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(*COLAPTES*) OF NORTH AMERICA

LESTER L. SHORT, JR.

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## INTRODUCTION

IN THE HUNDRED YEARS since the publication of Darwin's "Origin of Species," much work in evolutionary biology has resulted in the development and clarification of Darwinian concepts of the process by which species come into existence. The attainment of reproductive isolation is now known to be the critical point in the speciation process. Reproductive isolating mechanisms are achieved, to a greater or lesser degree, as a consequence of the genetic divergence of populations which have become geographically isolated (see Mayr, 1947, for arguments against the occurrence of sympatric speciation). Since divergence is gradual, it is to be expected that secondary contacts will occur at times between populations that have not achieved effective reproductive isolation. Sibley (1957, pp. 167-170) has discussed the hybridization phenomena resulting from the formation of such secondary contacts. Other discussions of hybridization following secondary contact were presented by Mayr (1942, 1949) and A. H. Miller (1949, 1955).

One of the most widely known situations of hybridization in the class Aves occurs between the yellow-shafted flicker (*Colaptes "auratus"*) and the red-shafted flicker (*C. "cafer"*). The interbreeding of these two forms in the central part of the continent was discovered by Audubon's party in 1843 on the Missouri River. The accounts of this discovery are contained in the journals of Audubon (M. R. Audubon, 1897) and of Edward Harris (Harris, 1951), who accompanied Audubon. The remarks of these pioneer naturalists upon encountering hybrid flickers are classical. Audubon, in his journal for July, 1843 (M. R. Audubon, 1897, vol. 2, p. 71), stated his belief that the flicker situation "will puzzle all the naturalists in the world." This followed the bringing in of five hybrid flickers by Harris and Sprague at Fort Union, along the Missouri at the present boundary of North Dakota and Montana. Harris in particular commented on the perplexing problem. His remarks of July 1 (Harris, 1951, pp. 121-122) are interesting enough to quote in part: "Here we are all in a heap with these Golden wings and Red-shafts—We have the *Red-shafted Bird* with *Red cheeks*, and *Newly-fledged birds* with *red*

*shafts* and *black cheeks*, *Yellow-winged* birds with *Red cheeks* and with *black cheeks*, both adults. I would give a great deal to have Dr. Bachman here with a dozen specimens of Golden-wings from our side of the mountains (i. e., the Appalachians), wouldn't we make a night of it?" Audubon decided that the hybrids were of a new species which he named "*Picus ayresii*," the "Missouri Red-Moustached Woodpecker" (1844, pp. 348-349, pl. 494; 1856).

Although the flicker problem has been widely commented upon since Audubon's time, there has been only one attempt to analyze the situation. This was J. A. Allen's study (1892) some 70 years ago. Allen was able to demonstrate that large-scale hybridization was taking place between the forms *auratus* and *cafer*. However, he lacked sufficient specimens to determine the exact areas of interbreeding and the effects of hybridization on the populations involved. He was also unaware of the interbreeding that was occurring between *cafer* and the form *chrysoides* in the Southwest. The purpose of the present paper is to describe hybridization among the North American flickers and to evaluate the effects of the interbreeding on the various flicker populations.

## METHODS

The analysis of hybrid situations is a relatively recent development in avian systematics. Meise's 1928 paper on hybridization in *Corvus* may be considered the earliest such study. Consequently it is important to present the methods used in an investigation of this nature.

The present study has involved both the examination of specimens and observations of the behavior and habits of flickers in captivity as well as in the wild. Behavioral and ecological notes were obtained for all three forms involved in hybridization. Hybrids between red-shafted flickers and yellow-shafted flickers were observed in the Plains.

Specimens were examined from many localities in the ranges of the forms concerned. Color patterns were analyzed in, and measurements were obtained from, all adult breeding

birds. Statistical methods were used in dealing with both color and mensural characters. This method of analysis allowed me to determine the limits of the hybrid zone, and the extent of introgression (see definition, p. 360) in populations away from the areas of interbreeding.

A study of the variation patterns of related woodpeckers was undertaken to aid in the understanding of variation patterns in North American flickers. Specimens of all races of flickers found in North and Middle America were studied with respect to color and mensural characters. The investigation of patterns of variation in characters not utilized in the analysis of hybrids allowed an appreciation of the normal variation expected in characters not affected by hybridization and introgression.

An effort was made to investigate the past history of conditions on the North American continent. The available information concerning past conditions was reviewed, and an attempt was made to evaluate the effects of these conditions on the past and present situations of hybridization.

Data obtained during the study were used to deal with the taxonomic status of the interbreeding forms.

### MATERIALS

The writer spent two field seasons (1955, 1956) in the zone of hybridization between the red-shafted flicker and yellow-shafted flicker. During these seasons Cornell field parties conducted transects and obtained specimens in Nebraska, South Dakota, and Colorado. A field party revisited a number of localities and obtained additional specimens in 1957. A sample of breeding flickers was obtained in New York State in 1957 and 1958. Interbreeding between the gilded flicker and red-shafted flicker was investigated in Arizona during the winter and spring of 1963. The total number of adult flickers collected for purposes of this study was 494. Additional specimens were examined during visits to various collections, or were obtained on loan from the persons and institutions listed under Acknowledgments. About 6000 specimens, including non-breeding and juvenile North American flickers and specimens of closely related woodpeckers, were examined. Data from about 3000 specimens were used in the

study. The sizes of samples from various areas differed greatly. Statistics were computed for samples of five or more birds, and in all tabular material in this paper parentheses surround figures that treat samples of fewer than five individuals.

Observations on behavior and ecology were made on the field expeditions mentioned above. The behavior of eastern flickers was studied in the field in the vicinity of Ithaca during the years 1955-1959. Through the courtesy of Dr. Charles G. Sibley it was possible to investigate the behavior of captive eastern flickers at the Department of Conservation Aviary during the years 1955-1958. Observations of the habits of red-shafted flickers and gilded flickers were made in Oregon (1953), Mexico (1954, 1963), and Arizona (1953, 1963).

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The portion of the study dealing with flicker hybridization in the Great Plains was part of a project involving the investigation of situations of avian hybridization in the Plains undertaken by Dr. Sibley and supported by a



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Drs. Richard Fischer and George M. Sutton made available specimens from their personal collections. I am indebted to them and to the authorities of the institutions who also made available specimens under their care.

Specimens were examined from the collections of the institutions that are listed below:

A.M.N.H., the American Museum of Natural History  
 A.N.S.P., Academy of Natural Sciences of Philadelphia  
 C.A.S., the California Academy of Sciences, San Francisco  
 C.M., Carnegie Museum, Pittsburgh  
 C.M.N.H., Colorado Museum of Natural History, Denver  
 C.N.H.M., Chicago Natural History Museum  
 C.U., Cornell University, Ithaca, New York  
 L.S.M.Z., Louisiana State Museum of Zoology, Baton Rouge  
 M.C.Z., Museum of Comparative Zoology at Harvard College  
 M.V.Z., Museum of Vertebrate Zoology, University of California, Berkeley  
 N.M.A.M.C., New Mexico Agricultural and Mechanical College, State College  
 N.Y.S.M., New York State Museum, Albany  
 O.C., Occidental College, Los Angeles  
 R.O.M.Z., Royal Ontario Museum of Zoology, Toronto  
 S.P.M., Saskatchewan Provincial Museum, Regina  
 T.N.H.C., Texas Natural History Collection, University of Texas, Austin

U.A.M.Z., University of Arizona Museum of Zoology, Tucson  
 U.C.L.A., University of California at Los Angeles  
 U.K.M.N.H., University of Kansas Museum of Natural History, Lawrence  
 U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor  
 U.O.M.Z., University of Oklahoma Museum of Zoology, Norman  
 U.S.N.M., United States National Museum, Smithsonian Institution

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#### RELATIONSHIPS OF NORTH AMERICAN FLICKERS

The genus *Colaptes* presently includes, according to Peters (1948), three "species" of North American flickers and three South American flickers. I favor the broadening of the genus to include the "genera" *Chrysomitris* and *Nesocleus* (Bock and Short, in preparation). The enlarged genus *Colaptes* consists of the following:

##### Genus *Colaptes* Vigors

Subgenus *Colaptes* Vigors: North America and mountains of Central America; one species  
 Subgenus *Soroplex* (Gloger): South America; three species  
 Subgenus *Chrysomitris* (Swainson): South America; three species  
 Subgenus *Nesocleus* (Sclater and Salvin): Cuba; one species

The species of *Colaptes* are medium-sized woodpeckers, having yellow in the remiges, except for one form of *Colaptes auratus*. They are more or less adapted for feeding on the ground; a large part of their diet consists of ants. The genus is closely related to the Central and South American genus *Piculus* (Bock and Short, in preparation).

There are in North and Central America five "groups" of well-differentiated flicker

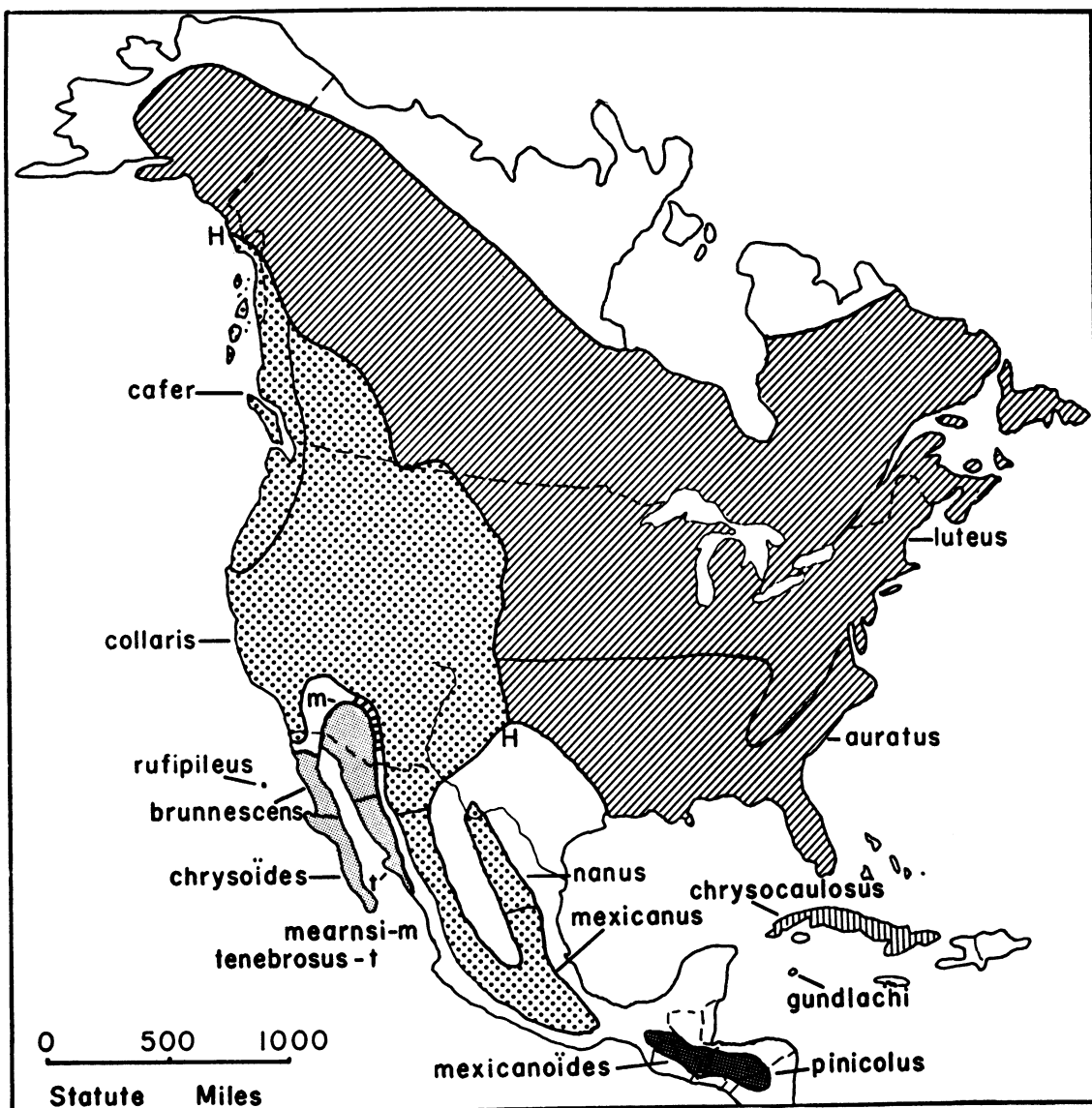


FIG. 1. Ranges of the subspecies and subspecies groups of North American flickers (*Colaptes auratus*). H marks the center of the hybrid zone between the *auratus* group and the *cafer* group. Slanting lines show the ranges of the populations of the *auratus* group. Vertical lines denote the distribution of the *chrysocaulosus* group. The large dotted area is the range of the *cafer* group. The area of fine stippling marks the range of the *chrysoides* group, and that of cross hatching is the range of the *mexicanoides* group.

populations which compose the subgenus *Colaptes*. Each of the groups is polytypic. Wherever members of different groups have come into contact, interbreeding has resulted. The "groups" of populations are here considered subspecies groups of one species, *Colaptes auratus* (Linnaeus), for reasons that are given below (pp. 419-420). The subspecies groups, with the subspecies that comprise

them, are as follows:

*auratus* group

*auratus* (Linnaeus)

*luteus* Bangs, including *borealis* Ridgway

*chrysocaulosus* group

*chrysocaulosus* Gundlach

*gundlachi* Cory

*cafer* group

*cafer* (Gmelin)

*collaris* Vigors, including *canescens* Brodtkorb,



*chihuahuae* Brodkorb, *martirensis* Grinnell,  
 and *sedentarius* van Rossem  
*rufipileus* Ridgway  
*nanus* Griscom  
*mexicanus* Swainson  
*mexicanoïdes* group  
*mexicanoïdes* Lafresnaye  
*pinicolus* Dickey and van Rossem  
*chrysoïdes* group  
*chrysoïdes* (Malherbe)  
*brunnescens* Anthony  
*mearnsi* Ridgway  
*tenebrosus* van Rossem

The ranges of the subspecies and subspecies groups are shown in figure 1.

The color-pattern features of the subspecies groups are summarized in table 1. The differences between the *auratus* group and the *cafer* group, and between the *cafer* group and the *chrysoïdes* group, are especially notable in view of the interbreeding that occurs among them. Apparently such differences are not necessarily associated with the presence of reproductive isolating mechanisms. In view of the nature of the color-pattern differences between the groups that hybridize, it seems likely that the two completely allopatric groups, *chrysocaulosus* and *mexicanoïdes*, have

not achieved reproductive isolation. The comments of Dickey and van Rossem (1938, p. 309) concerning the behavior of *mexicanoïdes* suggest that this form is similar to *cafer* and *auratus*, supporting the view that *mexicanoïdes* has not attained reproductive isolation while geographically separated from the other forms.

### ECOLOGY AND BEHAVIOR

Among the factors that determine the distribution of flickers in North America is the availability of a food supply. The diet of flickers of the *auratus* group consists of about 50 per cent ants (F. Beal, 1911). Other insects are taken when available, and fruit appears to form an important part of the diet of flickers wintering in the northern states. It is apparent from the migratory habits of flickers in the north that the winter distribution of these birds is affected by the lack of insect food, despite their feeding on fruit at this season. However, the widespread occurrence of ants in most types of habitats during the summer indicates that this factor alone is of little importance in limiting the distribution of flickers during the breeding season.

Related to the feeding of flickers on ants is

TABLE 1  
COLOR-PATTERN FEATURES OF NORTH AMERICAN FLICKERS (ADULTS ONLY)<sup>a</sup>

Character	<i>auratus</i> Group	<i>chrysocaulosus</i> Group	<i>cafer</i> Group	<i>mexicanoïdes</i> Group	<i>chrysoïdes</i> Group
Mean width of back bars, in mm.	2.8	3.0	2.8	4.0	2.2
Per cent with rump spots	45	100	55	100 <sup>b</sup>	50
Mean number of tail bars <sup>c</sup>	4.5	6.7	3.0	1.6	3.3
Black color in tail (mean extent from tip, in mm.)	37	37	48	40	55
Mean (maximum) depth of breast patch, in mm.	16.3	22.4	18.0	24.5	22.0
Malar-patch color					
Males	Black	Black	Red	Red and black	Red
Females	Tan	Tan or gray or both	Tan and gray	Rufous	Gray
Throat color	Tan	Tan	Gray	Gray	Gray
Crown color	Gray	Gray	Brown	Rufous	Rufous yellow
Ear-covert color	Tan	Tan	Gray	Gray	Gray
Shaft color	Yellow	Golden yellow	Salmon pink	Pink-orange	Yellow
Nuchal patch	Present	Present	Absent	Absent	Absent

<sup>a</sup> Sample sizes range from 14 to 25 birds from localities within the range of each group farthest removed from areas of contact with other groups. Female samples were checked, and differences from males are noted.

<sup>b</sup> All birds show spotting, but few are so heavily spotted as normal individuals of *chrysocaulosus*.

<sup>c</sup> Mean number of bars on outer (fifth) rectrix.

the type of ground cover. Flickers feed largely in open areas and are apparently unable to utilize areas covered with dense growth. Forested areas having little undergrowth, such as certain kinds of evergreen forests, are occupied by flickers. Bent (1939, p. 259) reports *Colaptes auratus auratus* as occurring commonly in pine barrens. The race *collaris* of the *cafer* group is found up to timberline in western mountain forests (Bent, 1939, pp. 287–88), especially in lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*), according to Snyder (1950). Flickers are common in open areas where trees are scattered, as along the river valleys of the Plains and in farming areas. The requirement of the flicker for open ground on which to forage approximates that of the robin (*Turdus migratorius*), at least in the northern part of the continent.

Flickers are limited in their distribution by the occurrence of trees (or substitutes for them) in which to nest. Although they largely excavate their own nesting holes in trees, flickers have been reported nesting in nest boxes, fence posts and telegraph poles, hay piles (Farley, 1901), buildings, wagon-wheel hubs (Agersborg, 1881), and in holes in banks (Elliot, 1892). The need for trees for nesting purposes has prevented flickers from occupying the tundra and large portions of the Great Plains. Flickers are also absent from desert areas lacking trees along water courses or arborescent cacti suitable for nesting, such as the Mohave Desert, parts of the Great Basin, and the deserts of northwestern Sonora and northeastern Baja California.

Factors limiting the southward distribution of flickers are little known. The southern limits of the distribution of the subgenus are reached at Grand Cayman Island in the Caribbean and in Nicaragua. Flickers have been unable to cross the water barrier separating Cuba from the rest of the Greater Antilles. They occur only in highlands in Central America. Other highland species that are

essentially North American or Holarctic and that extend only as far south as Nicaragua are: *Spizella passerina*, *Loxia curvirostra*, *Sialia sialis*, *Certhia familiaris*, *Cyanocitta stelleri*, and *Columba fasciata*. In addition the mountain-inhabiting, northern Middle-American species *Icterus gularis*, *I. wagleri*, *Setophaga picta*, *Peucedramus taeniatus*, *Dendroica graciae*, and *Contopus pertinax* reach only as far south as Nicaragua. Several North American forms occur south of Nicaragua in the mountains of Costa Rica and Panama, such as *Junco vulcani*, *Dendrocopos villosus*, and *Buteo jamaicensis*. Many other North American species extend south in the highlands only to the Isthmus of Tehuantepec, Guatemala, or Honduras. Climatic conditions, competition, and other possible factors responsible for the limitation of the ranges of these forms remain to be investigated.

Other habits were summarized by Bent (1939, pp. 259–308). Little is known of the habits of the *mexicanoides* and *chrysocaulosus* groups, which were not covered by Bent.

Early studies of flicker behavior include those of Sherman (1910) and Noble (1936). Noble demonstrated that individuals of *Colaptes auratus luteus* depend on the presence or absence of the malar patch for sexual recognition. He also found that females of this form give a vocalization immediately preceding copulation. Such a vocalization would be potentially important in regard to the formation of ethological isolating mechanisms. However, I have been unable to corroborate Noble's finding, despite careful observation of copulations in the same form.

A study of flicker behavior (Short, in preparation) and a review of the literature have failed to produce any evidence for the occurrence of major differences in behavior among the forms of flicker that hybridize. The ability of these forms to interbreed suggests that any behavioral differences among them do not function as ethological isolating mechanisms.



# HYBRIDIZATION BETWEEN THE YELLOW-SHAFTED FLICKER AND THE RED-SHAFTED FLICKER

## METHODS OF CHARACTER ANALYSIS

IN DEALING WITH HYBRIDIZATION, one must measure the phenotypic expression of various color characters in hybrid individuals. Such measuring has been accomplished by means of a "hybrid-index" system (which possibly should be called a "character-index" system rather than a "hybrid-index" system). Anderson (1936) developed a method of analysis utilizing a scoring system in dealing with a case of hybridization in plants (*Tradescantia*). In the same year (1936) Meise devised a similar method for use in his study of hybridization in sparrows (*Passer*). Anderson's method was independently developed for use in studies of hybridization in towhees (*Pipilo*) by Sibley (1950, 1954); this was followed by its use in other avian hybrid situations, such as those studied by Dixon (1955), Sammalisto (1956), and others by Sibley and his students. Meise's method was utilized in the study of hybridization in honeyeaters (*Melidectes*) by Mayr and Gilliard (1952).

Anderson's hybrid-index system was described in detail in Anderson (1949, pp. 88-91); a brief summary is given here. A character as it appears in one form is scored as 0. Gradations of the character that are readily discernible are given progressively greater scores (1, 2, 3, and so on) as they approach the condition of the character as it is in the other form; the character as it appears in the other form is given the score of the next number above that of the last gradation. Thus, if three gradations are recognized, the scores for the character would range from 0 to 4. The number of intermediate gradations varies

from character to character; some characters would thus have smaller ranges of scores than others. Scores for various characters may be totaled to give a summated score for each individual. If six characters are utilized, each having scores ranging from 0 to 4, the total score for individuals would range from 0 for a "pure" individual of one form to 24 for a "pure" individual of the other form. Meise's method is essentially similar; the pure forms are placed at the ends of a scale arbitrarily set at from 0 to 100. Each character is given a range of scores (such as 0-5, 0-15) depending upon its "importance" (Mayr and Gilliard, 1952, p. 327). It is doubtful that the difference between the systems is important enough to warrant the use of either one over the other. In the present investigation I have utilized Anderson's method, as developed by Sibley (1950, 1954) in dealing with avian hybrid situations. Gradations and scores are given in table 2 for each character (see discussion of the characters in the next section).

Gradations of characters used in this study were determined initially by an examination of specimens from all parts of the range of the forms involved, including hybrids. Scoring was usually accomplished by laying out individuals of a series in the sequence in which they showed expression of a single character. Occasionally, single specimens were scored for all characters. Reference specimens showing gradations of the characters were available at all times; these were constantly used to check the scoring of the characters.

## VARIATION IN COLOR CHARACTERS

Details of variation in those characters employed in an analysis of hybridization between the subspecies groups *auratus* and *cafer* are of importance, since effects other than those due to hybridization and introgression must be recognized.

### MOLTS AND PLUMAGES

Newly hatched flickers possess no down feathers (Test, 1945) and acquire their juvenal plumage in the nest. This plumage is molted after they leave the nest. All juvenal feathers are molted, except for the secon-

TABLE 2

SCORES AND SYNOPTIC DESCRIPTIONS OF GRADATIONS USED IN ANALYSIS OF COLOR CHARACTERS  
OF HYBRIDS BETWEEN THE *cafer* GROUP AND THE *auratus* GROUP

Character and Score	Description
Crown color	
0	Gray, as in <i>auratus</i>
1	Brown traces in forehead and crown
2	Intermediate, crown half brown, more gray on hind neck
3	Crown brown, hind neck gray toward back
4	Brown, confluent with back color, as in <i>cafer</i>
Color of ear coverts	
0	Vinaceous tan, as in <i>auratus</i>
1	Gray traces
2	Intermediate
3	Tan traces, especially below eye
4	Gray, as in <i>cafer</i>
Throat color	
0	Vinaceous tan, as in <i>auratus</i>
1	Gray traces, usually on lower throat
2	Mixed gray and tan
3	Tan traces, usually near chin
4	Gray, as in <i>cafer</i>
Nuchal patch	
0	Present; broad, as in <i>auratus</i>
1	Present, restricted in width (less than one-half of normal width)
2	Present, broken in one or more places
3	Traces, usually at sides of nape
4	Absent, as in <i>cafer</i>
Shaft color	
0	Yellow, as in <i>auratus</i>
1	Orange traces, either faint in all feathers or heavy in one or several
2	Shafts orange to red, barbs yellow-orange
3	Orange-yellow
4	Salmon pink, as in <i>cafer</i>
Malar color (males)	
0	Black, as in <i>auratus</i>
1	Some red (traces to 20% red)
2	Intermediate
3	Some black (traces to 20% black)
4	Red, as in <i>cafer</i>

daries, which are retained for a year until the first annual molt (Test, 1945, MS). One-year-old birds in the breeding season differ from older birds only in the retention of the juvenal secondaries. The shafts of the (juvenal) secondaries are often considerably paler than the primaries, so that some, but not all, first-year birds can be distinguished from older ones. Those year-old birds that can be

distinguished do not differ in measurements and color from older birds. Also, because not all first-year birds are separable from older adults, it is unlikely that a grave error is introduced by the inclusion of first-year individuals with older birds in analysis of hybridization and introgression. Other peculiarities of the juvenal plumage and post-juvenal molt will be discussed elsewhere. The

only molt in adult flickers is the annual molt, which is complete and takes place from about June to September or October (Test, 1945).

#### NUCHAL PATCH

The nuchal patch is generally present in all individuals of the *auratus* and *chryso-caulosus* groups. It is present in some individuals of all races of the species, adult birds as well as juveniles. There is a definite tendency in races generally lacking a nuchal patch for traces to appear in more males than females. This is probably correlated with the greater extent of the patch in juvenile males than in juvenile females. In the *cafer* subspecies group the tendency toward possessing a nuchal patch increases with increasing proximity to the zone of hybridization with the *auratus* group. Thus, traces of the nuchal patch in individuals of this group are to some extent due to the effects of introgression (see section on introgression below). Also, part of its occurrence may result from the latent genetic tendency of the *cafer* populations to produce this marking, and an increase in the appearance of the character from past introgression. Since it is impossible to separate effects due to introgression from those due to the genetic potential of *cafer* itself, a degree of error is incorporated in the use of this character in the color analysis of hybrids. The magnitude of the error can be seen by an examination of the occurrence of nuchal traces in those forms geographically isolated from populations of the *cafer* group. These include the subspecies *rufipileus* of the *cafer* group, and *mexicanoïdes* and *pinicolus* of the *mexicanoïdes* group. The *chrysoïdes* group, as is shown below, is in genetic contact with the *cafer* group. There is introgression of genes determining the presence of the nuchal patch from the *auratus* group into the *cafer* group, and thence into the populations of *chrysoïdes*. The occurrence of the nuchal patch in the subspecies mentioned above is as follows:

SUBSPECIES	TRACES OF NUCHAL PATCH
<i>mexicanoïdes</i>	Present in 1 of 24 males, 0 of 22 females (Test, MS, p. 42, found traces in 3 of 31 adults)
<i>pinicolus</i> , Honduras	Present in 3 of 16 males (extensive in 2 of 3), 0 of 14 females

<i>pinicolus</i> , northern Nicaragua	Present in 4 of 7 males (extensive in 1), 0 of 5 females
<i>rufipileus</i>	Present in 1 of 9 males, 0 of 11 females

The tendency toward presence of the nuchal patch in *pinicolus* may be due to selection in a more southern area, or to the continued presence of this trait in a form more nearly like the ancestral North American flicker, which probably arrived in North America from South America via Nicaragua and Central America. *Rufipileus* may have separated from the continental *cafer* population after hybridization and introgression had affected the latter. Comparing the number of male individuals of *mexicanoïdes* showing nuchal traces with the number of California *cafer* males showing nuchal traces (eight of 33 breeding male California flickers examined show nuchal traces), we find that more traces are found in the *cafer* males. Utilizing the chi-square test, the differences between the two samples (chi square = 5.30) is significant at the 5 per cent level, but not significant at the 1 per cent level. The observed difference is presumed to be due to some extent to introgression of *auratus* genes into the *cafer* populations. In those forms not usually possessing the nuchal patch, females tend to show indication of this character much less than do males. One of 21 California females, and none of 43 females of the two subspecies of the *mexicanoïdes* group show nuchal-patch traces. In hybrid flickers the nuchal patch is restricted and somewhat broken. Extremes range from traces of the nuchal at the sides of the neck, to a complete, but restricted, nuchal patch. Examination of hybrids indicated early in the study that the nuchal-patch character was controlled by a number of genes. This fact makes possible the use of the character in a hybrid-index system. Although variation in the character is continuous, three gradations were readily discernible, allowing scores of 0 to be assigned to the condition of the nuchal patch as in *auratus* and 4 to be assigned to the condition (absent) as found in *cafer*. The scores and descriptions of the gradations are given in table 2.

#### THROAT COLOR

The area considered as the "throat" includes the chin and throat regions. It is

bounded by the bill, the malar area, the ear coverts, the area of dorsal coloring on the neck, and the breast patch. The throat color of the *auratus* and *cafer* groups is vinaceous tan in the former and neutral gray in the latter. Juvenile birds of both groups generally have gray and tan throats, much resembling the intermediate throat color of hybrids. The throat color in juvenile *cafer* tends, however, to be more gray, and that of *auratus* juveniles more tan. Individual variation in the *auratus* group involves a "frosting" effect from the slight silver-gray cast of the throat color. When present, it occurs over the entire throat area, so is easily distinguished from evidences of hybridization, which involve the appearance of gray in place of tan in parts of the throat area. There is no detectable sexual variation in this character; however, males show indications of hybridization in the character to a greater degree than do females. There is no geographic variation in throat color in *auratus*. The *cafer* group possesses a gray throat which occasionally has a yellowish cast. There is little geographic variation; this involves the lightness or darkness of the gray color. Test (MS, p. 55) notes three gradations in the hybrids between the two groups. I am similarly recognizing three gradations (see table 2), the limits of which are somewhat subjective, since there is continuous variation from tan to tan with gray traces, to a half-and-half mixture, and so on. Generally gray appears in a tan throat just above the breast patch. Tan traces are most apt to appear first in the chin area of an individual with an otherwise gray throat. More intermediate hybrids and juvenile birds of both forms seem to show more tan in the central and upper parts of the throat and more gray on the lower throat. The scores given for throat color range from 0 for the expression of the character as it appears in *auratus* (all tan) to 4 for the character expressed as in *cafer* (all gray); the gradations are described and scores indicated in table 2.

#### COLOR OF EAR COVERTS

The area of the ear coverts as used here includes the auricular region and its suborbital continuation forward to the bill. It is bounded by the bill, the supraorbital line, the

eye, the crown, the side of the neck, and the throat and malar areas. This character might appear to be closely associated with throat color, as its color is similar to that of the throat in all flickers. However, the two are often expressed differently in hybrids. Also, juvenile birds show a difference between the color of the throat and that of the ear coverts. Juveniles of the *cafer* group generally have more gray ear coverts; when present, tan usually occurs in traces. Examination of 41 juveniles of *cafer* from far western states (California, Nevada) showed that the color of the throat area was completely gray in 10 per cent, while the intermediate half-gray, half-tan condition was found in 44 per cent. Ear-covert color in the same individuals was gray in 53 per cent and half gray, half tan in only 2 per cent (one individual). These differences are significant at the 1 per cent level according to chi-square tests. Juveniles of the *auratus* group generally have mixed tan and gray ear coverts. The tendency of juveniles of the *cafer* group to have grayer ear coverts seems reflected in *auratus* juveniles having less tan and more gray ear coverts; the throat patch is more tan and less gray. Of 45 juveniles of *auratus*, 58 per cent had half-gray, half-tan ear coverts, while only 40 per cent had half-gray, half-tan throat color, the difference being significant by the chi-square method at the 5 per-cent, but not at the 1 per-cent, level. Some 20 per-cent of the same individuals had an all-tan throat, while none had all-tan ear coverts (significant difference at 1 per-cent level by chi-square method). There is no apparent geographical variation in ear-covert color. Traces of gray in otherwise tan ear coverts in hybrids appear first in the auricular area; traces of tan in otherwise gray ear coverts appear first in the anterior part of the subocular area. The more intermediate ear-covert color is indicated by patches of gray and of tan, the patches of each comprising about half of the ear-covert area. Descriptions and scores of the various gradations of ear-covert color are given in table 2.

#### MALAR COLOR

The malar region extends from the bill back to an ill-defined area behind the eye. It is bounded by the bill, the subocular line, the



auricular area, and the throat. There is considerable variation in the shape of the patch, but usually it is broad posteriorly, tapering to a lesser width at the front. Both black and red pigments occur in the malar patches of all adult male flickers of the *cafer* and *auratus* groups (see discussion on pigments). However, the red is masked by black in *auratus*, and the black is restricted to the feather bases in *cafer* individuals. The macroscopically visible effects are discussed here and are the ones utilized in the hybrid index. Juvenile *auratus* individuals, including females, possess black malar patches; rarely is there any visible red (one in 50 individuals shows traces). Juvenile male *cafer* specimens generally possess red and black malar patches. The malar patches are mostly red, with some black traces, and occasionally are half black or all red. There is no detectable geographic variation in malar color, except from effects of hybridization. Female flickers possess tan, tan with some gray (*auratus* group), gray with some tan, or gray malar areas. Only the male malar color was used in the analysis of hybrids. Hybrid individuals show various combinations of red and black in the malar patch. The black condition of *auratus* was assigned a score of 0, and the red of *cafer* a score of 4. The three gradations are described and scores assigned them in table 2. Traces of red in an otherwise black malar patch are usually situated around the periphery of the patch. Black traces in an otherwise red malar patch may occur in the center or around the edges.

#### SHAFT COLOR

"Shaft color" refers to the color of the under side of the rachises and vanes of the primaries, secondaries, and rectrices. Virtually all feathers of the body possess shafts of the color shown on the under-wing and under-tail surfaces, but examination of the latter areas, where the yellow or red is best shown, was sufficient for the purposes of this study. Juvenile flickers have paler shaft color than do adults. "Paler" as used here refers to a more lemon-yellow color in *auratus* and a more pinkish red color in *cafer*. As a consequence, the effects of hybridization on shaft color are less noticeable in juveniles than in adults. The variation observed in

adult individuals of *auratus*, the shafts of which range in color from pale lemon-yellow to cadmium-yellow, is probably not related to age, for one-year-old birds (bearing juvenal secondaries) have the shafts of their primaries and rectrices fully as bright as those in other adults. There is no sexual variation in shaft color in either group. This is the only character used in the hybrid index in which females and males from a locality can be combined into a single sample. The *auratus* subspecies group shows little geographic variation in shaft color. The *cafer* group, however, varies to some extent. The subspecies *mexicanus* possesses (Test, MS, p. 217) more orange feathers than does the race *collaris*; it is therefore difficult to determine indications of introgression in this character in *mexicanus* individuals. The subspecies *cafer* has more scarlet-colored shafts than other races of the *cafer* group.

The effects of diet on shaft color were discussed by Test (MS, pp. 205-206). Test showed that off-color feathers occurring in *cafer* are more yellow than normal owing to their being replaced at a time other than during the annual (postnuptial) molt. Apparently animal foods provide the material from which the red pigments are produced. The diet of flickers during the time of the annual molt consists principally of ants and other animals. During the fall, winter, and early spring the diet consists largely of plant materials. Replacement of feathers lost during this period results in a more yellow color of such feathers, because the plant foods ingested at these times do not contain the proper carotenoids necessary for the production of the red pigment. Xanthophylls in the plant food allow the formation of yellow pigment instead. Presumably, certain local conditions might cause a more yellow shaft color in the feathers of *cafer* individuals during the breeding season, thereby introducing a possible source of error in any determination of introgression of yellow shaft color into the *cafer* population. This point is dealt with in the discussion of introgression; however, it might be pointed out that many occurrences of yellowish feathers in *cafer* individuals involve the symmetrical occurrence of such feathers. These could not be explained on the basis of feather loss and

replacement during a time when plant food was being ingested. The cause of this symmetrical appearance of yellow-shafted feathers cannot be explained at present, but it is not unreasonable to suppose that it is related to hybridization. Likewise, there are both symmetrical and asymmetrical occurrences of red feathers in a number of individuals of the eastern *auratus* type. Test did not see any of these individuals, but they occur with some frequency (as described below in the introgression section). Dietary factors like those described by Test could not be operating in this case, since yellow shafts are normally produced following the annual molt while insect food was being taken (the same conditions that normally produce red in *cafer*).

Test also (MS) discussed the effect of exposure to light on shaft color. The shaft color of *auratus* becomes yellower in time owing to the effects of light, while that of *cafer* becomes more red. As a result, birds taken in the spring are more yellow-shafted (*auratus*) or more red-shafted (*cafer*) than fall birds; however, spring and early summer birds are utilized in this study, so comparisons are not rendered invalid by this fact. Also, museum specimens with use, or with exposure to light, might be expected to fade in time. The result of all fading that occurs will be to lessen the indications of hybridization, since fading in both forms tends to make the color of the shafts more yellow (*auratus*) or more red (*cafer*). The effect of hybridization on this character is to make the yellow of *auratus* more red, producing an orange color, and to make the red of *cafer* more yellow, also producing orange. Fading reduces the orange coloring—the reverse of the effects of hybridization. Any bias incorporated into the color analysis from the above effects on this character will thus tend to lower the apparent incidence of introgression.

In the formation of a hybrid index, 0 was assigned to the yellow shaft color of *auratus*, and 4 was assigned to the salmon-pink shaft color of *cafer* (see table 2). A score of 1 indicates one of two conditions. One of these is the condition in which a slight orange or gold color appears in the shafts, while the vanes (of the flight feathers) remain yellow. The other condition is one in which deep orange or

red shafts occur symmetrically in one or more pairs of flight feathers. A score of 2 is likewise indicative of one of two conditions. The shafts of all flight feathers may be deep orange or red, while the vanes are but slightly orange. The second condition given a score of 2 is one in which the vanes and shafts of some flight feathers are red, while others are lighter in color. A score of 3 indicates either orange color of the vanes and shafts of all flight feathers, or the symmetrical occurrence of orange or yellow in one or several pairs of flight feathers, while the others are red.

#### CROWN COLOR

The crown area here includes the entire dorsal head surface from the forehead to the nuchal patch or the back. The lateral limits of the area are marked by the throat area, the ear coverts, and the superciliary line. The crown is normally brown in *cafer* and gray in *auratus*. The race *nanus* of the *cafer* group possesses a decidedly grayer crown than the others. The subspecies *cafer* of the humid northwestern coast has a very brown-black crown, while *rufipileus* of Guadalupe Island has a rufous crown as in the *chrysoides* group. Brodtkorb's (1935) "race" *canescens*, characterized by a grayer crown, shorter wings, and shorter tail than in *collaris*, tends toward *auratus* in all these characters as a result of interbreeding of the *cafer* and *auratus* groups (as surmised by van Rossem, 1936). Individuals of the *auratus* group acquire a gray (or grayer) crown by wear; the crown is much more brown in fall birds in fresh plumage (Test, MS). Many spring birds retain a slight indication of brown in the crown. This fact affects the value of this character in the study of introgression from *cafer* into *auratus*. The *auratus* populations along the rivers of the Plains, especially in Oklahoma and Kansas, possess very light gray crowns. The juvenile flickers of both groups exhibit a crown color similar to that of adults; in *auratus*, however, the juvenile crown color is like the fall adult crown color (gray-brown), rather than like the spring color (gray) acquired in the adults by wear. Sexual variation was not found, except in regard to the effects of hybridization. Here again females show the effects of introgression in crown color much less than do males.

The gray crown color of *auratus* (in spring plumage) is assigned a score of 0 (see table 2), while the brown of *cafer* is scored 4. Gradations between these extremes are about like those noted by Test (MS, p. 31) for hybrid flickers. Traces of brown appear first in an otherwise gray crown in the forehead and the occiput; traces of gray first appear in a brown crown in the nape region. Hybrids intermediate in crown color are largely gray behind the occiput and brown before the occiput. The scores for the various gradations are given in table 2.

#### CHEMISTRY OF COLOR DIFFERENCES

The pigments present in flicker feathers are of two basic types, melanins and carotenoids. Melanins produce the black, brown, and gray colors, while the carotenoids produce the reds and yellows (see Goodwin, 1954, chap. 10, for discussion of avian carotenoids). The genetic control of the two types of pigments differs somewhat, as shown by the fact that albino flickers lack melanins completely but have the red nuchal and yellow shaft color (see Deane, 1880, for an example). Melanins present are probably of two kinds of pigments (Test, MS). Test (*loc. cit.*) found three types of carotenoid pigments in flickers: xanthophylls, carotenes, and neutral red. The following notes concerning the color characters used in the hybrid index are taken from Test (MS):

Crown color: Due to melanin, or melanins; produce brown crown in *auratus* which by wear becomes gray.

Nuchal patch: Pigments are red carotenoids, with some xanthophylls.

Throat color: Due to melanin, or melanins.

Ear-covert color: Due to melanin, or melanins.

Malar color: All flickers have red in malar of males. In *auratus* the rhachises of the malar feathers are red; this is masked by (black) melanins. Red appears where black is lacking (but Test concluded that there is a set of genetic factors determining the extent of the black). Of red color in *auratus* malars, Test stated (p. 224), "It seems almost certain that this phenomenon has no connection with interbreeding between *auratus* and *cafer*, but is merely an 'incidental' restriction of the deposition of melanin in a few feathers." Red present in eastern *auratus* (only three individuals noted) was in same position as that in *cafer*. Black found in six adult females of *auratus*; red

also detected. In *cafer* Test found melanins at the bases of the red feathers, red in middle and at tips.

