relationships within the New World avian genus *Vireo* and draws some inferences on the origin of sympatry among members of the group. It is presumed that the present-day distribution, habitat ecology, and external morphology of these species might offer some information relating to the evolutionary history of the genus. Although species of vireos are well known to American bird systematists, little attention has been directed to the genus as such. It is hoped that the present report will serve as an outline to the numerous biological problems that are unresolved for this group, and that it will encourage others to use the approach of comparative systematics in the study of subgeneric affinities.

Specifically, this paper examines the following topics about the genus *Vireo*: (a) the distribution of species-specific characters of the external morphology, habitat preference, and foraging ecology throughout the several subdivisions of the genus, and the bearing of these data on the delimitation of subgenera and species groups; (b) the factors which may be responsible for the degree to which isolates or species have diverged from parental stocks while in allopatry; and (c) the manifested adaptations, presumably acquired in isolation, whereby the species can avoid competition and thus attain high degrees of sympatry. I have also used the apparent relationships in the genus *Vireo* as a point of departure for theorizing about the formation of species-specific characters and the development of sympatry. In consideration of the latter topic, it was found particularly useful to compare affinities in *Vireo* with those in the titmouse genus *Parus*; the papers of Hinde (1952), Gibb (1954), Snow (1954), and Dixon (1961) have been consulted especially concerning adaptation in the latter genus. I have already reported on trends of intraspecific variation for the widely distributed species of *Vireo* (Hamilton, 1958). That information will not be duplicated here except as it relates to the general problem of adaptation and divergence of members of the genus.

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METHODOLOGY, TERMINOLOGY, AND THEORIES

The conclusions of this paper are drawn for the most part from qualitative evidence. An effort is made to get at the causal basis of the species-specific characters of members of the genus *Vireo*, and constant reference is made to the hypothetical results of intraspecific, interspecific, and environmental selection pressures. An attempt is also made to emphasize the importance of phylogenetic divergence and zoogeographic source as factors influencing the kind of interspecific situation that occurs when congeners come in contact geographically and develop sympatry.

The following comments, definitions, and theories may prove useful in understanding and evaluating the several conclusions made later in the paper:

Allopatry and sympatry.—These two terms are used to describe, respectively, whether or not the breeding distributions of any two congeners are geographically separated (Mayr, 1942:148–149). Discussing the problem of sympatric species whose respective populations are in locally separated habitats, Cain (1953; 1954:91–93) suggested that the expression "genetical sympatry" be used for congeners which live either in contiguous habitats or in the same habitat. In this case, they have the opportunity to interbreed and, if they fail to do so, may be considered as truly sympatric. By his reasoning, ecological and geographic replacement are only two aspects of allopatry. Mayr (personal communication), however, was careful to use the terms allopatry and sympatry (Poulton, 1903) only for purposes of examining the possibility of geographic replacement or overlap of breeding distributions of congeners. In view of the wide acceptance of these two terms, both in zoology and botany (see Stebbins' comments, 1950: 35), I here leave them in the original meaning and adopt other terms for describing the biological relations of congeners whose distributions overlap geographically.

Habitat separation and habitat co-occupancy.—Much of the following discussion is based on whether or not sympatric species live side by side during the breeding season. From an empirical point of view, populations of sympatric species are usually either in different habitats or overlap within a common habitat. Thus, for describing the habitat relations of pairs of sympatric species, the expression "habitat separation" denotes spatial separation of their three-dimensional territories, whereas "habitat co-occupancy" denotes spatial overlapping. The usefulness of these two terms may be questioned, but for the present discussion they seem adequate for comparisons of sympatry within genera whose members in pair-bond tend to conduct the majority of their biological activities within the defended territory. Examples of such genera are *Vireo*, *Parus*, *Empidonax*, *Carduelis*, and many others whose members establish and defend breeding territories which encompass most courtship, nesting, and foraging activities (see Mayr, 1935: Nice, 1941; Armstrong, 1947; Hinde, 1956).

The terms habitat separation and co-occupancy refer to problems of ethology as well as to problems of space utilization, niche requirements, and foraging zones. They are here used deliberately for a less exclusive meaning than that which is usually connoted by use of the approximately equivalent terms of ecological segregation and co-existence. For example, sympatric species co-occupying the same habitat may or may not have co-extensive territories; the important point here is that there be at least some common zone of the habitat where they tend to occur side by side.

Development of sympatry.—Continuing the empirical approach of the preceding paragraph, when reproductively isolated congeners come in geographic contact and develop sympatry, selection pressures for the avoidance of interspecific strife may operate in a variety of ways which result in one or more of the following interspecific territorial situations: (a) territorial overlap—overlapping utilization of the same habitat; (b) territorial exclusion—occupation of the same habitat via mutual territorial exclusion; and (c) territorial separation—occupation of different, but necessarily contiguous, zones of the same habitat; or occupation of topographically separated habitats which may or may not be contiguous. Intermediate situations exist, and this is necessarily an oversimplification of conditions manifested in nature. Territorial overlap represents co-existence or habitat co-occupancy, and territorial exclusion and separation are here considered to be alternate ways that natural selection can operate for spatial isolation or habitat separation during the breeding season.

These observations are common knowledge to biologists, and Lack (1947) and many others have often pointed out that there are a variety of ways that natural selection can operate for ecological compatibility between congeners in sympatry. Our task now is (1) to inquire how ethological compatibility is achieved in sympatric situations and (2) to determine why selection operates in one pair of sympatric species for adaptations leading to territorial overlap but operates differently in another pair for territorial exclusion. On general theoretical grounds, we would expect biologically similar, potentially competing species initially to meet in sympatry in a situation not unlike that of territorial exclusion, and, then, in some cases to proceed in time to situations such as those of territorial overlap or separation. It is obvious that environmental and historical factors "route" the direction natural selection operates in these cases.

Biological isolating mechanism.—This widely used expression refers to any adaptation which directly or indirectly functions for the reproductive isolation of one species from another (Dobzhansky, 1937, 1951; Mayr, 1942, 1948). A part of the following discussion deals with the origin of ecological and ethological isolating mechanisms as species-specific characters or adaptations, and it must be kept in mind that we are here examining by inference two problems: one of cause or origin, and one of function. Strictly speaking, the two concepts are inseparable. Nevertheless, it seems useful to treat isolating mechanisms as ordinary adaptations, and to evaluate them abstractly in terms of ethology and ecology. In regard to this, it is useful to remember that the function or functions of an adaptation serving as an isolating mechanism for prevention of gene exchange between congeners need not be the same as the functions of that adaptation during its origin.

Thicket foraging and arboreal foraging.—These are terms which I use to describe the ways vireos exploit their breeding season habitats. They were first proposed by Grinnell and Swarth (1913:292) in a discussion of the habitat relations of the five species of vireos sympatric in the San Jacinto Mountains of southern California. For the present paper, thicket foraging refers to the tendency to utilize for territories either thickets or the shrub layers of woodlands, and arboreal foraging refers to the tendency to utilize for territories either the crown layer or the crown-to-shrub body of a woodland habitat. Whether arboreal foragers tend to have wider habitat tolerances than thicket foragers is uncertain. In terms of ecological amplitudes, however, the two categories are not equivalent, and, with strict usage, difficulty is encountered for interspecific comparisons. For example, in the deciduous woodlands of Massachusetts, populations of the Red-eyed Vireo (*V. olivaceus*) spend a majority of their daily foraging time in the crown layers and spend lesser, but significant, periods of time in the understory (personal observation). In the deciduous woodlands of piedmont Virginia, the Yellow-throated Vireo (*V. flavifrons*) spends virtually all of its time foraging in the crown layers, even though its territories may be situated in woodlands having a well developed shrub layer (personal observation). I consider both of these species as arboreal foragers, with the latter demonstrating a reduced ecological amplitude in comparison to the former. Whether these foraging characteristics are species-specific characters, or only local adjustments of populations to their immediate biotic environments, is a matter that will be resolved only when more information is available. For the present, I assume that distinctions between arboreal and thicket foraging are valid and useful for examination of taxonomic affinity within the genus *Vireo*.

GENERAL DESCRIPTION OF THE GENUS

The genus *Vireo* is composed of 18 to 21 species or superspecies having temperate and tropical distributions throughout the New World. So far as known, none of these species is endemic to South America, although representatives of two polytypic species or superspecies have breeding populations restricted to that continent. Most of the vireo species are essentially similar in external morphology (for example, shape of bill and plumage patterns such as wing-bars, eye-rings, eye-stripes, and other external characters due to the presence of absence of pigment), and taxonomists are now in general agreement that they represent a group of related species deserving a single generic designation. Similar to many other passerine groups, the characteristic feather pigments of vireos are lipochrome and melanin. The two pigments are deposited in the feathers in varying degrees of composition and/or intensity to give the general gray to yellow coloration of the species.

Continental members of the genus are relatively similar both in basic habitat preferences and in mode of food gathering. The specialized species of *Vireo* are endemic to certain islands of the Greater Antilles and probably owe their origin to consecutive invasions by the *V. griseus* complex from the American mainland. Two of these endemics, the shrike-like *V. osburni* on Jamaica, and the flycatcher-like *V. nanus* on Hispaniola, demonstrate noticeable morphological modifications and have feeding ecologies atypical for the genus. Excepting the *V. griseus* complex, the *V. olivaceus* complex seems to be the only other mainland vireo to reach the West Indies and establish breeding populations.

