THE CONDOR

VOLUME 53 JANUARY-FEBRUARY, 1951 NUMBER 1

CONGENERIC SPECIES OF BIRDS NESTING TOGETHER IN CENTRAL AMERICA

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Evolutionary theory leads us to believe that a genus is a monophyletic group, all its component species having sprung from a common ancestral stock. Indeed, proof that any genus, as currently recognized, did not fulfill this condition would provide a basis for its division. Whenever the bird fauna of a certain locality is studied, it is found that in many instances several species of a single genus intermingle in the same breeding area. For a long time this has been a challenging problem to the naturalist. In the early discussions of the subject, during the nineteenth century, the phenomenon was frequently cited as evidence for physiological or sympatric speciation, that is, the division of a single local population into two or more non-interbreeding groups sharing a common area. This theory, which was based on the concept of blending inheritance, finds so many obstacles in the Mendelian theory of inheritance that it has only few adherents today. It is now held to be much more likely that such similar species originated in geographical isolation, but have come together at a subsequent date through the extension of the area occupied by one or more of them (Mayr, 1942, 1947).

The problem of congeneric species nesting together has, however, by no means lost its attractiveness as a result of the rejection of the theory of sympatric speciation. It is now realized that the real problem is not how these species originally split into two, but rather what keeps them distinct, now that they have come together again. All the various biological factors which help to maintain the distinctness of species and to prevent interbreeding have been labelled isolating mechanisms by Dobzhansky (1941). The study of congeneric species nesting together is thus really a study of isolating mechanisms.

Most important among them are probably those characters which are directly connected with pair formation, such as external morphology and plumage pattern, song and call notes, and finally displays and courtship motions. However, as Lack (1944) has recently emphasized, an overlapping of the ranges of closely related species takes place usually only when ecological differences between the two species have developed in regard either to food or habitat preference. Such ecological differences not only decrease the amount of competition between such species but also reduce the number of contacts between unmated birds of different species and thus also help to prevent interbreeding.

The purpose of the present paper is, first, to place on record the instances of congeneric species breeding in the same area that have come to my attention in Central America; second, to try to discover what keeps such species from interbreeding; and finally, to discover some of the differences in habitat preferences. In table 1 information is given for twenty-nine groups of two, one group of three, and one group of four, congeneric species that I have found nesting in the same area or in contiguous or overlapping habitats.

I have omitted the trogons from this discussion. In this family it is difficult to steer a safe course between the shoals of lumping and the reefs of splitting. If I follow the somewhat narrow generic concepts of Ridgway (1911), I have no records of congeneric

species of trogons nesting together. If, on the contrary, I follow the older as well as some more recent authors and place in the single genus *Trogon* all the Central American members of the family, save only *Pharomacrus mocinno*, then there are a number of records of congeneric species nesting together. But by this course we place in the same genus species whose nests differ more fundamentally in form than those of any two species that have been treated as congeneric in this paper.

When more than a single pair of species is listed in table 1 under the generic name, the brackets indicate which were found nesting in proximity. Most of the species considered together occupy the same habitat; but in a few instances species of adjoining habitats have been placed in juxtaposition for the purposes of comparison. Even among the non-migratory species of the tropics, birds frequently make short excursions beyond their normal haunts; they often place their nests at the edge of the vegetational formation in which they dwell, or even beyond it, forest birds at times entering the neighboring clearings to build their nests and lay their eggs. Thus, birds of quite different preferences as to habitat often meet; and were there any strong tendency for them to hybridize, they would have ample opportunity to do so. It is not inconceivable that a bird of open country should mate with a bird of the forests and the two place their nest where field and forest meet.

The discovery of nests amid the heavy vegetation of the tropics is notoriously difficult. Observation of the habits during the breeding season of a number of pairs of congeneric species not listed here makes me feel sure that they nest in the same area; but it seems best to include in this discussion only species whose nests have actually been found in the same neighborhood. In a few instances the nests of the species bracketed together were two or three miles apart; but in the great majority of cases the two species were found nesting within a mile of each other; and often their nests were in the same dooryard, in the same bank, or even in the same tree. I feel confident that the discovery of a greater number of nests would show that all the species bracketed together breed at times within a few hundred feet of each other, for they intermingle during the season of reproduction. When the vast Central American avifauna is as thoroughly known in its biological as in its taxonomic aspects, it will be possible to compile a far longer list of congeneric species that breed together.