Shaft color: Analyzed feathers from one specimen of *auratus* and three of *cafer*, with use of chromatography and spectrophotometry. Found xanthophylls and carotenes also present. Stated that (p. 201) "... in general, the red color of *cafer* results from the presence of red pigments not found in *auratus*; both species contain yellow pigments." Thyroid extract fed to flickers led to the inhibition of carotenoid deposition.

The information obtained by Test needs verification, as Test himself suggested. Probably more recently developed biochemical methods would make possible a more satisfactory identification of the pigments involved. In regard to the malar patch, Test suggested that the amount of black in *auratus* males is under genetic control. I would add that such is probably also true of *cafer*. Some juvenile males of *cafer* have black in the malar region, and Test indicated that melanins are present at the bases of red malar feathers in *cafer*. In fact genes controlling the extent of black in the malar region of *auratus*, and thus allowing the red color to be seen, may occur in *auratus* populations owing to introgression from *cafer*. Test was premature in his statement that restriction of melanin allowing red to become visible in *auratus* "has no connection with interbreeding" between the two forms. In regard to the shaft color, Test's work suggests that all red traces found in *auratus* are due to introgression from *cafer*, since only *cafer* produces the red carotenoids apparently responsible for this color. It is most unfortunate that only one *auratus* individual was utilized (and that one a fall bird) in connection with the work on shaft color. Also, it should be noted that several "faint" bands of pigment in *auratus* were not analyzed chromatographically (it is quite possible that some red carotenoids may be present in this form). The three *cafer* individuals used by Test were winter and early spring birds; two of these had "off-color feathers" (Test, 1942, p. 378) which could be due to the effects of hybridization. More information concerning these pigments in critically determined specimens from the breeding season would be welcome. Besides work on the *auratus* and *cafer* groups, it would be interesting to have information concerning the

shaft color of the *chrysocaulosus* group (more golden than *auratus*), of the *mexicanoides* group, and of the subspecies *mexicanus*. Test's study must be followed up in considerably greater detail before we can make definite statements concerning the nature of the carotenoid pigments in *auratus* and *cafer*, and the effects of hybridization on them.

#### HYBRID INDEX

The hybrid index obtained with the six color characters discussed above gives a range of from 0 for a male individual which is

phenotypically like *auratus* in all six characters to a 24 for a male individual phenotypically like *cafer*. In females the index is based on five characters, since females lack the red or black malar, and the range is from 0 to 20. Although there are difficulties (in scoring certain individuals, in the equal weight given all characters, and in other respects) with this admittedly rough method, this technique "permits a more precise recording of the differences between the populations and of the hybridity of individual specimens than any other, more subjective method" (Mayr and Gilliard, 1952).

#### ANALYSIS OF ZONE OF HYBRIDIZATION

##### THE PLATTE RIVER TRANSECT

A transect of the Platte-South Platte River of Nebraska and Colorado was established in 1956 to determine the extent of interbreeding between eastern and western "species pairs" in contact along the river valleys of the Plains. The Platte River was selected because of its size (which indicated that trees would be present along the valley) and because of its fairly straight west-east flow from the Rockies to the Missouri River. The subspecies *luteus* of the *auratus* group was known to occur in eastern Nebraska, and *collaris* of the *cafer* group was known to breed in the Rocky Mountain region of Colorado. Previous reports (Weakly, 1940) had indicated that *luteus* occurred west at least as far as North Platte on the Platte River. Early observations, such as those of James (Thwaites, 1905) in 1819, indicated that a woodland connection existed from the Missouri to the Rockies along the Platte-South Platte River.

In planning the transect, we selected 10 collecting localities in advance at intervals of 50 miles. On the way west up the Platte the party made five camps at 100-mile intervals, and these were bisected on the return trip. One of the localities (Grand Island) was visited in 1955; the eastern six localities, including Grand Island, were revisited in 1957. Approximately three collecting days were spent at each camp in one visit by a party of three or four persons. Additionally, I visited the Crook, Colorado, locality for five days in 1963. Thus, three collecting days were spent at each of the three western localities, and

six days were spent at each of the eastern six localities, except for Grand Island where nine collecting days were spent. The localities visited were as close as possible to the actual 50-mile interval selected and to the localities that had been planned in advance. The locations of the 10 collecting stations, listed from east to west, follow; in parentheses are the symbols for each locality as given on the map (fig. 2) and the number of flickers obtained at each.

1. Platte River, 1300 feet, 2.5 miles east-south-east of Schuyler, Colfax County, Nebraska (Sch, 17 males, 20 females).
2. Platte River, 1550 feet, 3 miles south-south-west of Silver Creek in Polk County, Nebraska (SiCr, 13 males, 17 females).
3. Platte River, 1900 feet, 7 miles south-south-west of Grand Island, Hall County, Nebraska (GrIs, 16 males, 13 females).
4. Platte River, 2300 feet, 3 miles southeast of Elm Creek in Phelps County, Nebraska (ElmCr, 14 males, nine females).
5. Platte River, 2500 feet, 2 miles southeast of Gothenburg, Dawson County, Nebraska (Goth, 19 males, 14 females).
6. South Platte River, 2950 feet, 1 mile south-east of Sutherland, Lincoln County, Nebraska (Suth, 15 males, 14 females).
7. South Platte River, 3500 feet, 8 miles south-west of Big Springs, Deuel County, Nebraska (BigSp, five males, three females).
8. South Platte River, 3700 feet, 5 miles east-southeast of Crook, Logan County, Colorado (Crook, 11 males, 11 females).
9. South Platte River, 4300 feet, 8 miles west-northwest of Fort Morgan, Morgan County, Colorado; also South Platte River, 4400 feet, at

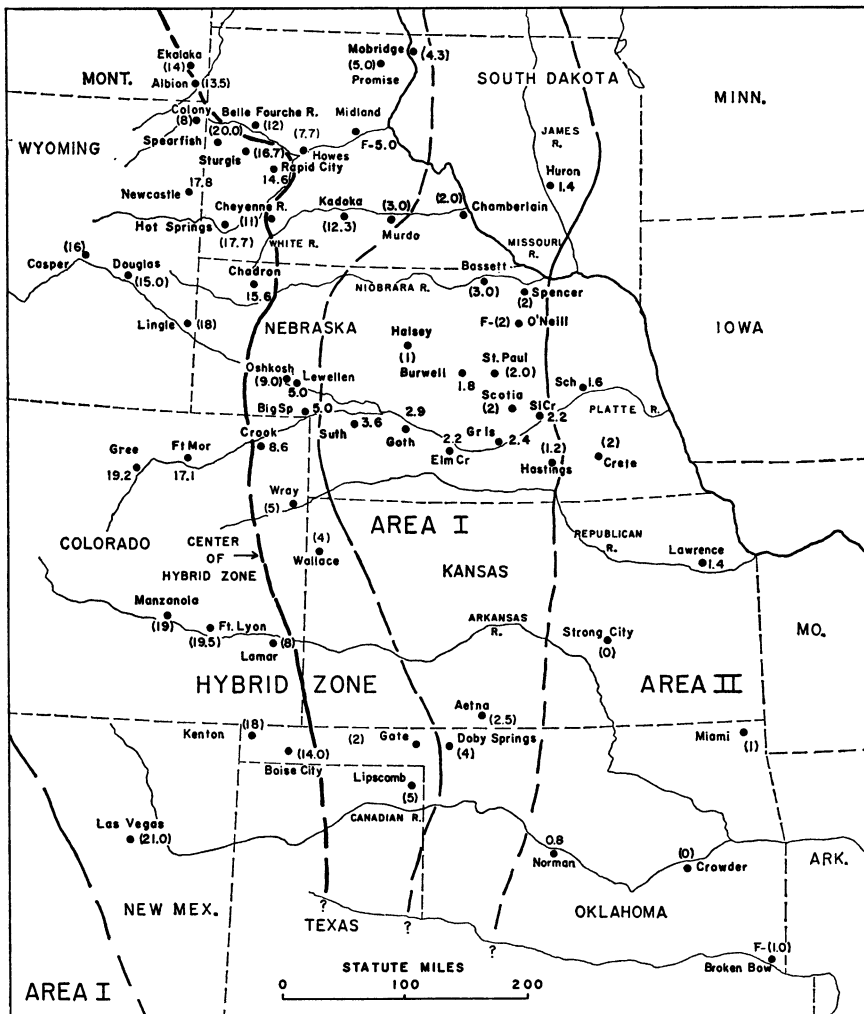


FIG. 2. The hybrid zone and areas of introgression in the southern Plains. Area I is the primary area of introgression, and Area II is the secondary area of introgression. Hybrid indexes are given for the samples from the various localities; samples of fewer than five specimens are shown by parentheses around the hybrid indexes. Indexes are for males, except in a few cases in which only females were available (F preceding the hybrid index).

*Abbreviations:* For the Platte River Valley, from east to west: Sch, Schuyler; SiCr, Silver Creek; GrIs, Grand Island; ElmCr, Elm Creek; Goth, Gothenburg; Suth, Sutherland; BigSp, Big Springs; FtMor, Fort Morgan; Gree, Greeley.

Goodrich, Morgan County, Colorado (FtMor, 12 males, seven females).

10. South Platte River, 4800 feet, 7 miles southwest of Greeley, Weld County, Colorado (Gree, nine males, six females).

The specimens obtained were analyzed with the hybrid-index technique as described above; weights were available for all specimens, and standard wing (chord), tail, bill

(from nostril), and tarsal lengths were taken (see tables 4 to 8). Examination of the color characters of the 245 adult flickers taken at the 10 localities indicated that only 20 could with certainty be called "pure" *auratus* (= 0 score in all characters). An additional 50 adults were indexed at 1, thus closely approximating *auratus*. All the specimens indexed at 0 or 1 were collected at the seven



TABLE 3  
HYBRID INDEXES OF PLATTE RIVER SAMPLES

Locality	Sex	N	Mean Hybrid Index	2 S. E.	1 S. D.	Range	Index Expressed as Per Cent of <i>cafer</i>
Schuyler	♂	17	1.59	0.66	1.37	0-5	6.63
	♀	20	1.95	0.50	1.10	1-4	9.75
Silver Creek	♂	13	2.23	0.94	1.69	0-5	9.30
	♀	17	1.82	0.84	1.73	0-6	9.10
Grand Island	♂	16	2.44	0.60	1.21	0-5	10.20
	♀	13	1.54	0.66	1.20	0-3	7.70
Elm Creek	♂	14	2.21	0.90	1.67	0-5	9.21
	♀	9	1.33	0.74	1.12	0-3	6.65
Gothenburg	♂	19	2.95	0.62	1.36	1-5	12.30
	♀	14	2.00	0.82	1.52	0-5	10.00
Sutherland	♂	15	3.60	1.74	3.38	0-15	15.00
	♀	14	2.71	0.90	1.68	0-7	13.60
Big Springs	♂	5	5.00	2.60	2.92	3-8	20.80
	♀	3	2.67	—	—	1-4	13.35
Crook	♂	11	8.59	3.32	5.49	3-20	35.79
	♀	11	11.64	2.64	4.39	3-17	58.20
Fort Morgan	♂	12	17.09	1.96	3.40	9-21	71.20
	♀	7	15.86	1.02	1.34	14-18	79.30
Greeley	♂	9	19.22	1.56	2.35	15-21	80.01
	♀	6	15.67	1.46	1.79	13-18	78.30

eastern localities; 0-indexed specimens were obtained only from Sutherland eastward. Specimens *cafer*-like (= 24 for males, 20 for females) in all characters were not obtained from the Platte River area in Nebraska (see fig. 3). None of the 52 adult flickers obtained at the three Colorado localities along the South Platte (Crook, Fort Morgan, and Greeley) was "pure" *cafer* in all characters. An additional 32 flickers (taken April-August) from southeastern (15) and western (17) Colorado were examined in connection with this study. Only three (all females) of the 32 were indexed at the *cafer* end of the hybrid index (20), while two others were one index point toward *auratus* (two females indexed at 19). These five specimens came from western Colorado. Thus, all flickers collected along the South Platte River from about the Nebraska-Colorado border west to the Rocky Mountains were ascertained to be hybrids. This point is significant, for it indicates that flickers of the parental types are not in contact; rather, between the eastern *auratus* and western *cafer* populations a population exists

consisting entirely of hybrids. "Hybrids" as utilized throughout this paper denote individuals that are products of the interbreeding of the two flicker populations, regardless of whether they are F1, F2, back-cross, or recombinant products.

The hybrid indexes of all adult flickers collected along the Platte-South Platte River are indicated in the histogram (fig. 3; see also table 3). Included in the histogram is a sample of flickers from the Rocky Mountains and western area of Colorado. The histogram indicates that the populations of the eastern portion of the Platte Valley (Missouri River to Sutherland, Nebraska) are composed of individuals that are either like *auratus* in all characters or that show a tendency toward *cafer* in one or more characters. One male (C.U. No. 28037) from Sutherland is intermediate in one character (nuchal), near *auratus* in one character (crown color), and tends toward *cafer* in the other four characters. This bird was taken July 6, 1956, in an area where other flickers were obtained; the testes were enlarged, and there is every indi-

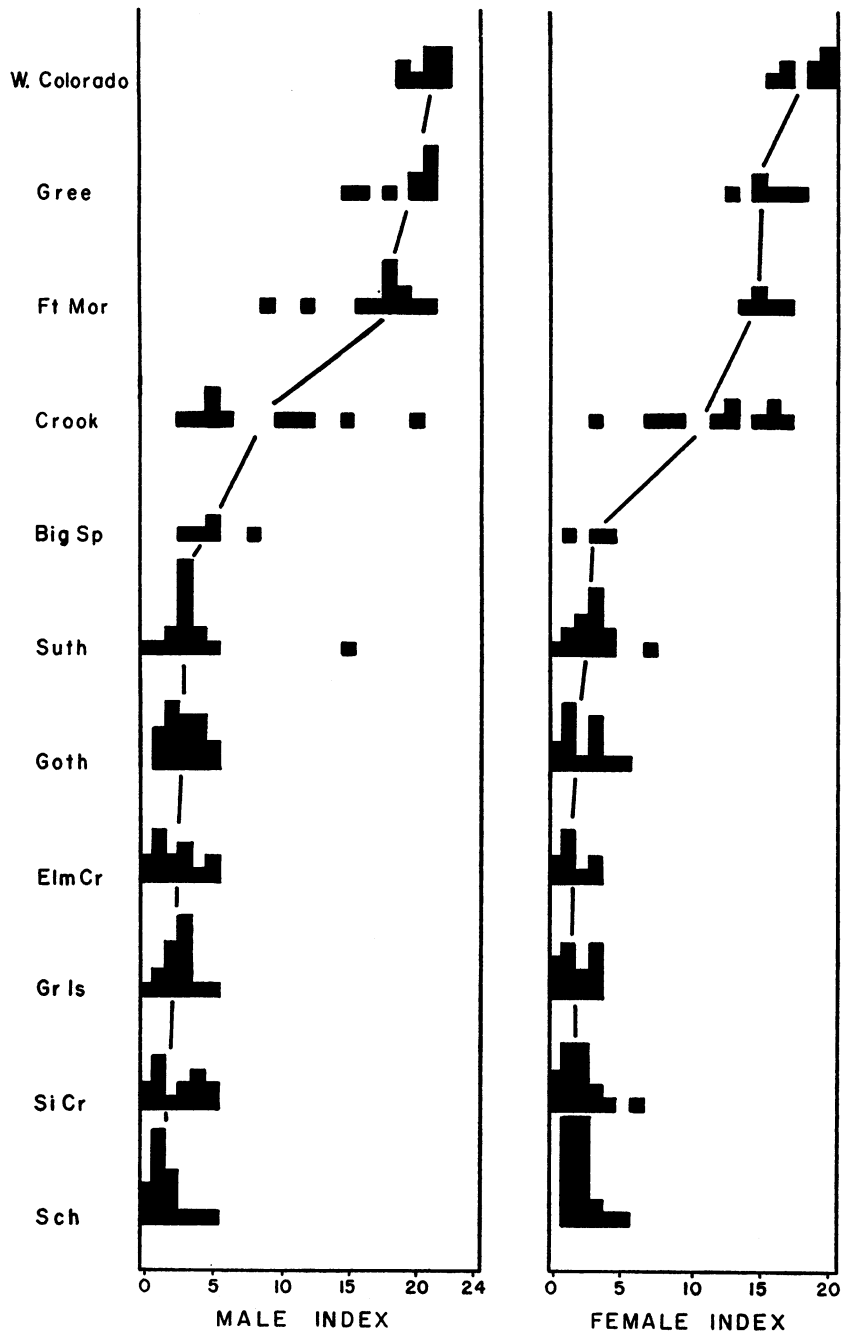


FIG. 3. Hybrid indexes of the Platte Valley samples. Each square in the histogram represents one specimen. Lines connect the means of the samples. Localities are approximately 50 miles apart. (See text for localities and mean hybrid indexes of samples.)

*Abbreviations:* From east to west (bottom to top): Sch, Schuyler; SiCr, Silver Creek; GrIs, Grand Island; ElmCr, Elm Creek; Goth, Gothenburg; Suth, Sutherland; BigSp, Big Springs; FtMor, Fort Morgan; Gree, Greeley.

cation that the bird had bred in the area. A female (C.U. No. 28052) taken at Sutherland tended more toward *cafer* than *auratus* in one character (throat color, score 3), but it was otherwise intermediate or tended toward *auratus*. The eight flickers obtained near Big Springs, on the Nebraska-Colorado border, indicate a trend toward *cafer*.

The specimens collected at Crook, Colorado, are extremely variable. The variability in color characters shown in table 9 is typical of situations of hybridization (see the summation of characters in the towhee population from Cerro Viejo in Sibley, 1950, p. 167, and characters of populations of honeyeaters from the Wahgi Mountains and from the Herzog Mountains in Mayr and Gilliard, 1952, p. 330).

The trend toward *cafer* continues west of Crook at Fort Morgan; several males from the latter locality are, however, considerably like *auratus*. The Greeley sample is nearly as *cafer*-like in its characters as is the sample from western Colorado. Several individuals from the Greeley station tend toward *auratus*; one female (C.U. No. 28129) has a pure vinaceous tan throat like that in *auratus*, but no other individuals are completely *auratus*-like (score 0) in any of their characters. The western Colorado sample is more typical of *cafer* than the Greeley sample. None of the specimens from this area exhibited the *auratus* condition in any of their characters.

For figure 4 the hybrid index has been converted into a percentage system; an index of 0 equals 0 per cent, while an index of 24 (or

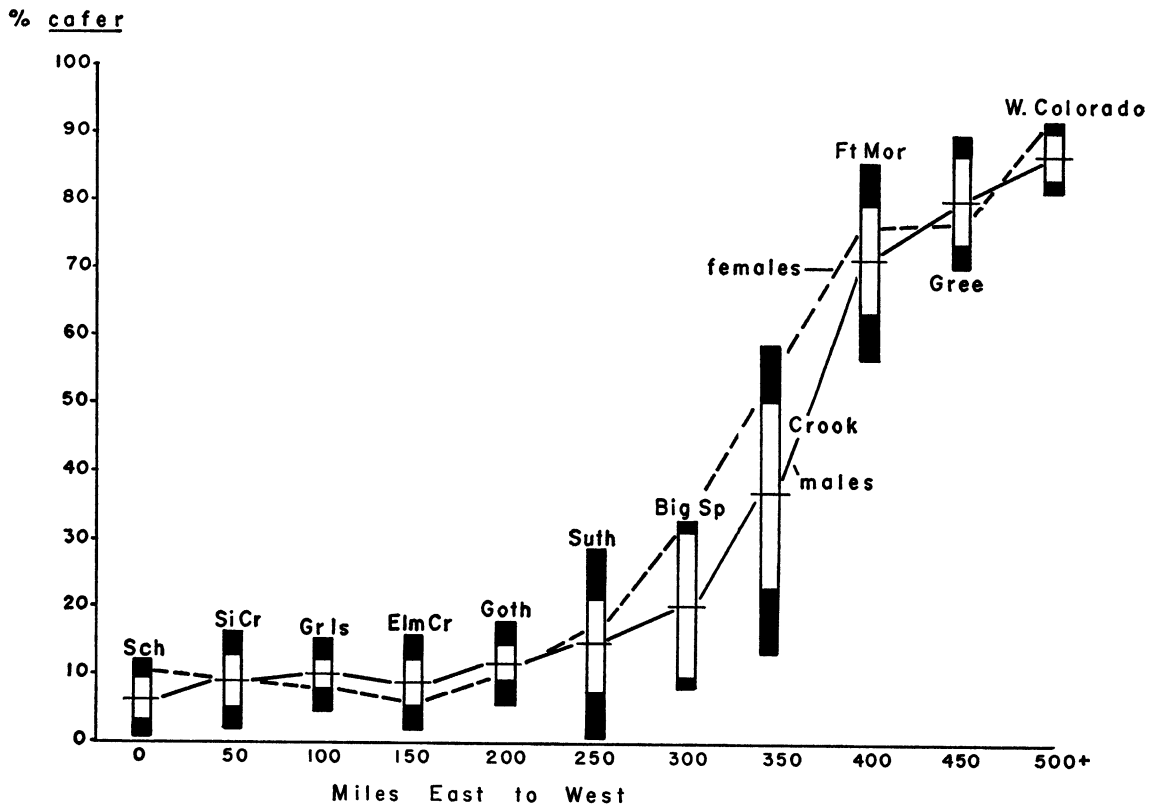


FIG. 4. Hybrid-index gradient in the Platte Valley samples. Hybrid indexes are indicated as per cent of *cafer* characters for comparison of male and female gradients (see text). For males the means of the various samples are shown by horizontal lines; light areas enclosed by lines include two standard errors of the means; and black areas indicate one standard deviation on each side of the means. The dashed line connects the mean values for females.

Abbreviations: Sch, Schuyler; SiCr, Silver Creek; GrIs, Grand Island; ElmCr, Elm Creek; Goth, Gothenburg; Suth, Sutherland; BigSp, Big Springs; FtMor, Fort Morgan; Gree, Greeley.

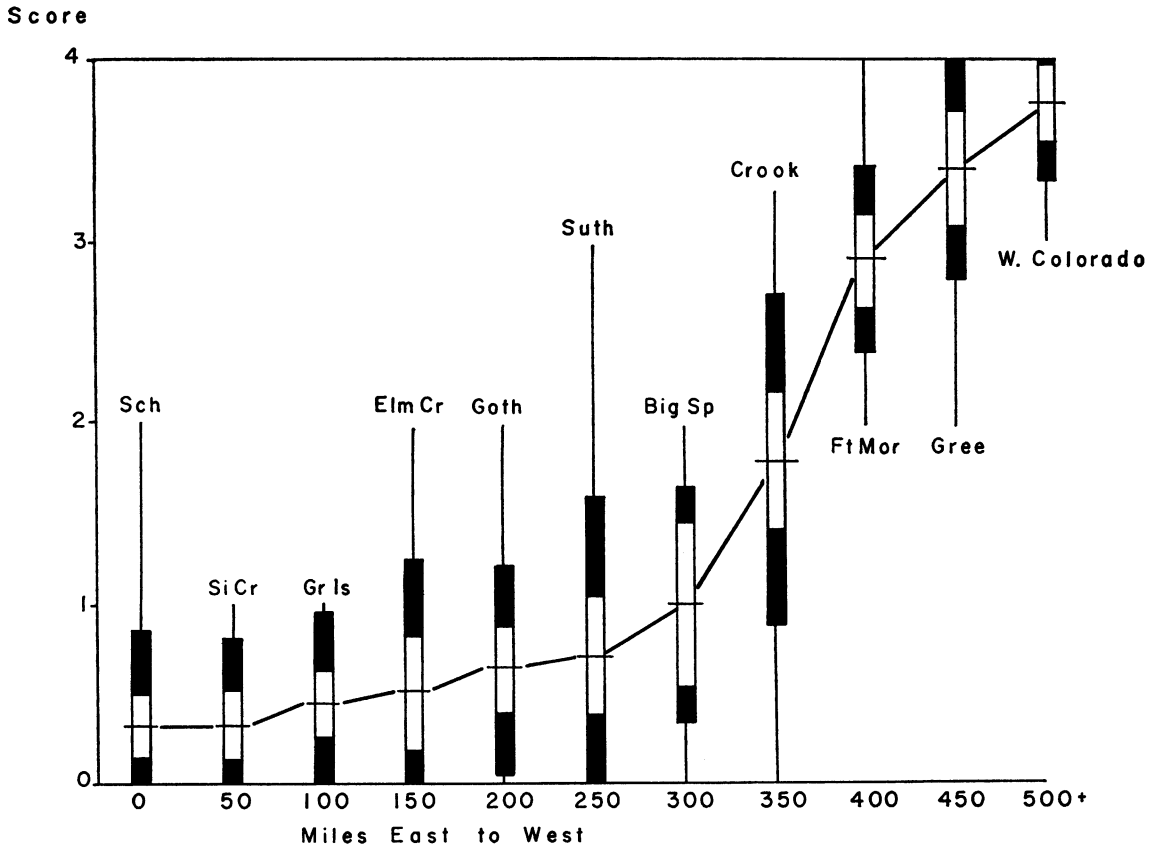


FIG. 5. Shaft-color gradient in the Platte Valley samples, which include both males and females. Vertical lines indicate the range in scores exhibited by individuals of each sample. The mean, two standard errors, and one standard deviation are indicated for each sample.

Abbreviations: Sch, Schuyler; SiCr, Silver Creek; GrIs, Grand Island; ElmCr, Elm Creek; Goth, Gothenburg; Suth, Sutherland; BigSp, Big Springs; FtMor, Fort Morgan; Gree, Greeley.

20 for females) is equal to 100 per cent (see table 3). The figure thus depicts the mean per cent of *cafer* characteristics in each sample. Conversion of the mean male hybrid index and mean female hybrid index for each sample into this system facilitates comparison of the male and female indexes. Several points are indicated by figure 4. The eastern four localities exhibit but a slight tendency toward an increase in *cafer* characteristics progressing westward. Beginning with the Gothenburg sample a definite trend toward an increase in *cafer* characteristics is apparent. This gradient increases rapidly beginning at Big Springs; a shift of 50 per cent (0.5% per mile) occurs within the next 100 miles. Crook is near the center of the east-west shift from *auratus* to *cafer* characters. West of

Crook the steep gradient continues at least as far as Fort Morgan before leveling off. The Greeley sample indicates that the gradient has begun to taper off. The western Colorado sample closely resembles *cafer*; the gradient probably reaches the level of the western Colorado population just west of Greeley at the base of the Rocky Mountains. West of western Colorado the gradient becomes almost imperceptible (see section on introgression below). The increased variability of the populations along the Platte from Sutherland to Greeley is indicated by the size of the standard errors and standard deviations shown by the samples from the localities in this area.

The indexes for the various characters undergo changes similar to those for the total

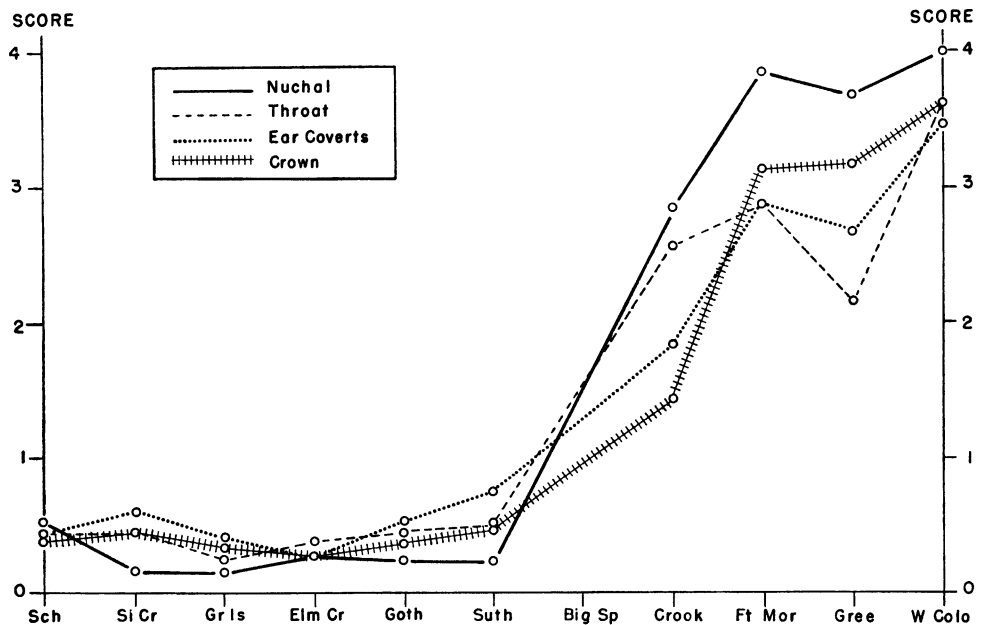
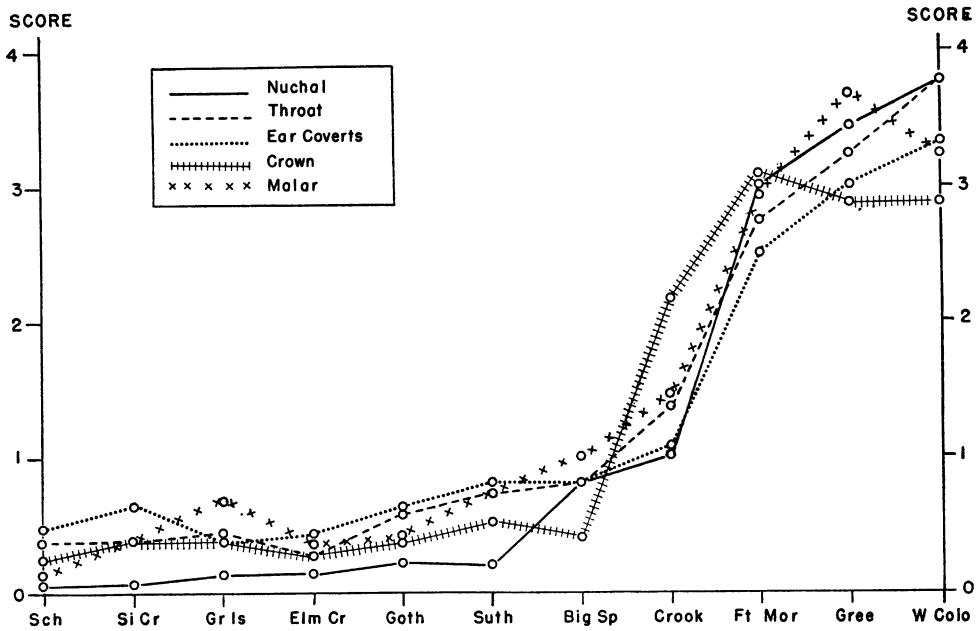


FIG. 7. Female color-character gradients in the Platte Valley samples. Localities are approximately 50 miles apart. Lines connect the mean scores for four characters in females from the various localities.

**Abbreviations:** Sch, Schuyler; SiCr, Silver Creek; GrIs, Grand Island; ElmCr, Elm Creek; Goth, Gothenburg; Suth, Sutherland; BigSp, Big Springs; FtMor, Fort Morgan; Gree, Greeley.



indexes just discussed. The clearest picture is presented by the shaft-color character (see fig. 5). As mentioned above, males and females may be treated together in regard to this character. The figure demonstrates the shift from an *auratus* condition to a *cafer* condition in a single color character. The gradient rises gradually from Schuyler west to Sutherland, followed by a sharper rise between Sutherland and Big Springs. Between Crook and Fort Morgan the greatest rise occurs; this is followed by a slightly less steep gradient which continues to the Rocky Mountains. The other character gradients are depicted in figures 6 and 7. The lines in these figures connect the mean indexes for the various characters in the samples from the Platte Valley localities. The gradients are similar for all characters. There is a general low level of incidence of *cafer* characters in the eastern six samples. The gradients become steep between Big Springs and Fort Morgan; the sharp rise is followed by a leveling off between Fort Morgan and Greeley.

The major portion of the change from *auratus* to *cafer* characters thus takes place over an area of from 100 to 150 miles. It should be noted that the shift from the general condition of the presence of a nuchal patch to its absence is the most complete shift for any character. The incidence of a restricted or absent nuchal patch in the eastern samples is very low; crossing the main zone of hybridization the gradient for this character rises to the opposite extreme. This character is useful, therefore, in the determination of the limits of the hybrid zone.

The various measurements and weights obtained from the specimens tend to corroborate the information presented by the color character analysis. Data on the weights of the specimens are summarized in table 4. The males from Greeley average about 16 grams heavier than those from the eastern six localities. The information for the females is of little value owing to the inordinately low (139.17 grams) weight of the Greeley sample, the reason for which is unknown. The

TABLE 4  
BODY WEIGHT (IN GRAMS) OF FLICKERS IN SAMPLES FROM THE PLATTE RIVER VALLEY<sup>a</sup>

Locality	N	Mean	2 S. E.	1 S. D.	Range	Coeff. Var.
<b>Males</b>						
Schuyler	17	139.59	± 3.90	± 8.08	129-154	5.79
Silver Creek	13	140.85	± 4.46	± 8.03	127-154	5.70
Grand Island	15	140.87	± 4.80	± 9.24	125-160	6.60
Elm Creek	14	138.04	± 3.74	± 6.97	130-150	5.05
Gothenburg	19	140.71	± 3.62	± 7.89	127-161	5.61
Sutherland	15	141.07	± 2.40	± 6.59	132-153	4.68
Big Springs	5	132.01	—	—	113-146	—
Crook	4	141.12	—	—	130-146	—
Fort Morgan	12	150.98	± 8.02	± 13.93	137-178	9.23
Greeley	9	156.45	± 5.24	± 7.85	143-167	5.02
<b>Females</b>						
Schuyler	20	131.83	± 3.34	± 7.46	117-150	5.66
Silver Creek	17	133.94	± 4.60	± 9.50	118-157	7.09
Grand Island	13	138.77	± 4.06	± 7.31	123-154	5.27
Elm Creek	9	133.18	± 5.52	± 8.27	122-144	6.21
Gothenburg	14	135.68	± 4.88	± 9.13	122-152	6.73
Sutherland	14	139.07	± 3.68	± 6.88	120-151	4.95
Big Springs	3	142.70	—	—	138-148	—
Crook	5	141.60	—	—	135-150	—
Fort Morgan	7	150.43	± 3.86	± 5.11	144-158	3.40
Greeley	6	139.17	± 3.78	± 4.63	130-145	3.33

<sup>a</sup> No weights are available for either males or females from western Colorado.

TABLE 5  
WING LENGTH (IN MILLIMETERS) OF FLICKERS IN SAMPLES FROM THE PLATTE RIVER VALLEY

Locality	N	Mean	2 S. E.	1 S. D.	Range	Coeff. Var.
<b>Males</b>						
Schuyler	17	151.06	±1.76	±3.61	145-156	2.39
Silver Creek	12	151.86	±1.88	±3.25	146-156	2.15
Grand Island	16	152.25	±1.30	±2.59	149-159	1.71
Elm Creek	13	151.15	±1.62	±2.91	146-155	1.93
Gothenburg	19	153.42	±1.30	±2.85	150-161	1.86
Sutherland	15	151.67	±1.72	±3.33	146-157	2.20
Big Springs	5	151.80	—	—	147-159	—
Crook	6	154.17	±0.60	±2.32	150-157	1.50
Fort Morgan	12	161.75	±2.98	±5.15	155-171	3.18
Greeley	9	163.22	±2.26	±3.39	157-167	2.08
Western Colorado	9	163.11	±1.60	±2.24	159-167	1.38
<b>Females</b>						
Schuyler	20	151.15	±1.72	±3.87	143-161	2.57
Silver Creek	17	149.77	±1.48	±3.05	142-154	2.04
Grand Island	13	152.08	±1.56	±2.81	148-158	1.85
Elm Creek	9	152.67	±2.82	±4.22	150-158	2.77
Gothenburg	12	150.75	±2.22	±3.85	145-159	2.56
Sutherland	14	152.86	±2.04	±3.82	147-162	2.50
Big Springs	3	151.33	—	—	149-155	—
Crook	10	156.80	±2.80	±4.42	150-165	2.82
Fort Morgan	7	159.72	±2.12	±2.80	155-163	1.76
Greeley	6	161.17	±1.96	±2.41	157-164	1.50
Western Colorado	7	163.71	±2.42	±3.20	161-169	1.96

TABLE 6  
TAIL LENGTH (IN MILLIMETERS) OF FLICKERS IN SAMPLES FROM THE PLATTE RIVER VALLEY

Locality	N	Mean	2 S. E.	1 S. D.	Range	Coeff. Var.
<b>Males</b>						
Schuyler	16	102.56	±2.32	±4.65	95-108	4.54
Silver Creek	12	103.50	±2.64	±4.58	96-112	4.43
Grand Island	15	103.60	±1.78	±3.44	98-108	3.33
Elm Creek	8	107.51	±2.92	±4.14	102-112	3.86
Gothenburg	16	106.13	±2.34	±4.66	101-117	4.40
Sutherland	9	105.33	±2.14	±3.20	100-110	3.04
Big Springs	3	107.67	—	—	102-114	—
Crook	7	107.42	±0.98	±1.29	106-109	1.20
Fort Morgan	9	115.01	±4.18	±6.29	106-125	5.47
Greeley	9	115.45	±2.98	±4.47	108-122	3.88
Western Colorado	7	110.16	±1.42	±1.73	108-113	1.58
<b>Females</b>						
Schuyler	19	104.43	±2.02	±4.39	95-112	4.21
Silver Creek	11	100.91	±1.98	±3.27	96-106	3.24
Grand Island	10	104.50	±2.44	±3.89	100-110	3.72
Elm Creek	6	107.33	±3.48	±4.32	101-113	2.68
Gothenburg	10	103.00	±2.34	±3.68	99-112	3.57
Sutherland	9	105.78	±2.70	±4.06	101-112	3.84
Big Springs	0	—	—	—	—	—
Crook	9	110.00	±2.76	±4.15	102-114	3.77
Fort Morgan	5	112.60	±3.72	±4.16	108-115	3.70
Greeley	4	111.75	—	—	108-117	—
Western Colorado	5	111.40	—	—	106-117	—

TABLE 7

BILL LENGTH (IN MILLIMETERS) OF FLICKERS IN SAMPLES FROM THE PLATTE RIVER VALLEY

Locality	N	Mean	2 S. E.	1 S. D.	Range	Coeff. Var.
<b>Males</b>						
Schuyler	15	26.02	$\pm 0.48$	$\pm 0.92$	24.9-27.6	3.54
Silver Creek	13	27.05	$\pm 0.66$	$\pm 1.19$	25.5-29.3	4.40
Grand Island	15	27.34	$\pm 0.44$	$\pm 0.85$	26.2-29.0	3.11
Elm Creek	13	26.57	$\pm 0.88$	$\pm 1.59$	25.0-28.8	5.98
Gothenburg	17	27.40	$\pm 0.60$	$\pm 1.25$	24.6-29.8	4.56
Sutherland	15	26.66	$\pm 0.92$	$\pm 1.77$	23.9-30.0	6.64
Big Springs	4	28.33	—	—	26.9-29.4	—
Crook	11	28.75	$\pm 0.96$	$\pm 1.61$	26.7-31.6	5.60
Fort Morgan	10	29.69	$\pm 0.54$	$\pm 0.85$	28.9-31.7	2.87
Greeley	9	29.78	$\pm 0.76$	$\pm 1.13$	27.9-31.6	3.80
Western Colorado	9	29.49	$\pm 1.22$	$\pm 1.84$	26.4-32.3	6.24
<b>Females</b>						
Schuyler	19	26.43	$\pm 0.54$	$\pm 1.19$	24.9-28.6	4.51
Silver Creek	17	26.25	$\pm 0.54$	$\pm 1.12$	24.8-28.5	4.27
Grand Island	11	27.12	$\pm 0.70$	$\pm 1.17$	24.8-28.3	4.31
Elm Creek	8	25.69	$\pm 0.82$	$\pm 1.16$	23.9-27.6	4.52
Gothenburg	14	27.46	$\pm 0.88$	$\pm 1.64$	24.4-29.9	5.98
Sutherland	12	26.49	$\pm 0.88$	$\pm 1.53$	23.9-29.0	5.78
Big Springs	3	26.13	—	—	25.8-26.6	—
Crook	10	28.24	$\pm 0.74$	$\pm 1.15$	26.3-30.0	4.07
Fort Morgan	7	30.46	$\pm 1.32$	$\pm 1.75$	27.3-32.0	5.75
Greeley	6	29.47	$\pm 1.38$	$\pm 1.69$	27.9-31.4	5.74
Western Colorado	8	29.65	$\pm 1.02$	$\pm 1.45$	27.0-31.8	4.90

TABLE 8

TARSAL LENGTH (IN MILLIMETERS) OF FLICKERS IN SAMPLES FROM THE PLATTE RIVER VALLEY

Locality	N	Mean	2 S. E.	1 S. D.	Range	Coeff. Var.
<b>Males</b>						
Schuyler	17	28.33	$\pm 0.28$	$\pm 0.59$	27.2-29.5	2.08
Silver Creek	13	28.55	$\pm 0.56$	$\pm 0.99$	27.0-30.1	3.47
Grand Island	15	28.56	$\pm 0.42$	$\pm 0.82$	27.1-30.1	2.87
Elm Creek	14	28.54	$\pm 0.42$	$\pm 0.78$	27.7-30.4	2.87
Gothenburg	17	28.81	$\pm 0.42$	$\pm 0.85$	26.8-30.5	2.95
Sutherland	15	28.63	$\pm 0.42$	$\pm 0.82$	27.5-30.0	2.87
Big Springs	5	29.38	—	—	29.1-29.8	—
Crook	11	27.80	$\pm 0.60$	$\pm 1.01$	26.4-29.5	3.63
Fort Morgan	12	29.68	$\pm 0.54$	$\pm 0.95$	27.9-30.6	3.21
Greeley	9	29.83	$\pm 0.74$	$\pm 1.10$	27.9-31.3	3.69
Western Colorado	9	29.22	$\pm 0.62$	$\pm 0.94$	27.8-30.6	3.99
<b>Females</b>						
Schuyler	20	27.82	$\pm 0.38$	$\pm 0.86$	26.3-29.9	3.09
Silver Creek	16	28.20	$\pm 0.32$	$\pm 0.63$	27.3-29.0	2.23
Grand Island	13	28.77	$\pm 0.48$	$\pm 0.86$	27.0-30.2	2.99
Elm Creek	9	28.33	$\pm 0.62$	$\pm 0.94$	26.4-30.0	3.32
Gothenburg	14	27.74	$\pm 0.48$	$\pm 0.88$	26.6-29.0	3.17
Sutherland	14	28.87	$\pm 0.36$	$\pm 0.68$	27.3-30.1	2.36
Big Springs	3	28.67	—	—	28.5-28.8	—
Crook	11	28.42	$\pm 0.54$	$\pm 0.88$	27.2-29.9	3.10
Fort Morgan	7	29.51	$\pm 0.78$	$\pm 1.02$	28.2-30.9	3.46
Greeley	6	29.72	$\pm 0.74$	$\pm 0.91$	29.1-31.4	3.06
Western Colorado	8	28.50	$\pm 0.66$	$\pm 0.92$	27.2-30.1	3.23

main shift in weight, as far as can be determined, occurs between Crook and Fort Morgan, slightly west of where most of the color characters undergo their shift from *auratus* to *cafer* condition.