The genus appears to be most successful in temperate regions of México and the southwestern United States, where, in some local regions, as many as five species may be sympatric during the breeding season. Occurring primarily in evergreen oak habitats of México and western United States, the Hutton Vireo (*V. huttoni*) is a sedentary species. The populations of the other nine species of *Vireo* in North America are mostly migratory, with their wintering quarters occurring in Middle or South America. Of the migratory species, four are monotypic and have relatively restricted winter distributions (*V. vicinior*, *V. flavifrons*, *V. atricapillus*, and *V. philadelphicus*). The other five are widespread, polytypic species (*V. griseus*, *V. bellii*, *V. solitarius*, *V. olivaceus*, and *V. gilvus*), having migratory as well as sedentary populations, with the latter occurring in Middle or South America.

In general, members of *Vireo* are monogamous, monomorphic, seasonally pair-forming species which normally glean broadleaved foliage for insects. Most of the continental species establish breeding territories in broadleaved, deciduous vegetation, and broadleaved woodland is considered to be the typical and historical habitat of the genus. The Solitary Vireo (*V. solitarius*) appears to be the only vireo sufficiently wide in habitat tolerance to utilize coniferous vegetation, and even in this species the breeding territories are usually in broadleaved or mixed broadleaf-conifer habitats (Bent, 1950).

For North American vireos, pair formation occurs at the beginning of the breeding season on the male's previously occupied and defended territory. It is presumed that all migratory races and species of vireos break the pair bond at the end of the breeding season. From the summaries of Bent (1950), it appears that in the majority of the North American species both sexes participate in nest construction, incubation, and feeding of young. However, Skutch (1960:40–42) has noted that the amount of assistance by the male varies among different species. After the breeding season, family groups disperse and, in migratory populations, depart for the wintering area.

Data on the behavior and breeding biologies of species of vireos.—There are few detailed accounts of the breeding biologies and ecological relations of vireo species. To date, the most extensive deal with the Bell Vireo, *V. bellii* (Nolan, 1960; Pitelka and Koestner, 1942; Nice, 1929), the Red-eyed Vireo (Lawrence, 1953; Southern, 1958), the Black-capped Vireo, *V. atricapillus* (Graber, MS; Bunker, 1910), and the Latimer Vireo, *V. latimeri* (Spaulding, 1937). For background information on the biology of these and other vireo species, the reader is directed to the references here cited, as well as to writings of Bent (1950) and Skutch (1960). It is noteworthy that in the literature on vireos there is a striking absence of information on the biology and ecology of such common and accessible North American species as the Hutton Vireo, the Solitary Vireo, the Yellow-throated Vireo, and the White-eyed Vireo (*V. griseus*).

SUBGENERIC RELATIONSHIPS AND SPECIES GROUPS

It is clear from basic similarities in ecology and external plumage characters that the vireos constitute a natural genus. With exception of allopatric complexes, both on the American mainland and in the West Indies, the majority of species boundaries in the genus are clear-cut by the test of sympatry. Following the warning of Miller (1955*b*: 2–10) and others (for example, see Selander and Giller, 1961:81), I now designate (*contr.* Hamilton, 1958:310–311) as separate species the allopatric subdivisions of the superspecies *V. griseus*, *V. olivaceus*, and *V. gilvus*. This is to emphasize the possibility of incipient speciation of continental isolates. In the case of the allopatric, insular segments of the *V. griseus* complex in the West Indies, I reduce to subspecific rank those segments that are essentially similar in plumage appearance and bill shape to members of *V. griseus* on the mainland. I realize that others may differ with me on these points. In either case, however, we are dealing—until more information is available—with problematic, allopatric situations.

The main problem of classification for this study was the determination of subdivisions of the genus and groups of "closely related" species. Comparing table 1 and table 2 for the generic distribution of species-specific characters, the members of the genus *Vireo* seem to divide naturally into two major groupings or subgenera: one group (*Vireo*) whose members possess eye-rings and wing-bars, and, except in three species, have thicket foraging preferences; and another group (*Vireosylva*) whose members all exhibit an absence of eye-rings and wing-bars, but possess eye-stripes and have arboreal foraging tendencies.

Relying on differences in morphological characters for subgeneric limits, and placing emphasis on ecological characters for species groups, a sequence of species groups is proposed for members of the genus *Vireo* (see opposite page).

This outline of the subgenera and species groups of *Vireo* summarizes the geographic variation, in terms of race formation, and also shows the migrational tendencies of individual members of the genus. Apart from rearranging the sequence of species to form two subgenera and four species groups, this listing represents no major departure from previous classifications, and the reader is referred to Hellmayr (1935) for detailed accounts of the distribution and taxonomic synonymies of the listed species.

As proposed by Salomonsen (1955), "allohiemy" refers to a migratory pattern which results in geographic separation of the wintering quarters of various populations or races of a species. "Synhiemy," he states, refers to a trend of migration which results in a common or "united" wintering quarters for the various subdivisions of a species. Salomonsen reasons that an allohiemic species will have reduced intraspecific gene-exchange as a result of both seasonal and geographic fragmentation of its geographic distributions. From this, he theorizes that allohiemic migration patterns facilitate the process of race formation.

SUBGENUS *Vireo*

(Eye-rings and wing-bars present)

griseus group

(Basically thicket foragers)

	Species and breeding distribution	Variation	Dispersal status
ss	*V. griseus.* Eastern United States, eastern México (to Veracruz), and West Indies. Includes segments *crassirostris, gundlachii, modestus,* and *caribaeus*	Polytypic	Allohiemic migration; resident in lower latitudes
	V. pallens. Coastal Middle America. Includes *ochraceus* segment?	?	Resident
	V. bellii. Southwestern United States east to Mississippi valley and south to eastern México	Polytypic	Allohiemic migration
	V. vicinior. Southwestern United States	Monotypic	Short distance migrant
	V. nelsoni. Southwestern México	Monotypic	Resident
	V. bairdi. Cozumel Island	Monotypic	Resident
	V. carmioli. Costa Rica and Panamá	Monotypic	Resident
	V. nanus. Hispaniola	Monotypic	Resident
	V. latimeri. Puerto Rica	Monotypic	Resident
	V. osburni. Jamaica	Monotypic	Resident

solitarius group

(Basically arboreal foragers)

Species and breeding distribution	Variation	Dispersal status
V. solitarius. Montane North Middle America	Polytypic	Allohiemic migration
V. flavifrons. Lowlands of eastern North America	Monotypic	Synhiemic (?) migration
V. atricapillus. Isolated foothills of southern Great Plains and northern México	Monotypic	Synhiemic (?) migration
V. huttoni. Western North America (Pacific mountain ranges) and mountains of México and Guatemala	Polytypic	Resident

Subgenus *Vireosylva*

(Eye-rings and wing-bars absent)

olivaceus group

(Basically lowland arboreal foragers)

	Species and breeding distribution	Variation	Dispersal status
ss	*V. olivaceus.* North America, mostly absent from southwestern United States	Polytypic	Allohiemic migration
	V. flavoviridis. Middle and South America	Polytypic	Allohiemic migration; some segments resident
	V. altiloquus. West Indies, includes *magister* segments	Polytypic	Migratory (pattern ?) *magister* segment resident
	V. hypochryseus. Pacific slopes of western México	Polytypic(?)	Migratory (?)

gilvus group

(Basically montane arboreal foragers)

	Species and breeding distribution	Variation	Dispersal status
ss	*V. gilvus.* North America south to northern and western México	Polytypic	Allohiemic migration
	V. leucophrys. Southern México south to South America	Polytypic	Resident (?)
	V. philadelphicus. Eastern North America	Monotypic	Synhiemic (?) migration

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Superspecies (ss) are denoted by brackets.

The validity of including certain species in particular species groups is subject to debate. For example, the Hutton Vireo is placed in the *solitarius* species group chiefly because it is an arboreal forager. However, apart from this so-called ecological character and the presence of eye-rings and wing-bars, the species seems not too closely related to the other members of the species group. Further study of this sedentary species might reveal characters indicating that it should be placed in a separate species group. Although the Black-capped Vireo is a thicket forager, I place this species in the *solitarius* group—a group which was designated previously as "basically arboreal foragers." I rationalize such a seeming contradiction in my methodology in the following manner: Breeding in thickets of foothills in the Great Plains, the Black-capped Vireo appears to be a smaller, allopatric "version" of the Solitary Vireo that has been "subjected" to selection pressures for intensification of head color from gray to black. If an isolate of the Solitary Vireo originally differentiated in the habitat and region that now is characteristic of the Black-capped Vireo, that isolate would necessarily have had to adapt to an environment lacking a crown layer. That is, the nature of the habitat being exploited would be associated with selection, or would "route" the operation of selection, for reduced ecologic amplitude in the ancestors of the Black-capped Vireo.

Incidentally, Bond (1956:137) has noted the close relation of *Neochloe brevipennis* to *Vireo* and has suggested that it be placed in the latter genus. This vireonid species of eastern and southern México (Rowley and Orr, 1960) is clearly allied to the genus *Vireo* on the basis of general plumage appearance and bill structure. However, since the arrangement of its plumage patterns is markedly different from that of *Vireo*, we should perhaps wait for more information on its breeding biology and vocalizations before assigning it to *Vireo*.

ISOLATE AND POPULATION DIVERGENCE

When one compares the effects of migratory pattern on race formation in the continental species of *Vireo*, it seems evident that allohiemic migration and disjunct distributions of local breeding populations are factors which facilitate the splitting of species into races and enhance the adaptation of local populations to their particular environments.