The present record is based upon field work during fourteen nesting seasons, in Guatemala, Honduras, Panamá, and chiefly Costa Rica. The nomenclature employed in the table is that of Cory and Hellmayr's "Catalogue of the Birds of the Americas" (1918-1938) except in the single instance of the genus *Phaethornis*, where Peters (1945) has been followed. The localities where the observations were made are indicated by the capital letters opposite the brackets at the left side of the table, in accordance with the following schedule, which is that followed in my paper (1945:14) on incubation and nestling periods:

A—El General, head of Térraba Valley, southern Pacific Costa Rica.
B—Vicinity of Vara Blanca in the Costa Rica highlands, on the Caribbean slope at 5000 to 6000 feet above sea level.
C—Caribbean Costa Rica, at lower elevations.
D—Caribbean Honduras, near Tela.
E—Los Amates, humid lower Motagua Valley, Guatemala.
F—Highlands of western Guatemala, Department of Chimaltenango, 7000 to 10,000 feet above sea level.
I—Almirante, western Panamá.
J—Barro Colorado Island, Canal Zone.
K—Near Cali, Colombia.

Many of these pairs of species that breed together come into contact over a vast extent of territory; hence there is no reason to suppose that their nesting in close proximity is a purely local condition. In other instances, a bird of great geographic extension meets and mingles with a congener whose homeland occupies only a small fraction of its own. Again, we have the interesting phenomenon of a wide-ranging species breeding alongside now one, now another, of two "representative species," that is, two quite similar species (members of the same superspecies) that may be thought of as representing each other in different areas. Instances of this are found in the genus *Troglodytes,* in which the wide-ranging *T. musculus,* the tropical House Wren, breeds in Guatemala in close proximity to *T. rufociliatus,* and in Costa Rica with the local representative of the latter, *T. solstitialis.* These little highland wrens are woodland birds, while the House Wren haunts the clearings. Yet in Guatemala I found *T. rufociliatus* and *T. musculus* nesting within hearing of each other in the same bank beside a road that led between woodland and pasture; while in Costa Rica, *T. solstitialis* and *T. musculus* nested in the same forest-encircled pasture. Similarly, the wide-ranging and common Blue Tanager (*Thraupis episcopus*) breeds in northern Central America with the Abbot Tanager (*T. abbas*), a "representative" of the Palm Tanager (*T. palmarum*), with which the first-mentioned nests in southern Central America. In Guatemala, *T. episcopus* and *T. abbas* nested in the same yard; in Costa Rica, *T. episcopus* and *T. palmarum* nested in the crown of the same cohune palm growing in a pasture.

In column four of table 1 is given the approximate altitudinal distribution of each species. These figures refer especially to the Central American portion of the bird's geographical range; where the species occurs also in México or in South America, it may have there rather different altitudinal limits. In most instances, the congeneric species that nest together have essentially similar altitudinal ranges—they are both lowland or both highland species—but one may occupy a broader vertical zone than the other. In a few cases, however, the altitudinal range of a lowland species overlaps that of a highland species, as may be seen in the genera *Elaenia, Myiodynastes, Troglodytes* and *Chlorospingus.*

In the fifth column, giving habitats, limitations of space make it necessary to characterize the vegetation in the most general terms. Usually the species bracketed together are both forest birds, or else both birds of the clearings and secondary vegetation; but they often differ in the density of the growth they prefer. Thus, in the genus *Leptotila,* the Rufous-naped Cassin Dove (*L. cassinii rufinucha*) frequents rather heavy, dense second-growth; while the Verreaux White-fronted Dove (*L. verreauxi verreauxi*) is at home in lighter, more open second-growth and fields with scattered trees, where one will seldom find the former. Yet there is a fairly broad zone in which their habitats overlap. So the Slate-headed Tody Flycatcher (*Todirostrum sylvia*) will be found in thickets too dense for its relative, *T. cinereum,* and the latter in shady pastures and dooryard shrubbery far too open for the former; yet along the edges of thickets the two often meet. Both of the little black manakins of the genus *Pipra* are at home in the high forest; but the scarlet-headed species, *P. mentalis,* displays and nests at somewhat higher levels of the understory than its blue-crowned relative, *P. coronata.*

The sixth column gives the breeding season for the Central American portion of the bird's range. In preparing this I have been aided by Harrower's (1936) comprehensive resumé of data on the breeding habits of the passerine birds of Central America. The nesting season of some of these birds appears to begin earlier, and to last longer, in Panamá than farther to the north. Unfortunately, the breeding seasons as given in this column are based on very unequal numbers of nests. In some instances, only one or two