Wing-length data are summarized in table 5. There is very clearly no gradient in wing length in flickers across the Platte River of Nebraska. The wing lengths of flickers from Big Springs do not show any increase from those of flickers farther east. Between Big Springs and Fort Morgan, a distance of about 100 miles, an increase of approximately 10 mm. occurs in the average wing length of male and female flickers. The samples from Greeley and western Colorado show similar mean wing lengths. The wing lengths of the Fort Morgan individuals are but slightly less. The shift in wing length matches extremely well the east-west gradient for the hybrid index. The tail-length data, presented in table 6, are similar to the wing-length data. A gradient in tail length occurs from east to

west. The major shift is primarily between Crook and Fort Morgan. Males from Greeley average from 8 to 10 mm. longer in tail length than those from the seven eastern localities. The picture is complicated by the greater overlap in tail length between eastern and western populations.

Bill-length data are presented in table 7. The bill length in western samples averaged more than 2 mm. larger than that of the eastern samples. The eastern six or seven localities are again uniform in respect to this character. From Sutherland and Big Springs westward there is a gradient of increasing bill length which continues as far as Fort Morgan (100-150 miles). The data for tarsal length (table 8) indicate a similar trend of increasing length from east to west. However, since there is a difference of only 1 mm. between eastern and western samples, the data are considerably less significant in regard to the hybrid situation.

TABLE 9  
SCORES OF COLOR CHARACTERS FOR SPECIMENS FROM CROOK, COLORADO

	Nuchal	Throat	Ear Coverts	Malar	Shafts	Crown	Total Index
<b>Males</b>							
	4	3	3	4	3	3	20
	0	1	0	1	1	2	5
	0	3	2	2	3	2	12
	2	0	1	1	3	3	10
	0	1	1	1	0+	1	4+
	2	3	2	3	2	3	15
	1	0+	0	0	1	2	4+
	0	0	0	0	0+	3	3+
	1	2+	2	2	1+	2	11
	0	0	0	1	0	2	3
	1	1	1	1	1	1	6
<b>Females</b>							
	4	3	3	—	3	4	17
	3	3	3	—	1	3	13
	4	4	3	—	1	3	15
	4	1	1	—	0	1	7
	1	2	2	—	1	2	8
	0	0+	1	—	0+	1	3
	4	2+	3	—	1+	2	13
	1	3	2	—	1	2	9
	2	3	2+	—	2	2	11+
	4	2+	2+	—	3+	3	15+
	4	3+	3	—	2	3+	16

## THE SOUTHERN PLAINS SITUATION

The southern Plains region is here considered to include that portion of the Plains south of South Dakota.

### NEBRASKA

A total of 250 adult flickers taken in the breeding season was available from Nebraska. This figure includes 50 adults from 13 localities outside the Platte-South Platte Valley. These localities are listed in table 10, along with the sample sizes, hybrid indexes and mean wing length of the specimens (see also map, fig. 2).

The presence of considerable *cafer* influence in the flicker populations of western Nebraska is indicated by the high indexes of Chadron specimens from the Pine Ridge region of northwestern Nebraska. Lying at the western edge of the Nebraska Sand Hills, the Pine Ridge area is a wooded upland which, while not directly connected by woodland with the Black Hills, is nevertheless closely adjacent and has a similar fauna. The Pine Ridge area apparently contains an outlying *cafer* population which is under strong influence of gene flow from the *auratus* populations of the river valleys to the northeast, east, and southeast.

The two samples from the North Platte River (Lewellen, Oshkosh) south of the Pine Ridge area show considerable evidence of introgression from *cafer*. There is a detectable difference in hybrid index between Lewellen (mean male index, 5) and Oshkosh (index, 9), although the localities are but 17 miles apart. The mean index for the Lewellen sample is the same as that for the Big Springs sample; the latter locality is some 23 miles southwest of Lewellen on the South Platte River (see map, fig. 2). The shift in index from Lewellen to Oshkosh shows a gradient greater than that between Big Springs and Fort Morgan, Colorado. The shift in hybrid index between the former two localities is 0.24 index points per mile. Between Big Springs and Crook, Colorado, the shift in female index is 0.18 index points per mile (hereafter designated as i.p.m.), while the male index changes 0.17 i.p.m. between Crook and Fort Morgan.

The samples from many eastern Nebraska

localities are too small for detailed analysis. The trend in increasing hybrid index demonstrated above for the Platte River populations was made possible through the securing of large samples. The specimen data that are available suggest that: (1) a great proportion ( $\pm 50\%$ ) of eastern Nebraska flickers show *cafer* tendencies; (2) the clinal decrease in these *cafer* characteristics from west to east is due to introgression; and (3) any large sample of flickers taken in eastern Nebraska will contain individuals that possess considerable evidence of *cafer* influence, owing probably to the effects of recombination occasionally producing more *cafer*-like individuals. The last point is suggested by specimens such as one from Hastings (C.U. No. 26943) with an index of 5, having much gray on the throat; one from Bassett (C.U. No. 26130) indexed at 4, which has quite orange shafts; and one from Schuyler (C.U. No. 27889) indexed at 4 and possessing only faint traces of a nuchal patch.

The increase in wing length from east to west demonstrated for the Platte River populations is also generally apparent for the rest of Nebraska (see table 10). The eastern Nebraska samples have a wing length similar to that of the eastern Platte River samples (mean near 150 mm.). The shift indicated along the North Platte (Lewellen, Oshkosh) is probably similar to that occurring along the Niobrara River. The Chadron sample has a wing length similar to that of western Colorado *cafer* noted previously. It should be noted that the connection between *cafer* and *auratus* populations across Nebraska is essentially limited to the several major river valleys (Niobrara, North Platte, South Platte, Republican). The total width of the connection in western Nebraska is estimated to be less than 5 miles. While flickers are common to abundant in the river valleys, the flicker populations of the valleys are tiny when compared to the populations in the woodlands of eastern Nebraska and of the Pine Ridge region. The connection is probably somewhat enhanced by the presence of small flicker populations in certain areas away from the valleys, as in villages, woods around ranches, and perhaps wooded areas around some of the lakes in the Sand Hills. Such populations add slightly to the size of the contact between



TABLE 10  
FLICKER SAMPLES FROM NEBRASKA

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
7 miles south of Hastings, Adams Co. <sup>a</sup>			
5 males	0, 0, 0, 5, 2	1.40	149.5
1 female	2	(2)	—
3 miles south of St. Paul, Howard Co.			
2 males	2, 2	(2)	150.7
5 females	0, 0, 1, 1, 2	0.80	—
3 miles south of Scotia, Greeley Co.			
1 male	2	(2)	(147)
1 mile west of O'Neill, Holt Co.			
2 females	1, 3	(2.0)	(152.5)
5 miles south-southeast of Spencer, Holt Co.			
1 male	2	(2)	(147)
8 miles west of Burwell, Garfield Co.			
5 males	1, 1, 2, 2, 3	1.80	153.8
1 female	0	(0)	—
13 miles north of Bassett, in Keyapaha Co.			
2 males	2, 4	(3.0)	(149.0)
1 female	0	(0)	—
2 miles west of Halsey, Thomas Co.			
1 male	1	(1)	(157)
1 female	1	(1)	—
16 miles south-southwest of Valentine, Cherry Co.			
1 female	2	(2)	—
5 miles east of Lewellen, in Keith Co. <sup>b</sup>			
5 males	2, 3, 4, 7, 9	5.0	155.2
2 females	1, 2	(1.50)	—
2 miles south of Oshkosh, Garden Co.			
4 males	4, 7, 12, 13	(9.0)	(156.75)
2 females	4, 5	(4.5)	—
2 miles northeast of Chadron, Dawes Co.			
5 males	12, 15, 16, 16, 19	15.60	162.5
3 females	13, 14, 15	(14.0)	—

<sup>a</sup> Includes one specimen from "Little Blue River."

<sup>b</sup> Includes two specimens from 1½ miles east of Lewellen, Garden County.

the main populations of the two subspecies groups.

For purposes of this study I have arbitrarily defined the hybrid zone as the area in which phenotypically pure individuals (indexes of 0 or 24 for males and 0 and 20 for females) are lacking. Large samples may include recombinant types so closely approaching the parental forms as to index as "pures," as is the case with the Forsyth, Montana, sample. I suggest that for larger samples the zone may be defined as the area in which 5 per cent or fewer specimens index as "pures." The eastern edge of the hybrid zone in Ne-

braska (see maps, figs. 2 and 10) lies between Big Springs and Sutherland on the South Platte River, just east of Lewellen on the North Platte and probably  $40 \pm$  miles west of Valentine on the Niobrara River. Another area I utilize is designated the "primary area of introgression." This area extends from the edge of the hybrid zone to areas where fewer than half of the flickers show indications of introgression. For this purpose specimens indexed 1 or 23 (males) and 1 and 19 (females) are considered as "pure" individuals of parental type. The eastern limit of this area in Nebraska (see maps, figs. 2 and 10) is reached

along a line extending from about the mouth of the Niobrara River south to Silver Creek and then south to the border of Nebraska and Kansas, passing east of Hastings.

#### SOUTH DAKOTA

The number of breeding flickers available from this state totaled 81. Cornell field parties collected 62 of these at 10 stations in 1955. Most of the localities represented by specimens are from the western part of the state (see table 11). The main feature of the hybrid situation in the state is the effect exerted by an outlying *cafer* population in the Black Hills on the river valley populations to the east. The zone of hybridization (see defi-

nition above) extends farther east in South Dakota than in Nebraska, nearly bisecting the state (see map, fig. 2). The river valleys providing direct contacts with *cafer* populations are: the White River which drains the northern Pine Ridge region of Nebraska; and the Cheyenne River which, with its tributaries, including the Belle Fourche River, drains the greater part of the Black Hills. Samples the indexes of which approach *cafer* more than *auratus* are those from Spearfish, Sturgis, Rapid City, and Hot Springs, all of which are in or near the Black Hills.

The gradients shown by the hybrid indexes of samples from the rivers mentioned above are indicated in figure 8. The hybrid-index

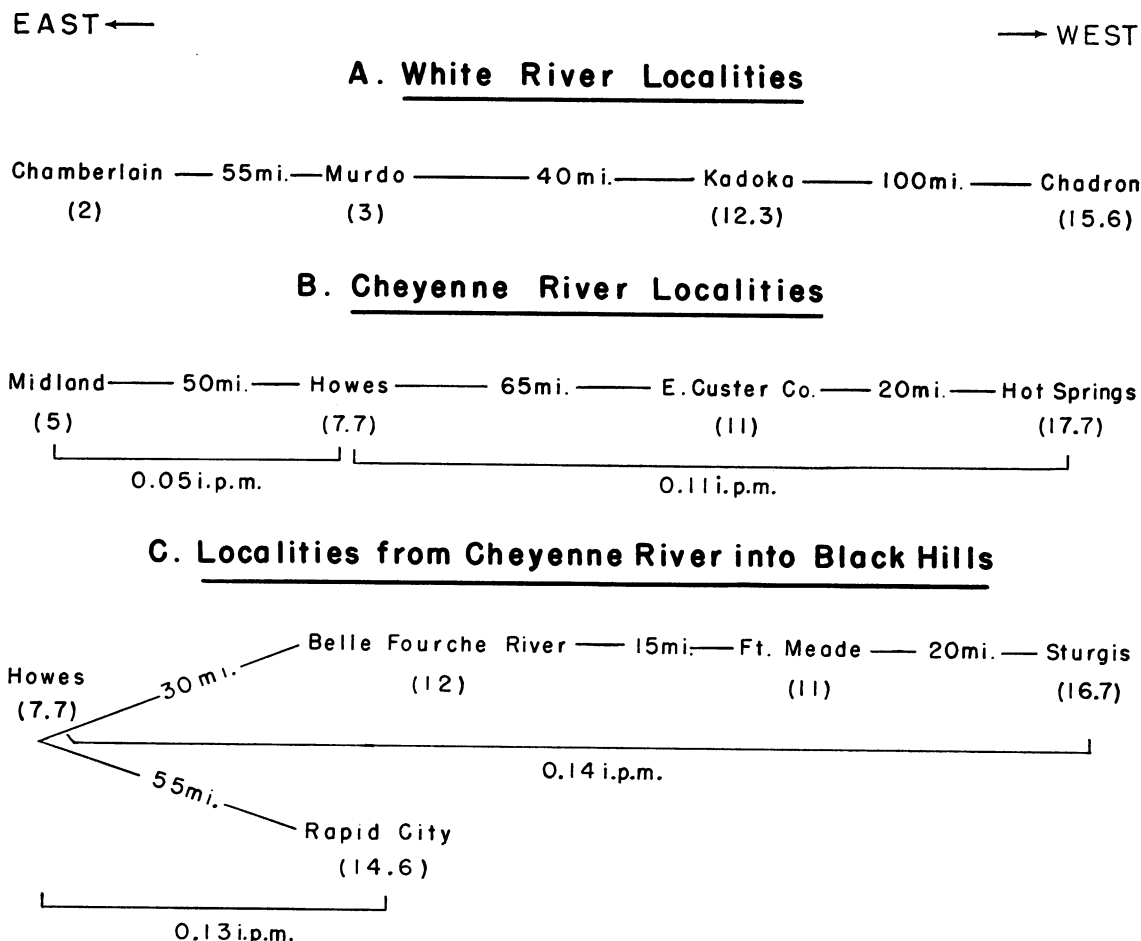


FIG. 8. Shifts in hybrid-index values of male flickers along three South Dakota transects. Localities are indicated, with distances between them (not to scale). The mean hybrid index for each locality is the figure below each locality name. Shifts in mean hybrid index over various distances are shown, with the change in index value per mile indicated as i.p.m.

TABLE 11  
FLICKER SAMPLES FROM SOUTH DAKOTA

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
3 miles northeast of Huron, Beadle Co.			
6 males	—, 0, 1, 2, 2, 2	1.4	152.5
1 female	2	(2)	—
10 miles southwest of Chamberlain, in Lyman Co.			
1 male	2	(2)	—
2 females	0, 0	(0)	—
10 miles south-southwest of Murdo, Jones Co.			
2 males	2, 4	(3)	(151.5)
3 females	3	(3)	—
9 miles north-northeast of Mobridge, Campbell Co.			
3 males	1, 5, 7	(4.3)	(158.7)
1 female	1	(1)	—
45 miles north of Midland, Haakon Co.			
5 females	0, 3, 5, 8, 9	5.0	155.2
15 miles west-southwest of Promise, Dewey Co.			
3 males	3, 5, 7	(5.0)	(153.0)
5 females	2, 4, 5, 9, 10	6.0	—
15½ miles southwest of Lemmon, Perkins Co.			
2 females	3, 5	(4.0)	(154.5)
6 miles south of Kadoka, Jackson Co.			
3 males	9, 12, 16	(12.3)	(156.0)
3 females	1, 6, 13	(6.7)	—
9 miles south-southeast of Howes, Haakon Co.			
3 males	6, 8, 9	(7.7)	(155.3)
4 females	6, 8, 12, 13	(9.8)	—
Belle Fourche River, east of Fort Meade, Meade Co.			
1 male	12	(12)	—
1 female	10	(10)	—
6½ miles north of Rapid City, in Meade Co. <sup>a</sup>			
9 males	9, 10, 11, 12, 13, 16, 17, 21, 22	14.56 ± 3.14 <sup>b</sup>	160.7
9 females	4, 8, 11, 12, 12, 16, 16, 16, 17	12.44 ± 2.92 <sup>b</sup>	—
12 miles east of Fort Meade, Meade Co.			
1 male	11	(11)	—
1 female	16	(16)	—
Fruitdale, Butte Co.			
1 female	16	(16)	—
Sturgis, Meade Co.			
3 males	15, 17, 18	(16.7)	(168.0)
1 female	15	(15)	—
Spearfish, Lawrence Co. <sup>c</sup>			
2 males	18, 22	(20.0)	(163.0)
Cheyenne River, east Custer Co.			
1 male	11	(11)	—
2 females	6, 10	(8)	(161.0)
7 miles northeast of Hot Springs, Custer Co.			
3 males	14, 17, 22	(17.7)	(159.0)
1 female	15	(15)	—

<sup>a</sup> Includes 11 miles north of Rapid City, Meade County, and 6 miles east of Rapid City, Pennington County.

<sup>b</sup> Mean hybrid index plus or minus two standard errors.

<sup>c</sup> Includes 5 miles north of Spearfish, Lawrence County.

gradient is similar along all three contacts, as indicated by the changes in index per mile (i.p.m.) along the contacts just east of the Black Hills. The populations on the Grand River (Lemmon sample), the Moreau River (Promise sample), and the Missouri River in northern South Dakota (Mobridge sample) are directly in contact with the Black Hills population via the Missouri-Cheyenne River populations (see map, fig. 2). The populations of northern South Dakota are subject to introgression indirectly from the Black Hills, and also from the contact area farther north and west on the Missouri. Thus the samples from this area show higher hybrid-index values than do the samples from south-central South Dakota (Murdo, Chamberlain).

The Huron sample is from a population inhabiting the James River Valley; there is no contact with the hybrid populations to the west except by way of the mouth of the James River and the Missouri River. The James River population is isolated from flicker populations to the east and west by an unfavorable habitat—open plains. This population might be expected to resemble closely the Nebraska flickers to the south, which it does. The mean index of 1.4 is perhaps slightly higher than means of samples as far east in Nebraska. It is of interest to note the possibility that the James River population could constitute a "peninsular" population in the sense that gene flow from other populations enters only at one end of the population. Thus, genes from the eastern *auratus* population, as well as genes from *cafer* which have through introgression reached the flicker population at the mouth of the James River, are able to enter only from the south. Such a condition could result in the more effective operation of selection on *cafer* and *auratus* genes, since the James River population is somewhat protected from the effects of selection in the populations to the east and of selection and hybridization in the populations to the west. A situation of this nature would merit detailed study (for such effects, see the discussion of the Saskatchewan situation regarding the Cypress Hills). Since all but one of the Huron specimens show indications of *cafer* influence, the eastern edge of the primary area of introgression is believed to be somewhat east of Huron.

Compared with the situation on the east face of the Rocky Mountains in Colorado, the Black Hills situation is more complex. The *cafer* population of the Rockies is large, and its connections with *auratus* are tenuous along the valleys of the Plains. The Black Hills are situated closer to the main *auratus* population of the east; consequently, the center of the zone of hybridization occurs at the edge of the Black Hills, rather than farther east in the river valleys. The center of this zone in Colorado lies 100 miles or so east of the mountains. The relatively high index values (17.7 and 20.0) attained by the Hot Springs and Spearfish samples (respectively) approach the value of the sample from western Colorado (20.78). The Rapid City sample is variable, with individuals separated by as much as 13 index points. The Crook, Colorado, sample of 11 males shows a maximum separation of 17 index points.

Scores for color characters of specimens in the Rapid City sample are given in table 12. The mean scores for the male color characters in the table are: nuchal color, 1.67; throat color, 2.78; ear-covert color, 2.44; malar color, 2.67; and crown color, 2.10. The mean score for shaft color for individuals of both sexes is 2.85.

The population of the Rapid City area tends to be more *cafer*-like in all characters except nuchal color, as reflected by the mean hybrid index for the sample of 14.6. The center of hybridization is therefore slightly east of Rapid City (see map, fig. 2). The wing length, utilized again to demonstrate the effect of hybridization on a mensural character, of South Dakota flickers is slightly greater than for Nebraska flickers. Birds with the shortest wings occur in the southern and eastern parts of South Dakota. Northern South Dakota specimens (Mobridge sample) are longer-winged, possibly owing partly to a south-to-north cline of increasing wing length, and partly to the effects of introgression from farther up the Missouri River. The Black Hills samples have wing lengths about the same as those of the western Colorado sample. The effect of introgression from the Black Hills population into the more *auratus*-like river valley populations is shown by the trend toward a decrease in wing length along the White River and from Rapid City and Sturgis to Howes (see table 11).

TABLE 12  
SCORES OF COLOR CHARACTERS OF SPECIMENS IN RAPID CITY SAMPLE

	Nuchal	Throat	Ear Coverts	Malar	Shafts	Crown	Hybrid Index
<b>Males</b>							
	0	2	1	3	2	1	9
	1	1	1	3	3	2	11
	2	1	0	1	3	3	10
	0	3	3	2	4	0	12
	4	4	4	2	4	4	22
	2	3	3	3	2	3	16
	1	4	4	4	2	2	17
	4	4	4	3	3	3	21
	1	3	2	3	3	1	13
<b>Females</b>							
	3	2	2		3	2	12
	4	3	3		2	4	16
	3	0	0		3	2	8
	3	2	2		3	1	11
	4	4	3		2	3	16
	2	0	0		2	0	4
	4	3	3		3	3	16
	1	2	2		3	4	12
	4	3	3		4	3	17

#### EASTERN WYOMING

The portion of Wyoming considered here is the area drained by the Belle Fourche, Cheyenne, and North Platte rivers (roughly the eastern third of Wyoming). The area is largely open steppe country, with cottonwood (*Populus*) and willow (*Salix*) cover along the major streams. Forests occur in the higher mountain masses, particularly along the eastern border, which is continuous with forests of the Black Hills, and between Laramie, Casper, and the North Platte River.

The flicker situation in this region is little known owing to the lack of adequate samples from the area. Nineteen adult flickers (breeding) were examined from eight localities in eastern Wyoming, with a fair-sized sample present only from Newcastle, Weston County (see table 13 and map, fig. 2). From the upper reaches of the Belle Fourche River at the northwestern edge of the Black Hills, two specimens were examined (male from Colony, female from Sundance). The specimen from Colony (U.M.M.Z. No. 86933) is intermediate between *cafer* and *auratus* in four characters (score 2 in nuchal, malar, crown, shafts)

and has a completely fawn-colored throat and ear coverts. This specimen, indexed at 8, is at the *auratus* extreme for Wyoming flickers. The Sundance specimen is a female indexed at 16. The Newcastle sample, taken from the area along Beaver Creek, a tributary of the Cheyenne River, is very similar to the sample from Hot Springs, South Dakota, at the south end of the Black Hills. Specimens from Newcastle generally approach *cafer* in lacking the nuchal, although a male (U.M.M.Z. No. 86941) has a complete nuchal scored at 0, in throat color, malar color, and ear-covert color. Crown color and shaft color are more nearly intermediate in this sample.

Along the North Platte River adequate samples are unfortunately lacking. Specimens from Lingle, near the Nebraska border, are very *cafer*-like (scores 3-4) in most characters, although one (male, M.V.Z. No. 69374) is intermediate, scoring 2 in nuchal and crown color. The five other specimens from the North Platte drainage area (Douglas, Laramie Peak, Casper specimens) are not so *cafer*-like as are those from Lingle. Both males from Douglas have extensive nuchal

patches (scores 0-1) and are intermediate in crown color. The male from Casper (M.V.Z. No. 69375) is intermediate in throat, ear-covert, and malar color.

It would appear that *auratus* genes are entering Wyoming *cafer* populations from around the edges of the Black Hills along the Belle Fourche, Cheyenne, and North Platte rivers. Further study of the eastern Wyoming situation is needed, particularly for us to ascertain more fully the effects of introgression on the Black Hills population, and the effects of that population on introgression from *auratus* into the western Wyoming *cafer* population. All that can be said with certainty regarding the flicker situation in eastern Wyoming is that the area is within the zone of hybridization, there are strong *cafer* characteristics in the flicker populations of the area, and there is less *auratus* influence shown, although the effects of introgression from *auratus* are considerable.

#### KANSAS

Only 30 specimens were available from the entire state of Kansas. These were mostly

from the southern and eastern parts (see table 14 and map, fig. 2). Fortunately, the specimens from southeastern Colorado enable the piecing together of the picture of the flicker situation in Kansas. Western Kansas is similar to southern Nebraska in that flickers are limited to the larger watercourses where sufficient arboreal vegetation exists. The rivers along which contacts between *auratus* and *cafer* definitely occur are the Arkansas and Cimarron. Contacts may also occur along the Republican and Smoky Hill branches of the Kansas River (see map, fig. 2). All samples from central and eastern Kansas are close to *auratus* in hybrid index. The eastern edge of the primary area of introgression crosses Kansas from north to south, passing through Harvey County, Kansas. Owing to insufficiency of material, no definite line can be drawn at this time. The westernmost locality in southern Kansas represented by specimens (Meade) is estimated to be approximately 100 miles east of the center of the hybrid zone; this is suggested by Oklahoma and Colorado samples. Failure to detect an appreciable amount of *cafer* influ-

TABLE 13  
FLICKER SAMPLES FROM EASTERN WYOMING

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
8 miles southeast of Colony, Crook Co. 1 male	8	(8)	(156)
Sundance, Crook Co. 1 female	16	(16)	—
Newcastle, Weston Co. <sup>a</sup> 5 males 3 females	14, 18, 19, 19, 19 10, 15, 15	17.8 (13.3)	165.8 —
4 miles west of Lingle, Goshen Co. 1 male 2 females	18 17, 19	(18) (18)	(157) —
Wheatland, Platte Co. 1 male	—	—	(166)
Laramie Peak, Albany Co. 1 female	16	(16)	(163)
Douglas, Converse County 2 males 1 female	14, 16 15	(15.0) (15)	(161.0) —
Casper, Natrona Co. 1 male	16	(16)	(166)

<sup>a</sup> Includes several localities, all within 5 miles of Newcastle.



TABLE 14  
FLICKER SAMPLES FROM KANSAS

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
Columbus, Cherokee Co. 1 female	0	(0)	(150)
Lawrence, Douglas County 11 males	0, 0, 0, 1, 1, 1, 2, 2, 2, 3, 3	1.36	151.45
5 females	1, 1, 2, 2, 3	1.80	—
Strong City, Chase Co. 1 male	0	(0)	(153)
Halstead, Harvey Co. 1 female	1	(1)	(151)
18 miles north of Stafford, Stafford Co. 1 female	2	(2)	(149)
Sharon, Barber Co. 1 female	1	(1)	(148)
4 miles southwest of Aetna, Comanche Co. 2 males	1, 4	(2.5)	(153.0)
5 females	1, 2, 2, 2, 3	2.00	152.4
12 miles east of Meade, Meade Co. 1 female	3	(3)	(151)
Wallace, Wallace Co. 1 male	4	(4)	(157)

ence in the Kansas samples is attributed to their small size. One specimen from Wallace County in western Kansas (see map, fig. 2) shows *cafer* influence in all characters except throat color and nuchal patch. The male from Wallace (U.K.M.N.H. No. 5577) is the only specimen with a wing length that suggests introgression (157 mm.), although this length is within the range of variation of eastern *auratus* individuals. Evidence from Oklahoma specimens indicates that the center of the zone of hybridization barely reaches the southwestern tip of Kansas. The eastern limits of the zone in Kansas are indefinite, although the sample from Comanche County indicates that they are east of that point. The Kansas situation, although far from clear, appears uncomplicated. Several river valleys provide contacts between *auratus* and *cafer*, and, while the center of hybridization is largely west of Kansas, introgression of *cafer* genes through the river-valley populations is indicated.

#### EASTERN COLORADO

Seven specimens were available from five eastern Colorado localities:

	INDEX	WING LENGTH, IN MM.
Wray, Yuma County 1 male	5	159
1 female	4	160
Lamar, Prowers County 1 male	8	159
Jimmie Creek, Baca County 1 female	15	166
Fort Lyon, Bent County 1 male	18	168
1 male	21	167
Manzanola, Crowley County 1 male	19	163

The specimens from Wray, near the Arikaree River in central-northeastern Colorado (fig. 2), have an index similar to that of individuals from Big Springs, Nebraska, some 65 miles north of Wray. It would be interesting to ascertain whether the population along the Arikaree at this point is in contact with a more *cafer*-like population to the west along the Platte-Arkansas divide. Presumably the latter area is steppe country, with virtually no arboreal vegetation. The Arikaree and several branches of the Republican River rise

in this area; there is little possibility of any contact in the headwaters of these rivers. However, introgression by means of dispersal from other contact areas may be causing *cafer* influence in the populations along such rivers.

The main flicker contact in southern Colorado is provided by the Arkansas River. Specimens from Lamar, Fort Lyon, and Manzanola indicate a rapid shift of color characters from the center of hybridization somewhere in the vicinity of Lamar, to Fort Lyon, a distance of 30 miles. Two male specimens from Fort Lyon fall within the range of specimens from central Colorado. The eastward extent of *cafer* influence along the Arkansas, suggested by the hybrid indexes and wing lengths of the Fort Lyon and Manzanola specimens, may be due to the effect of considerable gene flow from *cafer* populations to the south, perhaps from populations in the Raton Pass and Sierra Grande areas, as well as from gene flow from the mountain populations of south-central Colorado. A female specimen from Jimmie Creek in Baca County (C.M.N.H. No. 3703) is indexed at 15. There is a contact between *auratus* and *cafer* along the Cimarron River, which runs through the southeastern tip of Colorado (see Oklahoma discussion below). In the indications of *auratus* influence that it shows, the specimen from Baca County is similar to the specimens from Cimarron County, Oklahoma.

#### OKLAHOMA, NEW MEXICO, AND TEXAS

Contacts between *auratus* and *cafer* in this region occur along the Cimarron and Canadian

rivers. Connections farther south in Texas are possible but not probable. No large streams reach far enough west into New Mexico to allow contact with *cafer* populations in that state for any *auratus* populations that may occur along the eastern reaches of such streams. Specimens examined include 23 from Oklahoma, five from the northeastern corner of New Mexico, and one from north Texas (see table 16). Samples from Oklahoma west to Lamont, Grant County, exhibit only traces of *cafer* characters. Owing to the presence of phenotypically pure *auratus* west to this area, the eastern limit of the primary area of introgression is just west of Lamont and Norman, Oklahoma. The Oklahoma samples from Harper and Beaver counties and the Lipscomb, Texas, individual, from tributaries of the Cimarron and Canadian rivers, show definite indications of *cafer* influence. The Lipscomb specimen (U.S.N.M. No. 186710) is intermediate (score 2) in crown and shaft color. The female from Gate, Beaver County (C.U. No. 25109), is intermediate in crown color, while the male from Doby Springs, Harper County (U.O.M.Z. No. 3313), has orange shafts. The samples from Cimarron County, Oklahoma, indicate that the center of hybridization occurs east of Boise City, at about the border of Cimarron County and Texas County. The Boise City specimens show the variation typical of populations in proximity to the center of the zone.

The specimens that are listed in table 15 are intermediate or near *cafer* in most characters. The wing lengths (table 16) of these same specimens also indicate the strong in-

TABLE 15  
SCORES OF COLOR CHARACTERS OF SPECIMENS FROM BOISE CITY, KENTON (CIMARRON COUNTY),  
OKLAHOMA, AND BACA COUNTY, COLORADO  
(All males except the Baca County specimen.)

	Nuchal	Throat	Ear Coverts	Malar	Crown	Shafts	Hybrid Index
Boise City	2	3	3	3	2	3	16
	1	2	2	2	1	2	10
	2	2	1	2	2	1	10
	4	4	3	3	3	3	20
Kenton	3	3	3	3	2	4	18
Baca County	4	2	2	—	3	4	15

TABLE 16

FLICKER SAMPLES FROM OKLAHOMA, NORTHEASTERN NEW MEXICO, AND NORTH TEXAS

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
OKLAHOMA			
7 miles east of Broken Bow, McCurtain Co.			
1 male	0	(0)	(146)
4 females	1, 1, 1, 1	(1)	(146.5)
Miami, Ottawa Co.			
1 male	1	(1)	(149)
Crowder, Pittsburgh Co.			
1 male	0	(0)	(150)
Norman, Cleveland Co.			
6 males	0, 0, 0, 1, 2, 2	0.8	149.2
Lamont, Grant Co.			
1 female	0	(0)	(148)
Doby Springs, Harper Co.			
1 male	4	(4)	(154)
1 female	2	(2)	—
Gate, Beaver Co.			
1 male	2	(2)	(152)
1 female	4	(4)	—
13 miles north of Boise City, Cimarron Co.			
4 males	10, 10, 16, 20	14.0	(158.8)
8 miles east of Kenton, Cimarron Co.			
1 male	18	(18)	(160)
TEXAS			
Lipscomb, Lipscomb Co.			
1 male	5	(5)	(155)
NEW MEXICO			
Las Vegas, San Miguel Co.			
1 male	22	(22)	(162)
Willis, San Miguel Co.			
2 males	19, 22	(20.5)	(162.0)
Sangre de Christo Mts., Colfax Co.			
1 female	20	(20)	(163)

fluence of *cafer* in the populations they represent. Tail, bill, and tarsal measurements of the Cimarron County and Baca County specimens are also nearer to measurements of *cafer* than to those of central Oklahoma flickers.

The contacts along the Cimarron and Canadian rivers proceed into New Mexico from western Oklahoma and Texas. The north branch of the Canadian River and the Cimarron River probably provide connections from the western Oklahoma populations to the populations of *cafer* presumed to occur (no records available) in the Capulin Mountain-Sierra Grande area. The main branch of

the Canadian River probably provides a connection from north Texas to *cafer* populations in the Cornudo Hills area (Mora County) and Corazon Peak area (San Miguel County) in New Mexico. Specimens available are from the vicinity of the Sangre de Christo Mountains in Colfax and San Miguel counties. These are very close to *cafer* in color characters (see table 16) and in measurements. The female (A.M.N.H. No. 362322) is *cafer*-like in all characters, which suggests that the western limit of the zone of hybridization lies at the eastern edge of the Sangre de Christo Range. Further elucidation of the contacts in this area is needed to define the

situation accurately. Sutton's recent (1955) collecting of the Boise City and Kenton specimens indicates that a transect of the Cimarron River would be profitable. Another problem in this area involves the location of the southernmost contact between *auratus* and *cafer* in central and western Texas and eastern New Mexico. Information regarding breeding flickers in this area is virtually lacking. Hasbrouck (1889) listed *auratus*, *cafer*, and hybrids as breeding in Eastland County, east of Abilene, Texas.

### THE NORTHERN PLAINS SITUATION

Across the northern Plains flicker contacts occur in North Dakota, Montana, and northern Wyoming, and in the provinces of Saskatchewan and Alberta.

#### NORTH DAKOTA

Thirty-five adult flickers were examined from this state. However, 22 of these are from one locality in northeastern North Dakota (Grafton, Walsh County). The present material thus allows no exact determination of the hybrid situation in this state. The limits of the hybrid zone and the primary area of introgression (map, fig. 9) are tenta-

tive, although the maximum error involved is probably less than 50 miles. The large sample from Grafton (table 17) shows a mean hybrid index of 1.60, which is about that of certain eastern South Dakota and eastern Nebraska samples. Despite the considerable traces of *cafer* characteristics exhibited by the Grafton specimens, none of them is intermediate in any character. The wing lengths of the Grafton birds are greater than those of flickers to the south. There is a south-north cline of increasing wing (and also bill, tail, and tarsal) length in *auratus*, such that the difference between *cafer* and *auratus* is greatest in the south (Oklahoma), gradually diminishing to the north and west. In western British Columbia there is nearly a reversal of the differences. Thus, despite increasing *cafer* influence proceeding from eastern to western North Dakota, the measurements of the flickers do not show a corresponding increase, as was true farther south. The Turtle Mountains sample is similar to the Grafton sample in all respects. The two females from Fort Rice show little *cafer* influence, especially when compared with the Mobridge, South Dakota, sample from slightly farther south (see discussion of South Dakota situation). Only three specimens were available from western

TABLE 17  
FLICKER SAMPLES FROM NORTH DAKOTA

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length in Mm.)
Grafton, Walsh Co.			
10 males	0, 0, 1, 1, 1, 2, 2, 3, 3, 3	1.60	159.60
12 females	0, 0, 1, 1, 1, 2, 2, 2, 2, 2, 3, 3	1.58	157.50
Fairmount, Richland Co.			
1 male	5	(5)	(157)
Turtle Mt. area <sup>a</sup>			
4 males	0, 1, 3, 3	(1.75)	(160.5)
3 females	1, 2, 2	(1.67)	(156.3)
Fort Rice, Morton Co.			
2 females	1, 3	(2)	(158.5)
Oakdale, Dunn Co.			
2 males	8, 12	(10.0)	(161.5)
Sentinel Butte, Golden Valley Co.			
1 female	10	(10)	(156)

<sup>a</sup> Includes specimens from Ramsey, Rolette, and Towner counties.



abundant. On the Missouri River in western North Dakota (on the Montana border) is Fort Union, where Audubon's party obtained the first hybrid flickers in 1843 (M. R. Audubon, 1897; Harris, 1951).

#### MONTANA AND NORTHERN WYOMING

Specimens examined from Montana and that portion of northern Wyoming which is drained by the Missouri River totaled 112; most were from southeastern Montana (see map, fig. 9). The first area to be considered is the southeastern corner of Montana, through which the Little Missouri River flows. Two small samples were available from Carter County (see table 18). Three of the four specimens are nearer *cafer* in color characters than they are to *auratus*, while the other individual is intermediate. The region is probably slightly southwest of the center of hybridization which seems to be in Harding County, South Dakota. The Yellowstone River and its tributaries permit a contact between the hybrid flickers of the Missouri River Valley of western North Dakota and the *cafer* populations of the mountains of northern Wyoming and southwestern Montana. Specimens were examined from seven localities on the Yellowstone itself, and from 10 localities in the area drained by its tributaries (see table 18). The information provided by these specimens indicates that the center of hybridization is in the Glendive-Terry region (see map, fig. 9), perhaps slightly east of Glendive, and that the shift toward *cafer* west of the hybrid-zone center is a gradual one. Both Glendive specimens are more like *cafer* than *auratus*. However, one specimen from Terry, 40 miles southwest of Glendive, is intermediate (female; index, 10). Examination of specimens from farther west and south along the Yellowstone and its tributaries clearly indicates that the center of the zone of hybridization lies close to the North Dakota border. The series from Miles City contains no males with a hybrid index below 12 (or 10 for females). The mean male index (15.9) indicates that the center of hybridization is some distance east of this locality, probably east of Glendive.