If we contrast, for example, the differences achieved by the various races of the Solitary Vireo occurring throughout North and Middle America with the differences attained by the various populations of the Red-eyed Vireo occurring throughout the same geographic area, it is quite clear that the highly disjunct, montane segments of the former species are allohiemic and exhibit a far greater range of differences in mean values for wing length, bill length, tail length, and in coloration (see Hamilton, 1958). Thus, the reduction of morphologic divergence in the North American segments of the Red-eyed Vireo, which occur in a relatively uniform and consistent summer environment and have almost continuous breeding distributions in mesic woodlands of the Atlantic coastal lowlands, may indicate that continuity of breeding territories promotes a relatively high degree of gene-exchange and suppresses or holds down ecogeographic adaptation.

Related, possibly, to this conclusion is the problem of why the Black-capped Vireo, having disjunct breeding distributions in the southern Great Plains and northern México, has failed to differentiate into races. Moore's finding (1938) of what appears to be a wintering area for this species in Sinaloa, México, may mean that all or a large number of the populations of this species are united during the winter. If this is true, then this species may have a relatively high degree of intraspecific gene-exchange, which would, by Salomonsen's thesis, hold down tendencies for race formation in the species. This assumes that the habit of *Ortstreue,* or homing of individuals to the locality of their youth, is not strongly developed in this species. However, another possible explanation is that this species has only recently differentiated, that it is now exploiting throughout its distribution essentially the same ecological niche for the breeding season, and that selection pressures are not yet sufficiently differential for ecogeographic variation within the species.

These suppressions of adaptive divergences at the local population or isolate level might conceivably be caused by annual disruptions of the local genotypes by alien genes (influxing from dispersing offspring) adapted to other environments—disruptions which would swamp or hold down the tendencies of local populations to adapt to their respective biotic environments (see Mayr, 1954). While such a discussion as this rests, unfortunately, completely on inferences about gene-flow and panmixia, these conclusions are consistent with present-day knowledge of population genetics, and my ideas presented here stem essentially from the writings of Timofeeff-Ressovsky (1940), who clearly realized that territorial fragmentations or disjunct breeding distributions work against gene-exchange and thereby enhance population divergence or race formation.

An evolutionary factor operating at the population level in opposition to the swamping influence of panmixia or increased gene-exchange is that of isolation, and the effects of this factor are prominent when the striking radiation of the *griseus* species group in the West Indies is examined (see tables 1 and 2).

TABLE 1

DISTRIBUTION OF SPECIES CHARACTERS WITHIN THE GENUS *Vireo*

	Species characters:					
Species and common name	Wing-bars	Eye-rings	Eye-stripes	Functional 10th primary	Marked yellow throat	Thicket arboreal forager
Subgenus *Vireo*						
griseus group						
V. griseus. White-eyed Vireo	+	+	—	+	—	T
V. pallens. Mangrove Vireo	+	+	—	+	—	T
V. bellii. Bell Vireo	+	+	—	+	—	T
V. vicinior. Gray Vireo.	—	+	—	+	—	T
V. nelsoni. Dwarf Vireo	+	+	—	+	—	T ?
V. bairdi. Cozumel Vireo	+	+	—	+	—	T
V. carmioli. Yellow-winged Vireo	+	+	—	+	—	A ?
V. nanus. Lawrence Vireo	+	+	—	+	—	T
V. latimeri. Latimer Vireo	+	+	—	+	—	T
V. osburni. Osburn Vireo	—	+	—	+	—	T
solitarius group						
V. solitarius. Solitary Vireo	+	+	—	+	—	A
V. flavifrons. Yellow-throated Vireo	+	+	—	—	+	A
V. atricapillus. Black-capped Vireo	+	+	—	+	—	T
V. huttoni. Hutton Vireo	+	+	—	+	—	A
Subgenus *Vireosylva*						
olivaceus group						
V. olivaceus. Red-eyed Vireo	—	—	+	—	—	A
V. flavoviridis. Yellow-green Vireo	—	—	+	—	—	A
V. altiloquus. Black-whiskered Vireo	—	—	+	—	—	A
V. hypochryseus. Golden Vireo	—	—	+	+	—	A
gilvus group						
V. gilvus. Warbling Vireo	—	—	+	+	—	A
V. leucophrys. Brown-capped Vireo	—	—	+	+	—	A
V. philadelphicus. Philadelphia Vireo	—	—	+	—	—	A

TABLE 2

SYNOPSIS OF THE HABITAT PREFERENCES OF SPECIES OF *Vireo* (FOR BREEDING SEASONS ONLY)

griseus group (mostly thicket foragers):

- *V. griseus* and *V. pallens*
  Broadleaved, mesic or riparian thickets of lowlands (Bent, 1951). In Central America, *pallens* segments occur in coastal mangroves, according to Part II of the Mexican check-list (Pacific Coast Avifauna, 1957).
- *V. bellii*
  Thickets or scrub: normally low, broadleaved thickets of uplands or riparian lowlands (Pitelka and Koestner, 1942; Nolan, 1960).
- *V. vicinior*
  Arid thickets or open scrub: occurs in sagebrush and chaparral in southern California (Miller, 1951).
- *V. carmioli*
  Uncertain: Dr. A. Wetmore (personal communication) has observed this species in the highlands of Panamá foraging arboreally in the crown layers of forests. Carriker (1910), writing of this species in Costa Rica (6000 to 10,000 ft.), refers to it as occurring in shrub layers but cites no details.
- *V. bairdi* (wren-like?)
  Broadleaved thickets and shrubs of Cozumel Island (Paynter, 1955).
- *V. latimeri* (wren-like?)
  Low thickets and scrub vegetation of arid coastal plains of southern Puerto Rico (Spaulding, 1937; Bond, 1947).
- *V. nanus* (flycatcher-like)
  Low thickets (open, not closed?) of coastal lowlands of Hispaniola.
- *V. osburni* (shrike-like)
  Humid forests of highlands and foothills of Jamaica (most common in the Blue Mountains region; Bond, 1947).

solitarius group (except for *V. atricapillus*, arboreal foragers):

- *V. solitarius*
  Mostly montane broadleaved or mixed conifer-broadleaf habitats. Arboreal foraging in both crown and shrub layers (otherwise in the Cape Region of Baja California?; see Grinnell, 1928).
- *V. flavifrons*
  Lowland broadleaved woodlands; mostly a forager of crown layer foliage (personal observation).
- *V. huttoni*
  Woodlands of broadleaved, evergreen oak. Arboreal foraging in both crown and understory (Marshall, 1957). Mostly a montane representative in México and Guatemala.
- *V. atricapillus*
  Low scrub or dense broadleaved thickets of isolated foothills or plateaus of southern Great Plains region. In the mesa region of north-central Texas (Nolan County), occurs in mesic thickets of upper canyons (personal observation).

olivaceus group (arboreal foragers):

- *V. olivaceus* and *V. flavoviridis*
  Broadleaved, mesic or riparian woodlands of continental lowlands. In eastern United States, mostly crown-layer foragers. South American populations seem to have foraging habits similar to those of their northern counterparts (A. H. Miller, personal communication).
- *V. altiloquus*
  Coastal mangroves and broadleaved woodlands of the Carribean lowlands; crown to shrub layer foraging.
- *V. hypochryseus*
  Riparian, broadleaved habitats of tropical deciduous woodlands of lowlands and foothills of of western México (K. L. Dixon, personal communication).

gilvus group (arboreal foragers):
  V. gilvus and *V. leucophrys*
    Generally inhabitants of riparian, broadleaved woodlands throughout North, Middle, and South America. Usually occur in montane habitats in Middle and South America.
  V. philadelphicus
    Broadleaved woodlands and woodland edges of eastern North America.

Another evolutionary factor, also well known, but generally not discussed in systematic studies, is simply the geographic size of the isolate. The size of an isolate is very often inversely associated with the degree of divergence that the isolated gene pool undergoes while in isolation. Here, the size and divergence of the isolate is compared with that of the parental species or body of populations. For example, if the species-specific characters of the *griseus* group of vireos are compared, it will be noted that the species on the continent, having far greater geographical distributions, exhibit lesser amounts of biologic divergence than the endemic, *griseus*-derived members restricted to single islands of the Greater Antilles. Some of these small insular species demonstrate biologies atypical for the genus. The same conclusion, but to a lesser degree, seems valid when comparisons are made between continental members of the *griseus* group. The two most widespread members of this species group are the White-eyed Vireo and the Bell Vireo, which, although sympatric throughout much of south-central United States, have equivalent morphologies and basic similarities in foraging ecologies and habitat preferences. In contrast, monotypic members of this species group show slight departures from the "*griseus*" character and have noticeably smaller breeding distributions. This is true of the Dwarf Vireo (*V. nelsoni*) and of the desert-dwelling Gray Vireo (*V. vicinior*), the latter having lost most of the yellow pigment and one wing-bar (tables 1 and 2).

The meaning of the phenomenon of enhanced divergence of small isolates is not certain. It may mean that relatively small isolates have stronger or more effective extrinsic isolation than larger isolates which might arise as a result of continental fragmentation of what was previously a widely distributed species. In this case, the inverse association between divergence and size of the isolate would seem to be a secondary expression of effectiveness of isolation. Another possibility, and the one I favor, is that the gene-pool of a small isolate has a more favorable situation for adjusting to its own biotic environment since the diversity of environments to which its populations must adjust will be reduced. The adjustment to the diversity of environments within the isolate will, of course, be mediated via gene exchange. One can deduce from this that small isolates of relatively constant, tropical environments will have more favorable situations for divergence than isolates of equal or larger sizes occurring in more seasonally varying climates of the northern latitudes (see Dobzhansky, 1950).