Table 1

Examples from Central American Birds of Congeneric Species Nesting Together

Genus and species	Location	Range: Geographic	Range: Altitudinal	Habitat	Nests found	Comparison: Nest area	Comparison: Appearance	Comparison: Voice
PIGEONS, DOVES								
Columba								
nigrirostris	A	México—E. Panamá	0– 3000	Forest and clearings	Mch.-Apr.	Same	Very different	Very different
speciosa	A	S. México—Paraguay	0– 3000	Forest and clearings	Feb.-May			
Columbigallina								
passerina	K	S. U.S.A.—Paraguay	0– 8500	Open country	Jan. (1)	Same	Moderately different	
talpacoti	K	S. México—N. South America	0– 3500	Open country	Jan.-Aug.	Same	Very similar	
minuta	E	S. México—N. South America	0– 2000	Open country	May-June			
Leptotila								
cassinii	A	Guatemala—Colombia	0– 3000	Woodland	Mch.-Oct.	Overlap	Head different	Very different
verreauxi	A	S. Texas—Brazil	0– 8000	Thickets and clearings	Jan.-Sept.			
KINGFISHERS								
Chloroceryle								
amazona	E	S. México—Argentina	0– 3000	Water	Feb.-July	Same	Similar; striking difference in size	Very different
americana	E	S. U.S.A.—Argentina	0– 7000	Water	Mch.-May			
HUMMINGBIRDS								
Phaethornis								
longuemareus	A	México—South America	0– 4500	Forest and clearings	Nov.-July	Overlap	Similar; striking difference in size	Moderately different
superciliosus	A	México—Bolivia	0– 3000	Forest and edge	Jan.-May			
ANTBIRDS								
Myrmotherula								
axillaris	J	Honduras—Bolivia	0– 1500	Rain-forest	Apr.-May	Same	Very different	Moderately different
fulviventris	J	Honduras—W. Ecuador	0– 1500	Rain-forest	Jan.-May			
FLYCATCHERS								
Elaenia								
chiriquensis	A	S. Costa Rica—S. Brazil	0– 3500	Bushy pasture	Apr.-July	Overlap	Similar, but head different	Very different
flavogaster	B	S. México—N. Argentina	0– 6000	Open groves	Mch.-Aug.	Overlap	Similar, but head different	Very different
obscura	B	Guatemala—N. Argentina	4000– 8000	Shady pasture	Apr.-June			
Myiobius								
atricaudus	A	Costa Rica—Perú	0– 3000	Riverside thickets	Apr.-Aug.	Overlap	Very similar	
sulphureipygius	A	S. México—W. Ecuador	0– 3000	Rain-forest	Mch.-May			

Table 1 (Continued)

Examples from Central American Birds of Congeneric Species Nesting Together

Genus and species	Location	Range: Geographic	Range: Altitudinal	Habitat	Nests found	Comparison: Nest area	Comparison: Appearance	Comparison: Voice
Myiodynastes								
chrysocephalus	B	Costa Rica—Perú	3500– 6000	Cloud-forest	May (1)	Sometimes same	Moderately different	Moderately different
luteiventris	B	Arizona—W. Panamá	0– 6000	Open groves	Apr.-July	Sometimes same	Moderately different	Moderately different
Myiozetetes								
cayanensis	J	Panamá—S. Brazil	0– ?	Open country	Jan.-May			
similis	J	México—N. Argentina	0– 6000	Open country	Apr.-July	Same	Very similar	Different
granadensis	A, I	Honduras—E. Perú	0– 5500	Open country	Mch.-July	Same	Similar, head different	Very different
Todirostrum								
cinereum	A	S. México—Brazil	0– 4500	Open groves	Mch.-July			
sylvia	A	S. México—Brazil	0– 3000	Dense thickets	Apr.-July	Often join	Very different	Very different
MANAKINS								
Pipra								
mentalis	A	S. México—W. Ecuador	0– 3500	Rain-forest	Mch.-Jun.			
coronata	A	S. Costa Rica—Perú	0– 3500	Rain-forest	Feb.-Jun.	Same	Similar, head different	Very different
COTINGAS								
Tityra								
inquisitor	A	S. México—N. Argentina	0– 3000	Forest and clearings	Apr.-May			
semifasciata	A	México—S. Brazil	0– 6000	Forest and clearings	Mch.-July	Same	Similar, head different	Different
WRENS								
Thryothorus								
modestus	A	S. México—Panamá	0– 6500	Low thickets	Jan.-Sept.			
nigricapillus	A	E. Nicaragua—W. Ecuador	0– 3000	By rivers	Jan.-Aug.	Adjoin	Very different	Very different
Troglodytes								
rufociliatus	F	Guatemala—Salvador	7000–11000	Cloud forest	Apr.-July			
musculus	F	S. México—Patagonia	0– 9500	Open country	Dec.-Sept.	Overlap	Very different	Very different
solstitialis	B	Costa Rica—N. Argentina	4500– 8000	Cloud forest	Apr.-July	Overlap	Very different	Very different
THRUSHES								
Turdus								
assimilis	A	México—W. Panamá	1000– 6000	Forest and clearings	Mch.-Jun.			
grayi	A	México—Panamá	0– 8000	Open country	Mch.-Aug.	Overlap	Very different	Very different
ignobilis	B	S. México—South America	3000– 7000	Forest and clearings	May (1)	Overlap	Moderately different	Very different