The sample from Forsyth, 45 miles west of Miles City, is worthy of more detailed consideration, since the series obtained at this

locality is the largest examined from the Plains. The mean index of the Forsyth sample (16.78; see table 18 and fig. 9) indicates that this locality is considerably west of the center of the hybrid zone. Two of the specimens were intermediate in hybrid index, while only two of the total of 43 specimens approached *auratus* more than *cafer*. Despite the tendency toward *cafer*, the fact that individuals such as the male (M.V.Z. No. 69404) indexed at 5 occur in populations as far west of the center of the hybrid zone as Forsyth is presumed to be, suggests that recombination is producing individuals phenotypically like the parental forms. Extensive collecting throughout the zone of hybridization should result in the securing of such individuals both east and west of the center of the zone. The scores for color characters of 30 Forsyth flickers are presented in table 31 and are discussed in the section on mating preferences (p. 373). The means (in millimeters) of mensural characters of males (numbers in parentheses) are:

	GRAFTON, EASTERN NORTH DAKOTA	FORSYTH, SOUTH- CENTRAL MONTANA	MISSOULA, WESTERN MONTANA
Wing	159.60 (10)	161.52 (23)	162.85 (7)
Tail	106.77 (9)	110.06 (17)	112.00 (6)
Bill	28.62 (9)	29.36 (21)	30.81 (7)
Tarsus	28.97 (10)	29.70 (23)	30.32 (7)

The differences, although strongly suggesting clines of increasing size from east to west, are not great enough to merit consideration in respect to the hybrid situation. West of Forsyth the increase in hybrid index continues. The small samples from Custer, Big Timber, and Springdale are similar to the Missoula and the Forsyth samples in hybrid index, although approaching the mean of the former more than that of the latter. Samples from the area south of the Yellowstone River into Wyoming show a tendency toward an increase in *cafer* characteristics (see table 18), although the samples are small. The Powder River samples indicate this tendency to some extent. The Fort Howe, Campbell, and Sheridan County (Wyoming) specimens are indexed higher than are the Terry and Powderville specimens (see table 18). The Lame Deer sample

TABLE 18  
FLICKER SAMPLES FROM MONTANA AND, WHERE INDICATED, NORTHERN WYOMING

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
LITTLE MISSOURI RIVER DRAINAGE			
Ekalaka, Carter Co.			
1 male	14	(14)	(159)
7 miles northeast of Albion, Carter Co. <sup>a</sup>			
2 males	12, 15	(13.5)	(165.0)
1 female	15	(15)	—
POWDER RIVER			
Terry, Prairie Co. <sup>b</sup>			
1 male	12	(12)	—
1 female	10	(10)	(160)
Powderville, Powder River Co.			
1 male	13	(13)	(159)
4 miles west of Fort Howe, Powder River Co.			
3 males	14, 18, 19	(17.0)	(159.3)
3 females	15, 17, 17	(16.3)	—
Little Powder River, Campbell Co., Wyoming			
2 males	17, 17	(17.0)	(166.5)
Powder River, Sheridan Co., Wyoming			
1 female	18	(18)	(166)
ROSEBUD CREEK DRAINAGE			
Lame Deer, Rosebud Co.			
3 males	16, 16, 18	(16.7)	(163.7)
1 female	16	(16)	—
BIG HORN RIVER DRAINAGE			
8 miles southwest of Custer, Yellowstone Co.			
1 male	19	(19)	(160)
1 female	18	(18)	—
Fort Custer, Big Horn Co. <sup>c</sup>			
3 males	17, 18, 21	(18.7)	(165.0)
3 females	13, 13, 15	(13.7)	—
Big Horn Mts., Sheridan Co., Wyoming			
2 females	17, 18	(17.5)	(159.5)
Greybull, Big Horn Co., Wyoming			
2 males	20, 20	(20.0)	(165.5)
1 female	18	(18)	—
12 miles north of Worland, Washakie Co., Wyoming			
2 males	19, 22	(20.5)	(160.0)
1 female	16	(16)	—
Green River Lakes, Fremont Co., Wyoming			
1 female	15	(15)	(165)
YELLOWSTONE RIVER			
7 miles northeast of Glendive, Dawson Co.			
1 male	15	(15)	(163)
1 female	14	(14)	—
Terry, Prairie Co. <sup>b</sup>			
1 male	12	(12)	(160)
1 female	10	(10)	—
Miles City, Custer Co. <sup>d</sup>			
8 males	12, 13, 15, 15, 17, 18, 18, 19	15.9	162.87
3 females	13, 13, 17	(14.3)	—



TABLE 18—(Continued)

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
5 miles west of Forsyth, Rosebud Co. 23 males	5, 10, 12, 12, 14, 15, 16, 16, 16, 17, 17, 18, 18, 18, 19, 19, 19, 19, 20, 20, 22, 22, 22	16.78 ± 1.72 <sup>a</sup>	161.52
20 females	—, 11, 11, 12, 12, 14, 14, 15, 15, 15, 16, 16, 16, 16, 16, 16, 16, 17, 18, 20	15.05 ± 1.06 <sup>a</sup>	161.10
6 miles southwest of Custer, Yellowstone Co. 1 male	19	(19)	(160)
1 female	18	(18)	—
Big Timber, Sweetgrass Co. 1 male	20	(20)	(161)
Springdale, Park Co. 1 male	21	(21)	166
1 female	18	(18)	—
NORTHEASTERN MONTANA			
18 miles south of Lismas, Valley Co. 1 male	16	(16)	(161)
1 female	14	(14)	—
NORTH-CENTRAL MONTANA			
Fort Assiniboine, Hill Co. <sup>f</sup> 2 males	16, 20	(18.0)	(165.5)
WESTERN MONTANA			
St. Mary's Lake, Glacier Co. 1 male	19	(19)	(168)
1 female	13	(13)	—
Missoula, Missoula Co. <sup>g</sup> 7 males	19, 19, 21, 22, 22, 23, 23	21.28	162.85
4 females	15, 16, 17, 20	(17.0)	—

<sup>a</sup> Includes 12 miles west-southwest of Capitol, Carter County.

<sup>b</sup> Includes Calypso, Prairie County.

<sup>c</sup> Includes Crow Agency, Big Horn County.

<sup>d</sup> Includes Fort Keogh, Custer County, and collecting stations 4 miles east and 3 miles south of Miles City.

<sup>e</sup> Mean and two standard errors.

<sup>f</sup> Includes Bear Paw Mountains, 20 miles southeast of Fort Assiniboine, Blaine County.

<sup>g</sup> Includes stations 5 miles south and 7 miles south of Missoula, and also  $\frac{1}{2}$  mile southwest and  $6\frac{1}{2}$  miles west of Lolo, Missoula County.

has a mean hybrid index near that of the Forsyth sample. Since Lame Deer is in the Tongue River drainage, this sample would be expected to show a greater index than the Miles City sample. The Big Horn River specimens indicate the shifting hybrid index to a lesser extent than do the specimens from farther east. The population from 8 miles southwest of Custer, near the mouth of the

Big Horn, is similar to western Montana populations in its color characters. The northern Wyoming specimens from the Big Horn Mountains, Greybull, Worland, and Fremont County are indexed higher than are the Custer-Fort Custer specimens. The mean index for the combined Wyoming samples was 18.75 for males and 14.75 for females.

The Missouri Valley situation in Montana is not known. The two specimens available from Valley County are slightly more like *cafer* than *auratus*. Lack of an adequate sample in this area allows only speculation as to the actual situation. Farther west, two specimens were available from the Fort Assiniboine area (Milk River drainage). These show only that there is greater *cafer* influence in the populations of the area than there is *auratus* influence. From western Montana, two samples were available. One of these, from the Glacier Park area (St. Mary's Lake), contains a female indexed at 13. The hybrid situation in Alberta is such that considerable introgression from *auratus* should be detected in the northwestern Montana populations. The St. Mary's Lake specimen suggests that such introgression is occurring. Eleven specimens were available from the Missoula area of southwestern Montana. The mean hybrid index for this sample is high (21.28), and the presence in the sample of a "pure" *cafer* female (20) and a nearly "pure" *cafer* male (23) indicates that this area is west of the hybrid zone as it has been defined herein. Considerable effects of introgression from

*auratus* were noted, especially in the females. One is intermediate in two characters; one, intermediate in one. The Rocky Mountain population of *cafer* in southwestern Montana may be regarded as a somewhat introgressed *cafer* population, definitely within the primary area of introgression. Mensural characters of the Missoula sample are discussed above.

#### SASKATCHEWAN

Hybrid flickers have been known for some time to occur widely in the Cypress Hills region, but the contacts to the east of this area are virtually unknown. Outside the Cypress Hills area hybrids have been reported from Prince Albert on the Saskatchewan River, from Quill Lake (both reports from Ferry, 1910) and from Elbow on the Saskatchewan River northeast of the Cypress Hills (Todd, 1947). Specimens available from areas of Saskatchewan outside the Cypress Hills totaled but four (see table 19). Two of these are indexed at 0, one at 1, and one at 3. These specimens indicate only that the populations they represent are east of the hybrid zone. It is not known whether they are

TABLE 19  
FLICKER SAMPLES FROM SASKATCHEWAN

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
CENTRAL AND NORTHERN SASKATCHEWAN			
Cochran River			
1 female	0	(0)	(154)
Prince Albert			
1 male	3	(3)	(157)
St. Walberg*			
1 male	0	(0)	(161)
1 female	1	(1)	—
CYPRESS HILLS			
Eastend			
1 male	7	(7)	(164)
Cypress Hills Reserve			
4 males	5, 8, 10, 14	(9.25)	(162.75)
1 female	11	(11)	—
North Cypress Hills			
1 male	20	(20)	(163)
Maple Creek			
6 males	7, 10, 11, 12, 13, 17	11.67	163.50
6 females	8, 11, 11, 13, 14, 17	12.33	162.33

\* Includes one female from Paradise Hill.

within the primary area of introgression or not, although the Prince Albert specimen (index, 3) suggests that this locality is within or close to the primary area of introgression.

The Cypress Hills flicker population is connected by river-valley flicker populations with the main *auratus* population to the north and east (see map, fig. 9). Godfrey (1957, p. 327) gives an idea of the nature of these contacts as follows: "The flood plains of rivers often support profuse stands of willow and tall shrubbery, with poplars and other trees rising above the shrubs." The Cypress Hills are drained by the Saskatchewan River (western, northern, and northeastern parts of the Hills) and by the Frenchman River (tributary of the Missouri draining southern Cypress Hills). The Cypress Hills are described by Godfrey (1957, p. 327) as follows: "Isolated far out on the plains . . . are the Cypress Hills, a 100 mile-long wooded plateau which rises some 1600 feet above the surrounding grassland . . . Its higher parts are in marked contrast to the surrounding semi-arid treeless plains. Its flat top and upper north-facing slopes have extensive stands of lodgepole pine, white spruce, and aspen. Below the coniferous forest down to the middle and lower levels is a broad belt of aspen. Willow shrubbery is often dense in damp depressions and on drier ground is mixed with serviceberry, cherry, hawthorn, and red-osier dogwood. Such shrubbery often follows streams from the Hills down onto the plains."

The importance of this area in regard to flickers lies in the fact that the Cypress Hills provide a large area of suitable habitat in the middle of the region in which the two flickers meet. The flickers originally reaching the Cypress Hills following the last glaciation were probably individuals of *cafer*. The avifaunal affinities of the Hills are mostly with western North America (Godfrey, 1957, p. 327). Westward movement of *auratus* into the Hills resulted in hybridization and the build-up of a large hybrid population (see below). Thus, a fine opportunity is provided for the study of possible effects of selection on the characters of the two forms of hybrids. Limited introgression from east and west constantly introduces genes from *auratus* and *cafer* into the presumably large hybrid

population in the Hills. The effect produced by limited introgression into a large hybrid population may be termed the "peninsular effect" (see discussion concerning the James River, South Dakota, population). Nineteen specimens were examined from the Cypress Hills area of Saskatchewan (see also Walsh, Alberta, sample). The hybrid indexes of the Cypress Hills individuals are shown in table 19. The main problem concerning the flickers of the Hills is whether or not they comprise a single population. Unfortunately, the size of the samples available does not now permit the solution of this problem. It is apparent from perusal of table 19 that specimens of the three smaller samples fall within, or close to, the range of variation exhibited by the Maple Creek series. The possibility that the Cypress Hills support a large hybrid population interposed between the main *auratus* and *cafer* populations demands thorough investigation. The number of flickers that could be supported in an area the size of the Cypress Hills suggests that, if a single large hybrid population inhabits this area, the number of hybrid individuals may well be considerably greater than the total number throughout the river valleys of the entire Plains area.

In nuchal color (see table 20) the males tend more toward *auratus*, while the females tend toward *cafer*. Throat color in these hybrids tends slightly toward *cafer*. Ear-covert color is generally more intermediate or tends toward *auratus*. The malar color, showing the greatest variability, tends slightly toward *cafer* (mean score for 12 males, 2.17). Shaft color tends more toward *cafer* than toward *auratus*. In crown color males are generally intermediate, while females tend somewhat toward *cafer*. Thus, the male individuals of the combined four samples tend toward *cafer* in two characters, toward *auratus* in two, and are intermediate in two. Females, however, are intermediate in one character, while tending toward *cafer* in the other four. The center of hybridization passes through the Cypress Hills, perhaps including the entire population of the Hills. I have placed the limits of the zone of hybridization and the primary area of introgression (see map, fig. 9) at what seem to me to be appropriate intervals north and east of the Cypress Hills. The considerable doubt as to

TABLE 20  
SCORES OF COLOR CHARACTERS OF THE CYPRESS HILLS FLICKERS

	Nuchal	Throat	Ear Coverts	Malar	Shafts	Crown	Hybrid Index
<b>Males</b>							
Eastend	2	0	0	3	3	0	7
Cypress Hills Reserve	1	1	1	2	1	2	8
	1	0	0	1	2	2	5
	0	3	3	2	4	2	14
	2	2	1	2	2	1	10
North Cypress Hills	3	3	3	4	4	3	20
Maple Creek	0	2	1	1	2	1	7
	2	3	3	3	3	3	17
	1	3	1	2	3	3	13
	0	3	3	1	2	1	10
	0	3	2	3	2	2	12
	0	2	1	2	3	3	11
<b>Females</b>							
Cypress Hills Reserve	4	1	1	—	3	2	11
Maple Creek	4	4	3	—	3	3	17
	2	3	2	—	2	2	11
	4	0	1	—	1	2	8
	4	2	2	—	3	3	14
	3	3	1	—	1	3	11
	3	3	2	—	3	2	13

the actual limits of these areas has led me in this case, and in all similar instances, to broaden the lines that mark the limits of these zones. These broadened lines, extending through Saskatchewan, in all probability encompass the actual limits of the areas as I have defined them.

#### ALBERTA

The situation in Alberta is complicated by two factors: the presence of the Rocky Mountains in western Alberta, which support a large population of red-shafted flickers, and the fact that the Plains reach their northern limit in this province. As elsewhere, flickers in Alberta are limited in distribution by the presence of arboreal vegetation. Moss (1932) has presented a clear picture of the vegetation zones of Alberta. The "prairie" of Moss, herein called "Plains," covers all of southern and eastern Alberta from near the base of the Rockies north through the Calgary area to Didsbury, and then east-northeast to the north of Coronation and Sullivan Lake to Saskatchewan. Within this area flickers are confined to the valleys of the Milk River and

the Saskatchewan River and its tributaries, except for the region in and around the Cypress Hills (see Saskatchewan discussion). Along the east face of the Rocky Mountains from the Waterton Lakes area to Didsbury and then east (south of Red Deer) and north to Saskatchewan is the parkland area, containing scattered trees away from river valleys. The isolated groves are probably inhabited by flickers and provide for a more dense population than in the Plains. From Red Deer north to Westlock and then east (including Edmonton) to Saskatchewan above the parkland area is the poplar area. According to D. A. Boag (personal communication), from Red Deer northward (including the poplar area) vegetation is such that flickers are no longer confined to valleys but occur throughout the area. Thus, the situation is as follows: (1) *cafer* populations extend north in the Rocky Mountains (Moss's "Cordilleran Forest"); (2) a hybrid population with some individuals tending toward *cafer* occurs in the Cypress Hills; (3) introgression from *auratus* east and south of Alberta is passing through the river valley

populations to the Cypress Hills and into the Rocky Mountain *cafer* population; (4) northern Alberta is inhabited by a huge *auratus* population south to the plains; and (5) the critical point in terms of the hybrid situation exists northwest of Didsbury, where the massive northern Canadian *auratus* population is brought into contact with the sizable, but smaller, Rocky Mountain *cafer* population.

Specimens examined (see table 21 and map, fig. 9) from southern Alberta totaled 22. Two males were available from Walsh at the northwestern edge of the Cypress Hills. The indexes of these specimens are comparable to those from the Cypress Hills of Saskatchewan. The Edmonton area is in the "Poplar Area" of Moss (1932). Specimens from this region are very close to *auratus*, except for the female from Bon Accord which indexed at 3.

TABLE 21  
FLICKER SAMPLES FROM ALBERTA

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
CYPRESS HILLS			
Walsh 2 males	9, 11	(10.0)	(162.5)
EDMONTON AREA			
Bon Accord 1 female	3	(3)	(152)
Edmonton 2 males	1, 2	(1.5)	(162.0)
2 females	0, 0	(0)	—
Nisku 1 female	0	(0)	(156)
Camrose 2 males	0, 1	(0.5)	(161.5)
RED DEER AREA			
3 miles south-southwest of Ponoka 1 male	1	(1)	(159)
Red Deer 1 male	2	(2)	(159)
1 female	1	(1)	—
Didsbury 1 male	2	(2)	(159)
WEST-CENTRAL ALBERTA			
Brazeau River 1 male	1	(1)	(154)
CALGARY AREA			
Rosebud 2 males	1, 2	(1.5)	(158)
1 female	7	(7)	—
20 miles southwest of Calgary 1 male	5	(5)	(158)
Bowness 2 males	0, 3	(1.5)	(158.5)
BANFF AREA			
Banff 1 male	21	(21)	(162)

The Edmonton area is outside, but probably fairly close (within 50 miles) to, the limit of the primary area of introgression. The specimens from the Red Deer area all show indications of introgression from *cafer*. One male (R.O.M.Z. No. 24.4.14.470) was intermediate in crown color, scoring 2. The eastern limit of the primary area of introgression passes through this area, probably somewhere between Red Deer and Didsbury. The single specimen indexed at 1, from the Brazeau River, about 75 miles northwest of Red Deer, indicates that *auratus* occurs in "pure" form rather close to the Rocky Mountains. The primary area of introgression must be somewhat narrow and closely applied to the mountains in this area. Only one male from the Calgary area was indexed at 0. It would appear that the primary area of introgression includes the Calgary region. Information provided by Boag (personal communication) suggests that the zone of hybridization commences just west of Calgary. The Alberta Biological Station 20 miles west of Turner Valley (southwest of Calgary) is apparently well within the hybrid zone, according to Boag. I have placed the eastern limit of the zone between Calgary and the Station at a point 20 miles southwest of Calgary (see map, fig. 9) on the basis of Boag's observations and the specimen material available to me. Only one specimen approaching *cafer* in hybrid index was available for examination; this was a male from Banff (A.M.N.H. No. 56130). Although *cafer*-like in most respects, this specimen exhibited a tendency toward intermediate crown color with a score of 3. Clarke and Cowan (1945) have indicated that the hybrid zone crosses Banff National Park. They also stated that *cafer* is more common in the Park, although suggesting that most specimens of "*cafer*" might show signs of hybridization on close examination. From the east edge of the Park eastward, these authors found *auratus* more common. Other authors (Macoun and Macoun, 1909; Rand, 1948a; Soper, 1947; and Williams, 1946) have found *auratus* breeding to the eastern edge of the Rockies and even in the mountains in the Waterton Lakes Park and Banff areas. The center of the zone of hybridization appears to occur at the eastern edge of the mountains.

The *cafer* population of the Rockies is undergoing heavy introgression from *auratus* to the north and the east. The narrowness of the hybrid zone and of the primary area of introgression east of the mountains may be attributed to the strong influence of the large *auratus* populations not far from the mountains. The problem of the determination of these zones in southern Alberta and in west-central Alberta is greater than that in the Banff region. Information concerning the distribution of flickers in Alberta (Salt and Wilk, 1958) suggests that the *cafer* populations follow the Rocky Mountains into British Columbia.

The flicker situation north of the Rocky Mountains in western Alberta is unknown. It would be of interest to compare the situation there with that to the west and southwest. The effects of introgression from the northern *auratus* population may be more notable in the *cafer* populations of the Rockies north of Jasper Park. The situation between the Cypress Hills and the Rockies in southern Alberta also needs study. Hybrids have been reported in the Milk River Valley (Macoun and Macoun, 1909). However, the exact location of the hybrid zone between the Hills and the Rocky Mountains is not known. Since *cafer* has not been reported breeding between the Cypress Hills and the Lethbridge area, while *auratus* has (Williams, 1946), it may be that the Cypress Hills population is surrounded by more *auratus*-like populations. At any rate, this possibility should be explored.

#### THE SITUATION IN NORTH-WESTERN AMERICA

This area is of paramount importance as far as hybridization is concerned. Across the province of British Columbia from Jasper Park, Alberta, west to southeastern Alaska, the presence of timber has allowed the *auratus* and *cafer* populations to form a massive (500 miles long) contact. The size of this contact is the prime factor influencing introgression in North American flickers, since the Plains river valleys afford only a small fraction of the contact provided in British Columbia. The size of the British Columbia contact allows *auratus* genes to penetrate the *cafer* population, so that its effects can be measured in the *chrysoides* populations in the

Southwest, as a result of the interbreeding between the latter form and *cafer* (see p. 405).

#### BRITISH COLUMBIA

Optimum flicker habitat is provided in most of the 366,000 square miles of this province. Entering British Columbia from the south are the coastal race *cafer* and the inland race *collaris* of the *cafer* subspecies group. The race *cafer* extends up the coast to southeastern Alaska at about the Yukon-Alaska border. From the north and east, *auratus* populations extend southward over a large part of the province. The contact that developed in the area probably resulted from the nature of deglaciation there (see p. 410). Hybridization between the flickers has been noted by most authors dealing with British Columbian birds. Taverner (1934) expressed doubt that any flickers in the province were pure. He suggested that the *auratus* influence in the flicker populations was weaker along the coast and coastal islands than in the interior, although hybrids were reported from Vancouver Island. In reviewing the McCabe collection of British Columbian birds, Dickinson (1953) presented a report of the flicker situation in central British Columbia. He used 65 specimens, of which about a third were migrants or non-breeding individuals, and concluded that *Colaptes auratus* and *C. cafer* could not be maintained as separate species. Most of the specimens used by Dickinson were available for the present investigation. Adult breeding specimens from British Columbia that were examined totaled 119. Only two of these could be assigned to *auratus* in all characters, while but three could be assigned to *cafer*, thus justifying Taverner's suspicions. Specimens from British Columbia suggest that introgression from *cafer* is having much less effect on the *auratus* population in the north than introgression from the latter is affecting the *cafer* population to the south.

Specimens from Vancouver Island were considered as comprising a single sample (see table 22 and map fig. 9). Localities from Vancouver Island are as follows (number of male and female specimens from each locality given in parentheses):

Parkerville (2, 0)  
Albarine Valley (1, 0)  
(French) Creek (1, 0)

Little(?) River (2, 0)  
Union Bay (0, 1)  
Comox (1, 2)  
Nicomin Island (0, 1)  
Victoria (1, 0)  
Vancouver Island (0, 1)

The Vancouver Island specimens are similar in hybrid index to those of the rest of southern British Columbia. The mean hybrid index (20.88 for males) is similar to the mean indexes for the southwestern and south-central British Columbian samples. Indications of *auratus* influence are distinctly noticeable, however; only one of the 13 specimens is *cafer*-like in all characters.

Ten localities from southwestern British Columbia, excluding Vancouver Island, were represented by specimens. These localities are:

Agassiz (1, 0)  
Westminster (2, 2)  
Chilliwack (1, 0)  
Sumas (1, 0)  
Deer Park (1, 0)  
Goldstream (10, 6)  
Mt. Lehman (2, 1)  
Port Moody (1, 0)  
Lund, Melaspina Inlet (1, 1)  
Gibson's Landing, Howe Sound (1, 0)

The mean hybrid index approximates the indexes of the samples to the east and from Vancouver Island (see table 22). Specimens that exhibit extremely *auratus*-like characters are: a female from Goldstream (A.N.S.P. No. 30786) possessing fawn-colored throat and ear covert color (scores, 1, 1); and a male from Chilliwack (M.C.Z. No. 45604) having solid black malar stripes and a complete nuchal patch (scores, 0, 0).

Five localities from south-central British Columbia were combined for purposes of this study. The localities are Okanagan, Okanagan Landing, 4 miles north of Kamloops, Edgewood, and Shuswap. The combined sample shows a mean hybrid index similar to that from the other areas to the west. The fact that there is no discernible east-west gradient indicates that the hybrid situation of the eastern slope of the Rocky Mountains in Alberta is having little effect on the characters of British Columbian flickers. Only one locality in southeastern British Columbia was represented by a sample; this was Cranbrook,



TABLE 22  
FLICKER SAMPLES FROM BRITISH COLUMBIA

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
SOUTHEASTERN BRITISH COLUMBIA			
Cranbrook			
1 male	21	(21)	(163)
1 female	16	(16)	—
SOUTH-CENTRAL BRITISH COLUMBIA			
5 localities <sup>a</sup>			
8 males	16, 19, 19, 20, 21, 21, 22, 24	20.25	166.63
4 females	16, 17, 18, 20	(17.75)	—
SOUTHWESTERN BRITISH COLUMBIA			
10 localities <sup>a</sup>			
21 males	14, 18, 18, 19, 19, 19, 19, 20, 20, 20, 20, 21, 21, 21, 22, 22, 22, 22, 22, 23, 23	20.24	165.19
10 females	13, 16, 16, 17, 18, 18, 18, 18, 19, 19	17.20	163.20
VANCOUVER ISLAND			
9 localities <sup>a</sup>			
8 males	16, 17, 20, 22, 22, 23, 23, 24	20.88	163.12
5 females	16, 17, 18, 19, 19	17.80	—
QUEEN CHARLOTTE ISLAND			
Masset			
1 male	23	(23)	(166)
2 females	19, 20	(19.5)	—
WEST-CENTRAL BRITISH COLUMBIA			
Bella Coola			
1 male	11	(11)	(168)
Stuie			
1 male	16	(16)	(160)
Anahim Lake			
3 males	12, 14, 17	(14.3)	(162.7)
4 females	15, 15, 16, 17	(15.8)	—
CENTRAL BRITISH COLUMBIA			
Clinton			
1 male	20	(20)	(158)
1 female	17	(17)	—
100-Mile House <sup>b</sup>			
5 males	17, 18, 19, 20, 21	19.00	164.20
3 females	13, 16, 17	(15.3)	—
Clearwater			
9 males	10, 16, 17, 18, 19, 19, 20, 20, 21	17.78	164.11
8 females	12, 14, 14, 15, 15, 16, 17, 17	15.00	—

TABLE 22—(Continued)

Locality and No. of Specimens	Hybrid Indexes	Mean Hybrid Index	Mean Wing Length (in Mm.)
Indianpoint Lake			
4 males	8, 9, 11, 16	(11.0)	(160.8)
2 females	16, 17	(16.5)	—
Cottonwood			
1 male	7	(7)	(163)
2 females	6, 13	(9.5)	—
NORTHERN BRITISH COLUMBIA			
Hazelton			
4 males	4, 6, 7, 8	(6.25)	(161.0)
1 female	7	(7)	—
Kispiox Valley, 23 miles north of Hazelton			
1 male	1	(1)	(156)
4 females	0, 1, 1, 2	(1.00)	—
Telegraph Hill, Sawmill Lake			
2 females	0, 1	(0.5)	(162.0)
Glenora, Stikine River			
1 female	2	(2)	(163)

<sup>a</sup> Localities are listed in the text.

<sup>b</sup> Includes specimens from Lac La Hache.

with but a male and female. The female (R.O.M.Z. No. 24.4.14.473) had intermediate ear-covert color. No difference in index was detected between these two specimens and those from farther west.

Farther north, the small sample from Queen Charlotte Island comprises three specimens which are nearly, or completely, *cafer*-like in all characters. The hybrid indexes of these specimens are at the upper extreme of those from southern British Columbia. There may be limited gene flow from the mainland, allowing considerable inbreeding in this island population and perhaps others in the area.

Three samples were available from west-central British Columbia (see table 22). The two single-specimen samples do not tell very much, although the specimens are indexed somewhat lower than specimens from farther south. The Bella Coola specimen (C.N.H.M. No. 173012) in particular shows more *auratus* influence than *cafer* influence (nuchal score, 0; crown, 3; other characters scored 2). The sample from Anahim Lake shows an average hybrid index slightly more toward *cafer* than toward *auratus* (14.3). One male (M.C.Z. No. 282624) is exactly like the above-mentioned Bella Coola specimen in its approach toward

*auratus*. The center of the hybrid zone apparently lies north of the Bella Coola River-Anahim Lake area, within Tweedsmuir Provincial Park.

Five samples were available from central British Columbia (see table 22). The specimens from Clinton and from the 100-Mile House-Lac La Hache area are only slightly more *auratus*-like than are southern British Columbian specimens. East of 100-Mile House, specimens from Clearwater show more of an approach toward *auratus*. One male has a hybrid index of 10 and is scored 1 in four of six characters. However, the variability in hybrid index permits no definite statement that the apparent difference between the 100-Mile House and the Clearwater samples is significant, which is indicated by the following information for the two samples (males only):

	MEAN HYBRID INDEX	STANDARD DEVIATION	COEFFI- CIENT OF VARI- ABILITY
100-Mile House	19.00 ± 1.42	1.58	8.31
Clearwater	17.78 ± 3.42	3.92	22.04

The large standard error, standard deviation,

and coefficient of variability of the Clearwater sample preclude attaching significance to the apparent differences between the samples.

Indianpoint Lake and Cottonwood are evidently close to the center of the zone of hybridization, as is indicated by the mean hybrid indexes of the samples and by the low scores in many characters, especially in the males. Also, about equal numbers of the specimens are indexed above the midpoint of the hybrid-index scale (12 for males, 10 for females) as are indexed below it (four above, five below, for both samples). One important conclusion is that the strong *cafer* influence on the east face of the Rocky Mountains in Alberta is not maintained as the mountains curve westward into British Columbia. Thus, the center of the hybrid zone, which apparently extends into Jasper Park, moves out of the Rocky Mountains west of the Park. Most (all?) of the Rocky Mountain region of British Columbia is within the primary area of introgression. The flicker populations of these mountains are presumed to be strongly *auratus*-like, but with most individuals showing traces of *cafer* influence.

The center of the zone of hybridization crosses British Columbia from east to west about on a line between the Indianpoint Lake region and Tweedsmuir Park. Specimens from two localities (Hazelton, Kispiox Valley) north of Tweedsmuir Park are therefore important. The Kispiox Valley specimens are labeled as having been taken 23 miles north of Hazelton by Swarth and Strong. We thus have a remarkable picture of a shift in characters of a flicker population over a short distance (see table 23). Clearly the boundary of the primary area of introgression and the zone of hybridization lies between these localities. The gradient in hybrid index cannot be calculated exactly owing to the disproportionate number of individuals of each sex in both samples. However, the gradient must be approximately 0.20 or 0.25 i.p.m., a figure that has been matched only near the center of the hybrid zone in the Plains area. A comparison of the Hazelton and Anahim Lake hybrid indexes indicates that Anahim Lake is somewhat closer to the center of hybridization than is Hazelton. However, the sharp

gradient in hybrid index between Kispiox Valley and Hazelton may continue to the south for some distance. There is no reason to assume that the low gradient (0.037 i.p.m.) indicated by the difference in hybrid index between the two points actually holds throughout this distance. The center of hybridization between the two localities can be tentatively placed somewhere in the vicinity of Tweedsmuir Park, pending investigation of the situation in that area (see map, fig. 9).

SOUTHEASTERN ALASKA, SOUTHWESTERN  
YUKON, AND NORTHWESTERN  
BRITISH COLUMBIA

Individuals of *cafer* have been reported as far north as Carmacks in the Yukon (Taverner, 1934). Apparently *cafer* is the predominant form along the coast north to Sitka and Juneau. A hybrid reported from Sitka (J. A. Allen, 1892) is apparently the same individual noted by Taverner (1934). At the northern limit of its range, the subspecies *cafer* probably interbreeds with *auratus* (subspecies *luteus*). The Glacier Bay region may be near the center of the hybrid zone. Flickers north of this area in the vicinity of Chitina Glacier are reported to be strongly *auratus*, but gray has been noted on the throats of several (Taverner, 1934). A hybrid flicker has been reported from Prince Rupert on the northwest coast of British Columbia (Brooks, 1923). Inland flickers are predominantly *auratus* (Atlin, Telegraph Creek, Dease Lake). Contact between *auratus* and *cafer* may be restricted by the intervening Coast Range Mountains between southeastern Alaska and British Columbia. A male flicker (R.O.M.Z. No. 36.9.18.208) from Yakutat Bay, Alaska, showed faint gray traces in the auricular and throat regions, indexing at 2. A female (R.O.M.Z. No. 71332) from Snag in the Yukon is typical *auratus* in all characters (index, 0). British Columbia specimens from Glenora on the Stikine River, and from Telegraph Hill (see table 22) showed little indication of *cafer* influence. (Glenora female had faint crown and ear-covert traces.)

Mensural characters are of little value in an analysis of the hybrid situation in the Northwest, because *auratus* in this area approaches *cafer* in its measurements. A small

TABLE 23  
SCORES OF COLOR CHARACTERS OF SPECIMENS FROM KISPIOX VALLEY  
AND FROM HAZELTON, BRITISH COLUMBIA

	Sex	Nuchal	Throat	Ear Coverts	Malar	Shafts	Crown	Hybrid Index
Kispiox Valley								
	♂	0	0	0	1	0	0	1
	♀	0	0	0	—	0	0	0
	♀	0	0	0	—	1	0	1
	♀	0	0	0	—	0	1	1
	♀	1	1	1	—	0	0	2
Hazelton								
	♂	0	2	2	0	2	1	7
	♂	1	3	1	2	1	0	8
	♂	0	2	1	1	0	0	4
	♂	0	2	1	2	0	1	5
	♀	0	2	2	—	1	1	7

sample of *auratus* females from northern British Columbia, Yukon, and Mackenzie was compared with a sample of "*cafer*" females from southwestern British Columbia. The measurements (in millimeters) are:

	<i>auratus</i>	<i>cafer</i>
Wing length		
Mean	163.14	163.20
Range	160–170	157–165
N	7	10
Tail length		
Mean	109.60	113.00
Range	107–113	111–118
N	5	9
Bill length		
Mean	28.61	29.78
Range	25.9–31.3	26.0–32.3
N	7	9
Tarsal length		
Mean	29.97	29.50
Range	29.0–30.4	28.9–30.9
N	7	10

The samples indicate that wing length and tarsal length are of no value when one is dealing with hybrids from the intermediate area. The slight difference in bill length is rendered valueless owing to the great variability of this character. Tail length shows some difference which might be utilized with large samples. However, some overlap and considerable variability in this character make it undesirable, in view of the small samples presently

available, to use tail length in dealing with hybrids in the Northwest.

The center of the zone of hybridization passes across the British Columbia-Alaska border to the neighborhood of Juneau and Glacier Bay, where it reaches the coast. The contact in the Alaska-British Columbia area may be limited. The zone itself occupies most of southern British Columbia and possibly a narrow strip along the Alaska-British Columbia boundary. The southern limit of the zone barely cuts across the southern and western corner of the province. The primary area of introgression of *auratus* genes into the *cafer* population begins along the southern boundary and continues southward (see section on introgression in *cafer*). The primary area of introgression of *cafer* characters into *auratus* is apparently much narrower than the similar area south of the hybrid zone (see map, fig. 10). Most of northern and eastern British Columbia contains flicker populations which are essentially *auratus*, with some traces of *cafer*. Stronger indications of introgression, marking the primary area of introgression, occur only in a limited area extending as a belt 50–100 miles wide to the north and east of the hybrid zone (see fig. 9). These limits are tentative, and the "zones" are not very clear-cut. However, they must suffice until larger series become available from a greater number of localities.

INTROGRESSION IN POPULATIONS OF *AURATUS*

## DISCUSSION OF METHOD

The term "introgressive hybridization" was originally defined by Anderson and Hubricht (1938, p. 396) as "an infiltration of the germ-plasm of one species into that of another." However, in their discussion (p. 396) these authors apparently recognized the difficulty in applying this term to hybridization between "species." They stressed in particular the "difficult problem" of the application of the terms "hybrid" and "species." Anderson later (1949, p. 61) discussed the application of "introgressive hybridization" to situations of interbreeding between various kinds of populations: "In many ways the flow of genes from one genus into another presents the same phenomenon" (as introgressive hybridization between "species"). He then used the term "introgression" to "apply with equal validity whether the entities involved were subspecies, species or genera." Anderson further (1949, p. 64) used Woodson's study of *Asclepias tuberosa*, which shows introgression between well-differentiated geographical races, as an example of introgression.

Mayr (1955, pp. 331-332) favored the restriction of the term "introgression" to situations in which there is an "incorporation of genes of one species into the gene complex of another species." While I sympathize with Mayr's objection to the use of "introgression" to cover all types of gene exchange, I believe, as does Anderson (1949, p. 61), that we need much more information concerning situations of this nature before an exact definition for the term can be set. Introgression can be defined as gene flow: (1) between formerly isolated populations as a result of hybridization following the formation of a secondary contact; and (2) between normally reproductively isolated, sympatric populations. Introgressive hybridization in flickers is of type 1.

Ideally it would be best to trace indications of introgression along a transect from the zone of hybridization to the extremities of the ranges of the forms involved, which would require samples taken from many states, consisting of large series; these are at present unavailable. In the present report I

attempt only the demonstration of introgression in eastern *auratus* populations.

Introgression is usually demonstrated by one's proving the presence in one population of characters of another population, with which the first is in genetic contact; these are found to diminish gradually or sharply in populations farther and farther from the zone of hybridization. In such a demonstration of introgression, it is assumed that (1) the characters of the other form discovered in a population are present as a result of the interbreeding of the two populations; and (2) the cline of diminishing characteristics of the other form in a population as one progresses farther from the zone of hybridization is produced solely by the greater genetic influence of the other form close to the hybrid zone. These assumptions can be made only after an intensive study of the variation patterns of the forms involved has been made.

The *auratus* and *cafer* populations show differences in many characters. In addition to differences in color characters used in the hybrid index, *cafer* has longer wings, a longer tail, greater body weight, greater tarsal and bill lengths, more black in the tail, a broader breast band, and a grayer dorsal color. Genes responsible for the phenotypic expression of these and probably other characters are constantly being passed from *cafer* into *auratus* populations. In seeking evidence for introgression, one must realize that, despite the extensive hybridization between the two forms, it will be possible to detect the effects of introgression in only a few characters, because selection operating in local *auratus* populations has probably "cultivated" genotypes and gene combinations favorable to particular local conditions. Selection operates to maintain such gene combinations and genotypes, which results in the formation of local (microgeographic) races and sometimes subspecies. Genes responsible for the various characters of *cafer* that are forced into *auratus* populations are differentially acted on by selection. Many will be rapidly eliminated from the populations near the hybrid zone, because of their being disadvantageous in some way, while others more neutral or ad-

vantageous in *auratus* populations will be dispersed more widely. Some *cafer* characters are apt to be detected much farther east than others. Mensural differences between *auratus* and *cafer* are considerable, but there is no evidence that introgression into *auratus* populations of *cafer* genes determines such characters. One point that should be stressed in regard to the detection of introgression is the necessity of studying a number of characters. Lack of introgression in one or two characters offers no assurance that it is not occurring at all, for the characters may be of the type undergoing a rapid shift in the hybrid zone. Genes having favorable effects but not affecting characters that are studied may be passing freely into the hybridizing populations. The *Corvus corone-C. cornix* situation (Meise, 1928) may be a case of this sort. A beautiful example is shown by Dessauer, Fox, and Pough (1962), who demonstrated the extensive effects of hybridization from electrophoretic work on hybrid lizards (*Cnemidophorus*), compared to less extensive effects determined by conventional morphological methods (Zweifel, 1962).

Detection of introgression away from areas of hybridization probably depends on the presence and effectiveness of selection against genes that control the various characters. Since the color-character differences between *cafer* and *auratus* seemed to have little or no effect on interbreeding between them, and since various authors (Berier, 1880, 1881; Nelles, 1936; Ridgway, 1881) had found indications of *cafer* characters in *auratus* individuals, it seemed reasonable to use the color characters to study the possibility of introgression. Only these color characters are dealt with here.

#### CAFER CHARACTERS IN AURATUS POPULATIONS

Figure 10

The information obtained from color characters concerning introgression in *auratus* is summarized in tables 24, 25, and 26. I have placed the samples of *auratus* in three groups. Group I includes samples from eastern Nebraska in the area 150–350 miles east of the center of the zone of hybridization. Group II includes specimens from northern Canada

and from central Canada and the United States in the area from 350 to 1000 miles from the center of the hybrid zone. Specimens from beyond 1000 miles of the center of the hybrid zone are in group III.

#### NUCHAL COLOR

Nuchal-patch restriction is difficult to detect in *auratus* populations. Of 497 flickers examined from eastern North America, including Cuba, Grand Cayman Island, and northern Canada, only eight had a restricted nuchal patch. One female possessed only a broken, narrow patch scored at 2. In studying this character, I took into account the variation in the width of the patch. The patch is normally  $\frac{1}{2}$  inch in width (range, about  $\frac{1}{4}$  inch to 1 inch). Nuchal patches less than  $\frac{1}{4}$  inch in width were indexed at 1, as in the index method used for the analysis of hybrids. A score of 2 was given for the same expression of this character as in the hybrid-index system described above. The frequency of nuchal-patch scores of 1 and 2 (tables 24, 26) for groups II and III indicates little if any effect of introgression involving this character in eastern *auratus* populations. Group I shows a significantly higher frequency of individuals scored 1 than do groups II and III (see table 26 for *P* values obtained by testing differences shown in table 24 by the chi-square method). Also, one female from this area scored 2, and one scored 3. The restriction of the nuchal patch exhibited by the eastern Nebraska flickers (group I) is ascribed to the effects of introgression from *cafer*. The data for groups II and III do not indicate that the cases of restriction found in these groups is attributable to the effects of introgression, but such remains a distinct possibility.