It is important to note here that the logical extenuation of the above hypothesis leads to the evolutionary significance of the local, isolated population or small isolate, and the possible operation of the so-called Sewall Wright "effect." Whether or not random-fixation of genes as a result of fluctuations in population size is of evolutionary importance is a matter of considerable interest. However, following current theories on population genetics (see Sheppard, 1958; White, 1959; and Stone, Guest, and Wilson, 1960), populations or isolates of restricted size are expected to adjust to their biotic environments because of the operation of a variety of factors facilitating the establishment of new gene complexes—for example, freedom from swamping from parental populations or species; freedom to adjust to an environment differing from that of the parental stock; freedom to adapt to a new environment rather than to a diversity of many new environments interconnected by intra-isolate gene-exchange; and/or, if established by founder populations, representing an atypical sample of the parental species' gene-pool, freedom to adapt to the new environment starting with a new genetic background (Mayr, 1942, 1954; Carson, 1959).

In brief, for the genus *Vireo*, speciation by fragmentation of continental distributions, like the eastern and western divisions for *V. griseus* and *V. bellii* which now overlap geographically in south-central United States, seems to have resulted in species relatively similar in general biologies when compared to the results of speciation by peripheral isolation (as, for example, the cinnamon-colored, wren-like *V. bairdi* of Cozumel Island off Quintana Roo; see Paynter, 1955), or, perhaps, by establishment of founder populations (the aberrant, flycatcher-like *V. nanus* of Hispaniola?).

NOTES ON TRENDS OF SPECIATION AND ADAPTATION IN *VIREO*

The following comments are deduced primarily from the data on the ecological and external morphological characters of members of the genus (tables 1, 2). From this, a diphyletic history is postulated for the contemporary members of *Vireo*, with the subgenera *Vireo* and *Vireosylva* representing the two major evolutionary lines. It is further suggested that each line has divided into two fragmenting complexes or species groups. These hypothetical relationships are schematically summarized in figure 1.

Distributional history of the genus.—The vireos seem to have originated in the Middle American latitudes and to have radiated out from there to North America, the West Indies, and South America. The fact that both subgenera are rich in numbers of species on the American mainland, and that only a few species, typical and atypical forms, occur in the West Indies, suggests a continental origin for the genus. Although confirmatory evidence is lacking, I derive the genus from the tropical latitudes mostly on the observation that the ten-primaried species of *Vireo* are usually (1) sedentary or (2) members of superspecies consisting of migratory, northern breeding populations and/or sedentary, southern breeding populations. The loss of the functional tenth primary (outermost) is considered to be a specialization for migration (Averill, 1925). It will be noted (fig. 1) that three species or superspecies (*V. flavifrons, V. philadelphicus*, and *V. olivaceus-flavoviridis-altiloquus*) have only nine primaries. These species belong to different species groups and have more pointed wing tips than the sedentary members of their respective species groups (see Hamilton, 1958:328). From such observations, I speculate that these species are derived, respectively, from *V. solitarius*, *V. gilvus*, and a "*V. hypochryseus*-like" ancestor. Supporting the origin of *V. flavifrons* from *V. solitarius* is the presence of a hybrid specimen (U.S. Nat. Mus.) and the record (Hauser, 1959) of an unsuccessful pairing between the two species.

Five species or three superspecies have wintering and/or breeding populations in South America: *V. flavifrons* (wintering only in Venezuela and Colombia), *V. leucophrys* (having endemic races), *V. olivaceus* (wintering), *V. altiloquus* (wintering), and *V. flavoviridis* (having endemic races). Populations of these species breeding and wintering in South America have relatively more pointed wing tips than the vireo species that are endemic and sedentary to Middle America or the West Indies (Hamilton, *op. cit.*). I interpret this to mean that members of the genus *Vireo* have only recently exploited habitats in South America (the *V. gilvus-leucophrys* complex may be exceptional, see following). This implies that the sedentary populations of the "*flavoviridis*" segment have only secondarily become nonmigratory. If this is true, then it appears that, while a more pointed wing tip facilitates migratory flight, a less pointed wing tip is not

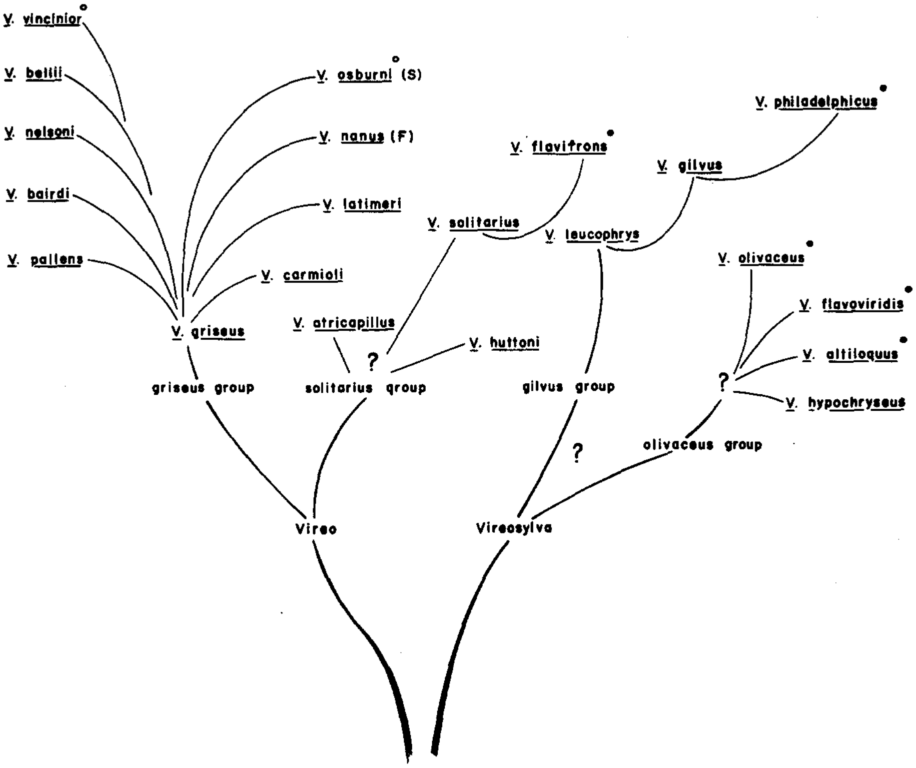

Fig. 1. Diagram of hypothetical relationships in the genus *Vireo*. With several exceptions, species to the left (subgenus *Vireo*) possess eye-rings and wing-bars and have thicket foraging habits. Species to the right (subgenus *Vireosylva*) lack eye-rings and wing-bars but possess arboreal foraging habits. Parentheses designate atypical forms that are either flycatcher-like (F) or shrike-like (S). Open or solid circles denote, respectively, species which are thought to have secondarily lost either wing-bars or the functional tenth (outermost) primary.

initially necessary for the development of the resident habit from that of migration; the same might be argued for the populations of the *alticola* segment of *V. solitarius* which now(?) winter in the lowlands of coastal, southeastern United States.

These conclusions on the phylogeny of *Vireo* are based on the usual taxonomic philosophy which assumes that, by common descent, the majority of similar species indicates the ancestral condition. Knowing full well that such a reliance on "characters-in-common" presents numerous intellectual boobytraps (see Simpson, 1953*a*:341–349), I use this approach here for two reasons: first, for the lack of a better one, and second, because I believe that one theory is better than no theory. Eventually, it may be decided by others that the present account of subgeneric affinities in *Vireo* is unrealistic. Here is one problem which I find difficult to reconcile with the relationships of *Vireo* as presented in figure 1. The external characters of the Brown-capped Vireo (*V. leucophrys*) are similar to those of some members of the vireonid genus *Hylophilus* (the "greenlets") of Central and South America. There is, I believe, a remote possibility that from the latter genus arose—as pioneering species in the Nearctic—the species we now designate as *V. leucophrys*, *V. gilvus*, and *V. philadelphicus*. Furthermore, there is a certain similarity between the Brown-capped Vireo and the Rufous-brown Peppershrike (*Cyclarhis gujanensis*), also of Central and South America. The chief differences of external characters between these confamilial species are those of size and intensity of coloration, the peppershrike being larger and having the same plumage pattern in greater intensity. The vocalizations of the three vireonid genera cited here are quite different (R. H. Barth, Jr., personal communication).

The standard conclusion on such a problem involving the affinities of members of different genera, within the same family, would be that their similarities are due to convergence and that their dissimilarities are due to divergence. However, for intergroup comparisons, we should always consider the possibility that, as species diverge or undergo radiation, their respective biological characters such as plumage patterns, vocalizations, and others may not diverge concomitantly. The point here is that it is conceivable that in the evolution of the Vireonidae divergences of vocalizations and behavioral characters have preceded those of the external morphology. Thus, the phylogeny of the Vireonidae might be obscured by the absence of appreciable divergence of external characters of the plumage.

Relevant to the foregoing is the knowledge derived from various bird genera (Beecher, 1950) that as species radiate, develop sympatry, and exploit new ecological niches, there may be little divergence in the totality of plumage characters as long as the congeners utilize the same basic habitat. Here, apparently, the demands of environmental selection pressures are overriding, and there is thus a "limit" to the array of plumage characters that can be influenced by intraspecific and interspecific selection pressures. Reciprocally, when congeners exploit different environmental habitats, changes in the array of environmental, interspecific and intraspecific selection pressures are expected to permit different or new plumage characters to be favored. Since most members of the Vireonidae are inhabitants of broadleaved woodlands, relatively similar environmental selection pressures might be factors which either promote convergence or suppress divergence of morphological characters.