Table 1 (Continued)

Examples from Central American Birds of Congeneric Species Nesting Together

Genus and species	Location	Range: Geographic	Range: Altitudinal	Habitat	Nests found	Comparison: Nest area	Comparison: Appearance	Comparison: Voice
WOOD WARBLERS								
Myioborus								
miniatus	B	México—Perú	2000– 7000	Forest and edges	Apr.-Jun.	Same	Very different	Very different
torquatus	B	Costa Rica—W. Panamá	3500– 9000	Forest and edges	Apr.-May			
FINCHES								
Saltator								
coerulescens	D	S. México—Paraguay	0– 5500	Open country	May-July	Overlap	Different	Very different
maximus	D	México—Brazil	0– 5000	Open country	Mch.-Sept.			
albicollis	A	S. Costa Rica—N. So. America	0– 3200	Open country	Mch.-Aug.	Overlap	Different	Very different
Sporophila								
aurita	C, D	S. México—S. Colombia	0– 5500	Grassland	Mch.-Sept.	Same	Very different	Moderately different
torqueola	C, D	S. U.S.A.—Costa Rica	0– 6000	Grassland	Apr.-Oct.			
TANAGERS								
Chlorospingus								
ophthalmicus	B	S. México-Argentina	1500– 8000	Forest and clearings	Apr.-Jun.	Same	Similar, head different	
pileatus	B	Costa Rica—W. Panamá	5500–10000	Cloud forest	Jun.-July			
Tanagra								
luteicapilla	A	Nicaragua—Panamá	0– 4000	Woods and clearings	Mch.-Jun.	Adjoin	Males very similar	Moderately different
imitans	A	S. Costa Rica—W. Panamá	0– 4000	Forest and clearings	Mch.-May		Females moderately different	
minuta	A	Guatemala—Brazil	0– 5000	Forest and clearings	Apr. (1)			
Calospiza								
chrysophrys	A	Costa Rica—N. So. America	1000– 3500	Forest and clearings	Apr.-Jun.	Same	All four very different	All four very different
gyrola	A	Costa Rica—Bolivia	0– 4000	Forest and clearings	Feb.-Sept.			
icterocephala	A	Costa Rica—Ecuador	0– 4000	Forest and clearings	Apr.-Sept.			
nigro-cincta	J	S. México—N. So. America	0– 5000	Forest and clearings	Feb.-Sept.	Same	Very different	Moderately different
inornata	J	W. Panamá—Colombia	0– ?	Forest and clearings	Apr.-Aug.			
Thraupis								
abbas	E	S. México—N. Nicaragua	0– 5000	Open country	Mch.-May	Same	Very different	Very different
episcopus	A, J	S. México—Brazil	0– 7500	Open country	Jan.-July			
palmarum	A, J	S. Nicaragua—Bolivia	0– 4000	Open country	Feb.-Jun.	Same	Very different	Moderately different

nest records were available for the species; in others, scores of nests had been found. Whenever the breeding season as given is very short, covering only a month or two, it is based on a small number of nests; and it is probable that a greater number of records would show a considerably wider spread of dates. It is important to emphasize that imperfect though our information is, it is sufficient to prove that in no known instance do the congeneric species of birds that nest in the same area in Central America have breeding seasons that are mutually exclusive. On the contrary, wherever there are sufficient records of nests, they show that the breeding seasons of the two species are very much the same, although one may nest over a period a month or two longer than the other.