In comparison with other characters (table 24), it is evident that for some reason the genes that restrict the nuchal patch are not being passed eastward to the same degree as genes that determine others (such as malar color). There is a distinct possibility that either (1) the nuchal patch is associated with some behavioral pattern of *auratus* and the tendency toward restriction of the patch is being "discouraged" by selection; or (2) genes determining the restriction of the

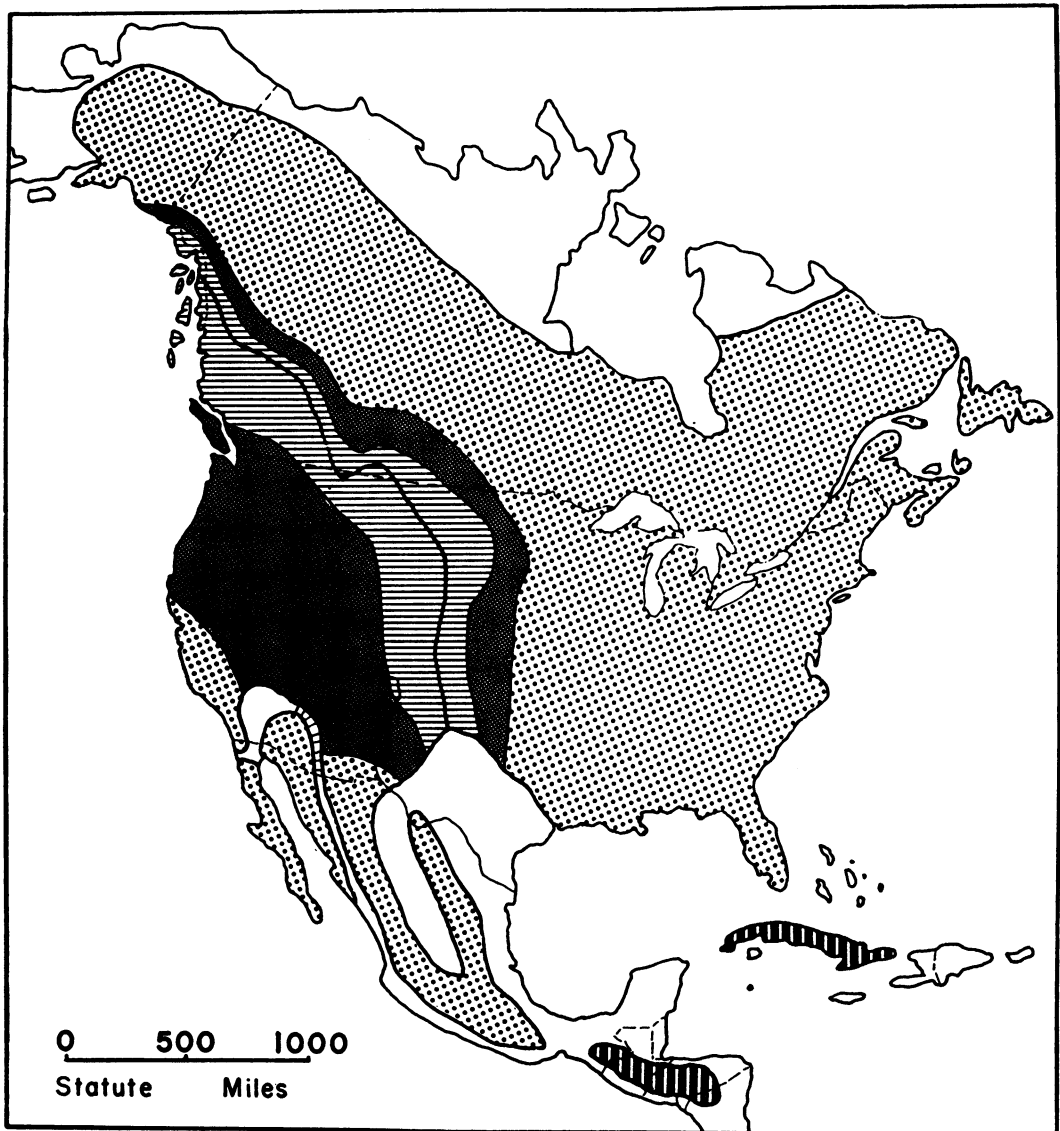


FIG. 10. Introgression in populations of North American flickers resulting from hybridization between the *auratus* group and the *cafer* group. Horizontal lines mark the hybrid zone. Dark areas are the primary areas of introgression. Spotting indicates secondary areas of introgression. Heavy vertical lines denote areas in which flicker populations show no indications of introgression.

nuchal patch are, directly or by association with other genes, disadvantageous and are being eliminated from the population. Behavioral study of this character would be of considerable value. This is the only character that differs by being present in one form and absent from the other. In regard to 2, it might be noted that, although the frequency of re-

stricted nuchal patches is low in eastern populations, such a low frequency (one or two per 100 individuals) for a gene (or genes) does not mean that this gene (or genes) is ineffective in the population. The increased variability conferred on a population by genes of low frequency is of potential importance in the evolution of the population.

TABLE 24  
INCIDENCE OF *cafer* CHARACTERS IN *auratus* POPULATIONS

Character	Group <sup>a</sup>	N	Males Score			Per Cent Scoring 1 or More	N	Females Score				Per Cent Scoring 1 or More
			0	1	2			0	1	2	3	
Nuchal	I	80	74	6	0	7.50	74	60	12	1	1	18.92
	II	106	104	2	0	1.89	70	67	3	0	0	4.29
	III	142	141	1	0	0.70	134	132	1	1	0	1.64
Throat	I	80	58	17	5	27.50	74	53	19	2	0	28.38
	II	106	101	5	0	4.72	70	66	4	0	0	5.71
	III	125	122	3	0	2.40	123	119	4	0	0	3.25
Malar	I	80	49	29	2	38.75	—	—	—	—	—	—
	II	106	91	15	0	14.13						
	III	142	129	13	0	9.15						
Crown	I	80	56	23	1	30.00	74	49	21	4	0	33.78
	II	106	80	22	4	24.53	70	50	17	3	0	28.57
	III	125	106	18	1	15.20	123	102	16	5	0	17.00
Shafts <sup>b</sup>	I	154	97	52	5	37.01	—	—	—	—	—	—
	II	176	114	58	4	34.20						
	III	266	177	85	4	33.46						

<sup>a</sup> Group I includes specimens from Nebraska 150–350 miles east of the center of the zone of hybridization; group II, specimens from the area 350–1000 miles east and north of the center of this zone; and group III, specimens from the area beyond 1000 miles east and north of the center of this zone.

<sup>b</sup> The number for this character includes both sexes.

#### THROAT COLOR

Traces of gray throat color in *auratus* individuals are easily detectable, provided careful distinction is made between the actual encroachment of gray in the tan of the throat and the gray "frosted" color that frequently appears over the entire throat. Of 469 *auratus* specimens (groups II and III; table 24), including Cuban specimens, 16 definitely showed gray in the throat, as their scores (1) indicate. With a larger number of specimens, the eastern (group III) sample shows fewer gray traces than does group II, although the difference is not considered significant. Group-I specimens showed considerable gray in the throat, with five individuals scoring 2 in this character. The difference between group I and the other two groups is highly significant (table 26). Many of the comments concerning nuchal color are applicable to throat color as well. Again, there is suggestive evidence of introgression in the east, but the levels of incidence are quite low.

The presence of gray color in such a high proportion (27.5% of males, 28.38% of females) of eastern Nebraska flickers indicates that considerable introgression is occurring. The reasons for the low frequency of this

TABLE 25  
HYBRID INDEXES OF THE THREE GROUPS OF  
*auratus* INDIVIDUALS DESCRIBED  
IN TABLE 24

	Group	<i>N</i>	No. Indexed 3 or More	Per Cent Indexed 3 or More
Males	I	80	25	31.25
	II	106	13	12.26
	III	124	7	5.64
Females	I	74	14	18.92
	II	70	9	12.85
	III	123	5	4.07



TABLE 26

SIGNIFICANCE (DETERMINED BY CHI-SQUARE METHOD) OF DIFFERENCES IN COLOR CHARACTERS AND HYBRID INDEX AMONG THE GROUPS OF *auratus* POPULATIONS DESCRIBED IN TABLE 24

Differences Between Groups	<i>P</i> Values <sup>a</sup>					
	Nuchal Color	Throat Color	Crown Color	Malar Color	Shaft Color <sup>b</sup>	Hybrid Index
Males						
I-II	0.05	0.01	0.50	0.01	0.50	0.01
II-III	—	—	0.05	0.10	0.80	0.05
I-III	0.01	0.01	0.01	0.01	0.50	0.01
Females						
I-II	0.01	0.01	0.50	—	—	0.50
II-III	—	—	0.01	—	—	0.01
I-III	0.01	0.01	0.01	—	—	0.01

<sup>a</sup> Being tested are the differences between groups in the number of individuals scoring 1 or more for each character; for hybrid indexes the difference being tested is in the number of birds indexed at 3 or more.

<sup>b</sup> Both sexes combined for this character.

character in groups II and III are probably similar to those given for nuchal color.

#### EAR-COVERT COLOR

The color of ear coverts is not included in tables 24 and 26. The difficulty encountered in dealing with gray traces in the ear coverts of *auratus* made it advisable to exclude the character. Gray appears at the rear edge of the ear coverts of many eastern *auratus* individuals; slight extension of this gray would give a score of 1. Totaling all individuals with any gray in the auricular area, it was found that roughly 65 per cent of specimens in group II and 65 per cent of specimens in group III had such gray indications. It is not known whether the slight amount of gray found in *auratus* was originally due to introgression, or whether this is a normal variation lacking in some individuals. At any rate it was not feasible to use this character for investigating introgression.

#### CROWN COLOR

Brown crown color is present in *auratus* individuals in "fresh" plumage (i.e., after the postnuptial molt), and the gray crown color present in the breeding season appears by spring owing to wear. Brown color may appear in *auratus* owing to (1) incomplete effect of wear in producing more gray crown color;

(2) normal brown variants in the populations; or (3) effects of introgression from *cafer*. The effect of wear, and of possible genes controlling brown color remaining from past periods of hybridization, may be expected to be constant throughout the population, thus introducing a constant error in the scoring of the specimens. Table 24 indicates that there is a gradient of traces of brown crown color from west (group I) to east (group III). The gradient is shown for both sexes. The significance of the observed differences is shown by the *P* values indicated in table 26. Although this demonstrates only that a gradient exists, there are two reasons for considering the gradient to be the result of introgression. First, the gradient in crown color is unlike other gradients detected in a study of the variation of 19 mensural and color characters, not including characters used in the hybrid index, in flickers. Second, the similarity shown by several other hybrid-index character gradients suggests that introgression is the cause of this gradient.

#### MALAR COLOR

Red in the malar patch of *auratus* males was noted frequently. If Test (MS) was correct in his conclusion that red and black are both normally present in *auratus* malars, then some difficulty is encountered in assign-

ing introgression as the cause of macroscopically visible red color. However, it can be assumed that the frequency with which (for some reason) *auratus* males show red, owing to the failure of black to mask the red color, is similar in all parts of the population. The effect of introgression is to add to the base level of incidence of red from other causes in such a way as to form a west-east gradient. This is observed (table 24) in malar color. The high incidence of red traces in the malar stripes of males of group I decreases progressively to the east. The significance of differences between the groups is shown in table 26. The gradient exhibited in this character is not so abrupt between group I and group II as the nuchal gradient. It is likewise not so shallow as the crown-color gradient. Red malar color is also shown by two of 15 male flickers from Cuba, and by three of 10 Grand Cayman males examined. The potential of these populations to exhibit this character (and in such frequency) is interesting. This genetic potential may be the result of retention of genes from an ancestral form, which either possessed them originally or had received them as a result of the interbreeding between *pre-cafer* and *pre-auratus* forms (*chrysocaulosus* is definitely derived from an *auratus*-like form). The red color could be due to mutation, or mutations, followed by selection for the gene, or genes, producing this character. Also, the red color may be present because of recent introgression from mainland *auratus* populations.

#### SHAFT COLOR

The incidence of orange or reddish shaft color in eastern *auratus* populations is rather high (table 24). According to the findings of Test (MS), *auratus* should (normally) not show any red shaft color, since red pigments are lacking in this form. Test's work is in need of corroboration and extension on a larger scale, to show what pigments are responsible for the presence of orange or red in the shafts of roughly one-third of the flickers of the eastern part of the continent. The slight differences observed (table 24) among the three groups are not significant (table 26), although the western groups (I, II) show a slightly higher incidence of red or orange

shaft color than does group III. In view of the high incidence of red or orange traces in eastern populations, there should be some definite indication of a west-east gradient of introgression responsible for these traces. There is some inconclusive evidence, however, which offers an explanation for the lack of such a gradient. If selection in certain local areas tended to favor an introgressive character, the grouping of specimens (as was done for this section) would result in the biasing of the value of the character shown by the large, collective sample in favor of the populations from areas that make up the greater part of such a sample. A comparison of shaft-color scores in samples from certain areas of eastern North America gave the following results:

AREA	N	No. SCORING 1 OR 2	PER CENT SCORING 1 OR 2
Cuba and Grand Cayman Island	45	29	64.4
Florida	44	18	40.9
Appalachian Mountains (from West Virginia to Georgia)	61	23	37.7
Group I (not including Florida and Appalachian Mountain samples)	169	53	31.4

The number of Cuban and Grand Cayman Island specimens showing orange traces is significantly different, at the 0.01 level according to chi-square tests, from the other eastern samples. The higher incidence of such traces in the samples from Florida and the Appalachian Mountains, while not significantly different from that of the collective sample of the rest of group I, suggests that local flicker populations in the east may differ in the incidence of red or orange shaft color. Further study of this problem is needed. Conclusive evidence of such differences would indicate that selection is acting on the level of incidence of this character in eastern flicker populations. Although introgression cannot be demonstrated to be the cause of red (or orange) shaft color in eastern flickers, it appears that the original source of this character in the eastern flicker populations was the western *cafer* population.

## HYBRID INDEX

For the study of possible introgression from *cafer* into *auratus*, I used the number of specimens indexed at 3 or more in the three groups (table 25) which eliminated the difficulties involved in the determination of slight traces of *cafer* characteristics in the various color characters. Specimens indexed at 3 or more clearly show such indications of *cafer* characters, either exhibiting slight traces (score, 1) in several characters or being intermediate (score, 2) in one character. There is a decrease in hybrid index from west to east, as is indicated in table 25. Table 26 gives the levels of significance attached to the differences among the various groups. The female indexes as well exhibit similar differences. Introgression is clearly indicated by the gradient thus demonstrated.

## CHANGES IN COLOR CHARACTERS WITH TIME

Specimens in groups II and III (see above) were separated into two chronological classes,

those taken before 1925 and those taken after 1925. The incidence of *cafer* characters (in malar, crown, and shaft color) in specimens in the two time classes was then determined for each group (see table 27). The results indicate no drastic change in the incidence of *cafer* characters in *auratus* populations in the past century. All the chronological differences observed are negated by other data. Thus, the difference in shaft color of group-II specimens collected before and after 1925 is rendered unimportant by the reversed difference observed in the time classes of group II (see table 27). The difference in crown color between pre- and post-1925 specimens of group-III males is likewise rendered unimportant by the close agreement found in group-II males and by the reversal noted by the two groups for female crown color. Differences in malar color noted in the two groups are slight and are considered insignificant. Other characters were not analyzed in this fashion owing to the low incidence of *cafer* traces (nuchal, throat) and to the difficulty encountered in dealing with the ear-covert character.

TABLE 27  
*Cafer* CHARACTERS IN *auratus* POPULATIONS WITH RESPECT TO TIME IN  
TWO GROUPS AS DESCRIBED IN TABLE 24

Character	Group	Time	N	No. Scoring 1 or More	Per Cent Scoring 1 or More
Malar Color	II	Pre-1925	48	7	14.58
	II	Post-1925	58	8	13.80
	III	Pre-1925	60	7	11.67
	III	Post-1925	82	6	7.31
Crown color (male)	II	Pre-1925	36	9	25.00
	II	Post-1925	69	16	23.18
	III	Pre-1925	60	12	20.00
	III	Post-1925	65	7	10.77
Crown color (female)	II	Pre-1925	25	8	32.00
	II	Post-1925	45	12	26.67
	III	Pre-1925	53	8	15.10
	III	Post-1925	70	13	18.57
Shaft color (both sexes)	II	Pre-1925	63	23	36.51
	II	Post-1925	106	24	22.64
	III	Pre-1925	113	34	30.08
	III	Post-1925	153	55	35.94

INTROGRESSION IN POPULATIONS OF *CAFER* AND *MEXICANOIDES*

The detection of introgression in western flicker populations presents the same difficulties as those found in the east, particularly in regard to *cafer* and *mexicanoïdes*, the subpopulations of which are often partially or completely isolated. For this reason it is desirable to discuss introgression in the west by populations rather than by characters.

## NORTH-SOUTH GRADIENT

As might be expected, the considerable interbreeding taking place in British Columbia is affecting the western flicker populations to a great extent. Samples from California and Nevada, Oregon and southwestern Idaho, and Washington, southern British Columbia, and northern Idaho were compared in regard to indications of *auratus* influence (tables 28 and 29). The California sample (hereafter only one state from each group is used to designate the group, as given in table 28) showed significant differences in all characters except female nuchal and female crown color when compared with the Oregon sample by means of the chi-square method. The level of significance of the differences observed in the

number of individuals in each sample indexed below 4 was  $P = 0.01$  for all except malar color ( $P = 0.05$ ).

Comparison of the Washington and Oregon samples shows little difference between them. The north-south gradients for the characters indicate that little shift occurs between the hybrid zone in British Columbia and that in Oregon, but a sharp break occurs between the population of Oregon and that of California, possibly because the California and Nevada flicker populations are considerably isolated, while the Oregon, Idaho, and Washington populations are in direct contact with the main center of hybridization to the north. The various differences indicate that introgression is responsible for at least a great part of the *auratus* characters in these populations. The hybrid-index differences (table 28) in particular indicate the north-south shift from a situation in which roughly 50 per cent to 75 per cent of the flickers show definite traces of *auratus* characters to one in which about 25 per cent in the California population do. It is to be noted that the high frequency of *auratus* color characters in the

TABLE 28  
HYBRID INDEXES OF FLICKER SAMPLES FROM WESTERN NORTH AMERICA  
AND FROM CENTRAL AMERICA

Group	Areas	Males		Females	
		<i>N</i>	Per Cent Indexed Below 22	<i>N</i>	Per Cent Indexed Below 18
Washington <sup>a</sup>	S. British Columbia, Washington, N. Idaho	55	70.9	31	41.9
Oregon <sup>a</sup>	Oregon, SW. Idaho	29	75.8	29	51.7
California	California, Nevada	37	29.7	25	24.0
Utah	SW. Montana, SE. Idaho, Utah, SW. Wyoming, W. Colorado, New Mexico, W. Texas	38	57.9	35	57.7
<i>rufipileus</i>	Guadalupe Island	9	00.0	11	00.0
Mexico <sup>b</sup>	Mexico, except Chiapas and NE. Mexico	24	12.4	12	8.3
<i>nanus</i>	NE. Mexico	5	(20.0)	4	(25.0)
<i>mexicanoïdes</i>	Chiapas and Guatemala	21	38.1	23	4.3
<i>pinicolus</i>	Honduras and Nicaragua	23	34.8	19	00.0

<sup>a</sup> Includes individuals of subspecies *cafer* and *collaris* (*cafer* subspecies group).

<sup>b</sup> Includes *mexicanus* and *collaris* specimens.

TABLE 29  
*Auratus* COLOR CHARACTERS IN FLICKERS FROM WESTERN NORTH AMERICA  
 AND FROM CENTRAL AMERICA<sup>a</sup>

Group	Nuchal Color		Throat Color		Ear-Covert Color		Crown Color		Malar Color		Shaft Color <sup>b</sup>	
	N	%	N	%	N	%	N	%	N	%	N	%
<b>Males</b>												
Washington	54	38.9	54	59.2	59	45.8	54	75.9	54	37.0	86	47.7
Oregon	29	41.4	29	62.1	29	65.5	29	65.5	29	31.0	58	36.2
California	37	18.9	37	35.1	37	29.7	37	40.5	37	18.9	63	20.6
Utah <sup>c</sup>	55	23.6	54	27.7	52	42.3	54	64.8	53	32.1	74	28.4
<i>rufipileus</i>	9	11.1	9	22.2	9	11.1	9	22.2	9	11.1	20	0.0
Mexico	24	4.2	24	20.8	22	9.1	24	25.0	24	4.2	38	44.7
<i>nanus</i>	5	(0.0)	5	(0.0)	5	(20.0)	5	(100.0)	5	(20.0)	9	44.4
<i>mexicanoides</i>	21	4.8	21	4.8	21	19.0	21	0.0	21	100.0	44	100.0
<i>pinicolus</i>	23	30.4	23	0.0	23	13.0	23	0.0	23	100.0	42	100.0
<b>Females</b>												
Washington	32	6.3	31	54.8	31	74.2	31	41.9	—	—	—	—
Oregon	29	3.4	29	65.5	29	79.3	29	44.8	—	—	—	—
California	25	4.9	26	42.3	26	53.8	26	32.0	—	—	—	—
Utah <sup>c</sup>	51	0.0	50	50.0	52	53.8	51	35.3	—	—	—	—
<i>rufipileus</i>	11	0.0	11	9.1	11	18.2	11	0.0	—	—	—	—
Mexico	12	0.0	12	25.0	12	33.3	12	25.0	—	—	—	—
<i>nanus</i>	4	(0.0)	4	(0.0)	4	(0.0)	9	(50.0)	—	—	—	—
<i>mexicanoides</i>	23	0.0	23	17.4	23	4.3	23	0.0	—	—	—	—
<i>pinicolus</i>	19	0.0	19	10.5	19	5.3	19	0.0	—	—	—	—

<sup>a</sup> The per cent of the individuals scoring less than 4 in a character is noted in the columns marked %.

<sup>b</sup> Both sexes combined.

<sup>c</sup> Same as in table 28, except that Arizona specimens are also included.

flicker samples from Oregon northward places the limit of the primary area of introgression somewhere in northern California (see map, fig. 10).

#### EAST-WEST GRADIENT

Introgression from the contact areas in the Plains apparently has less effect on the *cafer* populations than does the British Columbia contact. The "Utah" sample (tables 28 and 29) contains specimens from all the states between Nevada and the Plains (see states listed in table 28). When compared with the California sample, specimens of the Utah sample show higher frequencies in four of five male characters, in two of four female characters, in shaft color and in both male and female index values. However, only in the male and female hybrid index, and in crown color, were the differences significant at the  $P = 0.01$  level (chi-square). The tendency of

flickers in the Rocky Mountain area to show gray crown color was noted by Brodkorb (1935) as a basis for his "subspecies" *canescens*. The gray color may be associated with some adaptive physiological feature or may itself be adaptive. The probability that genes causing the gray color were originally derived from *auratus* is impossible to prove. It should be noted that specimens of *auratus* from the eastern plains are distinctly grayer in crown color than are specimens from farther east. When the Utah sample is compared with the Oregon sample, it is found that the former shows fewer *auratus* characteristics. The Oregon sample shows a higher incidence of *auratus* traces in four of five male characters, in all four female characters, in shaft color, and in male hybrid index. Chi-square tests showed the differences to be significant at the 1 per-cent level in female ear-covert color, in male ear-covert color, and in male

throat color. Since the Utah sample and the California sample are from areas about equidistant from the British Columbia contact, the somewhat greater incidence of *auratus* characters in the Utah sample is attributed to the effects of introgression from the Plains. However, the differences between the Utah sample and the Oregon sample indicate that introgressive effects from the north are stronger than the effects of introgression from the east.

#### GUADALUPE ISLAND POPULATION

The now extinct race *rufipileus*, represented by 20 specimens, apparently had been affected by introgression, as several of the specimens clearly show indications of *auratus* characteristics (see tables 28 and 29). Nevertheless, the frequency of traces in the sample indicates that this population showed fewer traces of *auratus* characters than did the California population. One might speculate on the basis of the data that the island was colonized at a time when *auratus* influence in *cafer* populations was less than at present, as perhaps during the last glacial period. However, in view of the drastic changes and fluctuations in gene frequencies to which small insular populations may be subjected (Mayr, 1954), more speculation is unwarranted.

#### MEXICAN POPULATIONS

Three races of the *cafer* subspecies group occur in Mexico. The few specimens of *colaris* examined (from Chihuahua) were included with specimens of *mexicanus* from farther south. Specimens of *nanus* were studied separately for reasons mentioned below. Much work must be done concerning the Mexican flickers before an accurate picture of introgression in the populations of the area can be obtained. Two extremely important considerations cannot be dealt with owing to inadequate material. The first of these concerns the nature of former Pleistocene contacts between the flora and fauna of Mexico and those of eastern North America. Detailed study of the effects of introgression in the northeastern Mexican flickers (*nanus*) and in the flickers of eastern Texas and Louisiana might provide important information regarding the presence or absence of

such a contact, as well as some idea of the nature and extent of any that might have existed. The second consideration involves the possibility of recent contact between *mexicanus* of the *cafer* group and the *mexicanoïdes* group across the Isthmus of Tehuantepec. Study of Oaxaca and Chiapas flickers might be expected to show indications of any interbreeding between these two forms that has occurred in the recent past.

Mexican flickers show a lower incidence of *auratus* characteristics than either the California sample or the Utah sample in all characteristics but shaft color. The differences indicated in tables 28 and 29 were found to be significant at the  $P=0.01$  level (by chi-square test) in all characters but female crown color, female nuchal color, and male throat color. The incidence of orange shaft color observed is significantly higher ( $P=0.01$ ) than that found for the Utah and California samples. While introgression may be involved, it is also likely that other factors are of importance in connection with this character. The orange trend exhibited by Mexican flickers may be the result of a residual genetic effect from the ancestral North American flicker population when it inhabited the area. The approach of *mexicanus* to *mexicanoïdes* in regard to the orange shaft color is notable. In order to rule out introgression as a factor, it is necessary to determine the presence (or absence) and direction of a cline in regard to this character. I have been unable to make such a determination owing to the inadequacy of samples from various parts of Mexico. The race *nanus* is similar to *mexicanus* in most respects, including the expression of *auratus* characters. In crown color *nanus* approaches the specimens of the Utah sample and eastern Plains *auratus*. The gray-brown color observed may be related to the aridity of the areas occupied by the three forms or may have some other significance. The possibility that this character is present in *cafer* populations owing to introgression should not be ignored.

#### CENTRAL AMERICAN POPULATIONS

The flickers of the *mexicanoïdes* subspecies group differ considerably from other North American flickers. The color characters

(involved in the hybrid index) of the specimens of the two races of this group were examined in an attempt to discover whether introgression had affected the populations.

Determination of introgression in this group is difficult because the forms exhibit certain characters of both *auratus* and *cafer* groups in a way that suggests that this condition has been maintained for some time in *mexicanoides* populations. Since introgression of *auratus* characters would have had to pass through the intervening *cafer* populations, the evidence for introgression between the *cafer* and *mexicanoides* groups would be of interest. However, the material for such a study is not available.

The crown color of the races *mexicanoides* and *pinicolus* is rufous, similar to the color of *rufipileus* of the *cafer* group, and also to the members of the *chrysoïdes* group. It is scored 4 for purposes of this study; no traces of gray were discovered in the 86 specimens examined. Malar color is red, with some black as in *Colaptes rupicola* of South America. In a few individuals the malar area was nearly as black as it was red. All specimens examined showed an orange-red shaft color approaching that found in certain hybrids. The very little variation in this character indicates that it is a stabilized color pattern in this group. The considerable traces of nuchal patches in *pinicolus* are interesting in view of their rarity in *mexicanoides*. Variation in this character from north to south indicates that introgression is not the cause of its incidence in *pinicolus*. Probably the ancestral flicker population in Central America originally possessed a nuchal patch. This was largely lost by the *cafer*, *chrysoïdes*, and *mexicanoides* groups. It was either retained or regained in the ancestral *auratus* population. Interbreeding of *auratus* with *cafer* resulted in increased nuchal traces in *cafer* and *chrysoïdes*, but apparently not in *mexicanoides*, which was isolated from the effects of introgression.

#### SUMMARY OF INTROGRESSION IN *AURATUS* AND *CAFER* POPULATIONS

The study of color characters of North American flickers indicates that introgression is the cause of the presence of *cafer*

characters in *auratus* populations, and vice versa. The evidence from six color characters suggests that the western *cafer* population is being affected by introgression to a greater extent than is the eastern *auratus* population. A comparison of West Coast (California) and East Coast (*auratus*, group III; see tables 24, 28, and 29) specimens indicates that nearly five times as many individuals of the former show *auratus* characters as individuals of group III show *cafer* characters. Nuchal traces are more common in *cafer* than is the restriction of the nuchal in *auratus*. There is a greater tendency for males to show the nuchal patch, which results in the fact that nuchal restriction (score, 1) is most common in females of *auratus*, while nuchal traces (score, 3) are much more common in males than in females of *cafer*. Tan or buff is more frequent in the gray throats of California *cafer* than is gray in the tan throats of eastern *auratus*. Gray crown traces and black malar traces are more frequent in *cafer* than are brown crown traces and red malar color in *auratus*, although the disparity between the two groups is not so great as in nuchal or throat color. Ear-covert traces (tan) in *cafer* are somewhat less common than gray traces in *auratus* (but see discussion under the latter). Yellow shaft-color traces in *cafer* are fewer than are red traces in *auratus*, despite the apparent tendencies of fading to reduce red traces in *auratus* and of dietary conditions to increase yellow shaft color in *cafer* (Test, MS). It has been suggested that the high incidence of red shaft-color traces in *auratus* is due to factors of selection. In *cafer* there is a cline of increasing yellow shaft-color traces approaching the hybrid zone; such a cline is lacking in *auratus*.

No change in the incidence of *cafer* characters in *auratus* populations was detected with respect to the last 100 years. Attempts were made to check *cafer* in this manner, but sample sizes for the different time intervals were too small.

On the basis of the variation in the color characters, which is presumed to be due to introgression, the primary area of introgression is more extensive in the west than in the east (see map, fig. 10). Using the definition of the area as given above, I found that

the primary area of introgression east and north of the hybrid zone is a narrow zone generally 50–100 miles wide. In the west, however, the area was found to cover all the western United States except central California. Mexican flickers show less evidence of introgression than other western North American flickers. The primary area of introgression in the west thus encircles California and also cuts across northwestern Mexico. While these areas of introgression are determined solely by these six color

characters, the variation exhibited by the characters suggests that such determination allows a reasonable approximation of the limits of the areas affected most strongly by introgression.

The extinct Guadalupe Island flicker (*rufipileus*) exhibited traces of *auratus* characters much less than other western *cafer*. Central American flickers of the subspecies group *mexicanoïdes* show *auratus* characteristics, but these are not thought to be due to introgression.

### CORRELATION OF COLOR CHARACTERS

As noted above, shaft-color scores of male and female individuals have been considered together, while the scores of individuals of the two sexes have been kept separate for other characters. Tables 24 and 28, showing the effects of introgression in eastern and western flicker populations, indicate rather effectively the sexual disparity in the various color characters. The discussion on variation of the color characters also gives many points in favor of keeping the scores for the sexes separate. Examination of the incidence of yellow or orange shaft-color traces in western flickers and of orange or red traces in eastern flickers indicated that the two sexes did not differ in the frequency of such traces. Representative samples with the differences in frequency of the traces shown are:

	MALES	FEMALES
Per cent with <i>auratus</i> traces		
California group	24.3	16.1
Oregon group	35.7	40.7
Per cent with <i>cafer</i> traces		
Midwestern flickers	35.7	30.4
Eastern (group III) flickers	34.5	30.3

The differences shown were not found to be significant; females often show a greater incidence of traces than do males. In addition, examination of samples from the hybrid zone indicated that the shaft color expressed by males differs little or not at all from that shown by females. The mean shaft-color scores shown by males and females, respectively, from Forsyth, Montana, for example, are: mean shaft-color score, 2.91, 2.95; standard error, 0.46, 0.44; standard deviation,

1.12, 0.99; range, 0–4, 1–4; coefficient of variability, 38.4, 33.6. Despite the considerable variability of shaft color in this sample, the means are nearly identical. For these reasons, treatment of male and female shaft-color scores together was deemed justifiable.

When several color characters are dealt with, the question arises as to whether two or more characters are so closely correlated as to render separate treatment of them invalid. This question is of importance when dealing with few color characters, as in the case of the grosbeaks (*Phœnicurus*) studied by West (1962). When more characters can be utilized, as in Mayr and Gilliard's (1952) study of hybridization in *Melidectes*, the question is of little importance, since combining two characters because of their correlation will change the picture but little. However, it is well to be certain that very close correlation between characters is taken into account.

Two factors enter into consideration in the possible correlation of color characters in flickers. The first is the expression of color characters in hybrids. A simple means of detecting the correlation of characters in the hybrid index is presented in table 30. Scores of characters of 50 male and 50 female "intermediate" hybrids (males indexed at 5 to 18 and females indexed at 6 to 16) from the hybrid zone were compared. Hybrids were selected randomly from various samples. For each pair of characters the number of individuals with the same score were tabulated and is expressed in table 30 as per cent of the individuals that exhibit this condition. Likewise the number



TABLE 30

CORRELATION OF COLOR CHARACTERS IN 50 MALE HYBRID FLICKERS INDEXED AT 5 TO 18  
AND 50 FEMALE HYBRID FLICKERS INDEXED AT 6 TO 16

Character	Nuchal Color		Throat Color		Ear-Covert Color		Shaft Color		Malar Color		Crown Color	
	% s <sup>a</sup>	% d	% s	% d	% s	% d	% s	% d	% s	% d	% s	% d
Nuchal color												
Males	—	—	16	46	22	42	28	48	20	46	24	40
Females	—	—	24	48	10	50	32	30	—	—	20	32
Throat color												
Males	16	46	—	—	40	6	20	34	40	22	26	26
Females	24	48	—	—	40	10	26	26	—	—	26	22
Ear-covert color												
Males	22	42	40	6	—	—	22	34	28	28	34	22
Females	10	50	40	10	—	—	26	30	—	—	24	28
Shaft color												
Males	28	48	20	34	22	34	—	—	30	34	30	32
Females	32	30	26	26	26	30	—	—	—	—	32	20
Malar Color												
Males	20	46	40	22	28	28	30	34	—	—	22	24
Females	—	—	—	—	—	—	—	—	—	—	—	—
Crown color												
Males	24	40	26	26	34	22	30	32	22	24	—	—
Females	20	32	26	22	24	28	32	20	—	—	—	—

<sup>a</sup> Symbols: % s, per cent of hybrid specimens in which any given two characters were scored the same; % d, per cent of hybrids in which scores for any given two characters differed by two or more.

of individuals differing in their scores by more than one point were tabulated. The per cent of individuals in this group is that given in table 30 for each character. The use of the various characters as separate entities actually depends on the frequency with which a given character is expressed differently from other such characters. The highest observed proportion of individuals (40%) showing similar expression of a pair of characters is low enough so that the use of the characters involved (malar color and throat color, throat color and ear-covert color) as separate characters is warranted. I would say that a proportion above 55–60 per cent for the similar expression of two characters would cast doubt on their use as separate characters in an index system. The per cent of specimens that differ by more

than one point in any pair of characters gives a rough idea of the correlation between two characters. Only throat color and ear-covert color appear to be quite correlated. However, owing to the considerable proportion (60%) of individuals differing in expression of these characters, their use separately is justified, despite their apparent correlation.

The second factor to be considered in relation to possible correlations exhibited by the characters is the expression of the characters in the areas of introgression. Two characters, even when correlated, may differ considerably in their appearance in populations owing to introgression. Examination of tables 24 and 28 provides a clear picture of the extent to which the various characters are expressed in areas of introgression. The

differences in the expression of the various characters are obvious. Further attention is here paid only to the throat color and ear-covert color, since these appear to be somewhat correlated in the hybrids. Specimens from Oregon and California were examined; particular attention was given to individuals that showed evidence of *auratus* influence in only one or two characters. Individuals with traces in several characters, but in only one or the other of ear-covert or throat char-

acters, were noted. The information from 74 specimens was as follows: number that showed ear-covert traces alone, 23; number in which only ear-covert and throat traces were found, 27; number that showed throat traces alone, 24. The difference in expression of these characters, despite their similar incidence in the populations, is considered further to justify their separate treatment. The manner in which the characters were utilized in the study of hybrids is thus upheld.

#### ANALYSIS OF MATED PAIRS OF HYBRIDS

The extensive contact, hybridization, and introgression occurring between the *auratus* and *cafer* populations indicate rather emphatically that free interbreeding is taking place between the two forms. It has been indicated that no "pure" parental types are found in the hybrid zone. Nevertheless, the opportunity to analyze mated pairs of hybrids for possible mating preferences pertaining to the various color characters should not be neglected. A sample of 15 presumed pairs of flickers secured at Forsyth, Montana, by F. H. Test, with a party from the University of California in 1940, was the basis for such an analysis. Although the sample is small, the information obtained is important in regard to mating preferences.

For purposes of this study, all 23 males of the Forsyth sample were considered as comprising the total "population" available to the 15 mated females that were obtained. Analysis of scores and indexes of males with which the females mated, in relation to scores and indexes of their mates and of the total number of available males, was thought to provide a means of detecting strong mating preferences with regard to color characters. No assumption is made that females actually select males, although such is probable. Similar results could be obtained by reversing the situation, i.e., by allowing all females to comprise a total female population available to the mated males.

##### NUCHAL COLOR

The color characters of all paired flickers from Forsyth are given in table 31. Scores and hybrid indexes for all males are included in table 32, with the scores for each character

in the mated pairs. Perusal of table 32 for nuchal color shows that the females scoring 4 in this character show no strong preference for males having no nuchal patch (3 or 4). Four (33%) of the 12 females scoring 4 mated with males scoring 1 or 2 in this character. There is also no strong preference for males with a partial nuchal patch, for if there were, more females would have been expected to have mated with lower-scoring males. On the whole, the pattern presented for nuchal color indicates a lack of mating preference for males with any particular condition of the nuchal color.

##### THROAT COLOR

The pattern of matings and scores for throat color (tables 32 and 33) indicates diversity of matings between differently scored individuals. Females scoring 4 were mated with both high- and low-scoring males. Females scoring 3 mated with males scoring from 1 to 4. Females scoring 2 mated with the more common (comprising 67% of the male "population"), high-scored males. There is no evidence for mating preference in regard to throat color.

##### EAR-COVERT COLOR

The ear-covert pattern (tables 32 and 33) is about what would be predicted on the basis of mating with complete lack of preference shown for individuals with a particular ear-covert color. The diversity of matings of intermediate-scored females, and the lack of a tendency for low- or high-scored females to mate with similarly scored males, are indicative of a lack of mating preference in regard to this character.

TABLE 31  
COLOR CHARACTERS OF MATED PAIRS OF FLICKERS FROM 5 MILES WEST OF  
FORSYTH, ROSEBUD COUNTY, MONTANA

Sex	Nuchal	Throat	Ear Coverts	Malar	Shafts	Crown	Hybrid Index
♂	3	0	0	3	3	3	12
♀	4	4	3	—	1	4	16
♂	3	4	3	4	4	4	22
♀	3	3	3	—	3	4	16
♂	4	4	3	3	4	4	22
♀	4	2	1	—	2	3	12
♂	3	3	3	3	4	2	18
♀	4	3	3	—	4	2	16
♂	1	4	4	4	3	3	19
♀	4	2	3	—	3	3	15
♂	2	3	4	4	0	3	16
♀	1	3	3	—	2	3	12
♂	4	2	3	4	1	3	17
♀	4	4	3	—	3	2	16
♂	3	3	3	3	1	3	16
♀	4	2	1	—	1	3	11
♂	3	2	2	2	3	3	15
♀	4	3	4	—	4	3	18
♂	3	3	3	4	3	3	19
♀	4	3	1	—	4	2	14
♂	3	4	4	3	3	2	19
♀	4	2	2	—	3	3	14
♂	1	1	1	3	3	3	12
♀	2	3	1	—	2	3	11
♂	2	3	3	4	4	3	19
♀	4	—	2	—	3	4	—
♂	2	4	3	4	2	3	18
♀	4	4	4	—	4	4	20
♂	1	4	2	4	2	3	16
♀	4	4	3	—	2	2	15

TABLE 32  
SCORES AND HYBRID INDEXES OF MALE FLICKERS FROM FORSYTH, MONTANA

	Score											
	0	1	2	3	4							
Nuchal color, <i>N</i>	2	4	5	8	4							
Throat color, <i>N</i>	2	1	4	8	8							
Ear-covert color, <i>N</i>	2	3	4	10	4							
Crown color, <i>N</i>	0	2	2	17	2							
Shaft color, <i>N</i>	1	2	3	9	8							
Malar color, <i>N</i>	0	0	3	8	12							
Hybrid index	5	10	12	14	15	16	17	18	19	20	22	
<i>N</i>	1	1	2	1	1	3	2	3	4	2	3	

TABLE 33  
SCORES AND HYBRID INDEXES OF MATED PAIRS OF FLICKERS FROM FORSYTH, MONTANA  
(The score or index value attained by the mate of each female is given. Compare male values with total population of males available, table 32.)

Character	Scores and Hybrid Indexes													
Nuchal color														
Females	4	4	4	4	4	4	4	4	4	4	4	3	2	1
Males	4	4	3	3	3	3	3	3	2	2	1	1	3	1
Throat color														
Females	4	4	4	4	3	3	3	3	3	3	2	2	2	2
Males	4	4	2	1	4	3	3	3	2	1	3	3	4	4
Ear-covert color														
Females	4	4	3	3	3	3	3	3	3	2	2	1	1	1
Males	3	2	4	4	3	3	3	2	0	4	3	3	3	1
Crown color														
Females	4	4	4	4	3	3	3	3	3	3	3	2	2	2
Males	4	3	3	3	4	3	3	3	3	3	2	3	3	2
Shaft color														
Females	4	4	4	4	3	3	3	3	3	2	2	2	2	1
Males	4	3	3	2	4	4	3	3	1	4	3	2	0	3
Hybrid index, females	20	18	16	16	16	16	15	15	14	14	12	12	11	11
Malar score, males	4	2	4	4	3	3	4	4	4	3	4	3	3	3
Hybrid index, females	20	18	16	16	16	16	15	15	14	14	12	12	11	11
Hybrid index, males	18	15	22	18	17	12	19	16	19	19	22	16	16	12

## CROWN COLOR

The pattern presented by crown color (tables 32 and 33) is similar to patterns for other characters thus far discussed. Abundant males scoring 3 in this character are found to be mated to females of all three scoring classes. There is no apparent tendency for low- or high-scoring females to mate with similarly scored males. No indications for mating preferences are evident in regard to crown color.

## SHAFT COLOR

The pattern of matings presents a clear picture of the occurrence of matings without regard to shaft color. High-scoring females are mated to males with low as well as high scores. Females with a more yellow-shafted condition mate with the common (74%) red-shafted or red-orange-shafted males as well as with intermediate or yellow-orange-shafted males. There is no indication of any mating preference exhibited in regard to shaft color.

## MALAR COLOR

In order to deal with this character, the scores of males were compared with the hybrid indexes of females to which they were mated. Because of the lack of black malars in available males, the pattern does not exhibit so clear a picture as do patterns for other characters. Females indexed at 1 to 16 mated with males having scores of both 3 and 4. The one mating involving a male

having considerable black (2) in the malar patch is interesting in that one of the two high-indexed females mated with a male of this type. While the picture presented is not clear, there seems to be no evidence for mating preference in regard to malar color.