Similar principles should also apply to behavioral characters such as vocalizations. Similarity between the vocalizations of, say, the *gilvus* species group and those of the other vireos could indicate convergence instead of affinity. As a result of identical environmental selection pressures, different groups exploiting the same habitat of the Nearctic environment are expected to acquire certain similarities in behavior patterns and vocalizations as well as in ecological and morphological characters. For vireonids, such problems of convergence, divergence, and affinity will be resolved only when biological character comparisons can be made within and between Nearctic and Neotropical members. I make these hypothetical observations about vireos only to demonstrate the tenuousness of my proposed classification of the genus *Vireo* when this is done independently of other genera of the Vireonidae.

BIOLOGIC ISOLATION AS MANIFESTED IN *VIREO*

SYMPATRIC SITUATIONS

Examining the genus *Vireo* as a whole, occupation of spatially separated habitats is demonstrated by most sympatric species during the breeding season. The kinds of situations demonstrated by the members in sympatry may be summarized as follows:

(1) *Lateral habitat separation.*—Local, sympatric populations in this case are separated by restrictions to different, but often contiguous, habitats. This kind of sympatry is generally exhibited by members of the same species group or subgenus. Possibly the

best description is that of Grinnell and Swarth (1913), who found, in the San Jacinto Mountains of southern California, four species of the subgenus *Vireo* (*V. bellii, V. vicinior, V. solitarius,* and *V. huttoni*) and the vireosylvid *V. gilvus* locally restricted to different habitats. In Indiana, Nolan (1960) also found that lateral segregation of breeding season habitats was realized for sympatric populations of the similar *V. griseus* and *V. bellii.* A similar, but less localized, situation seems to exist between *V. olivaceus, V. gilvus,* and *V. philadelphicus,* all of the subgenus *Vireosylva,* in northeastern United States and eastern Canada.

(2) *Stratal habitat separation.*—This sympatric situation is usually manifested by species having similar habitat preferences but different foraging positions. That is, one species will be a thicket forager in the shrub layer, and another will be an arboreal forager occurring primarily in the crown layer of the same habitat. Such species are usually members of different subgenera. Examples are: *V. olivaceus* and *V. griseus* in eastern North America (Hoiberg, 1954); *V. olivaceus* and *V. bellii* in central Texas (personal observation); and *V. gilvus* and several species of the subgenus *Vireo. Vireo gilvus* normally has foraging positions restricted to the crown layers of vegetation; this tendency enables it in certain regions to overlap ecologically with either *V. huttoni* or *V. solitarius,* two species having apparently greater ecological amplitudes (see data of Marshall, 1957).

(3) *Altitudinal habitat separation.*—Examining the distributions, habitat preferences, and modes of foraging of *V. olivaceus–flavoviridis* and *V. gilvus–leucophrys,* the importance of altitudinal differences becomes evident since the latter superspecies, unlike the former, is generally a montane-dwelling form (Zimmer, 1941). With virtually complete biologic isolation from one another, it is not surprising that these two superspecies, belonging to the same subgenus and having the same basic habitat requirements of arboreal foraging in riparian or mesic vegetation, should have the most extensive sympatry and geographical distributions of all the species of *Vireo.* In the strict sense, this "altitudinal" type of sympatry represents another manifestation of lateral habitat separation; this point becomes clarified when it is recalled that in the higher latitudes of Canada these two species occur in spatially separated ("lateral") habitats. The altitudinal differences between these superspecies become more obvious in Middle and South America.

Another case might be the relationship between *V. solitarius* and *V. atricapillus* in northern México (Miller, 1955*a*) or in western Texas (K. L. Dixon, personal communication), where these species of the *solitarius* group occur at different elevations in a small area of sympatry. However, it should be noted that any two congeners are "altitudinally" separated if one chooses to consider local differences in elevation such as is found in *V. vicinior* and *V. solitarius* in southern California. At best, this scheme for evaluating sympatry between avian congeners is of value for comparisons between very closely related species or members of superspecies having narrow zones of geographic overlap.

(4) *Habitat co-occupancy.*—Although occupation of separated habitats during the breeding season seems to be the rule for sympatric vireos, two possible cases of habitat co-occupancy deserve attention. An examination of breeding bird censuses taken in eastern North America and reported in Audubon Field Notes indicates numerous instances of *V. flavifrons* and *V. olivaceus* occurring on the same study tract. Unfortunately, no one has yet investigated this case of apparent co-occupancy of the same unit of habitat by two species of *Vireo* belonging to different subgenera. Of interest here is the fact that both sexes of *V. flavifrons* possess a bright yellow throat sharply separated

from a white abdomen and belly. The second case is that of the *modestus* segment of *V. griseus* and the aberrant relict, *V. osburni*, on Jamaica. Here a double invasion by the *V. griseus* complex seems to have resulted in two species which now co-exist in the Blue Mountains (James Bond, personal communication). The striking differences between the two species, the former being typical and the latter (a shrike-like form that has lost the wing-bars) atypical or specialized in ways unique for the genus, are such that biologic strife should be negligible in sympatric situations.

Conclusions

It thus seems valid to state that biologically similar vireos belonging to the same subgenus or species group are usually restricted to spatially segregated, three-dimensional units of the environment when they are sympatric during the breeding season. Biologically different vireos belonging to different subgenera appear to be able to utilize the same habitat during the breeding season because of stratal differences in positions of foraging territories. The observations that such cases, as well as the instances of habitat co-occupancy, are usually manifested between vireo species having different modes of foraging in addition to different external morphological characters warrants by inference the tentative conclusion that for this genus only the older or more diverged species can exist in close proximity to one another during the breeding season. The relative importance of interspecific competition as an agency influencing the habitat preferences and ecological amplitudes of vireos remains to be examined. In this connection, it should be emphasized that the four sympatric situations just listed for *Vireo* are categorical and eventually will have to be reconciled with situations as they actually occur in nature.

The means of avoiding ecological competition in these cases of sympatry are clear; solutions to the problem of ethological isolation—if that problem really exists—are less clear. Where vireos occupy spatially segregated habitats in the breeding season, sympatric congeners should have relatively few opportunities for interspecific encounters. It is suggested, therefore, that habitat separation enhances ethological isolation as well as ecological isolation. Such trends of adaptations for sympatry help to explain the general drabness and lack of diversity of morphological characters for this successful passerine genus.

It is well known for bird species that species-specific vocalizations serve for conspecific defense of established territories, and, in addition, for enforcement of spatial isolation in cases of interspecific encounters (see Dilger, 1956*a*). Such species differences in vocalizations in members of the genus *Vireo* may be the important devices instrumenting habitat selection and restriction in sympatric situations. That vireos have characteristic vocalizations is known, and Saunders (1951) has described some differences in call notes for members of this genus. The need for further research on the intraspecific and interspecific functions of vocalizations in vireos is obvious.

THEORETICAL CONSIDERATIONS ON THE DEVELOPMENT OF SYMPATRY AND THE FORMATION OF SPECIES-SPECIFIC CHARACTERS

During the speciation process, isolates, in some unknown way, attain certain genetic attributes which are manifested in varying degrees in the phenotype of their individuals. After the origin of a species, adaptive adjustments to the environment continue. These post-speciation or phyletic adjustments continue to occur both as species exploit new geographic environments and as the environment of *in situ* species changes in time. When various spatio-temporal factors in some way result in geographic contact of reproductively isolated congeners, a new array of selection pressures begins to operate on the individuals of the species in contact. For the sake of simplicity in this discussion, selection pressures are listed in three ways that are undoubtedly not mutually exclusive: intraspecific, interspecific, and environmental. Environmental selection pressures represent a host of selective operations associated with the adjustment of populations to that part of their environment which is independent of conspecific and/or congeneric individuals.

To me, it is instructive to compare sympatric relationships in genera such as those of *Vireo* and *Parus* for trends of adaptations permitting ecological and ethological compatibility, that is, the biologic compatibility necessary when congeners develop sympatry. Such an analysis must distinguish clearly between two matters: (1) the methods or adaptations by which compatibility is effected in sympatry, and (2) the selective factors which have determined the pathways of adaptation leading to biologic compatibility in sympatry. A comparison of sympatry in birds can only describe the first, and any conclusions on the second must be speculative.

As mentioned in the beginning of this paper, historical and environmental factors obviously play roles in determining the kind of sympatric situation that is realized between congeners. To cite a hypothetical, but plausible, example, if a congener has acquired in isolation a preference for spruce habitats of the mountains, then interspecific competition will be zero or negligible when that congener's distribution overlaps geographically with that of a congener whose habitat preference is oak woodland of the lowlands. The following account deals mostly with congeners which in allopatry have not diverged markedly from one another in habitat preference. In these cases, we may expect interspecific competition either to be currently in operation or to be a factor that was operative during previous evolutionary history.

The ways that bird species avoid ecological competition in sympatry are well known, and Lack (1944, 1947, 1949), Moreau (1948) and many others have described and enumerated these methods. Less clear, however, are the various methods whereby sympatric congeners maintain ethological isolation. Concerning this, the importance of recognition marks (Sibley, 1957; Marler, 1957) and instinctive displays (see, for example, Tinbergen, 1959) are also well known, but the origin of these characters remains one of the major problems of speciation theory. To set the stage for a discussion of the formation of species-specific characters, I prefer to begin with an account of the functions and causes of interspecific territorialism (Simmons, 1951).