One of the forms of physiological isolation most easily discovered is that resulting from mutually exclusive breeding seasons; if two species are not in the reproductive state at the same time, obviously they cannot interbreed, although they live side by side. This condition is sometimes found among plants, although more commonly all the congeneric species of the same region flower at the same season, as violets (*Viola*) nearly all blossom in the spring, and golden-rods (*Solidago*) in the late summer and autumn. But I am aware of no instance of congeneric species of birds that nest at quite different periods. So far as their nesting seasons are concerned, any of the species bracketed together in the table could interbreed and hybridize. Yet hybrids between these species appear never to have been discovered; and in my experience with Central American birds, I have never found individuals of two species even trying to mate together. When two closely related species build nests of the same form, in the same tree, and at the same time, how is it that they never interbreed? In the last three columns, I have attempted to analyze the factors which keep them separate.

Appearance.—Some of these congeneric species are so different in appearance that no observant person, be he ornithologist or not, could possibly confuse them. This is true of the two species of *Myrmotherula, Todirostrum, Pipra* and *Thryothorus,* of the two sets of species of *Thraupis,* and of all five of the species of *Calospiza.* At the other extreme, a few of our congeneric species are so closely similar that, in regions where they occur together, even the experienced bird watcher must exercise great caution in his field identifications—especially if he depend upon appearance alone for their recognition. Among the ground doves, *Columbigallina talpacoti* and *C. minuta* are confusingly alike. So long as the Northern Elaenia (*E. flavogaster*) keeps its crest laid flat, it may readily be confused with the other two gray species with which it lives; but when raised, its higher crest, white in the center, is a good recognition mark. So, too, the species of *Myiobius* are of similar aspect. The males of all three species of euphonias (*Tanagra*) listed in our table are much alike in appearance; those of *T. luteicapilla* and *T. imitans* are confusingly alike even after long familiarity with them. The females of these two species are far more readily separated. I frequently see both of these euphonias in the trees about my house; and *T. luteicapilla* sometimes nests here; but the only nest of *T. imitans* that I have found was in the neighboring forest.

Among the flycatchers of the genus *Myiozetetes, similis* and *granadensis* are similar in size and general aspect, both being olivaceous above and bright yellow below; but they are easily distinguished by their head markings, *similis* having a dark forehead and white superciliary stripes, *granadensis* a white forehead but no superciliary bands. These two species build oven-shaped nests which I cannot distinguish, one pair of each frequently nesting in the same small tree. This past season, two orange trees and a lemon tree close by my house each contained a nest of *similis* and one of *granadensis,* separated by only a few yards; all four nests in the orange trees were successful. I have never found in the same tree two nests of *similis,* nor two of *granadensis.* Yet the terri-

torial instinct is only weakly developed in these birds, for two nests of the same species will often be found not far apart, with indistinct boundaries between the domains of the two pairs; one often trespasses upon the other's land without being chased. *Myiozetetes similis* and *cayanensis* are so very similar that only the sharpest eyes can distinguish them in the field. Yet once, in Panamá, I found nests of both in the same small orange tree.

Voice.—The species that are so similar in plumage are readily distinguished by their voices. The quite distinctive call notes of *Myiozetetes similis* and *M. cayanensis* furnish by far the simplest means of field identification; while *similis* and *granadensis* may be distinguished by their voices at a greater distance than is possible with good field glasses. So, too, the three species of *Elaenia* are more easily distinguished by the ear than by the eye; and this is true to a high degree of the two euphonias, *Tanagra imitans* and *T. lutcicapilla*. In fact, all these congeneric species that nest together are quite easily distinguished by their voices, save possibly in the few instances where I have left blanks in the ninth column, for I have not heard one member of the pair for many years, and finding no explicit statements on this point in my notes, I think it safest not to lean too strongly upon memory.

The longer my period of association with the birds of any region, the less I depend upon field glasses and the more I rely upon my ears for the recognition of those I meet from day to day. Since birds have acute hearing and make frequent use of their voices in keeping in touch with their mates or companions, we may be sure that voice plays a most important part in their recognition of each other. Whether this part is more important than that taken by sight I hesitate to say, but in many instances I suspect that it is.

How well birds can recognize each other as individuals may be illustrated by an observation that I made some years ago, while I dwelt in the valley of the Río Pacuar, near the western end of the Basin of El General in southern Costa Rica. In a neighboring pasture was a flock of three Smooth-billed Anis (*Crotophaga ani*) and a lone Groove-billed Ani (*C. sulcirostris*). The first species is very rare in Costa Rica; there is, I believe, only one published record (quoted in Bent, 1940); and these three individuals, with one other soon to be mentioned, are the only ones I had at that time seen in the country. The Groove-billed Ani, although generally abundant in cleared districts at lower elevations throughout the length and breadth of Central America, is for some unexplained reason rather rare in El General. The lone bird in the pasture had no close neighbors of its kind. In another pasture higher up the mountain there was a small flock of Groove-billed Anis; but an intervening belt of high forest served as an effective barrier between these birds which avoid the heavy woodland.