## HYBRID INDEX

The pattern presented by the hybrid indexes of mated pairs (tables 32 and 33) is similar to that offered by the individual color characters. Females with high (18, 20) indexes and with low (11, 12) indexes generally mated with the common (52%) males indexed between 16 and 19. The more common females indexed at 14 to 16 mated with males with diverse hybrid indexes. No clear indication of mating preferences is evident.

## CONCLUSIONS

Although the evidence offered above is not conclusive owing to the small size of the sample, there are distinct indications that the different color patterns of *auratus* and *cafer* are not being utilized in preventing the interbreeding of diverse types. It might be noted that in two breeding seasons, during parts of which I was in or near the hybrid zone, I observed no indication of differences between *auratus* and *cafer*, or among the hybrid types, in mating preference (or in habitat preference or behavior), which is what might be expected on the basis of the extensive hybridization and introgression that occur between the two forms.

## HYBRIDIZATION BETWEEN THE RED-SHAFTED FLICKER AND THE GILDED FLICKER

THE PROXIMITY OF TWO FORMS of North American flickers without interbreeding, as appeared to occur in the Southwest between *cafer* and *chrysoïdes*, was looked upon with suspicion after I became aware of the extent of hybridization between *auratus* and *cafer*. A review of the literature showed that a number of supposed hybrids between *cafer* and *chrysoïdes* had been taken.

### HABITS

The gilded flicker is similar in behavior to *cafer* and *auratus*. Information concerning the behavior and habits of *chrysoïdes* was summarized by Bent (1939, pp. 299-308). Perhaps the best description of the habits of the form is that of Gilman (1915). Vocalizations of *chrysoïdes* are similar to those of the other North American forms, according to Brewster (1882-1883), Gilman (1915), and my own observations.

The intimate association of gilded flickers with giant cactus (*Cereus giganteus*) has long been realized. Some authors have considered the form to occur only in cacti (Huey, 1926; Law, 1929; Swarth, 1929). Huey (1926, p. 350) went so far as to contend that gilded flickers of the race *brunnescens* are "restricted" by the occurrence of giant cactus. While association of the gilded flicker with cactus areas is apparent, there is no evidence that the form is truly restricted by the occurrence of giant cacti. Rather, it seems that its restricted range is due chiefly to the presence of the closely related form *cafer*, with which *chrysoïdes* interbreeds, in areas surrounding the latter. Just as the presence of *auratus* in eastern North America precludes the extension of *cafer* into the area, *chrysoïdes* is prevented from extending its range to the north and east by the presence of *cafer* populations. A biological barrier of this type is effective in limiting the ranges of the forms involved as long as reproductive isolating mechanisms are absent. Even when these are present the species will continue to occupy contiguous ranges until the ecological requirements of the two become sufficiently different to permit them to exist sympatrically with reduced

competition (see discussion of "pseudo-con-specific" species by Vaurie, 1955). The area where forms such as the gilded and red-shafted flickers are in contact, imposing biological barriers on each other's distribution, has been designated a "biological front" by Gentili (1949, p. 123). Other factors that restrict the range of the gilded flicker are the presence of the sea to the south and west, the occurrence of dense thorn forest in southern Sinaloa, and the absence of trees or cacti in areas such as the Mohave Desert and elsewhere.

Gilded flickers not uncommonly nest in plants other than giant cacti. Scott (1886) reported *chrysoïdes* in mesquite far from cactus in the Tucson area. Gilded flickers have been found nesting occasionally to commonly in willows and cottonwoods, as do red-shafted flickers. Nesting in cottonwoods and willows occurs along the Gila River (Gilman, 1909, 1915), the Santa Cruz River (Bailey, 1924), about small streams near cities like Tucson (personal observation), and, indeed, wherever such trees are available to this desert-inhabiting form. Stephens (1903) found *chrysoïdes* in the Big Sandy Creek region (Arizona) most common in willows near the stream. Grinnell (1928, p. 127) found *chrysoïdes* in the Colorado River area "apparently restricted to the riparian timber along the Colorado River and its distributaries." Brewster (1902) found several gilded flickers in the higher mountains of the Cape Region of Baja California.

### DISTRIBUTION

The distribution of the *chrysoïdes* group is shown in figure 1. The group is divided into four races (*mearnsi*, *tenebrosus*, *brunnescens*, and *chrysoïdes*); there are two races in each of two isolated populations. The race *mearnsi* inhabits the Sonoran Desert of southern Arizona and northern Sonora, with the westernmost population occurring in the Colorado River Valley to the Gulf of Baja California. The race *tenebrosus* inhabits the arid Tropical Zone of southern Sonora and northern Sinaloa (Miller *et al.*, 1957), intergrading to

the north with *mearnsi*. The western races (*brunnescens* and *chrysoïdes*) occupy Baja California. Apparently *brunnescens*, the northern of the two intergrading races in Baja California, is separated from *mearnsi* of the Colorado River by a barren stretch of uninhabitable terrain (see Grinnell, 1928; and C. H. Beal, 1949). Gilded flickers seem to be absent from northwestern Sonora (van Rossem, 1945; Phillips and Amadon, 1952). Further distributional comments are made below.

#### HYBRIDIZATION BETWEEN *cafer* AND *chrysoïdes*

The first possible hybrid obtained between *cafer* and *chrysoïdes* is a specimen mentioned by Baird (1858, p. 125). This individual, probably the second *chrysoïdes* specimen taken, had a "slight tinge of orange in the yellow of the shafts." Baird thought this might represent a distinct species or a hybrid. Coues (1881) described a hybrid flicker from Fort Whipple, Arizona, which could be either an *auratus* × *cafer* or a *cafer* × *chrysoïdes* hybrid. Considerable difficulty arises in the determination of hybrids, because shaft color is the only obvious character by which *cafer* and *chrysoïdes* differ; this character is one by which *auratus* and *cafer* also differ. Brewster (1882–1883) reported a hybrid between *chrysoïdes* and *cafer* as having orange shaft color and a dark crown. I consider this to be the first definite *chrysoïdes* × *cafer* hybrid reported. Scott (1885) reported another cross between *cafer* and *chrysoïdes* but gave little information concerning it. Brenninger (1898) referred to several presumed hybrids between the two forms; he also described a "hybrid" between *chrysoïdes* and *auratus* which had red traces in the nuchal area. Swarth (1905) reported a hybrid from Tucson.

Grinnell (1914) found that four of five gilded flickers from the lower Colorado River Valley had reddish shafts. He found no evidence in general size and other color characters by which to call the specimens "hybrids" and concluded (p. 137), "the strain of *chrysoïdes* occurring at the present time in the lower Colorado Valley shows proneness to replacement of yellow by red, without there having been any interbreeding with another species."

If correct, this information would cast doubt on most, but not all (see Brewster's 1882–1883 discussion), hybrid reports. Even in the early 1900's there were reasons to doubt Grinnell's conclusion. Stephens (1903) found *cafer* breeding in an area along the Colorado River where *chrysoïdes* normally occurs. Howell and van Rossem (1915) secured two hybrids in the lower Colorado Valley. These authors also reported (p. 233) a male individual of *cafer* courting a female *chrysoïdes*, indicating that the forms occurred together during the period of pair formation. When commencing this study, I believed it to be unlikely that *chrysoïdes*, which resembles *cafer* in most characters other than shaft color (and also resembles *cafer* in habits and behavior), would approach *cafer* in shaft color in the area in which interaction occurs. The lower Colorado River flicker population is actually a hybrid swarm (see below). The idea that polymorphism is responsible for red shaft color in some *chrysoïdes*, originating in Grinnell's work, is also shown to be incorrect. Other reddish-shafted flickers probably referring to hybrids were reported by Huey (1935) and Sutton and Phillips (1942).

Perhaps the most pertinent previous observations on the flicker situation in the Southwest were those of Monson (1942) concerning southeastern Arizona. Monson did little collecting of flickers but obtained a hybrid between *cafer* and *chrysoïdes* near Elgin, Santa Cruz County, in June, 1940. Regarding the supposed preference of *cafer* for the Transition Zone, and of *chrysoïdes* for saguaro cactus areas of the lower Sonoran Zone, Monson reported that many records were obtained of *cafer*-like individuals in cottonwoods and willows outside the Transition Zone. He concluded that either *cafer* and *chrysoïdes* breed outside their supposed zones of preference, or hybrids occur in the areas that separate them. Monson recorded *chrysoïdes* and *cafer* (hybrids?) together in the breeding season (May–July) in Cochise County at St. David, Hereford, and Charleston, and in Santa Cruz County near Elgin, where he obtained the above-mentioned hybrid. Phillips (MS) has reviewed the flicker situation in southeastern Arizona. He recorded the distribution of *cafer* (race *collaris*) as common "from the more heavily wooded parts of the

Upper Sonoran Zone up to timberline" (p. 173). The race *mearnsi* of *chrysoïdes* was listed (p. 174) as a "common resident in saguaro, willow-cottonwood, and mesquite forest associations (Lower Sonoran Zone) of southern and western Arizona." Phillips stated (p. 174): "Flickers breeding in the Mayer-Big Bug Creek region, about Camp

Verde, and in the Sonoita Plains district of Santa Cruz and Cochise Counties, and perhaps also those of the San Pedro Valley from St. David to Hereford are variously intermediate between *collaris* and *mearnsi*." Phillips (1961, pp. 341-342; MS) considered all the flickers of continental North America as comprising one species, *Colaptes auratus*.

### VARIATION IN COLOR CHARACTERS

Flickers of the *chrysoïdes* and *cafer* subspecies groups differ in several mensural characters (wing, tail, tarsal lengths, for instance) and in five color characters. The color-character differences involve crown color, back barring, shaft color, amount of black in the tail, depth of the breast patch, size and shape of ventral spots, and dorsal color. It was feasible to deal with only the first three of these in the forming of a hybrid index. The differences in these color characters and the gradations found in the hybrids are listed below, with the score assigned for each:

CHARACTER AND SCORE	DESCRIPTION
Crown color	
0	Rufous buff, as in <i>chrysoïdes</i>
1	Buff, with brown traces
2	Intermediate (buff-brown)
3	Brown, with buff traces (usually at rear or side)
4	Coffee brown, as in <i>cafer</i>
Back barring	
0	Narrow, as in <i>chrysoïdes</i>
1	Intermediate in width
2	Broader, as in <i>cafer</i>
Shaft color	
0	Lemon-yellow, as in <i>chrysoïdes</i>
1	Golden-orange or orange traces (either faint in all feathers or heavy in one or several)
2	Orange to red, barbs yellow-orange
3	Shafts and barbs orange to orange-pink
4	Salmon-pink, as in <i>cafer</i>

The hybrid index then ranges from 0 for individuals like *chrysoïdes* in all three characters to 10 for individuals like *cafer* in all characters.

An indication of some lack of correlation of the color characters used in the index, and also an indication of the great variability and

number of recombination types present among the hybrids, are shown by the following information. The total number of combinations of the above characters in hybrids (indexed from 3 to 7) was found to be 55. The number of combinations attained in 157 Arizona birds at these values was 43 (78%).

#### CROWN COLOR

The area used as the "crown" is identical with that described for *auratus* and *cafer*. Crown color in all races of *chrysoïdes* is buff to rufous brown, similar to that of *rufipileus* of the *cafer* group and to that of the *mexicanoides* group. There is no apparent sexual variation in this character. Individual variation is limited; crown color is somewhat more buff in some individuals and more rufous in others. All races have similar crown color, except for *brunnescens* which exhibits a decidedly more rufous crown. When it is present, brown (attributed to *cafer* influence) is as easily detectable in an otherwise rufous crown as in an otherwise buffy crown.

Three gradations of crown color were readily discernible in the hybrids. Brown traces (score, 1) appear usually at the back of the crown or at the sides above the auricular areas.

In an intermediate condition (score, 2) the crown is buffy or rufous in front and brown to the rear. A score of 3 denotes the condition in which rufous or buffy traces are present (on the forehead especially) in an otherwise brown crown.

#### BACK BARRING

This character is used, although but one intermediate condition between *cafer* and *chrysoïdes* can be recognized. There is considerable individual variation (0.9 mm. to 2.3 mm.) in the width of dorsal bars in



*chrysoïdes*. Dorsal bars in *cafer* of Arizona generally range from 2.0 to 3.5 mm. Moreover, it is not only the width of the bars that is considered in respect to indexing, but also the relative extent of the barring on the dorsum. Specimens of *chrysoïdes*, in addition to having narrower bars than *cafer*, also show a definite "spacing" effect, whereby some feathers show only one or two bars instead of three. This tendency toward loss of bars, together with the narrowing of the bars that are present, results in the less barred appearance considered typical of *chrysoïdes*.

No sexual variation was noted in this character. The race *brunnescens* showed somewhat heavier barring than other races of the *chrysoïdes* group. In the indexing of hybrids, a score of 0 was assigned if the bars were narrow and more widely spaced as in *chrysoïdes*. A score of 1 was given for the intermediate condition of broader and more closely spaced bars. A score of 2 was assigned to the broad bars and "normal" spacing found in *cafer*. The use of three scores for this character (five are used for the others) produced no undesirable effects in the applying of the hybrid index.

#### ANALYSIS OF HYBRIDIZATION AND INTROGRESSION

In the course of this study, 610 adult flickers, from Arizona (371), Sonora (63), Sinaloa (12), and Baja California (164), were examined. These include 475 breeding *cafer* and *chrysoïdes*, and 135 winter *chrysoïdes* from Tucson, Arizona (46), and Baja California (82). Winter specimens of the Tucson, Arizona, sample were compared with those taken later in the spring and early summer in order to determine the extent of differences. Means of measurements (in mm.) of the winter specimens differed from those of breeding birds only in wing length and tail length, as shown below (number of specimens given in parentheses):

	WINTER SAMPLE	"BREEDING" SAMPLE
Males		
Wing length	149.00 (20)	145.00 (16)
Tail length	95.60 (20)	96.40 (16)
Females		
Wing length	145.90 (18)	143.73 (15)
Tail length	96.20 (15)	93.07 (13)

#### SHAFT COLOR

This character is used here in the same manner as in the preceding section. The yellow-shafted condition of *chrysoïdes* is scored 0. The intermediate gradations are the same as those described for the *cafer-auratus* situation.

Because slight golden-orange traces in the yellow shaft color are difficult to detect, standard lighting conditions were used in the scoring of individual specimens, as was attempted in the study of all the color characters so far as practicable.

No sexual variation in this character was noted. Individual variation occurs in the relative paleness of the shaft color, when the paling effect due to exposure to light is taken into account.

Geographic variation was not observed, except in regard to the increased tendency of Sonoran and Arizona gilded flickers to show orange shaft traces, attributed to the effects of introgression (see also discussion in next section). No information is available concerning the nature of pigments responsible for the shaft color of *chrysoïdes* compared with those found in *auratus* and *cafer* by Test (MS).

Probably the generally shorter wings and tails of the breeding specimens are due to wear. No significant differences in hybrid index were found between the two groups. Examination of samples from Baja California showed no notable differences between summer and winter specimens. It was concluded that gilded flickers do not move about greatly in winter; they may be considered essentially resident. Winter red-shafted flickers and hybrids phenotypically resembling them were excluded from study. A considerable number of these was available.

#### MENSURAL CHARACTERS

Measurements of southwestern flickers were taken in the same manner as described above. A summary of the wing, tail, bill, and tarsal lengths of southwestern flickers (males only) appears in table 34. The mensural data indicate that: (1) Arizona and California *cafer* differ but little; (2) the northern races

TABLE 34  
MEASUREMENTS (IN MILLIMETERS) OF SOME MALE FLICKERS OF THE SOUTHWEST

Form	Wing Length	Tail Length	Bill Length	Tarsal Length
<i>cafer</i> subspecies group				
<i>collaris</i> , California				
N	35	35	23	25
Mean	162.91	113.86	30.31	29.54
Range	157-171	107-123	28.0-33.2	27.1-30.9
<i>collaris</i> , Arizona				
N	19	16	18	14
Mean	163.68	111.56	31.93	27.97
Range	159-171	107-120	30.0-33.6	26.5-30.4
<i>chrysoïdes</i> subspecies group				
<i>mearnsi</i> , <sup>a</sup> Arizona				
N	20	19	22	16
Mean	144.85	95.58	30.50	27.40
Range	140-151	90-101	28.6-31.6	25.8-29.4
<i>tenebrosus</i> , southern Sonora				
N	10	10	9	10
Mean	142.40	95.10	28.74	27.40
Range	140-146	92-100	27.3-31.0	26.3-29.6
<i>brunnescens</i> , northern Baja California				
N	5	5	5	5
Mean	141.20	90.10	28.90	27.10
Range	138-144	88-93	27.5-30.1	26.0-28.3
<i>chrysoïdes</i> , southern Baja California				
N	27	24	28	28
Mean	141.11	93.04	27.44	26.77
Range	135-147	88-97	25.5-29.4	24.8-27.9

<sup>a</sup> Includes gilded flickers from desert areas away from contacts with *collaris*.

of *chrysoïdes* exhibit longer wings, bills, and tarsi than does the southern race *chrysoïdes*; and (3) the Arizona race *mearnsi* shows rather greater measurements for these char-

acters than do *brunnescens* and *tenebrosus*, thus tending toward *cafer*. It is suspected that the larger measurements of *mearnsi* are partly the result of introgression from *cafer*.

### THE ARIZONA SITUATION

Generally, a physical barrier prevents contact between the gilded flickers and the red-shafted flickers of Arizona during the breeding season. This barrier is the grassland and open oak-juniper woodland generally found between lowland cactus desert and upland pine-oak woodland. Neither flicker can breed in the intervening area owing to the lack of nesting sites. Nevertheless, contacts of two types occur, or have occurred in the past. First, there are sporadic contacts in foothills surrounding certain mountains (e.g., the

Santa Catalina Mountains) near the upper altitudinal limit (3500 feet to 4500 feet) of the desert. Such contacts and resulting hybridization are to be expected as a consequence of the migratory habits of *cafer*. Red-shafted flickers move from the uplands to lower levels in the fall, and some individuals occasionally winter within the range of *chrysoïdes*. These birds may remain there into late winter, when the breeding season of *chrysoïdes* commences. Under certain circumstances mixed matings may then take place.

A second and more important type of contact occurs in riparian vegetation along major streams issuing from mountain masses around the rim of the Sonoran Desert. These streams once provided continuous suitable habitat between major populations of the two flickers. Man's activities in central and southern Arizona have greatly altered the situation by disrupting the continuity of riparian woodlands, thereby breaking the connections between the two. Only one river, the Agua Fria, still retains partial continuity of cottonwood-willow cover along its banks and those of tributary streams. This permits direct, if somewhat impeded, gene flow between populations of gilded and red-shafted flickers. Valleys of the lower Colorado, Verde, San Pedro, Babocomari, and Santa Cruz rivers (fig. 11) were once areas of connection or contact between the two flickers, for geographically isolated populations of hybrid origin today occupy portions of these valleys.

#### HYBRIDIZATION AT THE BASES OF MOUNTAINS

Two comparisons should indicate whether any degree of interbreeding occurs at the bases of mountains inhabited by red-shafted flickers, and near gilded-flicker populations. One need compare: (1) red-shafted flickers from such mountains with those farther removed from gilded-flicker populations; and (2) gilded flickers inhabiting deserts near such mountains with those from more distant areas.

Comparison of samples (approximately 35 adults for each sample) from mountain areas near gilded flickers with those from mountains farther removed (to the north and east) showed no significant differences between them in nine characters analyzed. However, suggestive of a trend toward *chrysoïdes* in the sample from mountains near gilded-flicker populations is the fact that both males and females in the sample tend toward *chrysoïdes* in seven of the nine characters (the first seven of these nine: wing length, tail length, breast-patch depth, depth of back bars, width of breast spots, amount of black in tail, crown color, back barring, and shaft color). Females of the two samples showed identical mean back-barring scores of 1.58, but males from the sample taken near *chrysoïdes* populations

tended toward that form (mean score, 1.44, compared with 1.71 for males farther from *chrysoïdes* and 0.46 for desert *chrysoïdes*). The shaft-color scores of males in the two samples were nearly identical (3.58, 3.57). However, females from the sample taken near *chrysoïdes* tended toward the latter form, the mean score being 3.56 compared with 3.79 for *cafer* away from *chrysoïdes*, and 0.77 for desert *chrysoïdes*. Thus, the male *cafer* sample from areas adjacent to gilded-flicker populations tends toward *chrysoïdes* in eight of nine characters examined, as does the female sample from the same area. Although the actual differences between *cafer* samples are too slight to be statistically significant, agreement in direction of the differences in nearly all characters and in both sexes suggests that hybridization occasionally occurs where the two forms are close together, with introgression resulting in the trend toward *chrysoïdes* evident in *cafer* populations nearest that form.

Interbreeding between the two flickers in foothills at the bases of mountains occupied by *cafer* is also indicated in a comparison of a gilded-flicker sample from the Santa Catalina Mountain foothills with a sample from the vicinity of Tucson, 15-20 miles to the southwest. The Tucson sample is comprised of specimens taken mainly about Rillito Creek and old Fort Lowell at the edge of Tucson, although it may include a few birds collected in the foothills of the Santa Catalina Mountains. Any bias such birds may introduce into the comparison will lessen and not enhance the differences between the samples. The samples differ significantly in both width of the back bars and scores for back barring as used in the hybrid index (see table 35). Differences not statistically significant, but nevertheless apparent, are those in shaft color and tail length (table 35). In width of the back bars, back-barring score, tail length, and shaft color (latter two, females only), the Tucson sample seems somewhat intermediate between the sample from the lower desert region and that from the Santa Catalina foothills. Differences are suggested by data for two additional characters. The mean wing lengths of the male samples from Tucson and from the foothills are very similar, but female sample means grade from 143.75 for

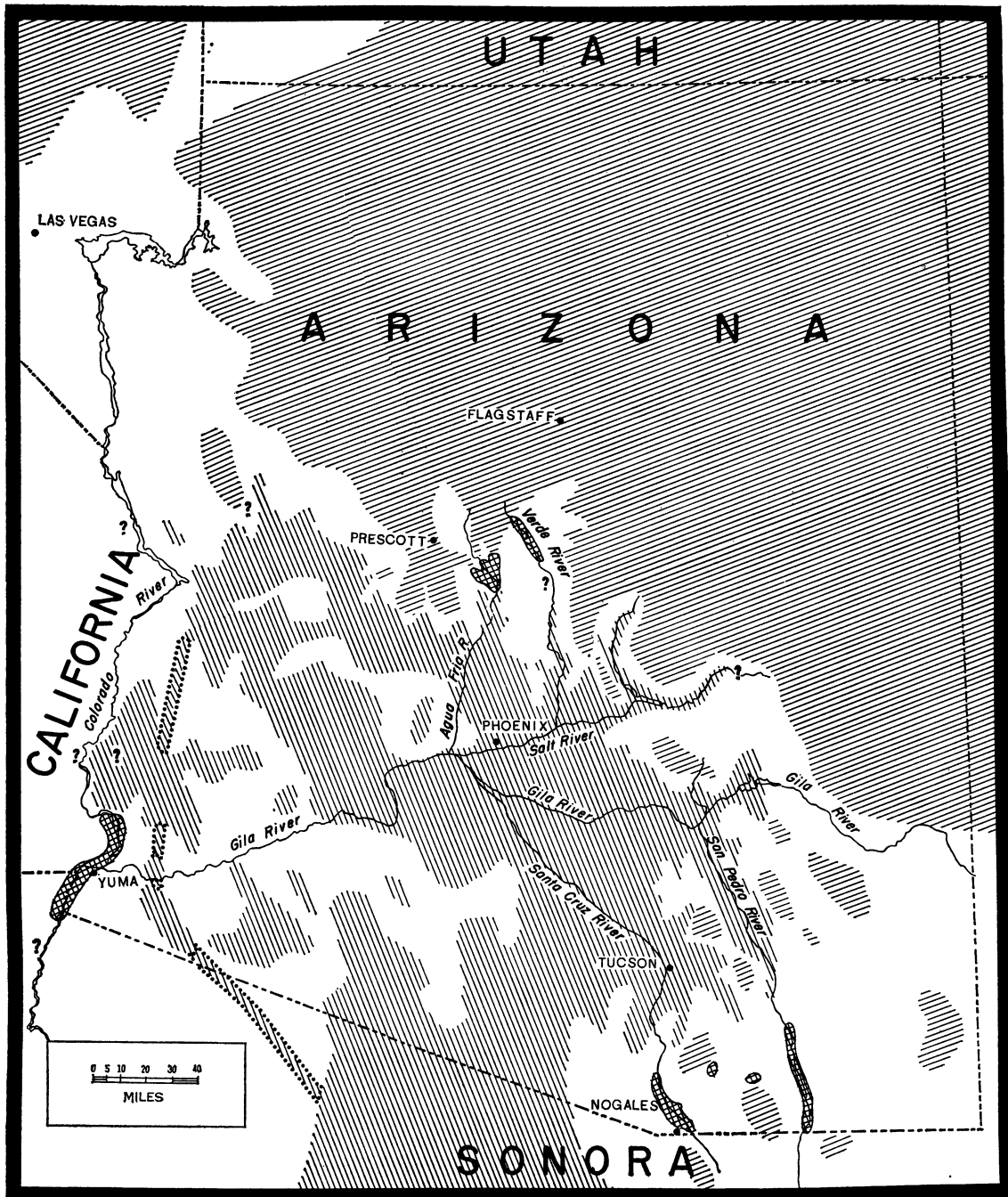


FIG. 11. Distribution of red-shafted flickers and gilded flickers in southern Arizona. The breeding range of *cafer* is shown by lines slanting upward to the right. Lines slanting down to the right show the range of giant cactus (*Cereus giganteus*), modified from Benson (1950). The range of *chrysoides* generally coincides with that of the cactus, except to the west where down-trending lines surrounded by spots enclose an area in which *chrysoides* may inhabit cactus areas or wooded stream sides. Location of hybrid swarms (see text) is shown by cross hatching.

TABLE 35  
COMPARISON OF FLICKERS IN TUCSON SAMPLE WITH SAMPLE FROM THE  
SANTA CATALINA FOOTHILLS, NORTHEAST OF TUCSON

	<i>N</i>	Males $\bar{X}$	$\pm 2$ S.E.	<i>N</i>	Females $\bar{X}$	$\pm 2$ S.E.
Tail length (in mm.)						
Tucson	13	95.57 [95.58] <sup>a</sup>	1.14	25	95.36 [94.07]	1.40
Tucson NE.	35	97.15	1.16	3	(96.67)	—
Back-bar depth (in mm.)						
Tucson	67	2.00 [1.93]	0.10	53	2.07 [1.90]	0.11
Tucson NE.	20	2.26	0.14	9	2.26	0.07
Shaft-color score						
Tucson	65	0.73 [0.77]	0.14	53	0.85 [0.73]	0.14
Tucson NE.	20	0.93	0.18	9	1.22	0.34
Back-bar score						
Tucson	44	0.59 [0.46]	0.20	33	0.61 [0.37]	0.22
Tucson NE.	20	1.20	0.32	9	1.39	0.32

<sup>a</sup> Figures in brackets are means for desert *chrysoides* in south-central and southwestern Arizona.

the sample of the lowland desert to 144.90 for that from Tucson to 146.67 for the foothill sample. Likewise, males from Tucson and the foothills average about the same in crown color, but mean scores of the female sample range from 0.47 to 0.76 to 1.17 (desert, Tucson, and foothill samples, respectively). No differences were detected in breast spotting and the amount of black in the tail.

Gilded and red-shafted flicker populations from adjacent areas thus appear to approach each other in some characteristics. There is a possibility, which cannot at this time be disproved, that this tendency of the two forms to approach each other in the various characters is due to similar adaptive responses of the two in areas where their environments are more similar. It is questionable that similar adaptive responses by the two would involve so many characters. The above data, the fact that the two forms interbreed elsewhere, and the potential for interbreeding afforded by the migratory habits of *cafer* suggest occasional hybridization as an equally good, or even better, cause for the approach in some characteristics.

#### AGUA FRIA RIVER POPULATION

The Agua Fria River and its tributaries drain the mountains around Prescott, the

Mingus Mountains, and the New River Mountains. Large red-shafted flicker populations, continuous with the main upland Arizona population of that form, inhabit the first two of these mountain areas. Major tributaries draining them include Black Canyon Creek, Big Bug Creek, the Agua Fria itself, and Ash Creek. These streams issue from the mountain areas accompanied by riparian vegetation which supports flickers. Leaving pine-oak woodland, they descend in turn through oak-juniper woodland, grassland, and desert grassland and finally enter the desert itself. Sonoran desert vegetation meets and mixes with the riparian and even with upland vegetation, so that one can find junipers, scrub oaks, mesquites, and acacias growing close together. It is evident that continuous cottonwood growth formerly covered most of the banks of this river system from the uplands down onto the desert. Old-timers, such as William West who ranches along Yarber Wash north of Cordes, recall the presence of cottonwoods 50 to 60 years ago along even the minor streams in the area. Apparently water once flowed much of the year in these washes, and the year around in major streams. The water table has suffered constant lowering because of drier conditions in the past half century, plus man's ever-increasing demands on the water supply. In

any event, both Big Bug Creek and the Agua Fria River were dry in the vicinity of Cordes during the late spring of 1963. Trees along both streams were restricted to the vicinity of habitations, except in a few instances. Certainly much of the upper river system lacks sufficiently large trees to support flickers. Ash Creek, however, runs through country having springs, so that several large portions of it are well watered, including the southern 8 miles of its length. The fairly continuous cottonwood growth along this creek, and along the Agua Fria below its junction with Ash Creek, constitutes optimum riparian flicker habitat. This habitat is nearly continuous (gaps of up to 3 miles occur, however) between the red-shafted flicker population of the Mingus Mountain region, and the gilded flicker population of the Sonoran Desert. About 7 miles southeast of Cordes Junction the Agua Fria enters a narrow canyon. At this point cottonwoods are sparse, the uplands are desert grassland, with small cacti much in evidence, and the vegetation around the stream is largely that of the Sonoran Desert. Within 5 miles to the south, saguaro cacti are presumed to occur along the river, as they are visible near the main road about 5 miles to the south. Thus, approximately 25 miles separate the two major flicker populations. A strong connection between them presumably occurred when riparian growth was actually continuous. The connection is now weak, and the hybrid population in the intervening area is small (although the birds are common wherever there are trees). Despite the weakness of this contact, it represents the only known area where there is continuous, if impeded, gene flow between populations of the two flickers.

Except for specimens from the Phoenix area, but one bird (taken in the Bumblebee Creek area south of Cordes) is available to represent the gilded-flicker population of the desert portion of the Agua Fria drainage. This bird, a male (A.M.N.H. No. 789329), is in nearly all respects a gilded flicker. The specimen was secured in an isolated saguaro patch near the limit of the range of cactus in the Black Canyon-Bumblebee Creek area. Lack of suitable riparian cover precludes the possibility of a contact between gilded flickers and red-shafted flickers at the base of the Bradshaw Mountains in this portion of the

Agua Fria drainage. Specimens of the red-shafted flicker were generally absent from mountain areas in the Agua Fria region. The two adult females available from near Prescott are all that represent these mountain populations. One of these birds (A.M.N.H. No. 51953) is somewhat intermediate, especially in crown color (score, 2), wing length (155 mm.), and tail length (102 mm.). The other (R.O.M.Z. No. 22.420.366) indexes at 9 and is within the range of variation of *cafer*, except for its intermediate tail length (103 mm.).

I worked the Ash Creek-Agua Fria River-Big Bug Creek area in the spring of 1963, securing 27 breeding adults. Available additionally were two apparently breeding birds taken along Big Bug Creek by earlier collectors, and three breeding adults secured by J. T. Marshall, Jr., and his students in 1962 at the junction of Ash Creek and the Agua Fria River. Localities (all in Yavapai County) represented by breeding specimens are (hybrid indexes of adult males and females in parentheses):

1. Ash Creek-Agua Fria River junction (males, 2, 4.5; female, 5.5)
2. Ash Creek, 3700 feet, 4 miles north of Agua Fria junction (males, 4.5, 5, 5.5)
3. Ash Creek, 3950 feet, 8½ miles north of Agua Fria junction (males, 2.5, 4, 4.5, 5, 7; females, 5, 5.5, 7, 8)
4. Ash Creek, 4150 feet, 11 miles north of Agua Fria junction (males, 8, 8.5; female, 7)
5. Ash Creek, 4650 feet, 15 miles north of Agua Fria junction (males, 9.5, 9.5; female, 8)
6. Yarber Wash, 4600 feet, 2½ miles southwest of locality 5 (male, 9; female, 8)
7. Agua Fria River, 3750 feet, 5½ miles north of Ash Creek junction, 3½ miles west of locality 2 (males, 4.5, 4.5, 6.5, 7, 7.5, 8; female, 4)
8. Mayer, 4400 feet, Big Bug Creek, 14 miles northwest of its junction with Agua Fria (male, 4.5)
9. Big Bug Creek (female, 2)

Both birds available from Big Bug Creek are hybrids. The Mayer specimen (U.S.N.M. No. 299909) is intermediate in most characters but *cafer*-like in wing length (160 mm.). The other specimen (A.M.N.H. No. 51984) is badly worn but seems close to *chrysoïdes* in most respects. From the village of Mayer continuous riparian cover leads directly into the uplands to the west. At Mayer the cottonwood cover all but ceases, and no flickers

were found (only a few old flicker holes in rotted-out stubs) in the few patches of generally small trees between Mayer and the junction of Big Bug Creek with the Agua Fria some 14 miles to the southeast. This situation leads me to believe that *cafer* influence is probably stronger in birds presently living in the groves within the village of Mayer than those that lived there in the past, when the presence of more continuous cover southeastward from there allowed greater infiltration of *chrysoïdes* genes.

Except for one major cottonwood growth (locality 7 above) and a few trees about habitations, the Agua Fria River banks were devoid of trees between the Dewey-Humboldt area and the junction of Ash Creek with the Agua Fria. The river bed was dry in April and May, 1963. The two flickers have no opportunity for direct contact along the river itself. The one Agua Fria locality is considered with the Ash Creek samples below.

Two of three adults taken in extensive cottonwood cover near the junctions of Ash Creek and Big Bug Creek with the Agua Fria River are nearly intermediate, while the other is close to *chrysoïdes*. Wing lengths of these birds span the range from *chrysoïdes* to *cafer*, the male indexed at 2 measuring 148 mm.; the male indexed at 4.5, 152 mm.; and the female, indexed at 5.5, 160 mm. Shaft color in all three specimens is nearer yellow (scores, 1-1.5) than red. Along Ash Creek for 4 miles to the north of this area trees occur continuously but are not sufficiently large to permit breeding by flickers. Willows and cottonwoods then become more numerous (though still not large), and a few pairs were encountered here. One nest was found in a dead willow at a point where the outside diameter of the tree was but 6 inches. One male was taken from this nest hole, and two males giving Long Calls (the flicker "song," rendered "wick-wick-wick . . .") were secured within 400 yards of the first. The three specimens are variously intermediate in all characters except back barring, in which two birds are *cafer*-like.

Favorable habitat extends 5 miles to the north from just above the last-mentioned locality to a series of springs that issue from beneath a bluff at the north end of the Orme School Ranch (the Quarter-Circle V-Bar

Ranch). Massive cottonwoods and large willows along Ash Creek here support approximately 45 pairs of flickers. A sample of nine adults, including three mated pairs, was secured at the north end of the ranch (locality 3 in list above) during May, 1963. The mated pairs (A.M.N.H. Nos. 789426 and 789430, 789427 and 789431, 789428 and 789432) consisted of birds with nearly matching hybrid indexes (5-5, 4.5-5.5, and 7-7.5). Scores comprising the index values varied. In the mated pair having both partners indexed at 5, for example, the male exhibits red-orange (3) shafts, while the female has off-yellow (1) shafts. The mean index for the five males is 4.60, while that for the four females is 6.50. Those specimens from which measurements could be obtained (i.e., those not badly worn) were intermediate or more like *cafer*.

North of the spring-fed portion of Ash Creek at the Orme School Ranch, the stream bed was dry and the banks were virtually devoid of trees. Several isolated, old sycamores were the only large trees within 2½ miles north of the springs. Small junipers were scattered about the grassy hills around the stream. Then, just north of the confluence of Cienega and Ash creeks, medium-sized cottonwoods and willows again began to line Ash Creek. Here, in two groves on the Thompson (Mulberry) Ranch, flickers were again encountered, and three adults were secured (locality 4 above). All were strongly red-shafted in their characters, though showing indications of *chrysoïdes* influence (in crown color, breast-patch width, and tail length especially). Along Ash Creek on the Thompson Ranch mesquites and acacias disappear, and scrub-oak thickets with scattered junipers begin to cover the hills. Suboptimal cottonwood cover is essentially continuous to the north from this point, with taller trees only occasionally out of view from the stream bed. Three more adult flickers were taken in a grove 4 miles farther north along Ash Creek (locality 5 in list above). Except for a slight orange tinge in shaft color of the two males, and *chrysoïdes* influence evident in the crown color and back barring of the female, these birds could be designated as true *cafer*. The somewhat intermediate measurements (wing, 158 mm.; tail, 104 mm.) of one male (A.M.N.H. No. 789439) are discounted be-

cause this bird showed an almost fully female condition of the malar patches, though it sang and its testes were much enlarged.

A pair of predominantly red-shafted flickers was obtained at a nest hole in one of six stunted, old cottonwoods beside a deserted house along Yarber Wash (locality 6 above). The hillsides surrounding the stream were partly grassland and partly covered with dense thickets of scrub oak. Such isolated, small areas of suitable habitat are probably colonized by migrant or winter-wandering flickers from Ash Creek and nearby populations of *cafer*.

Isolated by open grassland and miles of barren river bed from cottonwood groves along Ash Creek, from groves farther up the Agua Fria and Yarber Wash, and from those farther down the river near its junction with Ash Creek, is an extensive cottonwood-willow area beside the Agua Fria at the H Lazy A Ranch (locality 7 above). Flickers were abundant in a large stand of mature and old cottonwoods kept as a woodlot, and in small patches of large trees that lined irrigated fields nearby. Six adult males and one female were secured here on May 13, 1963. The hybrids are intermediate or tend toward *cafer*. The single female (A.M.N.H. No. 789415) is intermediate in wing length and tail length, has orange shafts, and is near *chrysoïdes* in back barring and crown color. Two of the males are strongly yellow-shafted but are in other characters within the range of variation of the remaining specimens. The mean index for the six males is 6.33, somewhat higher than the 4.60 for the Orme School Ranch (Ash Creek) male sample, but approximating the 6.50 registered by the female sample from the latter locality. The total range in index for the 16 hybrids from these two localities is from 2.5 to 8. Some character scores for the same birds range as follows: shafts, 1.5–4; crown, 0.5–3.5; back barring, 0–2; tail length, 99–110 mm.; wing length, 154–163 mm. No two birds are alike or even very similar in the totality of their characters, thus exhibiting the extensive recombination typical of such situations.

The 32 breeding adults available from the upper Agua Fria and its tributaries are all definite hybrids, with the possible exception of one male (A.M.N.H. No. 789437) from

the most northern Ash Creek locality. This male indexes at 9.5 because of slightly orange shafts; it is in all other characters like *cafer*. The hybrids are variable, no two being alike. There is a progression from hybrids more like *chrysoïdes* to those more like *cafer* from south to north over a distance of 15 miles. Unfortunately, adequate samples from populations farther north and south are lacking. There can be no doubt, however, that the habitat is sufficiently continuous from the hybrid area into the regions inhabited by the parental populations to enable constant gene flow between them. The hybrids exist in a true hybrid zone, with individuals phenotypically like the parental forms generally lacking in these populations. The hybrids are common and occasionally abundant in the limited riparian situations they occupy. Population pressure in the hybrid zone seems great enough to cause some utilization of suboptimal habitat. It is evident that the hybrids are breeding successfully, and that their genotypes are not strongly disadvantageous (if, indeed, they are at any disadvantage) when compared with those that occur elsewhere under similar environmental conditions in populations of the parental forms.

#### LOWER COLORADO RIVER HYBRID SWARM

From various museums I assembled a sample of 20 adults, which represents populations of flickers in the lower Colorado River area. Specimens were available from these localities (hybrid indexes in parentheses):

1. Yuma Indian Reservation, 18 miles south of Yuma, Yuma County, Arizona (males, 1, 2, 4, 6, 6)
2. Yuma, Yuma County, Arizona (female, 0)
3. Colorado River, Potholes to 4 miles north of Potholes, Imperial County, California (males, —, —, 5.5, 6; females, 2, 3, 3.5, 4)
4. Colorado River, 5 miles north of Laguna, Arizona (male, 3; females, 4.5, 6)
5. Bard to 2 miles south of Bard, Imperial County, California (females, 1, 1, 2)
6. Fort Mohave, San Bernardino County, California (specimens taken by Cooper in 1861, male, 0.5; female, 2)

The Colorado River has undergone tremendous changes in the past half century, owing to the building of dams, cultivation,



and other activities of man. The sites where most of the above specimens were taken are under water behind dams, including the only extensive giant cactus stand formerly found in California (Potholes area). Former groves of large cottonwoods and willows have been destroyed, although new stands are growing and are in various stages of maturity in parts of the valley. Around Yuma, flickers apparently inhabit scattered trees about irrigated fields and drainage ditches. Farther north the present occurrence of flickers is doubtful. Trees growing beside the river on the Arizona side north from Imperial Reservoir to Ehrenberg are not large enough to provide nesting sites for flickers. Giant cacti are scattered and small along the river and in washes from Cibola eastward to the Chocolate, Dome Rock, and Kofa Mountains, but I was unable to find flickers or flicker-sized holes in cacti near negotiable dirt roads and paved roads in this region. Trees around Parker, Arizona, were not large enough to support a flicker population. Unfortunately, I was unable to investigate the river personally north of Parker and in the Yuma area. Certainly flickers in the area have recently been subjected to drastic changes, and it is unfortunate that we cannot assess the effect these have had on the population.