INTERSPECIFIC TERRITORIAL SITUATIONS

Although this topic was outlined on page 41, it is useful to examine the several kinds of interspecific territorial situations that are demonstrated by sympatric congeners and to look for certain morphological and behavioral characters which may be associated with the development of a given situation. The following pertains chiefly to diurnal, territory-defending passerine species.

(1) *Territorial overlap within the same habitat* (*habitat co-occupancy*).—For the North American passerine bird fauna, this situation seems relatively infrequent (Dixon, 1961:204, 206). In this situation, congeners live side by side in the breeding season, and, apparently, interspecific antagonism is relatively low. Some species of *Dendroica* show this kind of interspecific territorial situation (see MacArthur, 1958; Marshall, 1957:109–110). The same may be true for two species of *Aimophila* in northern México (Marshall, *op. cit.*:119), for two species of *Ammospiza* on the Atlantic coast (Woolfenden, 1956), and, undoubtedly, in some others.

I am particularly concerned with this phenomenon as it is shown by *Parus* in the western Palearctic region. Gibb's study (1954; see also Hartley, 1953) indicates that in Marley Wood, near Oxford, populations of at least four species of *Parus* (*P. major*, *P. caeruleus*, *P. ater*, and *P. palustris*) are annually present and that they establish overlapping territories. Here, it would seem that conspecific individuals in pair bond defend their established territories from conspecific, but not against congeneric, individuals. Hinde notes (1952:87–88) for several of these sympatric congeners that there is no interspecific territorial exclusiveness except in the immediate vicinity of the nest hole, and that these interspecific contests are usually accomplished by displays other than those utilized in intraspecific encounters. Each of the four species cited above is noticeably different from the others in plumage appearance, and each belongs to a separate species group or subgenus (Snow, 1954). Since these species are essentially alike in the qualitative nature of their behavior (Hinde, 1952:190), I have suggested previously (Hamilton, 1958:313) that for "members of this genus occupying the same habitat . . . selection has favored (along with necessary adjustments in feeding ecology) traits of behavior which promote disregard of nonconspecific individuals." Dixon (1961:203) points out that such adjustments may be necessary for prevention of unnecessary energy expenditures in interspecific contests.

Through what means could natural selection operate for interspecific disregard or for prevention of energy loss in interspecific encounters? The problem is partly one of inter-individual communication, and it may be of use here to recall that the presence or absence of hostility may be communicated between individuals by a variety of display systems that operate by plumage and/or vocal and/or motion releaser signals (Hamilton, 1961). A territorial male may defend his territory by directing aggression to the source of certain releaser stimuli "emitted" by another conspecific, territorial male. We would thus expect, *a priori*, nonconspecific males during the breeding season to occur in closer proximity than conspecific males, particularly if their species-specific releaser systems are different. This generalization may be derived from Moynihan's (1960) study of the adaptations which promote gregariousness in birds. He states that a variety of adaptations permit the formation of mixed-species flocks in the Central American tropics, and that among these are the "neutral" plumages which lack specific plumage marks. He reasons (*op. cit.*:535) that both morphological and behavioral characters help to control hostility.

From the viewpoint of ethology, it is thus useful to examine the problem in the genus *Parus* cited previously. For example, during the breeding season, when an individual of one species of *Parus* encounters another of a different species, do they disregard each other because the afferent stimuli they each receive is of a nature that suppresses hostility and yields an "anti-releaser effect," or do they simply disregard each other because the afferent stimuli they each receive is not of a nature that elicits hostility?

The above distinctions may not be valid and may even represent circular reasoning. Nevertheless, there is an evolutionary problem here: Do these species live side by side partly because of differences in species-specific plumage patterns evolved after contact? Or do they live side by side because previously in their allopatric evolutionary histories they evolved differences in species-specific plumage patterns and vocal characters, which secondarily permit them to live in close proximity during the breeding season. In terms of the origin of species-specific characters, the first possibility implies an important role for interspecific selection pressures, and the second delegates a key role to initial divergences in allopatry as a result of the operation of intraspecific and environmental selection pressures. I draw no conclusions on the problem and suggest only that marked species-specific differences in plumage characters and behavioral traits facilitate the development of habitat co-occupancy by reducing interspecific hostility or antagonism.

(2) *Occupation of the same habitat via mutual territorial exclusion.*—Here, pair-bonded individuals exclude, by directed hostility, from their defended territories other individuals that are both conspecific and congeneric. Detailed observations are necessary for determination of this situation, and for the North American avifauna there are three good examples: the Eastern and Western meadowlarks (*Sturnella* sp.; see Lanyon, 1957) of central and eastern United States; the Red-bellied and Golden-fronted woodpeckers (*Centurus* sp.; see Selander and Giller, 1959) of central Texas; the Great-tailed and Boat-tailed grackles (*Cassidix* sp.; see Selander and Giller, 1961) of the eastern coast of Texas. Many of the examples of "pseudo-subspecies" listed by Vaurie (1954) for Eurasian birds may eventually be found to demonstrate this kind of interspecific territorial situation in small zones of marginal overlap.

Discussing the first three examples simultaneously and briefly, mutual territorial exclusion within a common environmental habitat seems to be another adaptation permitting sympatry among congeners which are essentially similar in external plumage characters and ecological requirements. In these instances, males are apparently responsible for the mutually exclusive territories, and females are responsible for the mating of only conspecific individuals. Thus, prevention of mixed species pairing is instrumented by the females' innate choice of conspecific males only. With such similarities in morphology, ecology, and behavior, the adaptive significance of territorial exclusion for these "sibling" species seems evident—namely, avoidance of both intraspecific and interspecific competition.

Since territorial defenders exclude both conspecific and non-conspecific individuals in this situation, mutual territorial exclusion may well be serving here for partial alleviation of potential wastage of energy in interspecific contacts during the breeding season (Dixon, 1961). In a general way, the evidence cited here for territorial exclusion between morphologically similar species or sibling species serves as a "natural experiment" for the thesis that differences in species recognition characters facilitate the development of habitat co-occupancy among congeners or non-conspecific individuals.

(3) *Occupation of different habitats or of different subdivisions of the same habitat.*—In this interspecific situation, the three-dimensional territories of pairs or trios of congeneric species are essentially spatially segregated. This is the usual way that bird congeners avoid competition (Lack, 1949), and numerous examples could be cited for the avifauna of North America.

(4) *General comments and exceptions.*—I have deliberately avoided discussing in any detail the ways ecological competition is realized between individuals at the breeding population level. For this, the reader is referred to several of the references just cited and particularly to the more recent papers of Pitelka (1951), Udvardy (1951), Marshall (1957), MacArthur (1958), and Dixon (1961). I have also ignored the probability that the habitat relations of many sympatric congeners are such that they demonstrate interspecific territorial situations intermediate between those here delimited and have only discussed examples which, so to speak, fall neatly into one of the three categories.

An attempt to apply the methodology just used to the intriguing findings of Marshall (1960) demonstrates only too vividly the weakness of this abstract examination of conditions in nature. Throughout most of their ranges, the Abert Towhee (*Pipilo aberti*) and the Brown Towhee (*P. fuscus*) occur in different habitats. Marshall (*op. cit.*), however, finds in southern Arizona a locality where both species occur in the same habitat. The two species are fairly similar in plumage characters, and Marshall's data indicate that their foraging territories may overlap. However, he states that their nests are usually 30 feet or more apart. It would be interesting to know for these congeners if interspecific hostility increases in intensity as an individual of one species penetrates farther into the territory of the other species and approaches the nest of the latter. The defended boundaries of the territory of pair-bonded individuals are relative and, in some species, "move" as the individuals move in the habitat. Furthermore, directed intraspecific and interspecific hostility can be expected to vary seasonally, sexually, and, within the territory, areally. In these species of *Pipilo*, defense of the area in the immediate vicinity of the nest might be a crucial factor in interspecific relations. I am obliged to Dr. Ernst Mayr for the suggestion that in these species territorial hostility against conspecific individuals may be so vigorous that members of the species stake out territories for areas larger than those demanded by their feeding requirements. In this case, the two species could ecologically "afford" to overlap. This can occur only if there is no ethological strife between overlapping species during the breeding season. The fact that these two species are in spatially separated habitats throughout most of their sympatric distributions may relate to this problem. Pitelka has shown (1951) that the operations of competition at the population level are slight and subtle, and, as a result of reciprocal selection pressures, average differences may develop only over a period of years.

The generalizations, outlined above, for interspecific territorialism must not be considered as "rules." Special circumstances may "permit" biologically similar congeners to have overlapping territories within a common habitat or between two contiguous habitats. The habitat relations of the Darwin finches serve as a reminder that morphologically similar congeners can co-exist or co-occupy the same unit of the environment. In these instances, congeners have specialized within the habitat, and, presumably, behavioral motions, size configurations, and vocalizations are of more importance than plumage patterns in enforcement of ethological isolation (Lack, 1947). Although the topic of evolutionary opportunity is not developed in the present paper, one might reason that the absence of yellow pigment in the ancestors of the Geospizidae is a factor bearing on the problem, for in these finches, unlike the Hawaiian honeycreepers, striking plumage recognition characters have not developed. Finally, in addition to vacant niches, superabundance of food may be a factor permitting biologically similar species to co-exist (Moreau, 1948:114; Stewart and Aldrich, 1952; and MacArthur, 1958).