Few birds are more sociably inclined than the anis which build communal nests in which several females lay their eggs in a common heap, all the cooperating members, both male and female, taking turns at incubating them, and all joining in nourishing the young. The lone Groove-billed Ani in the pasture, finding itself somehow separated from all others of its own kind, attempted to satisfy its thwarted social instincts by attaching itself to the flock of three Smooth-bills. These two species resemble each other so closely that only by examining their bills through field glasses at close range, and under the most favorable conditions of lighting, could I distinguish them visually; but their distinctive calls at once betrayed their separate identity. Again and again, day after day, the soft-voiced Groove-bill attempted to join the trio of louder-voiced Smooth-bills, only to be rebuffed and chased away by one or another of them. In the evening, it would try to enter the little clump of bushes in the midst of the pasture where the Smooth-bills

roosted; but one would issue forth and chase it away; and this would be repeated until the light had grown dim and the poor Groove-bill was obliged to go off and spend the night alone. For well over a month, the Groove-billed Ani hovered about the three Smooth-bills and was driven off by them innumerable times. Since it so greatly resembled them in outward aspect, it might be suspected that it was treated as a foreigner only because it spoke a strange language and that if it had learned to silence the soft *ti-ho* which it repeated almost every time it flew, it might have succeeded in attaching itself to the only others of its genus in sight.

However, this explanation is not necessarily correct. It is well known that anis can recognize members of their own flock by sight (see Davis, 1940); in fact, a fourth Smooth-bill, that from time to time appeared and wished to join the three, was chased away exactly like the lone Groove-bill.

These two species of *Crotophaga* in general occupy complementary parts of the vast extent of the American tropics; but they are found together in Panamá and along the west coast of South America as far as Ecuador, where I have seen both in the same neighborhood. Without much doubt they at times nest not far apart; but I have no actual record of this.

Voice is of the greatest aid to the field ornithologist in distinguishing closely similar races, species, and even genera of birds, and its probable rôle in the differentiation of species has never received the attention it merits. Especially among the American flycatchers (Tyrannidae) it appears to be of importance, not only among the small grayish species that so greatly try the patience of ornithologists, but even among the big kinds clad in bright and contrasting colors. The two largest flycatchers of Central America, the Kiskadee (*Pitangus sulphuratus*) and the Boat-billed Flycatcher (*Megarhynchus pitangua*), both wide-ranging, common species often found in the same district, are, despite their generic distinctness, sufficiently alike in appearance to confuse the beginner —and they are by no means plainly colored birds, but are dressed in a boldly variegated pattern. This color-pattern is amazingly similar to that of the two species of a third genus, *Myiozetetes*, which we have already noticed as being so confusingly alike in appearance; these are, however, considerably smaller than *Pitangus* and *Megarhynchus*. A bird of yet a fourth genus, *Myiodynastes chrysocephalus*, so closely resembles *Myiozetetes similis*, that when I first entered the highland region where this rare bird dwells, I confused it with the latter until its sharper notes drew my attention to its distinctness. All these species are easily known by their very distinct voices. So, too, the two races of *Myiozetetes similis* inhabiting Central America are in the field more readily distinguished by voice than by any other means. The southern race, *columbianus*, singing at dawn during the breeding season in April and May, repeats over and over the phrase *chips-â-cheery*, very clearly enunciated. The northern race, *texensis*, uses at best a garbled and scarcely recognizable version of the same phrase.

It would be easy to extend the list of closely allied birds that are more readily distinguished in the field by voice than by appearance. Another excellent example is furnished by two congeneric woodhewers: *Lepidocolaptes souleyetii* of the lowlands utters a beautiful, clear trill; *L. affinis*, its highland counterpart, has a weak, sad trill. Saunders (1929) concluded from studies of the voices of North American birds that "no two species of the same genus, breeding in the same area, have songs that are just alike." But when closely related species occupy different breeding ranges, there often are few or no definite differences in their songs. To the examples he gives in support of this last statement, I might add that of two pigeons which replace each other altitudinally in Central America, *Columba nigrirostris* of the lowlands is not only confusingly similar

in appearance to its highland representative, *C. subvinacea,* but I can not with certainty distinguish their melodious, far-carrying calls. Perhaps every widely travelled bird watcher has had the experience, when visiting a new region, of hearing an old familiar bird voice which he at first supposes to belong to a species well known to him, only to find, upon tracing the sound to its source, that it is the utterance of some related bird. Under these circumstances, it is the close resemblance of the songs of the two species that seems important. Since a considerable interval of time often separates our hearing the songs of the two kinds of birds, differences are apt to be forgotten or overlooked. Could we hear them both within an hour, I believe that we should far more often detect differences in the voices of these closely related allopatric species.