These birds range in hybrid index from 1 to 6. The low index values reflect the tendency toward low crown-color and back-barring scores, on the one hand, and high shaft-color scores on the other. For males scores are higher than those from samples of *chrysoïdes* elsewhere for back barring and crown color. Females score well within the range of *chrysoïdes* in these characters. Eight of the 16 measurable adults from the lower Colorado were intermediate in wing or tail length, or both. Only two of the 20 adults from that area have the breast patch as deep as that of normal *chrysoïdes*. In this character nearly all the adults fall well within the range of *cafer*. Likewise, the amount of black in the tails of these birds is not extensive, as in *chrysoïdes*, but is restricted (narrower black tips) as in *cafer*. Only two of the 20 adults show as extensive an amount of black as is found in *chrysoïdes*. The lower Colorado sample tends to be intermediate also in width of back bars and in size of breast spots.

Although very variable in some characters, the lower Colorado birds are less variable in others, such as depth and width of breast spots and amount of black in the tail. Variation in these characters is of the order found in *chrysoïdes* samples and not so extensive as in the Agua Fria hybrid samples, which suggests partial stabilization of certain characters in the Colorado Valley population, owing presumably to the action of selection on genes responsible for the characters. Such stabilization can occur when a population of hybrid origin loses genetic contact with the parental populations. Such appears to be the case in this instance. The sparse cover and poor condition of scattered saguaros east of the river preclude a contact with major *chrysoïdes* populations to the east. Probably only occasional wanderers permit slight gene flow between the hybrid population and populations of *chrysoïdes*.

The uncertainty concerning the occurrence of breeding flickers farther north in the Colorado Valley makes it difficult to conjecture about contact between the hybrids and *cafer* populations. The two birds taken by Cooper (locality 6 above) are of significance in this connection. The male (U.S.N.M. No. 109301) is slightly intermediate in wing length (150 mm.) and tail length (100 mm.), and strongly like *chrysoïdes* in other characters, except for its round rather than broad breast spots. The female (M.V.Z. No. 4329) is worn, but seems to be like *chrysoïdes* in measurements and is more like *chrysoïdes* than *cafer* in other characters as well. Only in the restricted black in the tail, intermediate back-barring condition, and shaft color (score 1) does this bird tend toward *cafer*. These birds, if the locality information is correct, indicate former occupation of the Colorado River bottomlands as far north as Nevada by a *chrysoïdes*-like population. Where hybridization originally occurred along the river is unclear, although it may have been near the Utah-Nevada border. At present there seems to be no opportunity for interbreeding between birds of the lower Colorado Valley hybrid population and *cafer*, other than that afforded by *cafer* individuals wintering in the valley. Some *cafer* genes may enter into the hybrid population if over-wintering birds of that form occasionally remain in the valley and mate

with hybrids there. The nearest red-shafted flicker population appears to be that in the Hualpai Mountains, far from where wandering hybrids might be expected.

The lower Colorado Valley flicker population apparently represents a partially stabilized hybrid swarm, presently having little or no genetic contact with populations of the parental forms.

#### UPPER VERDE VALLEY POPULATION

The Verde River drains the eastern New River Mountain area, the western slopes of the Mazatzal Mountains, and a broad region extending from the Mingus Mountain and Ashfork-Williams area east to Flagstaff and the western portion of the Mogollon Mesa. All highlands in these areas, except for the New River Mountains, support red-shafted flicker populations. Major tributaries leaving the highlands are well wooded and suitable for flickers. Among these streams are the upper Verde River, the East Verde River, and Sycamore, Oak, Beaver, and Clear creeks. Fine stands of cottonwoods extend along the tributaries to the river and along the river south to about 6 miles below Camp Verde. At that point, at an elevation of about 3000 feet, the river is restricted by rising mesas and mountains, so that its path becomes tortuous. Through this rugged area for more than 20 miles to the south there exist only small patches of cottonwoods, often a mile or more apart. Despite the low elevation along the river, a temperature-inversion effect produced by the steep slopes of the valley keeps it sufficiently cool to prevent some desert plants (including saguaros) from extending farther north along the river. However, many Sonoran Desert plants have managed to pass through this "bottleneck," and places near the river around Camp Verde (especially at Montezuma Castle National Monument) are very desert-like in aspect.

South of the mid-Verde bottleneck, saguaros occur in true Sonoran Desert from about Table Mountain southward. Flickers live among the saguaros and in streamside vegetation from near Table Mountain (although none were observed in a brief visit to the Verde River at Sheep Bridge Crossing, south of that mountain) southward along

the river toward the Phoenix region. Samples were taken from breeding populations at these localities, both in Maricopa County, Arizona:

1.  $\frac{1}{2}$  to  $2\frac{1}{2}$  miles west of Verde River, 1650 feet,  $24\frac{1}{2}$  miles north-northeast of Mesa (10 males)
2. Verde River, 1950 feet, just north of Horse-shoe Dam, 18 miles northeast of Cave Creek (5 males; 5 females)

Males from the second locality tended slightly more toward *cafer* than those from the first, but the two samples can be combined to present a picture of the situation along the lower Verde River. The localities are  $19\frac{1}{2}$  miles apart. An apparent gap in flicker distribution occurs in the "narrows" north of Sheep Bridge Crossing. I searched for flickers in the lower Cottonwood Basin south of Camp Verde, and along the Verde River near Cottonwood Basin, but had no success. Likewise, I found no flickers along the Verde River from Verde Hot Springs (Childs) south nearly to the confluence of the East Verde and Verde rivers, and including 1 mile along Fossil Creek above its junction with the Verde. Desert plants, except saguaros, predominate on the steep slopes adjacent to the river. Cacti are abundant and palo verdes (*Cercidium*) occur; the latter are absent north of Verde Hot Springs. With the exception of the lower part of Fossil Creek, which was wooded, only scattered, small groups of trees were found. Gila woodpeckers (*Melanerpes uropygialis*) were observed in these trees, but flickers were lacking. Although it is possible that a few flickers inhabit groves in the area, they are certainly not of general occurrence. It seems likely, however, that wandering birds from the south and migrants from the north occasionally pass through the area.

Extensive cottonwood forests occur along the river around Camp Verde, with especially luxuriant vegetation where streams enter the river. The forest breaks up into scattered larger, then smaller, groves before disappearing as the river becomes narrow near Cottonwood Basin, 6 miles south of Camp Verde. Within a few miles of the latter, I took seven breeding adult flickers in May, 1963, supplementing three secured there by Joe T. Marshall, Jr., and his students in May, 1962. The population in this cotton-

TABLE 36  
CHARACTER COMPARISON OF SAMPLES FROM THE VERDE RIVER AREA

	Males			Females		
	N	$\bar{X} \pm 2$ S.E.	Range	N	$\bar{X} \pm 2$ S.E.	Range
Wing length (in mm.)						
Phoenix	6	144.83 $\pm$ 3.64	140-151	8	143.37 $\pm$ 0.84	142-145
Lower Verde	9	147.67 $\pm$ 1.64	145-152	—	—	—
Camp Verde	(2)	—	(160)	(2)	—	158-160
Tail length (in mm.)						
Phoenix	6	95.67 $\pm$ 2.62	92-100	7	93.57 $\pm$ 1.84	90-97
Lower Verde	14	99.07 $\pm$ 1.52	94-104	(3)	(96)	94-98
Camp Verde	(3)	(109)	105-112	5	111.80 $\pm$ 2.92	109-117
Breast-bar depth (in mm.)						
Phoenix	6	20.50 $\pm$ 1.52	18-23	8	19.50 $\pm$ 1.64	17-24
Lower Verde	15	23.67 $\pm$ 1.90	18-32	5	23.40 $\pm$ 2.58	21-28
Camp Verde	(4)	(19.5)	18-21	6	21.17 $\pm$ 1.90	18-24
Back-bar width (in mm.)						
Phoenix	5	1.78 $\pm$ 0.59	1.5-2.0	9	2.06 $\pm$ 0.21	1.7-2.5
Lower Verde	15	2.43 $\pm$ 0.24	1.5-3.1	5	2.00 $\pm$ 0.19	1.7-2.2
Camp Verde	(4)	(2.13)	1.5-2.6	6	2.17 $\pm$ 0.32	1.8-2.9
Breast-spot width (in mm.)						
Phoenix	—	—	—	—	—	—
Lower Verde	15	5.46 $\pm$ 1.96	4.1-8.5	5	4.78 $\pm$ 0.72	3.9-6.0
Camp Verde	(4)	(4.1)	(3.0-5.0)	6	3.93 $\pm$ 0.66	2.7-5.1
Black in tail (in mm.)						
Phoenix	5	51.80 $\pm$ 2.18	50-56	7	51.00 $\pm$ 3.00	45-55
Lower Verde	14	55.00 $\pm$ 2.56	47-62	(3)	(54.3)	53-56
Camp Verde	(3)	(46.3)	44-50	5	51.80 $\pm$ 3.70	48-58
Crown-color score						
Phoenix	6	0.33 $\pm$ 0.42	0-1	9	0.00 $\pm$ 0	0
Lower Verde	15	0.93 $\pm$ 0.36	0-2	5	1.20 $\pm$ 0.74	0-2
Camp Verde	(4)	(2.4)	1-3	6	3.00 $\pm$ 0.74	2-4
Back-barring score						
Phoenix	6	0.50 $\pm$ 0.44	0-1	9	0.33 $\pm$ 0.32	0-1
Lower Verde	15	1.40 $\pm$ 0.38	0-2	5	0.80 $\pm$ 0.74	0-2
Camp Verde	(4)	(1.13)	0-2	6	1.42 $\pm$ 0.40	1-2
Shaft-color score						
Phoenix	6	0.83 $\pm$ 0.62	0-2	9	0.55 $\pm$ 0.36	0-1
Lower Verde	15	1.00 $\pm$ 0.22	0.5-2	5	1.10 $\pm$ 0.20	1-1.5
Camp Verde	(4)	(2.5)	1-3	6	3.33 $\pm$ 0.20	2.5-4
Hybrid index						
Phoenix	6	1.67 $\pm$ 0.84	0-3	9	1.00 $\pm$ 0.34	0-2
Lower Verde	15	3.33 $\pm$ 0.52	1.5-5	5	3.10 $\pm$ 1.20	1-4.5
Camp Verde	(4)	(6.0)	5.5-7	6	7.58 $\pm$ 0.94	6-9

wood forest is continuous with red-shafted flicker populations along the river and its tributaries to the north.

Flickers from the two lower Verde localities are mostly like *chrysoïdes* but tend toward *cafer* in certain respects. Compared with gilded flickers from the Phoenix area (see table 36), the lower Verde birds exhibit *cafer* influence in the gold, orange, or red in

their shafts, their broader back bars, browner and less rufous crowns, and longer wings and tails. However, they are strongly *chrysoïdes*-like in depth of the breast patch, width of breast spots, and the amount of black in the tail. The lower Verde flickers show more black in their tails than do gilded flickers from anywhere in the range of that form. For reasons discussed above, it is likely that

the lower Verde population is geographically isolated from populations north of the "narrows." There may also be isolation from desert gilded flickers to the south, as areas north and east of Scottsdale and Mesa lack saguaros. Whether the lower Verde population represents the remnant of a formerly more extensive hybrid population once connecting the two forms along this river, or whether its attributes are due to present limited infiltration of *cafer* genes is a moot question. The lower Verde population can at any rate be considered an introgressed gilded-flicker population.

The sample from Camp Verde, 42 miles north of the Horseshoe Dam locality and from beyond the "narrows" north of the lower Verde population, contains birds ranging from intermediate to nearly *cafer*-like in appearance. The mean hybrid index values for the sample are given in table 36. In shaft color the specimens show scores of 2.5 to 4, except for one strongly yellow-shafted male (U. A. M. Z. No. 4735), which scored 1. This individual also tends toward *chrysoïdes* in having broad breast spots. It is intermediate in tail length (105 mm.), but is *cafer*-like or nearly so in other characters (160 mm. wing length, narrow breast patch, fairly small black area in tail, back-bar depth of 2.6 mm., back-barring score of 2, and crown-color score of 3). Indexing less than the latter individual are two males at 5.5. These have reddish orange shafts but are more like *chrysoïdes* in other characters, including crown color and back barring. Two females index about the same (6, 6.5) as the yellowish-shafted male. They tend toward *cafer* in having orange to red shafts, but are less *cafer*-like than the male in other respects.

The Camp Verde sample differs from *cafer*, since most specimens show indications of *chrysoïdes* influence in a number of characters. Only in depth of the breast patch and in breast-spot width do the Camp Verde birds appear identical with *cafer*. In some characters they are strongly *chrysoïdes*-like. Notable among these are the depth of back bars and the amount of black in the tail. Data for the latter character are particularly interesting. The Camp Verde flickers have considerably more black in their tails than does *cafer*. In fact, the mean value for

females exceeds that of gilded flickers from Phoenix (mean areas of black in the tail from the tip toward the base for the two samples are 51.80 and 51.00 mm., respectively). Although these values are comparable, and considerably greater than the 45–48 mm. registered by samples of *cafer* from Arizona, it should be noted that the amount of black in the tail in the Camp Verde birds is relatively less than in *chrysoïdes* from Phoenix, for the latter have shorter tails. Thus, Arizona *cafer* samples usually average 40 per cent to 43 per cent of the tail black, and *chrysoïdes* samples average 49 per cent to 55 per cent. The black areas in the tails of the Phoenix birds extend farther (54.5% of tail length) toward the tail bases, while the Camp Verde females show less extensive (46.3%) black areas. Thus, although like *chrysoïdes* in actual amount of black, the Camp Verde sample is intermediate between *cafer* and *chrysoïdes* in amount of black relative to tail size.

It is likely that the upper Verde River population is subject to some introgression from *chrysoïdes*, owing to sporadic dispersal into the population of individuals from the lower Verde River, and possibly also from the Agua Fria region. The hybrid populations along Ash Creek are separated from Camp Verde by only 15–20 miles. The Verde River Valley may have once been inhabited by flickers to a greater degree than at present, so that formerly more extensive hybridization may have been responsible for the present attributes of the populations along the river.

#### UPPER SAN PEDRO VALLEY HYBRID SWARM

The San Pedro River is a northward-flowing tributary of the Gila River (see map, fig. 11). The lower (northern) portion of the San Pedro is surrounded by desert from about Redington north to its junction with the Gila. The upper San Pedro drains what was once a lush grassland and two high mountain areas (the Huachucas and the San Jose Mountains), which support red-shafted flickers. The lowlands have a long history of intensive ranching; man's activities and demands on the water supply, coupled with a drying trend in the climate, have greatly

restricted arboreal vegetation and have favored xeric plants. Cottonwoods and willows grow almost continuously along the river from the Mexican border north to St. David. Conditions away from the river are such that none of its tributary streams support continuous riparian woodland. Hence, there is no contact or connection between the San Pedro population and *cafer* populations in the Huachuca and San Jose Mountains. The gap between the valley and mountain populations is about 10–15 miles. Cottonwood groves lining the river to the north thin out near St. David, giving way between there and Benson to low trees, primarily mesquites, but including some small cottonwoods. Although a few pairs of flickers may occupy sporadic, favorable sites near the river, the area between St. David and Casabel (about 25 miles) does not support a flicker population. The upper portion of the San Pedro River for about 30 miles is thus inhabited by a population of flickers geographically isolated from both mountain *cafer* populations, and the desert gilded-flicker population along the lower part of the river. Only sporadic immigration across habitat unsuitable for nesting is possible from populations of the parental forms into the upper San Pedro population.

Again, it is likely that conditions of the past were more favorable than those of the present for riparian growth, and that the upper part of this valley once contained continuous vegetation sufficiently suitable for the nesting of flickers as to permit contact and interbreeding between populations of *chrysoïdes* and *cafer*. The present flicker population of the upper river is a remnant of this past, connecting population and can be considered a stabilized population of hybrid origin. I secured a series of 23 breeding adults in 1963 from an area within  $7\frac{1}{2}$  miles north of Hereford, 4050 feet to 4150 feet, Cochise County, Arizona. An additional male was available (C.M. No. 195674) from the San Pedro at Hereford. These all proved to be hybrids that were indexed from 3.5 to 8.5. One other hybrid male (U.C.L.A. No. 33676) taken near Fairbanks, Cochise County (11 miles north of the northern limit represented by the above series), comes from this population. This bird is

indexed at 4.5 and is not included with the others in the analysis below.

In most characters the upper San Pedro flickers exhibit little variation (see table 37). Only in shaft color, back barring, and amount of black in the tail does variation nearly bridge characteristics of both parental forms. Males are all intermediate in wing length and tail length, varying only within 7 mm. and 6 mm., respectively, in the two characters. The females range from being *chrysoïdes*-like to being intermediate in these characters. Coefficients of variation for these characters are among the lowest recorded for flicker samples in the Southwest, which indicates that the population has attained a considerable degree of stability and that its variation in some characters is comparable to the normal variation found in the populations of the parental forms. Breast spotting is similar to that in *chrysoïdes*, the spots being typically broader than deep as in that form. The San Pedro flickers have moderately deep breast patches, and the mean could represent a low extreme of *chrysoïdes* or high extreme of *cafer*. Mean values for breast-patch depth in relation to wing length in *chrysoïdes* samples range from 14 per cent to 16.5 per cent, while for *cafer* they range from 11 per cent to 13.5 per cent. The San Pedro males average 14.2 per cent and the females average 13.7 per cent, in this respect. The back bars of these flickers average broader than those of *chrysoïdes* and narrower than those of *cafer*. In index characters the birds tend slightly toward *chrysoïdes* in shaft color, while they are more like *cafer* in crown color and back barring. Variation is considerable, but only in back barring are extremes represented by the parental forms attained.

Most of the adults secured in 1963 were taken at nests. It was generally possible to collect both adults of a pair by waiting and observing near the nest. In this manner I took five definite pairs (actually more; see below), and also was able to take three probable pairs. The latter cases involved birds taken feeding together (away from any nest), or cases in which an adult was taken near a nest but not so near as to be certainly the mate of the bird obtained at the nest. These pairs are listed in table 38. The three-bird group in table 38 represents a male paired

TABLE 37  
STATISTICAL ANALYSIS OF FLICKERS OF THE UPPER SAN PEDRO VALLEY

	N	$\bar{X} \pm 2 \text{ S.E.}$	Range	S.D.	Coeff. Var.
Wing length (in mm.)					
Males	10	$152.20 \pm 1.40$	150-157	2.20	1.45
Females	12	$150.33 \pm 1.64$	146-155	2.84	1.89
Tail length (in mm.)					
Males	8	$104.00 \pm 2.04$	100-108	2.88	2.77
Females	10	$99.90 \pm 2.16$	94-105	3.41	3.41
Black in tail (in mm.)					
Males	10	$53.60 \pm 3.38$	45-64	5.34	9.96
Females	10	$49.30 \pm 2.96$	43-57	4.67	9.47
Breast-spot width (in mm.)					
Males	10	$5.75 \pm 0.14$	4.4-6.6	0.21	3.65
Females	13	$5.33 \pm 0.62$	4.2-7.6	1.13	21.20
Breast-spot depth (in mm.)					
Males	10	$4.05 \pm 0.30$	3.4-4.9	0.49	12.09
Females	13	$4.03 \pm 0.18$	3.3-4.5	0.33	8.18
Breast-patch depth (in mm.)					
Males	11	$21.55 \pm 0.56$	17-25	2.98	13.83
Females	13	$20.54 \pm 1.28$	17-25	2.30	11.20
Width of back bars (in mm.)					
Males	11	$2.24 \pm 0.20$	1.5-2.6	0.33	14.64
Females	13	$2.32 \pm 0.27$	1.7-3.6	0.49	21.03
Crown-color score					
Males	11	$2.23 \pm 0.50$	1-3.5	0.82	36.77
Females	13	$2.81 \pm 0.28$	2-3.5	0.52	18.51
Back-barring score					
Males	11	$1.45 \pm 0.40$	0-2	0.65	44.83
Females	13	$1.38 \pm 0.36$	0-2	0.65	47.10
Shaft-color score					
Males	11	$1.82 \pm 0.68$	0.5-3.5	1.12	61.54
Females	13	$1.81 \pm 0.44$	1-3	0.81	44.75
Hybrid index					
Males	11	$5.45 \pm 0.86$	4-8.5	1.44	26.42
Females	13	$6.00 \pm 0.70$	3.5-8.5	1.26	21.00

with female 1 and later with female 2. Female 1 was observed entering and leaving the same nest as the male. I then collected the female. After two weeks I returned to the nest and secured apparently the same male with female 2. Both entered and left the nest several times, and the male appeared identical to the one observed two weeks earlier. The four-bird group in table 38 is comprised of a pair, the female of which was collected at the nest hole two weeks prior to my securing, at the same hole, two females and apparently the same male. Of the four, female 1 was mated to the male, but the other two females (2 and 3) were displaying before the male just below the nest hole. When I fired, one

female was wounded, and the other female and male flew away. I was able to draw them both back immediately with a whistled imitation of the territorial Long Call. Despite my presence and the obvious (to me) injury of the female I had wounded, the returning uninjured female flew directly to the wounded bird and began alternately to display and to attack her. The male perched nearby, permitting me to secure all three. Thus, the male of the three-bird group had apparently remated, and the male of the four-bird group was in the process of so doing, following my securing of their earlier mates.

Although the number of pairs is not great,

TABLE 38  
MATED PAIRS AND PROBABLE PAIRS OF FLICKERS FROM THE UPPER SAN PEDRO VALLEY

	Wing Length	Shafts	Crown	Back	Index
Definite Pairs					
Male	150	0.5	2	1.5	4
Female	146	3	3.5	2	8.5
Male	157	1	3	1	5
Female	152	3	3	2	8
Male	153	1	2	1	4
Female	148	1.5	3	1	5.5
Male	151	1	2	2	5
Female 1	153	1	3.5	1	5.5
Female 2	148	1.5	2	2	5.5
Female 3	—	2.5	2	2	6.5
Male	—	0.5	2	2	4.5
Female 1	151	1.5	3	1	5.5
Female 2	151	3	2.5	1	6.5
Probable Pairs					
Male	152	3	2	1.5	6.5
Female	151	1.5	2	0	3.5
Male	150	3	1	2	6
Female	155	2	3	1	6
Male	154	3.5	3.5	2	8.5
Female	153	1	3	2	6

the data given in table 38 suggest the occurrence of random mating in the population. Birds with a given score (or index, or measurement) for any character appear to mate with higher-scoring or lower-scoring individuals, as well as with birds of similar or identical scores. Thus, of six pairs in which at least one member has strongly yellowish shafts (score, 1 or less), three birds were paired with strongly or moderately yellowish-shafted individuals, while the other three were mated with strongly reddish-shafted birds.

The upper San Pedro Valley flickers appear to represent a partially stabilized hybrid swarm. Variability in some characters remains great, but in others it is about that which is found in populations of the parental forms. Geographic isolation of the

population from its parental populations is apparently sufficient to permit the operation of selection on a local level. This has resulted in reduction of (phenotypic) variation in the population, in accordance with the dictates of local selective forces.

#### BABOCOMARI RIVER HYBRID SWARM

The Babocomari River is a small stream draining the eastern Sonoita Plains, the Whetstone Mountains, and the northern Huachuca Mountains. It flows into the upper San Pedro River near Fairbank, within the area along that river inhabited by the hybrid swarm discussed above. The Babocomari is dry, and its banks are treeless for most of its length. Only in a few scattered spots near habitations are there trees of any

size. The only extensive growth of trees of which I am aware occurs on the Babocomari Ranch east of Elgin, and some 15 miles west of the San Pedro-Babocomari junction. The ranch is one of the original Spanish land-grant ranches, and the lush riparian setting there attests to a long history of irrigation, damming, and protection of trees. A dam behind the ranch buildings was maintaining swampy conditions at the time of my visits in the spring of 1963. Altogether, about 1 mile of the river's length is well wooded, with trees growing in stands away from the immediate vicinity of the stream bed, as well as along it. Trees straggle along the river for about 1 mile to the west and  $\frac{1}{2}$  mile to the east of this area before disappearing. On the west side of the ranch are several sizable stands of cottonwoods along draws well back from the river. Surrounding the ranch on all sides is an expanse of open grassland. The elevation at the ranch is 4650 feet, the greatest elevation at which a hybrid population has been found. Oaks and junipers occur in small numbers near the river. Characteristic birds of uplands observed here were acorn woodpeckers (*Melanerpes formicivorus*), bridled tits (*Parus wollweberi*), and bush-tits (*Psaltiriparus minimus*). However, the south-facing slopes north of the river are xeric in aspect, with many acacias. Flickers were common late in the spring and were abundant in late February when I first visited the area. Red-shafted flickers apparently winter here in numbers, along with the resident birds. Seven breeding adults were obtained in 1963; also available was one male (U.A.M.Z. No. 103) taken there in June, 1940, by Gale Monson.

The flickers at the Babocomari Ranch are isolated by grassland from the Huachuca Mountain *cafer* population and from the hybrid swarm in the upper San Pedro Valley. Since they inhabit an area closer to *cafer* and farther from *chrysoïdes* than the San Pedro population, it was to be expected that these flickers would tend more toward *cafer* than do the San Pedro birds. They are indeed more *cafer*-like in some characteristics (wing length, tail length, breast spots, amount of black in the tail, and shaft color). Surprisingly, however, they tend more toward *chrysoïdes* in breast-patch depth, depth of back bars,

crown color, and back barring. The population is apparently isolated enough from other populations to permit effective local selection and its differential effects on genes responsible for the various characters.

The Babocomari birds have longer wings and tails than the San Pedro Valley hybrids. Four adults of both sexes average nearly 154 mm. in wing length and 106.8 mm. in tail length, compared with means of 151.1 mm. ( $N$ , 22) and 101.7 mm. ( $N$ , 18), respectively, for the San Pedro adults. The breast spots of the Babocomari flickers are rounder than those of San Pedro birds. Means, with two standard errors, for males of the two samples are: Babocomari,  $5.08 \pm 0.44$  mm. ( $N$ , 5); San Pedro,  $5.75 \pm 0.14$  mm. ( $N$ , 10). The difference is significant at the  $P=0.05$  level. Babocomari flickers tend to have deeper spots (mean of males, 4.34 mm., compared with 4.05 mm. for San Pedro males), which contribute to the rounder and not so barlike appearance of the spots. The males have spots averaging 0.74 mm. broader than deep, compared with values of 1.70 mm. for San Pedro males,  $-0.05$  mm. to 0.50 mm. for *cafer* samples and 1.00 mm. to 1.80 mm. for *chrysoïdes*. The Babocomari flickers are hence intermediate in this character. The black area at the distal ends of the tails of the Babocomari flickers averages 47 per cent to 48 per cent of tail length, intermediate between that of *cafer* and that of *chrysoïdes* (San Pedro males average 51.5% and are *chrysoïdes*-like). In shaft color the Babocomari birds all score from 3 to 4 (only seven of 24 San Pedro birds score 3 to 3.5). Means and two standard errors for males of the two samples are: Babocomari,  $3.30 \pm 0.40$  mm. ( $N$ , 5); San Pedro,  $1.82 \pm 0.68$  mm. ( $N$ , 11). The difference is significant ( $P=0.05$  level). The five Babocomari males show an average breast-patch depth of 24.80 mm. compared with 21.55 mm. for the San Pedro males, but the small size of the Babocomari sample makes it impossible to attach significance to the difference. Three of the five Babocomari males have back bars narrower than 2 mm., while but one of 11 San Pedro birds measures below 2 mm. Females of the two samples appear not to differ in this feature (there are only three Babocomari females).

Most Babocomari birds approximate



*chrysoïdes* in crown color, with only one of eight birds scoring above 2. The mean score for males is 1.60, while the three females average 2.0. More than half (14 of 24) of the flickers of the San Pedro sample score above 2, with mean sample scores of 2.23 for males and 2.81 for females. Back-barring scores for males of the two samples are 0.80 and 1.45 (Babocomari and San Pedro, respectively). Hybrid-index values for the two samples are comparable (Babocomari males at 5.70, females at 7.0; San Pedro males at 5.45, and females at 6.00).

The strong trend toward *cafer* in shaft color of the Babocomari birds compensates for reverse trends in the other index characters, resulting in the similar index values of the two samples. The isolated population along the Babocomari River thus differs from both parental forms and from the San Pedro population as well. All eight birds in the sample appear to be hybrids. It is suspected that the Babocomari once supported sufficient vegetation to enable direct connections with the Huachuca Mountain red-shafted flickers and with hybrids in the San Pedro Valley. Owing probably to overgrazing, over-utilization of water by man, and drier climate, the once-continuous riparian vegetation was fragmented and largely eliminated. Long maintenance of favorable conditions on the Babocomari Ranch seems to have allowed a remnant of the former hybrid population to endure. Effectively separated from other breeding flicker populations, this isolate has developed its own combination of features in response to local selective pressures.

#### UPPER SANTA CRUZ RIVER POPULATION

The Santa Cruz River lies west of the San Pedro River, which it parallels in its upper portion. It, too, drains mountains (Santa Rita, Patagonia, Pinitos) along the Mexican border and flows northward to join the Gila River near Phoenix, after a westward swing. Red-shafted flickers occupy pine-oak woodland in the Santa Ritas and Sierra del Pinitos. They appear to filter down along streams to lower elevations (Gardner Canyon, upper Sonoita Creek), where effects of gene flow from *chrysoïdes* are evident. Sonoita Creek is particularly well wooded in the vicinity of Pata-

gonia, where flickers have been observed during the breeding season (J. T. Marshall, Jr., personal communication). Cover becomes sparse as the creek approaches the Santa Cruz River north of Nogales. The river itself provides very favorable flicker habitat from the Mexican border nearly to its confluence with Sonoita Creek. Some minor tributaries such as Potrero Creek, which flows from Nogales northward into the river near the Sonoita Creek-Santa Cruz junction, also possess sufficient arboreal vegetation to support flickers.

To the north cottonwoods become restricted to the vicinity of habitations and irrigation ditches (as at Tumacacori, Tubac, and Carmen). A mesquite forest containing some large mesquites exists from Sonoita Creek northward a few miles along the Santa Cruz River. Scattered pairs of flickers may nest there, as birds have been observed in the breeding season (J. T. Marshall, Jr., personal communication). Habitat is sparse northward along the river to Continental and beyond. Desert conditions begin to prevail in the vicinity of Continental, and saguaro cacti may be encountered in the low hills near that town. Presumably, gilded flickers are sparse inhabitants of the desert south to Continental. They probably filter southward along the river toward Nogales. The river in the early Spanish exploration period seems to have had an abundance of water throughout the year, and held to some extent in the upper valley by beaver operations. Evidently riparian vegetation flourished, surrounded by extensive mesquite forests.

The present fine growth of timber at places along the upper river provides evidence that flickers were once able to inhabit the entire upper valley from desert to mountains, which would have enabled contact and interbreeding between *chrysoïdes* and *cafer*. The remnant of this earlier connecting population exists today in favorable situations along the river and its tributaries. Conditions appear to favor considerable influx into this population of *chrysoïdes* individuals from down the valley and *cafer* individuals from the Santa Rita Mountains. Hence, the upper Santa Cruz population is less isolated from genetic influence of the parental populations than is that inhabiting the upper San Pedro Valley.

Five adults and two juveniles were taken

along Potrero Creek at 3520 feet, about a mile south of the junction of that creek with the Santa Cruz River (6 miles north-northwest of Nogales) in late May, 1963. The adults, all hybrids, are indexed at 2, 3.5, 6, 7, and 8. Character scores range from 1 to 3 for shaft color, 1 to 3 for crown color, and 0 to 2 for back barring. The adults are extremely worn, a fact that prevents the use of their wing and tail measurements. However, the range for wing length was 148 mm. to more than 154 mm., and for tail length from 99 mm. to 108 mm., indicating their intermediacy in these measurements. All but one of the adults have fairly round breast spots, as in *cafer*. The one female (A.M.N.H. No. 789388) that exhibits the typical *chrysoïdes* condition of spots tending toward bars is indexed at 8 and is strongly *cafer*-like in other respects. None of the adults possesses a breast patch less than 23 mm. in depth, the average for all five being 24.6 mm. These hybrids thus tend to be like *chrysoïdes* in this character. One male (A.M.N.H. No. 789390), the individual assigned the lowest index value, exhibits narrow (1.7 mm. deep) back bars, while the remainder have broader bars that range from 2.3 mm. to 3.1 mm. in depth. The average of 2.4 mm. for all five birds is higher than the averages of samples from other hybrid populations. The tails of the hybrids are too worn to allow measurement of the black distal area, although comparison with birds equally as worn suggests that the Santa Cruz Valley birds are generally intermediate in this feature. When all characters of individuals in this small sample are considered, the population seems generally similar to that inhabiting the upper San Pedro Valley. The Santa Cruz River birds differ from San Pedro flickers principally in their rounder breast spots and to a lesser degree in their broader back barring. In hybrid-index characters, especially shaft color, they tend more toward *cafer*. They will probably prove to be more *cafer*-like in size than the San Pedro birds, when more specimens become available.

Two adult flickers (C.A.S. Nos. 29467 and 29470) taken in late May, 1927, 7 miles north of Patagonia, are of considerable significance. These birds, a male and a female (not a pair), were secured apparently in the vicinity of Big Casa Blanca and Wood creeks, between

4500 feet and 5300 feet. Their existence there at the base of the Santa Rita Mountains, and the presence of considerable riparian cover from there down Sonoita Creek toward the Santa Cruz River, suggest that there is occasional contact and interbreeding between *cafer* in the Santa Ritas and hybrids of the upper Santa Cruz Valley. The two flickers from north of Patagonia are definitely hybrids (indexes, 5 for the male, 4 for the female) that fall within the range of variation of the upper Santa Cruz birds. The female is in worn plumage and tends toward *chrysoïdes* in shaft color (score, 1), crown color (score, 1), amount of black in the tail, and in having barlike breast spots. This individual is more like *cafer* in back barring (score, 2), back-bar depth (3.0 mm.), and in having a rather narrow breast patch. The male approaches *cafer* in shaft color (score, 3), amount of black in the tail, back-bar depth, and roundness of breast spots. It is intermediate or tending toward *chrysoïdes* in wing length (153 mm.), tail length (99 mm.), breast-patch depth, crown color (score, 1), and back barring (score, 1).

These hybrids, presumably breeding birds, may represent a small population in the lower canyons along the south and east slopes of the Santa Rita Mountains. Further study of flickers in the entire upper Santa Cruz-Patagonia-Santa Rita Mountain area is necessary. In any event, a population undoubtedly of hybrid origin today inhabits portions of the upper Santa Cruz River and its tributaries.

#### SUMMARY

Conditions in Arizona in the past seem to have favored more extensive contact between the two flickers than occurs at the present time. The only area where contact presently takes place between them, through an intervening hybrid population, is along the Agua Fria River and its tributaries. Once such contacts prevailed along the other major streams mentioned above, but recent climatic changes and human activity in the region have combined to limit and, indeed, essentially to cut off gene flow along these streams. As a result, the original hybrid populations, which were probably not all alike, evolved and diverged because of the exigencies of local selective pressures in the environmentally different

TABLE 39  
MEAN VALUES OF THE HYBRID-INDEX CHARACTERS FOR MALES OF SOME ARIZONA SAMPLES

Sample	N	Shaft Color	Crown Color	Back Barring <sup>a</sup>	Mean Range <sup>b</sup>	Hybrid Index
<i>chrysoïdes</i>	20	0.77	0.46	0.92	0.46	1.68
Hybrids						
Lower Verde River	15	1.00	0.93	2.80	1.87	3.33
Lower Colorado River	8	2.10	1.00	1.60	1.10	4.19
San Pedro River	11	1.82	2.23	2.90	1.08	5.45
Lower Ash Creek	10	1.90	1.65	1.80	0.25	4.45
Babocomari River	5	3.30	1.60	1.70	1.70	5.70
<i>cafer</i>	21	3.57	3.57	3.42	0.15	8.74

<sup>a</sup> The score is doubled to facilitate comparison with other characters.

<sup>b</sup> The range of variation in means for all three characters.

areas. Distinctive hybrid populations now exist along portions of these streams, separated from one another as well as from parental populations.

That different effects of selection have resulted in the various isolated hybrid populations seems evident in the differing characteristics they exhibit, as mentioned above. Tables 39 and 40 present a comparison of some of the hybrid samples. Mean index values for these samples are intermediate and fairly similar, but samples with similar means actually differ greatly in the scores of the individual index characters (table 40). Also, mean character scores for any one sample vary considerably, except for those of the parental forms and the Ash Creek sample.

The column headed Mean Range in table 39 gives the range of greatest difference among mean character scores for each sample. The mean character scores of the Ash Creek hybrids, as well as of the *chrysoïdes* and *cafer* samples, are relatively less variable than those of hybrid-swarm samples. The Ash Creek *chrysoïdes* and *cafer* samples vary less than 0.47 in the means of their character scores. The hybrid-swarm samples vary from 1.08 to 1.87 in their ranges of character scores. Genes affecting the index characters appear to be fed into the Ash Creek population about equally for all characters, because this population retains direct genetic contact with both parental populations. This inflow of genes into the Ash Creek population prevents a

TABLE 40  
CHARACTER SUMMARY FOR SOME ARIZONA HYBRID POPULATIONS

Character	Lower Colorado River	San Pedro River	Lower Verde River	Babocomari River	Lower Ash Creek
Wing length	(G) <sup>a</sup>	(G)	G	I	I
Tail length	(G)	I	(G)	(R)	I
Breast spot	I	G	G	(G)	I
Breast-patch depth	R	I	(G)	G	G
Back-bar depth	I	I	R	G	G
Tail black	R	G	G	(R)	G
Shaft color	I	I	(G)	(R)	I
Crown color	(G)	I	(G)	(G)	I
Back barring	(G)	R	R	(G)	I

<sup>a</sup> Symbols: G, *chrysoïdes*-like expression of a character; I, intermediate; R, *cafer*-like expression of a character. Letters in parentheses indicate intermediate but tending toward either *cafer* (R) or *chrysoïdes* (G).

differential response to local selection pressures that act on genes controlling the various characters. The hybrid swarms are buffered by their partial or complete geographic isolation from effects of constant genetic inflow. Each hybrid swarm occupies a different region, with different selection pressures. Hence, each swarm has evolved differently from the others. Furthermore, selection has acted differently on genes responsible for the various characters of each. Genetic drift may also have played a role in bringing about these differences.

Table 40 summarizes the average condition of characters of five hybrid populations in terms of their relative similarity to and inter-

mediacy between *cafer* and *chrysoïdes*. It is readily apparent that the hybrid swarms vary from one extreme to the other in their characters. Each swarm presents a different picture. The varying intermediacy and tendencies toward both forms shown by these samples are explainable on the basis of effects of local selection in isolated populations of hybrid origin. The sample from lower Ash Creek, representing three localities within the southernmost 8 miles of Ash Creek, varies only between the intermediate and gilded-flicker conditions. Local selection pressures in this population must work against an influx of alien genes from parental populations, thus largely overriding their effects.

### THE SONORAN SITUATION

The distribution of the red-shafted flicker in Sonora has been discussed by Marshall (1957), while the most adequate information concerning the gilded flicker is contained in van Rossem's (1945) treatise. Marshall (personal communication) believes that the grassland area (mesquite grassland of Leopold, 1950) prevents contact between *cafer* and *chrysoïdes* in Sonora. Our knowledge of the state is far from complete, and it seems unwise to disregard the possibility that some contacts do occur, perhaps in the upper valleys of central and southern Sonora.

Available from Sonora were 55 adult flickers taken from February through July. Also examined were some 25 specimens taken during the fall and winter. Only six of the specimens collected between February and July were obtained in northern Sonora, and these include the only two (presumed breeding) *cafer* individuals that I have seen. The bulk of the specimens represent the flicker population that occupies the Sonoran Desert-Thorn Forest intergradient region of southern Sonora. Much of this area contains particularly suitable gilded-flicker habitat, with excellent nesting sites (giant cacti) and open areas for ground foraging. Flickers are often abundant in this region, which is doubtless why such a great majority of the specimens come from there.

The two breeding specimens of *cafer* come from the Sierra de Oposura. These are indexed between 8 and 10, but one is in such

worn condition that no exact scores can be assigned to it. Certainly, neither exhibits strong *chrysoïdes* influence. Red-shafted flicker samples are especially needed from mountain areas (Sierra de Pinitos, San Jose Mountains, Sierra Azul, Sierra de Oposura, west slopes of southeastern Sonoran mountains) adjacent to gilded-flicker populations.

The paucity of *chrysoïdes* specimens from northern Sonora precludes determination of the effects of interbreeding. Non-breeding birds from the desert along the Arizona border (Sonoita area primarily) are like neighboring Arizonan *chrysoïdes*. Farther inland, Opodepe and Rancho Carrizo are each represented by a single specimen; both are *chrysoïdes*-like, but the Rancho Carrizo bird scores 2 in shaft color. A bird from Tiburon Island is nearly typical of the race *mearnsi*, while a specimen (U.C.L.A. No. 33956) taken inland from Kino Bay tends toward *cafer* (but also the subspecies *tenebrosus*) in its long (103-mm.) tail, round breast spots, narrow breast patch, and chestnut-brown (score 2) crown. Before we can evaluate the possible indications of the effects of hybridization, breeding samples of *chrysoïdes* must be secured from the northwestern desert, and the upper Río Magdalena, Río Sonora, Río Yaqui, and their tributaries.