On the Causes of Spatial Segregation of Sympatric Congeners

One can envision two major causes for an observed sympatric difference in habitat preference: (1) to prevent ecological competition, and (2) to reduce inter-individual strife or hostility. These alternates will now be discussed in some detail.

Are closely related, sympatric congeners usually in different habitats because they are so similar in ecologies that selection has favored occupation of separated habitats as a means of preventing congeners from competing for the same niche or habitat requirements? Answered in the affirmative, this carries the implication that interspecific competition has a causal role in the determination of the habitat preferences of sympatric congeners. At first glance, we might say that genera such as *Vireo*, *Empidonax*, or *Spinus* (in England), or the *Poecile* group of the genus *Parus* (Old and New World), tend to exhibit noticeable tendencies for spatial segregation of habitats in sympatry, and, furthermore, that habitat separation precludes competition. However, this does not prove that competition is the chief factor responsible for the initial species differences in habitat selection, nor does it prove that congeners, initially equivalent in ecological requirements, develop habitat separation as an ecological isolating mechanism, when they come in contact and develop sympatry.

Dixon (1961) has discussed this problem in some detail, and points out, for the Nearctic species of *Parus*, that pre-existing differences in biological characters may be altered or modified in sympatry by selection pressures operating for the avoidance of competition. Dilger (1956*b*) has reached the same conclusion from his studies of the morphological differences for thrushes of the genus *Catharus*. Thus, it is usually concluded that the major genetic basis of habitat preference is gained in isolation or allopatry, and that later in sympatry, selection pressures for the avoidance of competition may further the differences between congeners. However, habitat preferences tend to vary geographically, and such changes may or may not have a genetic basis (see Miller, 1942; Marshall, 1957). This is outside the scope of the present paper, but do the initial species differences in habitat preference of sympatric congeners always have a genetic basis? Hinde discusses this (1959:117–118) and raises the possibility that populations actively restricted to a certain habitat by interspecific competition may in time acquire a genetic basis for selection of the habitat occupied as a result of the Baldwin effect *sensu* Simpson (1953*b*)—an acquisition which then may lead to relaxation of competition (cf. Snow, 1954).

Are sympatric species, such as are found in the genus *Vireo,* in different habitats because they are so similar in ethological characteristics that selection has favored habitat separation as an ethological isolating mechanism, and is this a result of interspecific interaction? In brief, it will be noted that species exhibiting habitat separation are often fairly equivalent or similar in terms of species recognition marks; witness the similar appearances of sympatric members of *Vireo*, *Empidonax*, or the *Poecile* group of *Parus* in contrast to the differing appearances of the co-existing congeners of *Dendroica*, some of the Central or South American tanagers, or the other species of the genus *Parus* in the western Palearctic Region. Could it be that in certain groups of species natural selection has operated for spatial separation of breeding season habitats as a means of reducing in sympatry the probability of non-conspecific encounters or mixed-pair formations? As with the problem of the origin of differences in ecologies, discussed above, it is difficult to see how a choice between the two alternatives could be made on the basis of evidence normally presented in systematic or ecological studies of bird groups. One possibility of the origin of species differences as a result of interspecific interaction might be that of the "character displacement" exhibited by two species of nuthatches (*Sitta*) in southwestern Asia (Vaurie, 1951), but even in this case there is no evidence that the "displaced" ecological and morphological characters can become species-specific characters.

The most likely explanation here would seem to be that the development of habitat separation in sympatry serves both for ecological and ethological isolation. However, although ethological compatibility is probably a component of the biologic differences necessary for sympatry, we might expect it to be secondary in initial importance since isolates or species in allopatry cannot come into contact and develop sympatry unless they have developed certain genetic differences (isolating mechanisms) via the speciation process in isolation. Thus, enhancement of species' characteristics in sympatry, in the case of the array of plumage differences in the Holarctic sympatric species of the duck genus *Anas,* would represent strengthening of the effectiveness of isolating mechanisms.

Since the development of sympatry is partly a result of the accumulation of adaptations in isolation or allopatry, we may examine the results of speciation in genera or species groups at different stages of evolution and compare the ways in which sympatry is manifested. Examining the distributional history of *Parus*, it is clear that the New World members are derived, by way of the Bering Strait, from the Old World members, probably the *Poecile* group, and seem to be less specialized both ecologically and morphologically than are their Old World counterparts. In the New World, Dixon's studies (1961) indicate that species of the genus *Parus* are relatively recent, and that they rarely live side by side during the breeding season. He concludes (p. 185) that biologic isolation in this genus is manifested by "geographic replacement and/or habitat segregation." Thus, comparing sympatry among members of the genus *Parus* occurring in different zoogeographic regions and representing the results of different time periods of differentiation, we may postulate that habitat separation usually occurs between biologically equivalent, recently separated members of a genus, and that habitat co-occupacy tends to occur only between the older and/or more diverged members of a genus or species group.

Conclusions on the development of sympatry.—In the preceding paragraphs, I have attempted to stress the point that the development of sympatry by a given pair of congeners is regulated by the adaptive resolution of immediate problems at the time of interspecific contact and by the nature of adaptations which each species "carries" into sympatry. It is concluded from a comparison of sympatry in *Vireo* and *Parus* that biological differences acquired in allopatry are the differences which later partly enable or permit congeners to develop sympatry, and that the greater these differences, the greater the opportunities for co-existence or habitat co-occupancy during the breeding season. This, however, is not to exclude the possibility that selection pressures stemming from interspecific interactions may further adjust the "fit" of genotypes.

Is there a sequential progression from one interspecific territorial situation to another during the course of the evolutionary history of specific pairs of sympatric congeners? As mentioned earlier in the paper, we expect, on general theoretical grounds, biologically similar species initially to resolve their problems by territorial exclusion. Even though such species are territorially exclusive, their territories are contiguous, and interspecific antagonism must be relatively frequent along territorial boundaries. If natural selection continues to operate for biologic isolation, two adaptive pathways are available: selection for adjustments permitting habitat co-occupancy (territorial overlap), or adjustments for utilization of spatially separated habitats (territorial separation). With the exception of congeners occurring in regions with sparse or few available habitats such as small islands, desert regions, or crests of mountain ranges, it would appear for many passerine bird genera that the usual sympatric progression is from territorial exclusion to territorial separation. The reciprocal, or one-sided, adjustments necessary for sympatric congeners to go from territorial exclusion to territorial overlap are expected to require greater biological differences, both for ecological and ethological isolating mechanisms, than those necessary for the former shift.

I believe that the few continental genera that have developed territorial overlap from a previous situation of territorial exclusion have done so mostly when certain congeners of restricted or small distribution have come into contact, and, thereafter, they have had the opportunity for relatively drastic mutual adjustments in ethological and ecological isolating mechanisms to become species-specific. Here, it follows, the absence of gene-flow in at least one of the interacting species will be a permissive evolutionary factor enabling that species to "diverge" from its counterpart, thus effecting biologic compatibility in sympatry.

ON THE FORMATION OF SPECIES-SPECIFIC CHARACTERS

Current theories on the origin of isolating mechanisms.—Recently, Moore (1957) has challenged the old theory that isolating mechanisms are reinforced devices decreasing hybrid pair formation and arise as a result of interspecific contact in hybrid zones. He argues that such devices would have to move back, except in populations on small islands (an exception that may be of importance; for example, in consideration of the evolution of the Drepaniidae) into the outlying, conspecific populations away from the zone of contact. And, he asks, how can this be explained? Mayr (1959:228) has discussed this problem and suggests that the preponderance of evidence indicates that "by far the greatest part of the genetic basis of the isolating mechanisms is an incidental by-product of the genetic divergence of isolated gene pools."

Avian systematics offers a variety of cases which might support Moore's and Mayr's criticisms of the theory of a hybrid-origin for basic isolating mechanisms. For instance, in many cases of hybridization (for example, *Corvus corone* and *C. cornix* in Europe; see Mayr, 1954) or "character displacement" (for example, species of the genus *Sitta* of southwestern Asia; see Vaurie, 1951, and Brown and Wilson, 1956), there is no evidence for back-flow of the hybrid or "displaced" characters for establishment in populations away from the area of hybridization or sympatric overlap. Presumably in such cases, the swamping effect would work against the infiltration of these characters into either species' populations away from the hybrid zone (Dixon, 1955:191) or sympatric zone (Selander and Giller, 1961:80). Accordingly, hybrid or "displaced" characters seem to be of value only in zones of contact or overlap.

The importance of interspecific interactions in the origin of species-specific characters.—Can the presence or absence of congeneric or associated species represent an element of an isolate's biotic environment and thereby play a causal role in determining the specific biological characters most efficient for the isolate (Mayr, 1942:49–50)? The present study does not permit definite conclusions on this problem. Theoretically, the answer must be yes, and we need only to examine relationships in the duck genus *Anas* (Sibley, 1957; 1961) to see possible examples. In this genus, members in allopatry or strong isolation tend to exhibit a lack of dimorphism in contrast to their geographic, markedly dimorphic counterparts occurring in sympatry in the Holarctic Region. However, even here caution is necessary in drawing conclusions on the possibility of interspecific interactions. Geographic representatives of the genus *Anas* exhibiting a lack of, or decrease in, plumage sexual dimorphism, such as certain members endemic to Pacific islands (Sibley, 1957), are usually resident forms whose pair bond is probably maintained throughout the year. In contrast, the sympatric, dimorphic members in the Holarctic are mostly migratory, and tend to break the pair bond immediately after the breeding season and to reform pairs (with other individuals?) on the wintering grounds. Thus, there may well be strong intraspecific selection pressure for strengthening intersex communication and pair-bonding processes operating for dimorphism in migratory populations or species of *Anas*, in addition to the operation of interspecific selection pressures for dimorphism as a means for avoidance of non-conspecific pairings.