Among the resident birds of the tropics, the method of pair formation is even more difficult to discover than in the migratory birds of higher latitudes. Because many males of migratory species, upon arriving in the spring, take up territory, isolate themselves, and make themselves conspicuous before the arrival of the females, their behavior at this critical period is relatively easy to follow. But tropical birds as a rule pair long before the beginning of the nesting season, sometimes while living in flocks, more often in seclusion or while roaming among the tree-tops. At least a third of the species listed in the table are seen by twos at all seasons and probably pair for life; many of these birds appear to choose their mates at an early age, and by processes difficult to fathom. But whatever the method of pair formation, we may be sure that recognition of the potential partner as to species and as to sex is an essential part of it; and it is reasonably certain that with most birds this recognition is effected through both the eye and the ear.

On the other hand, among the hummingbirds, manakins, and flycatchers of several genera, including *Myiobius,* no lasting bonds are formed between the sexes, and the male takes no share in the activities of the nest, not even guarding it. The flycatchers of the genus *Myiobius* are rather silent birds but display by spreading their black tails, drooping their short wings, and exposing their bright yellow rumps as they flt among the boughs. Male hummingbirds of many kinds, including *Phaethornis,* are found in the same spot day after day during a long breeding season, tirelessly repeating a little "song," in some species the mere repetition of monotonous, squeaky notes, in others a charming musical performance. While calling in these courtship assemblies, the hummingbirds display little or not at all; the hermit hummingbirds of the genus *Phaethornis* merely wag mechanically a long, white-tipped tail. Male manakins likewise center their activities around certain definite posts, where they call tirelessly; and in some species the males "dance" and indulge in the most bizarre antics, by means of which their often striking peculiarities of plumage are displayed for the benefit of the other sex. In this family, voice and color-pattern may vary so greatly even among species of the same genus that it is almost inconceivable that the female of one species should be attracted by the male of another.

While studying the White-eared Hummingbird (*Hylocharis leucotis*) in the Guatemalan highlands, I found amazing differences between the "songs" which different males repeated tirelessly during the breeding season. Frequently, after laboriously tracing a strange bird note to its source, I was surprised and somewhat vexed to find it just another White-eared Hummingbird. The male hummingbirds usually gathered to sing in little groups of from two to seven individuals; and those in the same assemblage as a rule used a rather similar "song," often strikingly distinct from that in vogue among a neighboring group. It was impossible to decide whether these differences in voice were genetic or merely arose from the fact that the birds in any assemblage imitated one individual who perhaps had been there first or was somehow dominant. If one of these hum-

mingbirds had joined another group that sang a very different tune, one wonders whether it would have been capable of following the fashion there prevailing. The variation among the voices of the White-eared Hummingbirds was so great that I at first inclined to the belief that it might be caused by differences in the structure of the vocal organs, which in turn were of genetic origin. However, if one thinks of the variety of sounds produced by a single flicker, starling, chat, or song sparrow, or of the ease with which certain captive birds adopt new songs, this hypothesis loses much of its attractiveness. The lack of a genetic basis for these differences of song would invalidate any idea that these song populations might be incipient species. For a reference to the genetic difficulties involved in any hypothesis of sympatric speciation, see Mayr (1942:204). It would be very difficult to imagine a mechanism that would produce males homozygous for a specific song type and simultaneously females equally homozygous in their exclusive preference for males of this kind of song. All these difficulties are removed if it is assumed that both the new song as well as the preference for it were developed during geographical isolation.

I believe that variations in voice, which are generally neglected, may be of no less importance as starting points in the evolution of new forms of birds than those slight differences in size and color that now receive such painstaking study and minute description. In the past it was not possible to preserve the notes of birds for future objective study and to make direct comparisons between species or races with diverse ranges, as has long been done with their skins. It is to be hoped that the recently developed art of recording bird voices will soon be perfected to the point where it will be called into service by students of taxonomy and geographic variation. Perhaps, before many years have passed, our handbooks of birds will be accompanied by phonographic records reproducing the songs and calls of each species. If this happy day arrives, such groups as the small, plainly clad flycatchers, now the despair of the field ornithologist, should present no greater difficulties in identification, to one with a moderately good ear, than the multihued tanagers to one who is not color-blind.