It is difficult to say that a species owes its specific characteristics to the presence, or former presence, of another congener. One can always argue that the differences were acquired in unknown ways during isolation or allopatry. This is only a suggestion, but I believe that the importance of interspecific selection pressures, such as factors influencing the development of species-specific characters, becomes progressively greater as the sizes of the ranges of the pairs of competing or interacting isolates or congeners become progressively smaller. For bird species, I develop this thesis from Moore's comment (1957:337) that interspecific interactions may be of importance in the case of small island populations. It seems to me that there are two facets to this problem: (1) are most populations of both, or at least one, of the competing congeners in actual interspecific contact, and (2) are the ranges of both, or at least one, of these congeners relatively small? In the first case, genetic swamping will not operate against the results of interspecific selection pressures in at least one species. In the second case, both, or one, of the competing congeners will have, by virtue of restricted isolate size, a more favorable situation for reorganization of the gene pool in response to intraspecific, interspecific, and environmental selection pressures (see p. 47).

While one could apply the suggestion of the previous paragraph to either the Darwin finches of the Galapagos Islands or certain genera of the Drepaniidae of the Hawaiian Islands (see Brown, 1958), I prefer to cite several possibilities for continental genera. Some of the species of *Parus* (p. 55) in the western Palearctic Region might have had their "specific distinctiveness" (Marler, 1957:13) adjusted in this way. I have previously discussed such a possibility for the origin of *Vireo flavifrons* from *V. solitarius* in eastern North America (Hamilton, 1958:338–342). The first of these congeners is monotypic and is quite similar in plumage characters to the latter, which is polytypic and has a wider breeding distribution. The chief morphological difference between the two is that *V. solitarius* shows a posterior increase in yellow pigment, whereas *V. flavifrons* shows an anterior increase in yellow pigment, culminating in a bright yellow throat which is atypical for the genus (table 1). In brief, I believe that *V. flavifrons* originated as a small isolate in secondary contact with the more widespread former species and that swamping due to gene-flow from conspecific populations away from the zone of contact prevented the competing populations of *V. solitarius* from developing specific plumage characters as a result of the operation of interspecific selection pressures. *V. flavifrons* now seems to be expanding its range and thus may be "carrying with it" the characters formerly developed by the combined operation of interspecific and intraspecific selection pressures (Hamilton, *op. cit.*).

A final example may be of interest to some readers. Moreau (1957) in his study of the relationships within the African *Zosterops* complex describes for two species of the complex what may well be termed an example of character divergence (Darwin, 1859: 86–93) or of multiple character displacement (Brown, 1958:164). Throughout most of Africa south of the Sahara Desert occur the mostly allopatric members of the *Zosterops* complex. These continental species are essentially alike in plumage characters. In western equatorial Africa, in the higher elevations of Cameroon Mountain, and on the islands of the Gulf of Guinea occur endemic members of the zosteropid genus *Speirops*. Both Moreau (*op. cit.*) and Amadon (1953) derive these insular endemics from the mainland, and Moreau points out that Cameroon Mountain is essentially a member of the islands of the Gulf of Guinea in terms of avifaunal affinities. *Speirops melanocephalus* occurs on Cameroon Mountain at an elevation of from 6000 to 9000 feet, and Serle (1950) notes that at its lower elevations this species overlaps and associates with the smaller *Zosterops stenocricota*. Moreau's list (*op. cit.*:387) of the external characters of the two species indicates that they differ markedly in the color of the feathers of the head, upper parts, underparts, and in the color of the legs and bill. Unlike the latter species which has normal eye-rings, the former species has vestigial eye-rings. Could interspecific selection pressures, for a variety of purposes, such as avoidance of interspecific hostility, have operated here for the different colors of the plumage characters of *Speirops melanocephalus?* The possibility here is that, during the secondary contact between the montane isolate and the parental *Zosterops* population, reciprocal interspecific selection pressures would affect the montane isolate more strongly (from "zosterops to speirops") than the *Zosterops* populations, since the latter would probably be subjected to the swamping effect of gene-flow from conspecific populations away from the montane zone of contact (that is, from the Cameroon lowlands). This is speculation and is based on the presumption that the more widely distributed *Zosterops* gave rise to *Speirops*, and that the latter developed its contemporary species-specific characters after, not before, secondary contact with *Zosterops*.

The examples of sympatry just mentioned are here interpreted to mean that interspecific selection pressures may be of importance in the formation of species characters. Moore (1957) and Mayr (1959) may be justified in arguing that hybridization is generally not an important factor in the origin of species-specific isolating mechanisms. However, this does not rule out the possibility that interspecific selection pressures, for avoidance of competition (Moore, *op. cit.*:334) or of hostility, may in certain cases operate for differences which then or later become species-specific. For developing reproductive isolation from congeners, an isolate needs only to acquire a certain adaptation which later curtails the influx of non-conspecific genes to the degree that the isolate, or incipient species, can maintain its reorganized gene pool, or have time to complete that reorganization. Thereafter a variety of selection pressures (intraspecific, interspecific, and so on) are expected to contribute to the process of perfecting or adjusting a species' biological characteristics.

SUMMARY

From comparisons of the external morphological characters with the ecological characters, two phyletic divisions are postulated for individual members of the American genus *Vireo*: the subgenus *Vireo* whose members possess eye-rings and wing-bars and, except for three species, have thicket foraging tendencies; and the subgenus *Vireosylva* whose members lack eye-rings and wing-bars but possess eye-stripes and have arboreal foraging habits.

A survey of the genus *Vireo* for tendencies for race formation in relation to dispersal potentials suggests that allohiemic migration facilitates race formation and that either synhiemic migration or continuous breeding distributions or both (presumably by increasing intraspecific gene-exchange) work against race formation. Insular species of the West Indies and continental species having small geographic distributions exhibit, respectively, relatively greater and lesser biologic divergences from the wide-ranging continental species that probably gave rise to them. Examining the genus *Vireo* as a whole, the major factors influencing the differentiation of isolates seem to be: isolation or absence of the swamping effect, the size of the isolate, and environmental opportunity.

By a combination of differences in foraging levels and habitat preferences, the vireos have been able to develop extensive sympatry. As many as five species may be sympatric during the breeding season in some continental regions. These sympatric situations are usually realized by occupation of spatially separated habitats. Since spatial separation of the breeding territories of congeners will operate for prevention of non-conspecific matings as well as for avoidance of competition, it is suggested that species-specific differences in habitat preference may function for ethological as well as for ecological isolation.

Habitat co-occupancy rarely occurs in members of the genus *Vireo*, and the few species of the genus that utilize the same habitat seem to do so by occupation of different, but contiguous, layers of that habitat. The few cases of the latter phenomenon ("stratal" habitat separation) known for vireos involve pairs of congeners that come into sympatry bearing different plumage characters such as presence or absence of eye-rings and wing-bars and possessing different ecological amplitudes such as thicket or arboreal foraging. This seems to be a result of differences or adaptations acquired in

allopatry, not in sympatry. This is evident since this type of sympatry is demonstrated by congeners which belong to different subgenera (for example, *V. griseus* and *V. olivaceus* in eastern United States) and possess approximately the same biological characters as their fellow subgeneric members.

An analysis is made of the sympatry exhibited by members of the genera *Vireo, Parus,* and others. Using a modification of Simmon's concept (1951) of interspecific territorialism, three categories are delimited for interspecific territorial situations: territorial overlap, territorial exclusion, and territorial separation. Examples are cited, and the possibility that many (or most?) sympatric congeners exhibit intermediate situations is noted.

For congeners to overlap spatially during the breeding season, it is suggested that reciprocal, or one-sided, adaptive adjustments are necessary for the avoidance of interspecific hostility as well as for the avoidance of interspecific competition.

Comments are made on the ways that selection pressures may operate for the differentiation of ethological isolating mechanisms. In terms of "reducing the distance" (Tinbergen, 1959) between non-conspecific, congeneric individuals, some alternative adaptations for avoidance of interspecific hostility are adjustments in (1) habitat selection, (2) vocalizations, (3) behavioral motions or postures, and (4) plumage signals.

Since the importance of interspecific selection pressures in furthering the differences between congeners will depend in part on the adaptations which congeners "carry" into sympatry, the problem of the development of sympatry is related to that of the factors promoting the divergence of isolates and allopatric species. Evidence from this study of the genus *Vireo* indicates, as would be expected from the findings of previous workers, that species of small areas or distributions have more favorable opportunities for undergoing divergent adaptation. The role of interspecific selection pressures as a factor influencing the formation of species-specific characteristics would thus appear to be greatest when one or both of the interacting congeners have small distributions. Here, all, or nearly all, populations of at least one congener may be in interspecific contact. In this case, presumably, the absence of gene-flow away from the zone of contact is a permissive factor promoting the biologic divergence of species characters.

On the basis of these conclusions, it is contended for territory-defending passerines that the sympatric development of habitat co-occupancy, or territorial overlap, generally occurs between relatively old and/or more diverged congeners, and that relatively young and/or less diverged congeners tend to develop territorial exclusion or territorial separation (habitat separation) in sympatry.

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