We must admit our complete ignorance of whether any of the pairs of congeneric species that have occupied our attention are prevented from interbreeding by sterility barriers. So far as we know, no two of these species have attempted to interbreed. But in view of the cross-fertility of numerous other species of birds that have been bred in captivity, it is fair to suppose that some at least of those we consider here could be successfully crossed under the conditions of the aviary. In nature, however, there seems rarely to be need of a sterility barrier to prevent the blending of related species of birds that occupy the same area. In all but a few exceptional cases, as the well-known hybridization of the Golden-winged Warbler (*Vermivora chrysoptera*) and the Blue-winged Warbler (*V. pinus*), another, subjective, factor prevents their even attempting to interbreed. We might call this for brevity "psychological isolation," and it appears to operate chiefly through differences in plumage and voice.

Habitat preferences.—A third way in which subjective factors may operate in keeping congeneric species distinct is through habitat preferences. Moreau (1935), after a detailed analysis of the local distribution of birds in an area of tropical Africa, could in many instances find no physical or biological differences between contiguous habitats that seemed adequate to explain the well known restriction of so many tropical birds to definite and often narrow altitudinal belts, or slightly differing vegetational formations. With apparent reluctance, he concluded his patient study with this statement: "Much of the Usambara distribution appears to be explicable only by subjective factors." Similarly, here in Costa Rica, many facts in the local distribution of birds appear

inexplicable except on the hypothesis of purely subjective preferences of certain species for certain surroundings—preferences which seem in some instances to be understandable from a consideration of the ancestral history of the birds in question. We shall limit ourselves to two examples among the local birds.

Why should the wren *Thryothorus nigricapillus semibadius* remain so closely attached to the courses of the wider streams, although it appears to derive no nourishment from the rivers themselves, but forages among the marginal bushes and vine tangles in exactly the manner of many another wren that ranges through thickets at a greater distance from running water? The only explanation that has occurred to me is that for many generations before the recent human settlement and extensive clearing of land in this region, the type of vegetation which it prefers was hardly to be found except along the banks of the broader streams. Although human activities have resulted in the creation of rather similar vegetation elsewhere, as in the vine tangles at the edge of the forest where it borders pastures and other clearings, where these birds could without doubt find adequate concealment and almost with certainty a sufficiency of the proper kind of food, the Riverside Bay Wrens remain close to their ancestral haunts because they do not "feel at home" at a distance from them.

The two doves of the genus *Leptotila* inhabiting this region are so similar in coloration that they can be distinguished only by careful scrutiny. The Verreaux White-fronted Dove (*L. v. verreauxi*) forages over shady lawns and close-cropped pastures, as well as beneath somewhat open thickets. The Rufous-naped Cassin Dove (*L. cassinii rufinucha*) hunts beneath these same thickets and others heavier, where the White-fronted Dove is not found; but it usually avoids the lawns and pastures. Yet it is hard to believe that one of these brownish pigeons should shun the open spaces because it would be a more conspicuous mark for birds of prey than the other, expecially in this region where bird-eating hawks are rare; and the food that one finds in the pasture would certainly seem to be good nourishment for its congener. The White-fronted Dove is a far-ranging species that probably grew accustomed to open country in regions that have been long shorn of their forest covering; the Cassin Dove is a species of restricted range that has not yet learned to take advantage of the recently made pastures.

SUMMARY

Twenty-nine pairs of congeneric species of birds, one group of three species, and one group of four, have been found nesting in the same or in contiguous areas during fourteen seasons of field work in Central America. An attempt is made to discover what prevents the interbreeding of these closely related species that come in contact during the nesting season. In no instance do the congeneric species have mutually exclusive breeding seasons; hence it is not possible that interbreeding is prevented by the circumstance that they do not enter the reproductive state at the same time. Some of these congeneric species may be distinguished at a glance, whereas others are confusingly similar in appearance; but nearly all are readily recognized by their distinctive voices. It is not known whether any of these congeneric pairs are physically able to produce hybrids; but for these species to remain distinct, sterility barriers do not appear to be necessary, because subjective or psychological factors seem to keep them from intermating. This "psychological isolation" appears to operate chiefly through differences in plumage and voice, but also through divergent habitat restrictions, some of which at least seem to be based upon subjective preferences rather than upon the physical or biological unsuitability of neighboring habitats from which the species is absent.

ACKNOWLEDGEMENTS

The subject of this paper was suggested to the writer by Dr. Ernst Mayr. To him and to Dr. Josselyn Van Tyne I am greatly indebted for assistance in the preparation of the manuscript.

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