The south-central and southern Sonoran specimens are difficult to analyze for two reasons: (1) there are no large series available from the interior and few from elsewhere;

TABLE 41  
MEANS FOR MALES OF SONORAN SAMPLES COMPARED WITH MALES FROM ARIZONA  
AND SOUTHERN BAJA CALIFORNIA

Character	Southern Baja California	Arizona	Central Coast	Sonora Central Interior	Southern Sonora
Wing length (in mm.)	141.5	144.9	142.3	145.8	146.7
Tail length (in mm.)	93.6	95.6	95.0	94.8	97.7
Breast-spot width minus depth (in mm.)	1.20	1.16	1.15	—	0.70
Depth of breast patch*	15.3%	15.9%	14.2%	14.8%	14.2%
Depth of back bars (in mm.)	2.09	1.93	1.86	2.00	1.81
Black in tail (in mm.)	52.1	51.4	46.5	49.0	48.6
Shaft-color score	0.47	0.77	0.70	0.78	0.40
Crown-color score	0.30	0.45	0.37	1.56	1.30
Back-barring score	0.68	0.46	0.47	0.72	0.50
Hybrid index	1.52	1.68	1.53	3.05	2.20

\* Mean depth as proportion of mean wing length.

and (2) the specimens tend more or less strongly toward the race *tenebrosus*, which shows a resemblance to *cafer* in its characters (see discussion below). Specimens were pooled for the analysis, as follows (parentheses enclose numbers of males and females, respectively, taken between February and July, unless otherwise indicated):

Central coast area: Guaymas (12, 9), Batamotal (1, 1), Ortiz (1, 0), Ciudad Obregón (1, 0)

Central interior area: Tecoripa (5, 2), San Javier (1, 0), Bonancita (December male), San Marcial (November male, female), Las Chinchas (November male)

Southern Sonora: Guirocoba (5, 1), Alamos (0, 2), Tesia (1, 0), Camoa (3, 2), Agiabampo (1, 1)

The means for various characters in males of these samples are compared with those of southern Baja California (*N*, 20–60 for various characters) and Arizona (*N*, 20) *chrysoïdes* in table 41. Central and southern Sonoran birds are similar to Arizona *chrysoïdes* in back barring and depth of back bars and in shaft color. They tend to have narrower breast patches and less black in their tails than do Arizona birds. Birds from interior central and southern Sonora tend strongly toward *tenebrosus* in browner crown color and, as a result, in hybrid index as well. Finally, southern Sonoran birds tend more than interior or coastal specimens toward *tenebrosus* in wing length, tail length, and rounder condition of

breast spots. It is significant that, in their divergence from Arizona *chrysoïdes*, the Sonoran flickers from the coast and interior tend toward *cafer* as well as toward the subspecies *tenebrosus*. The latter form is closer to *cafer* in all characters by which it differs from Arizona *chrysoïdes*.

Five birds, from Rancho Carrizo, Guirocoba, Guaymas, Las Chinchas, and Ciudad Obregón (all but the last are males), score 2 in shaft color, a score attained by three of 41 desert *chrysoïdes* specimens from Arizona. Similarity of the Sonoran samples to Arizona *chrysoïdes*, which does receive *cafer* genes, suggests present or past interbreeding as a possible cause of the incidence of scores away from 0. Sonoran flickers thus exhibit fully as much (and in their trend toward *tenebrosus*, more) *cafer* influence as do Arizona gilded flickers. Whether interbreeding between *cafer* and *chrysoïdes* occurs in Sonora is a moot point, requiring for an answer collecting in the areas mentioned above. Since all Sonoran and Sinoloan flickers are thought to be (see below) descendants of an ancestral population invading Arizona from Baja California, the observed effects could be due to earlier *cafer-chrysoïdes* hybridization in Arizona. Present or prior, or both, hybridization between the two forms may well have provided genetic material valuable to *chrysoïdes* in its invasion of Sonora and in its encounter with and partly successful penetration of the Thorn Forest.

## THE SINALOAN SITUATION

The distribution of the two flickers in Sinaloa is known only generally. Red-shafted flickers breed in the Sierra Madre Occidental along the eastern Sinaloan border. Specimens of *cafer* are available from Babizos, at 6400 feet in northeastern Sinaloa (three males), Santa Gertrudis at 6200 feet, also in the northeastern part of the state (one male), and from near Santa Lucia, 6200 feet, in east-central Sinaloa (one male). Additional birds were available from close to the Sinaloan border in adjacent Chihuahua and Durango. The lower altitudinal limit of *cafer* in Sinaloa is not known.

Gilded flickers inhabit the Thorn Forest and Short-tree Forest in the northern and central lowlands of Sinaloa. They nest primarily in hairbrush cactus (*Pachycereus pecten-aboriginum*) and are common in northern Sinaloan lowlands wherever human activities have left sufficient vegetation. South of Culiacán the Thorn Forest becomes dense, and low vegetation limits the amount of open ground surface available for feeding. The flickers become markedly less numerous south of the Río San Lorenzo. I encountered a single calling bird just north of the Río Elota, but was unable to find flickers along Federal Highway 15 south of that river. Despite extensive searching near the main highway, and between Marmol and El Quelite, I failed to find flickers. Chester Lamb took the male "of a pair in the top branches of a palo blanco tree" at El Quelite in February, 1934 (from Lamb's notes, courtesy of J. W. Hardy). This is the southernmost record of the form in Sinaloa. The upper altitudinal limit attained by *chrysoïdes* is not known. Twelve specimens of *chrysoïdes* taken in the spring and the early summer were available for study.

There appears little opportunity for contact between *cafer* and *chrysoïdes* in Sinaloa. Near the southern limit of *chrysoïdes*, Tropical Deciduous Forest of the lower mountains intervenes between Thorn Forest and upland pine-oak woodland. Although large cacti are frequent in the Tropical Deciduous Forest, the dense low growth of vegetation offers little opportunity for ground foraging by flickers. Human activity in the Tropical De-

ciduous Forest seems to favor large cacti somewhat, for fields are often hacked from the forest, with removal of all vegetation except the cacti. Hence man is creating suitable flicker habitat which may eventually result in contact between the two forms of flicker. In northern Sinaloa several streams cut into high mountains, carrying lowland vegetation close to pine-oak woodland. Investigation of areas such as the Río Culiacán around Tamazula, and the upper Río Humaya northeast of Culiacán might prove interesting from the standpoint of flicker contacts.

Examination of Sinaloan flickers for indications of hybridization was hampered by the tendency in *cafer* and *chrysoïdes* to converge, in respect to their characters, in the state. In central Sinaloa the gilded flicker occupies not open deserts like those farther north, but fairly dense Thorn Forest. Here *chrysoïdes* shows more prominent back barring, generally darker plumage, and browner crown color. Red-shafted flickers are smaller than those that occur farther north; they also exhibit narrower back bars and more rufous crowns. Differences between the flickers are thus lessened.

Available Sinaloan specimens of *chrysoïdes* came from around El Fuerte (three males), Guamuchil (two males, one from mouth of Río de Sinaloa, and one female), and Culiacán (Culiacán, one male, one female; El Molino, three males; and Cieneguita, one male). Further material is needed before the characteristics of the population can be evaluated. The birds are small, the wing length averaging 143 mm. and the tail length 95.1 mm. (the latter is inordinately lower than expected, since *tenebrosus* should have longer tails). Breast spotting is highly variable, some birds having broad spots while others exhibit very round spots. The breast patch is consistently narrow, about as in *cafer* (17–23 mm.), except that the patch is relatively deeper when the smaller size of these *chrysoïdes* is taken into account. Most of the specimens are intermediate in depth of back bars; a few are like *chrysoïdes*, while others have bars as broad as those of *cafer*. The amount of black in the tails of these birds is like that of Arizona

*chrysoïdes*. In shaft color none of the birds scored 0, while one (O.C. No. 8703) was strongly orange-tinted. Others showed fewer indications of orange. All specimens but one (a male from El Fuerte, O.C. No. 8252) scored between 1 and 3 in crown color, showing chestnut and brown rather than the strongly rufous color typical of the subspecies *mearnsi* farther north. Only two of the 12 birds scored 0 in back barring; the remainder scored 1 or 2.

Specimens of *cafer* available from Sinaloa measure 154 to 165 mm. in wing length and 107 to 116 mm. in tail length. The breast spots of these birds are round, generally, though tending toward bar spotting in one specimen. In depth of the breast patch these specimens are typical of *cafer*. Their back bars are very narrow, the mean for five males being 1.68 mm. Thus, these specimens are *chrysoïdes*-like in this character. Should further collecting bear out the narrowness of back bars in Sinaloan *cafer*, the two forms of flicker then show reversal in their normal condition of this character, with *cafer* exhibiting slightly narrower bars than *chrysoïdes*. Likewise, the amount of black in the tails of Sinaloan *cafer* individuals is greater than that in *cafer* to the north, a condition generally true of the race *mexicanus* in comparison with *collaris*. In shaft color no approach toward *chrysoïdes* is evident. The narrower condition of back bars is reflected in low back-barring scores of Sinaloan *cafer*. Crown color is quite rufous brown in these specimens, as in *mexicanus*, again showing an approach to *chrysoïdes*.

The increased similarity of *cafer* and *chrysoïdes* in Sinaloa is attributed to two major factors. First, the environment of the Sinaloan Thorn Forest is considerably different from that inhabited by *chrysoïdes* elsewhere, and perhaps more similar than deserts to the woodland habitats occupied by *cafer*. Hence, the "*cafer* tendencies" of *chrysoïdes* in Sinaloa may reflect that form occupying a more *cafer*-like habitat. Second, I consider *mexicanus* to be more like the progenitor of the *cafer* group than any other of the races of the group. In certain respects the *chrysoïdes* group may have diverged less from original "*pre-cafer*" flickers than have more northern races (*collaris*, *nanus*, *cafer*) of the *cafer* group.

Until we have more specimens available that represent other parts of the state (particularly areas where ranges of the two forms approach each other), the occurrence of hybridization between them can be neither proved nor disproved.

For reasons discussed above (the Sonoran situation), it is possible that effects of hybridization are still being manifested in the Sinaloan gilded-flicker population, as a consequence of the recent entry into the area of *chrysoïdes* from the north, where contacts had earlier been established with *cafer*. Evidence that suggests that *chrysoïdes* has only recently entered the Thorn Forest from the north is of several kinds. The gilded flicker seems to be penetrating into the Thorn Forest of central Sinaloa as a newcomer. It is local in distribution south of Culiacán. Though man's activities have created many favorable situations for these flickers between Culiacán and Mazatlán, few birds seem to be infiltrating the region, as would be expected of this adaptable bird if the Culiacán area were already fully exploited and supported a large flicker population. Conditions appear particularly favorable (more desert-like) for gilded flickers along the more arid coastal region. These conditions have not been affected by man's activities and appear to be long-standing. It is difficult to conceive of why *chrysoïdes* does not occupy this area fully if the form was in Sinaloa throughout the Wisconsin and post-Wisconsin glacial period. In this line of reasoning, the mixed Thorn Forest and savanna areas south of Mazatlán, especially in northwestern Nayarit, appear particularly suitable for gilded flickers. Again, gilded flickers should have been able to reach this area from the north, if populations of this form have been in the region for a long period. Finally, giant cacti of the genus *Pachycereus* and its relatives occur continuously from Sinaloa into Nayarit and the cactus scrub areas of central Mexico. These cacti are eminently suitable for nesting by gilded flickers. It seems that an adaptable bird like the gilded flicker would have at some time been able to extend its range southward into savanna areas along the western coast and into interior desert scrub situations, if the form had a long history in Sinaloa throughout the late Pleistocene.

## BAJA CALIFORNIAN FLICKERS

The distribution of flickers in Baja California has been discussed by Grinnell (1928; map of flicker distributions included). The only possible area of contact between the *cafer* group and the *chrysoïdes* group is along the southwestern edge of the Sierra San Pedro Mártir Range. Particular areas that need investigation are the upper reaches of the Río San Quintín and Río del Rosario and the region north of San Fernando in northern Baja California.

A total of 174 adult flickers (88 taken January–August, 86 fall birds) was examined from Baja California. Color analysis by means of the hybrid index used for Arizona specimens was difficult owing to the variation shown by Baja California flickers in back barring (see discussion below). Despite this difficulty, the use of a constant index system, with due regard for variation, was considered desirable. In the question of possible hybridization affecting gilded flickers of Baja California, three essential problems were encountered. The first is whether hybridization presently occurs in Baja California. The second problem is: Are there indications of *cafer* characters in the gilded flickers of Baja California? Finally, there is the problem of whether such indications (if present) could be due to normal variation in gilded flickers of this area, or are the result of introgression owing to past or present hybridization, or both.

The first of the three problems—whether hybridization is occurring in Baja California at present—cannot be answered.<sup>1</sup> Critical observations and the securing of specimens in the likely area pointed out above are required to provide clear information on this point. Specimens of *chrysoïdes* available from near the San Pedro Mártirs numbered only five (from near El Rosario, San Juan de Dios, and Aguaita). These appear not to differ from birds of the San Fernando region to the south. Gilded flickers are known to occur around San Quintín (Huey, 1926) and may follow the fringe of the desert northward beyond there. Huey noted (p. 350) the occurrence of

gilded flickers in the foothills of the mountains as well as in the desert itself. Whether they make contact with *cafer* remains to be determined. In view of the narrowness of some hybrid zones, lack of indications of hybridization in populations farther removed from possible areas of contact and interbreeding does not rule out its occurrence. Only three breeding red-shafted flickers were available from the mountains of northern Baja California. Two are from the north end of these mountains (Nachagüero Valley). The other is from Vallecitos. None of these show definite signs of *chrysoïdes* influence. Three additional specimens of *cafer* taken in the fall are also of no help. The latter have quite brownish crowns, approaching in color those of the race *brunnescens* representing the *chrysoïdes* group in the adjacent desert. Another specimen (M.V.Z. No. 47263) is of interest in that it was taken May 5 in the upper end of the Arroyo San Telmo at an elevation of but 2500 feet. This bird exhibits slightly more black in its tail than the others and scores 2 in crown color and 3 in shaft color. Whether breeding at that elevation or not, this bird suggests that *cafer* may be present in the foothills farther south (near or within the range of *chrysoïdes*) into the breeding season of *chrysoïdes*. At least sporadic interbreeding between the two appears to be likely.

The second problem can be attacked by an analysis of available specimens. Table 42 presents a comparison of the color-character scores of Baja Californian and Arizonan *chrysoïdes*. There is no difference in back barring of flickers from the two areas, a fact that may be attributable to the less arid conditions in the lower part of the peninsula (two-thirds of the specimens are from southern Baja California). Fewer Baja Californian than Arizonan *chrysoïdes* show crown-color evidence of *cafer* influence, despite bias toward higher scores in the Baja Californian sample from the inclusion of *brunnescens* specimens (*brunnescens* has a browner crown than the races *mearnsi* and *chrysoïdes*) with those of *chrysoïdes*. Baja Californian flickers show significantly less golden orange in the shafts than do Arizonan flickers. Strong effects of

<sup>1</sup> The answer is "yes," for Richard Banks and I have recently discovered a hybrid population of flickers in the foothills east of San Quintín.



TABLE 42

COMPARISON OF HYBRID-INDEX CHARACTERS OF GILDED FLICKERS FROM ARIZONA AND BAJA CALIFORNIA<sup>a</sup>

Character	N	N Scoring 0	Per Cent Scoring 0	Significance of Difference
Crown color				
Baja California	78	48	62	$P=0.01$
Arizona <sup>b</sup>	123	56	46	
Shaft color				
Baja California	167	95	57	$P=0.01$
Arizona	154	40	26	
Back barring <sup>c</sup>	—	—	—	
Hybrid index				
Baja California	78	38 <sup>d</sup>	49 <sup>e</sup>	$P=0.01$
Arizona	118	35	30	

<sup>a</sup> Adults of both sexes taken from January to August, except that, for shaft color, adults taken throughout the year were used.

<sup>b</sup> All Arizona birds taken from desert areas, including series from Phoenix and Tucson.

<sup>c</sup> No difference between samples.

<sup>d</sup> Number indexed from 0 to 1.

<sup>e</sup> Per cent indexed from 0 to 1.

introgression from *cafer* are presumed to be responsible for tendencies toward *cafer* in crown and shaft color of Arizonan birds. About two-fifths of the Baja Californian flickers show traces of orange-gold in their shafts, probably from the effects of present or past interbreeding, or both, between *cafer* and *chrysoïdes*. Finally, Baja Californian *chrysoïdes* exhibit significantly lower hybrid index values than do Arizonan birds (table 42), evident not only in the proportion of low-indexed specimens, but in that of high-indexed birds as well. Specimens indexed at 3 or more must tend toward *cafer* either slightly in all three characters or strongly in at least one character. The incidence of specimens achieving an index value of 3 or more in the Arizonan and Baja Californian samples used in table 42 is as follows:

	N	No. SCORING 3 OR MORE	PER CENT SCORING 3 OR MORE
Arizona	118	39	33
Baja California	78	13	17

The difference is statistically significant at the  $P=0.01$  level. Baja Californian *chrysoïdes* thus show fewer traces of *cafer* characteristics than do Arizonan *chrysoïdes*. That they do in

fact show such traces, however, is substantiated by the data.

The problem of proving that the *cafer* characteristics in the Baja Californian population are due to introgression is difficult, especially since *chrysoïdes* is believed to have originated from a pre-*cafer* flicker in Baja California. Retention of a low residue of ancestral genes now prevalent in *cafer* could account for observed indications of *cafer* characteristics. In such a case it is assumed that the incidence of such traces would be about the same in all segments of the Baja Californian population. Such does not hold true, for *cafer* indications are demonstrably more numerous in northern peninsular flickers, i.e., toward the area of potential contact with *cafer*, than in populations farther south. Comparison of hybrid-index values of adult *chrysoïdes* taken (January–July) in Baja California north of latitude 26° N. with those taken farther south shows the following:

	N	No. INDEXED AT 2 OR MORE	PER CENT INDEXED AT 2 OR MORE
Northern peninsula	39	26	67
Southern peninsula	39	14	36

The difference is highly significant. However, it may be argued that, since features of *brunnescens*, the northern Baja Californian race, include crown color and back barring more like those of *cafer*, the hybrid index would tend to be pushed in that direction. Such an argument does not apply to shaft color. When all adult *chrysoïdes* specimens from Baja California were considered for shaft color, the following data were obtained:

		NO. SCORING 1 OR MORE	PER CENT SCORING 1 OR MORE
N			
Northern peninsula	52	33	63
Southern peninsula	115	39	34

Again, the difference is highly significant. The partial retention of ancestral patterns of

plumage color may account for some degree of incidence of *cafer* characteristics in the Baja Californian gilded-flicker population. However, it is probable that past or present (or both) hybridization and introgression have provided at least an additive effect.

In other respects the Baja Californian *chrysoïdes* population (especially the race *chrysoïdes*) differs little from desert *mearnsi* of Arizona (see table 41). Adaptation in the northern peninsular Baja Californian population (*brunnescens*) has not involved trends toward *cafer*-like condition of the characters showing such modification in Sonoran-Sinaloa gilded flickers (*tenebrosus*). Only in crown color and back barring are comparable patterns evident in populations of the two areas.

#### YELLOW-SHAFTED FLICKER CHARACTERS IN GILDED-FLICKER POPULATIONS

I show above that populations of the subspecies group *cafer* in western North America exhibit considerable *auratus* influence owing to introgression from the hybrid zone. An analysis of Arizona *cafer* samples indicated that, as in surrounding populations, the Arizona population of this form showed indications of *auratus* characters. In view of the interbreeding between *cafer* and *chrysoïdes*, I undertook an examination of the hybrids and gilded flickers to ascertain whether *auratus* characters could be detected. The results indicated that hybridization between *cafer* and *chrysoïdes* is, or has been in the past, sufficient to allow the passage of *auratus* genes, as well

as *cafer* genes, into the gilded-flicker gene pool.

The incidence of five characters of *auratus* (all color characters used in the *auratus-cafer* index except shaft color) was determined in various southwestern flicker samples. The number of individuals in each sample showing scores of 3 or less for one or more of these characters was ascertained. Results appear in table 43. The picture presented is a clear one, showing a decreasing incidence of *auratus* characters in the *cafer* × *chrysoïdes* hybrids and a further decrease in the *chrysoïdes* samples. Many important points are indicated by these data. The decrease in *auratus* char-

TABLE 43  
TRACES OF *auratus* COLOR CHARACTERS OF ADULTS OF BOTH SEXES OF  
SOUTHWESTERN FLICKERS TAKEN JANUARY TO JULY

Form and Area	N	No. with Traces	Per Cent with Traces	Significance of Difference <sup>a</sup>				
				A	B	C	D	E
<i>chrysoïdes</i>								
Southern Baja California, A	48	12	25		—	x	x	x
Arizona, B	117	42	36	—		x	x	x
Hybrids, Arizona, C	104	49	47	x	x		—	x
<i>cafer</i>								
Arizona, D	71	40	56	x	x	—		x
California, E	80	52	73	x	x	x	x	

<sup>a</sup> Letters refer to the letters after the areas in the left-hand column. x indicates significance at the  $P=0.01$  level.

TABLE 44  
YELLOW SHAFT-COLOR TRACES IN SOME SOUTHWESTERN RED-SHAFTED FLICKERS,  
INCLUDING SPECIMENS OF BOTH SEXES

Area	N	No. with Traces	Per Cent with Traces	Significance of Difference
Arizona <sup>a</sup>	69	31	45	$P=0.01$
California	78	24	31	

<sup>a</sup> Includes specimens showing no strong indications of *chrysoïdes* influence in other characters.

acters from *cafer* in California to those of Arizona is expected because of the greater distance of the Arizonan populations from the main northern contact (British Columbia), and the occurrence of Arizona *cafer* in somewhat isolated mountain populations. Arizona hybrids show less indication of *auratus* characters than do *cafer* individuals. The individuals of *chrysoïdes* from Arizona exhibit considerably less *auratus* influence than do hybrids, although 36 per cent is still a considerable portion of the population. The incidence of *auratus* characters in Baja Californian flickers indicates that there is probably some introgression from *cafer* into the peninsular flicker population. Those gilded flickers from Baja California that exhibit *cafer* characters (index 2) show 12 per cent greater indication of *auratus* traces (the difference is significant at the  $P=0.10$  level) than do the gilded flickers that exhibit no *cafer* characters (index 0 and 1). The presence of *auratus* characters due to introgression into the Baja Californian gilded-flicker population is an indication of the effectiveness of the genetic contacts among the three subspecies groups. The implication is also clear that Baja Californian gilded flickers are either in contact and hybridizing with *cafer*, or have in the

recent past received *auratus* genes from the Arizona *chrysoïdes* population via a former contact in northern Baja California.

The study above involved all the *auratus-cafer* color characters except shaft color, which was omitted because of the possibility that Arizona *cafer* receive yellow shaft color via introgression from both *auratus* and *chrysoïdes*, which suggested testing the possibility of such two-way introgression. The incidence of yellow traces in shaft color of Arizona *cafer* (only individuals exhibiting no other apparent *chrysoïdes* characters) was compared with the incidence of such traces in California *cafer* (table 44). If introgression from *auratus* were solely responsible for the yellow traces in shaft color, Arizona *cafer* might be expected to exhibit fewer traces than California *cafer*, as found for other *auratus* characters (table 43). The incidence of yellow traces in shaft color was determined to be about 50 per cent greater in Arizona *cafer*, which indicates conclusively that considerable introgression is occurring between the two forms of Arizona flickers. It also attests to the ability of populations of the three forms to partake of one another's genetic variability.

## DISCUSSION

### HISTORY OF HYBRIDIZATION IN *AURATUS* AND *CAFER*

THE RECENT ADVANCES in our knowledge of past climatic and geological changes (see Flint, 1957) make it feasible to deal with the history of North American flickers. Wetmore (1931) has indicated that flicker-like woodpeckers existed in North America in the Lower Pliocene. The probable history of flickers in the Plains is presented below, beginning with the Pliocene; this follows a summary of conditions prevailing since that time.

#### CONDITIONS IN CENTRAL NORTH AMERICA SINCE THE PLIOCENE

Early in the Pliocene the climate in the central and western part of the continent was more moist, and probably warmer, than it is at present (Axelrod, 1948). Increasing aridity and cooling in the west began in mid-Pliocene time, owing largely to the uplift of mountains (Axelrod, 1950). With some reversals, this trend has continued up to the present and has culminated in the formation of the American deserts. A major feature of the Plains in the Pliocene was the general north-south, rather than east-west, drainage pattern (Frye and Leonard, 1952; Meneley *et al.*, 1957). By the end of the Pliocene, wooded areas in the Plains were restricted to the vicinity of major streams, as they generally are today (Chaney and Elias, 1936).

About four major advances of glaciers south into the United States occurred during the Pleistocene (Flint, 1957). The periods of glacial expansion were followed by warmer interglacial periods. At their maximum extent the glaciers covered most of the northeastern United States and virtually all of Canada. Glacial advances were not steadily progressing phenomena but were marked by gradual advances, with some interruptions or withdrawals with varying times and distances. The advances were ultimately followed by fast or slow retreats of the ice, punctuated by periodic halts and re-advances (Sears, 1948). Changes in sea level of considerable magnitude ( $400 \pm$  feet) occurred in response to the uptake and release of water by the glaciers as they advanced and receded (Lawson, 1942;

Fisk, 1944; Kuenen, 1950; and Gealy, 1955). In addition to changes in sea level, areas such as the northern Gulf of Mexico were the scene of large-scale submergence of land areas (Deevey, 1950; Gealy, 1955; Neill, 1957). Former land areas may have been of considerable importance in providing refuges for the biota pushed south from the more northern part of the continent. Centers of maximum ice depth during glacial periods occurred in the region of the northeastern United States and southeastern Canada, and in British Columbia. The ice was at its thinnest in the northern Plains at the base of the Rocky Mountains (Flint, 1957). Effects of the glaciers were apparently restricted to the immediate vicinity of their borders, beyond which they were of little direct importance (Deevey, 1949). There is some evidence that a woodland border extended across the Plains in front of the ice (Gleason, 1922; Flint, 1957). Recent botanical work (Hafsten, 1961; Wendorf, 1961) suggests that open boreal woodlands may have connected eastern and Rocky Mountain vegetation across the southern Plains during glacial maxima. Isolated glaciers occurred in the higher mountain areas of the west (Flint, 1957). Climatic conditions fluctuated greatly during the Pleistocene. Generally, moist, cool conditions prevailed during glacial periods, while interglacial periods were warmer and more dry (Flint, 1957). An excellent account of the climates of the various glacial periods in the Plains is that by Frye and Leonard (1952). According to these authors, the earlier glacial periods (Nebraskan, Kansan) were marked by considerable moisture in the Plains, followed at the end of the Yarmouth interglacial or beginning of the Illinoian Glacial by a pronounced arid trend, which is still progressing. Wisconsin and post-Wisconsin climatic shifts in the southern high Plains were discussed by Wendorf (1961).

During the last major ice advance (Mankato) of the Wisconsin glaciation the continental ice sheet did not extend so far south in the northern Plains region as it did in earlier advances. The Altamont moraine of the Mankato indicates that the greater part

of South Dakota, the southwestern half of North Dakota, eastern Montana, southeastern Alberta, and southwestern Saskatchewan were free of ice during this advance (Horberg, 1952; Horberg and Anderson, 1956). Rapid shrinkage of the ice north of this area occurred during deglaciation, owing to the thinness of ice in the area and to the "warming of the Plains before the central and eastern regions were affected" (Flint, 1957, p. 324). As deglaciation progressed, the extension northward of an open area in the form of a corridor from Alberta to Mackenzie occurred (Banfield, 1961). Eventually this ice-free corridor extended to the unglaciated area of Alaska, while ice still remained to the east and west. Gradually the ice retreated in the east toward centers in Quebec and Labrador. The last glaciers disappeared from the Great Lakes area about 8500 years ago, and from Labrador and Quebec perhaps as late as 3000 years ago (Flint, 1957, pp. 324-326). Large bodies of water pooled south of the glaciers as they retreated; the remnants of these are the Great Lakes. West of the corridor the ice retreated toward the center in British Columbia, at about latitude 53° N. in the area of the Cariboo parklands (Flint, 1957). Pluvial and glacial conditions south of the ice sheet in the west occurred concurrently with glaciation in the north, although maximum conditions may have been somewhat later (Antevs, 1941a, 1941b).

Since the glaciers receded, conditions have been far from stable. Postglacial time was marked by at least one period, the Climatic Optimum, which was somewhat warmer than the present (Zeuner, 1950, 1959; Flint, 1957). During this time grasslands extended eastward, reaching New York and North Carolina, and affecting the fauna of the east (Transeau, 1935; Schmidt, 1939; Frey, 1951; Smith, 1957; Neill, 1957; and Short, 1963). In the cooler period that followed, glaciers that had become virtually extinct in the Climatic Optimum re-formed and underwent expansion. Other warm and cool periods followed; the latest cool period ended in the nineteenth century. Increasingly warmer climate has occurred since that time (Flint, 1957).

The effects of Pleistocene conditions on the biota have been discussed by many authors.

The southward displacement of the biota under the influence of the advancing glaciers was amply covered by Braun (1955), Deevey (1949), Dillon (1956), Flint (1957), Neill (1957), and Savage (1960). The possible connection between eastern North American and Mexican biotas has been discussed by Martin and Harrell (1957). Pleistocene effects on evolution in moths of the genus *Platysamia* (= *Samia*) were discussed by Sweadner (1937). The influence of glaciation and related conditions on evolution in birds has been stressed by Rand (1948b), Mayr (1942, 1963), A. H. Miller (1941), and Howell (1952). Rand (*loc. cit.*) reviewed the effects of glaciation on certain North American birds. Sibley and his students have studied situations of hybridization in the Plains, caused by secondary contacts following separation of populations during glacial periods (Sibley, 1961; Sibley and Short, 1959, 1964; Sibley and West, 1958; West, 1962). Steinbacher (1948) and Moreau (1954) have reported on Pleistocene effects on the European avifauna. Gentili (1949), Serventy (1953), Condon (1954), and Keast (1961) reviewed Pleistocene conditions in Australia and their effects on the avifauna of that continent.

Following the last glaciation, man, in the form of the Indian, became a factor affecting plants and animals in North America. Indians using fire, and the presence of great buffalo herds, probably limited the extent of woodland along river valleys in the plains. Fires, accidental or set (see Dickens, 1928, p. 9), were important in restricting trees to the vicinity of streams. Early explorers were struck by the "ravages of fire" (see P. Allen, 1902, p. 245) in the area. Trees were also confined to river valleys and other sheltered areas by "the presence of millions of buffaloes [which] severely grazed the grasses [and] attracted the Indians, who set fire to the grass, thus confining the trees to the river banks, mountains and broken lands" (Harshberger, 1911, p. 517; see also Sauer, 1950). Thus, apparently owing to a combination of the semi-arid conditions of the plains, the effects of grazing by bison, and the activities of Indians as fire-causing agents, trees were confined largely to river valleys of the Plains in later postglacial times.

Along the river valleys of the Plains, the early explorers and pioneers found considerable quantities of timber. Beside the Missouri River a continuous woodland connection existed from its mouth to the Rockies (via the Yellowstone River and the Missouri), as indicated in the accounts of the Lewis and Clark expedition (P. Allen, 1902; see also J. J. Audubon's journal of his Missouri River trip in 1843, in M. R. Audubon, 1897). Pike's expedition (Quaife, 1925) found trees along the length of the Arkansas River from Kansas into the Rockies of Colorado. James, accompanying Long on the latter's expedition of 1819-1820 (Thwaites, 1905, vol. 15), found woodlands along the eastern Platte River which continued into Colorado (along the South Platte). Trees were less numerous in eastern Colorado, where isolated groves of cottonwoods and willows occurred. Groves of trees were observed continuously as the party progressed westward, however, and trees were found to the base of the Rockies along the South Platte River. The same account (Thwaites, 1905, vol. 16) also indicated a riparian woodland connection along the Canadian River in Texas and Oklahoma. The observations of these early explorers concerning the occurrence of trees along these rivers are further corroborated by their notes on the wildlife. Beaver, porcupines, and deer, all of which were restricted to the vicinity of the woodland border along streams, were found commonly along the entire Missouri (P. Allen, 1902; M. R. Audubon, 1897) and along the Platte and South Platte rivers (Thwaites, 1905, vol. 15).

The general effect of the white man's entrance on the scene in the Plains has been an increase in woodland and in the fauna dependent upon it. Early pioneers at first removed most of the tree cover in the Plains for various purposes (Thwaites, 1905, vol. 15, p. 224; Dickens, 1928, p. 9). This period of tree utilization was followed by a period of tree planting, which is still continuing. Natural tree growth since the cessation of the practice of tree removal has led to the formation of woodland borders along the streams in the Plains. Man has also provided more stable conditions for the growth of riparian vegetation by bringing to a halt the devastation of prairie and woodland by

fires, and by the damming of major streams in the area (although ever larger and more numerous dams result also in destruction of much riparian woodland).

#### HISTORY OF *auratus* AND *cafer* SINCE THE PLIOCENE

It is evident that the original separation of the ancestral *auratus-cafer* population could have occurred either (1) because of increasing aridity in the central part of the continent in the Pliocene, or (2) during one of the glacial periods of the Pleistocene when a combination of the ice sheet in the north and arid conditions in the south restricted gene flow between eastern and western populations. In view of the importance of the present contact provided by forests in western Canada, separation of the populations in the Pliocene would have necessitated a barrier in Canada as well as an arid climatic barrier in the Plains. There is no evidence to indicate that the taiga was broken in central Canada during the Pliocene, and it is therefore unlikely that initial separation of *auratus* and *cafer* occurred during this period.

Conditions favoring separation of the populations of these forms occurred during glacial periods of the Pleistocene. Partial or complete isolation may have first occurred in the Nebraskan Glacial period, which was the earliest glacial period. The work of Frye and Leonard (1952) suggests that the first two glacial periods were too moist to have resulted in elimination of the river-valley connections between the forms. The great increase in aridity these authors ascribed to the late Yarmouth Interglacial or early Illinoian Glacial suggests that this was the first period of complete separation of *auratus* and *cafer*.

It should be noted that complete isolation was not absolutely essential for the divergence in these forms. Divergence could have taken place, even with narrow contacts along river valleys in the Plains, through the isolation provided by distance alone (Wright, 1946). It is difficult to estimate the time necessary for development of differences such as those occurring between *auratus* and *cafer* on the basis of the nature of the differences. More precise information on rates of evolution would be useful. The various

differences exhibited by the various subspecies groups suggest that the *chrysocaulosus* and *chrysoïdes* groups originated from pre-*auratus* and pre-*cafer* stocks, respectively. The former two forms have undergone considerable differentiation since their isolation. Since the origin of *auratus* and *cafer* probably antedates the origin of *chrysocaulosus* and *chrysoïdes*, it is unlikely that a period of 15,000 to 40,000 years has been long enough to allow for differentiation of all these forms. The available evidence suggests that *cafer* and *auratus* underwent initial separation, which may or may not have been complete, during the early glacial periods of the Pleistocene. Once this occurred, divergence of the groups continued as long as conditions (such as those during glacial periods) limited interbreeding. Divergence was probably halted or even reversed owing to considerable interbreeding at times when greater contact was permitted, as during interglacials.

During late stages of the last (Wisconsin) glacial period, *cafer* apparently entered the ice-free Cypress Hills area of Saskatchewan. This form may have existed in the Black Hills of South Dakota throughout the Wisconsin glaciation, as this area was not glaciated. The corridor that opened up in central Canada provided an avenue for *auratus* populations to enter northern Canada, while conditions prevented *cafer* from moving north in this area. The eastern affinities of the avifauna of northwestern Canada are attributable to the fact that this area became available to eastern, rather than western, forms; the central Canadian corridor is the probable cause of this phenomenon. The contact between *auratus* and *cafer* in British Columbia generally bisects the area where the center of the Cordilleran ice sheet lay during the Wisconsin. During deglaciation, while the opening of the corridor enabled *auratus* to reach Alaska, *cafer* remained restricted to the area south of the receding ice sheet in the western United States. As the ice sheet retreated toward the British Columbian center, *auratus* and *cafer* gradually converged on this center, from the north and south, respectively. With the final breaking up of the ice sheet, contact

ensued, resulting in extensive hybridization and introgression. Similar contacts have been formed in this area between *Junco* "*hyemalis*" and *Junco* "*oreganus*" (A. H. Miller, 1941), and between *Sphyrapicus varius varius* and *S. v. ruber* (Howell, 1952).

Flicker contacts along the river valleys of the Plains, probably in existence during most of the Pleistocene, were perhaps obliterated by arid conditions during the Climatic Optimum. The warm, dry climate of this time, and the extension of grasslands to the east at the same time, make it unlikely that contacts persisted in the Plains. With the advent of cooler and more moist conditions following the Climatic Optimum the contacts were rejoined.

Since man has been effective in increasing the habitat suitable for flickers in the Plains, contact between the two forms has increased. The Plains contacts are, however, relatively unimportant in relation to the much greater gene flow permitted in the northwest by a continuous woodland contact. Man's activities have thus had little effect on hybridization between *auratus* and *cafer*.

Dillon (1956, p. 176, map p. 175) has described the flicker situation in terms of the pushing southward of flicker populations by conditions in the area of glaciation. He pointed out that flicker hybridization occurred in the past, probably during periods of glaciation as well as during interglacials. I fully agree with his contention but find it difficult to accept his other suggestions. Chief among these is the view that the various subspecies of the flicker groups were in existence during past glacial periods, and that their ranges were condensed in response to the narrowing of the life zones during glaciation. I believe that clinal subspecies such as those of the *auratus* group may originate over a short period of time in response to differing selective pressures in various areas. The races of *auratus* may well have originated since the last glacial period, as populations of this form extended northward. There is no need to assume that such races have been in existence for very long periods. The supposed similarity of the *mexicanoïdes* group to the dark northwestern race *cafer* or the *cafer* group, which

Dillon mentioned (from J. A. Allen, 1892), is a superficial one. All the races of the *cafer* group differ from the *mexicanoides* group in a number of characters which are constant in both the groups. Dillon (1956, p. 175) presented maps showing the present ranges of North American flickers and the hypothetical ranges of the various forms during maximum glaciation. While the ranges of the races shown are very questionable, the overall ranges of the *auratus* and *cafer* groups are of interest. Following the last glacial period, *auratus* populations expanded tremendously, as they were able to extend into northern and western Canada. Populations of *cafer* expanded slightly. The ranges probably occupied in the last period of glaciation and those occupied at present are estimated for *auratus* and *cafer* as follows:

	<i>cafer</i> GROUP	<i>auratus</i> GROUP
Area of range at maximum glaciation, in square miles	660,000	880,000
Area of present range, in square miles	1,020,000	3,400,000
Per cent of increase	50% $\pm$ 50%	315% $\pm$ 50%

If the sizes of the populations are assumed to be directly proportional to the areas occupied, it seems clear that the *auratus* population greatly increased its numbers, while *cafer* increased but slightly. It is conceivable that this expansion of *auratus* had some effect on hybridization and introgression between the forms. The greater size of the *auratus* population at present is apparently reflected in the much greater introgression in *cafer*.

## HISTORY OF HYBRIDIZATION IN *CAFER* AND *CHRYSOIDES*

### CONDITIONS IN THE SOUTHWEST SINCE THE PLIOCENE

The climate in the southwest during the Lower Pliocene was fairly cool and moist (Axelrod, 1950). Xeric conditions leading to the formation of the southwestern deserts originated in the mid-Pliocene. The increasingly arid conditions were caused by the uplift of the Sierra Nevada and the peninsular mountains. By the end of the Pliocene, more mesic plants had been forced out of arid areas. During the Pliocene, woodlands extended from northern Baja California to the Cape region (C. H. Beal, 1949; Axelrod, 1958).

Pluvial cycles, generally correlated with periods of glaciation, characterized the southwest during the Pleistocene. Periods of increased rainfall alternated with periods nearly as dry as those of the present time (Flint, 1957). A recent dry period occurred some 4000 to 5000 years ago (Antevs, 1938), at the time of the Climatic Optimum. Interpluvials early in the Pleistocene were probably more moist than conditions are at present, as mountains to the west were not so high, resulting in less arid effects on the areas to the east. Volcanic activity, crustal up- and down-warping, and changes in sea level and lake level characterized Baja Cali-

fornia during the Pleistocene (C. H. Beal, 1949; Arnold, 1957). The eastern side of the peninsula became increasingly arid as the peninsular mountains were uplifted continually during this period. The western side was probably more moist during pluvial periods than it is at present. It seems likely that the Cape region was separated from the rest of the peninsula by a sea barrier during several of the pluvial periods (C. H. Beal, 1949). The shallow northern part of the Gulf of California was probably above sea level during glacial maxima, allowing a possible "connection with the mainland (Sonora) across the gulf" (C. H. Beal, 1949, p. 118).

Dillon (1956), Flint (1957), Axelrod (1950), and Antevs (1954) have discussed the lowering of the life zones in the west during pluvial periods. It is evident that woodlands covered much more of the southwest during glacial maxima than they do at present. According to Antevs (*loc. cit.*), transition-zone forests ranged down into much of the present Upper Sonoran Zone. Vegetation in the Sonoran Desert was much more dense during pluvial periods than it is at present. Norris (1958, p. 314) stated that during glacial maxima in the Sonoran Desert "vegetation was probably a great deal denser and composed of plants that now occupy the



desert region and components of the peripheral floras." The arrival of the white man in the southwest has apparently had little effect on the vegetation of most of the region, except in Arizona, where urbanization and marked lowering of the water table have drastically affected some areas. Some tree planting has occurred in certain places, and the control of fires may be permitting the extension of arboreal vegetation into areas formerly grassland (Brown, 1950).

#### ORIGIN AND HISTORY OF THE GILDED FLICKER

A fossil gilded flicker has been reported (L. Miller, 1943) from Nuevo Leon, Mexico, far east of where *chrysoïdes* presently occurs. This record is discounted, as I fail to detect the characters of the humerus that supposedly distinguish *chrysoïdes* from *cafer* (L. Miller, 1943, p. 165). I concur with Wetmore (1962, p. 11) that no trenchant osteological characters separate our three "species" of the American Ornithologists' Union "Check-list" (1957), and I expect that one would encounter great difficulty in distinguishing *chrysoïdes* from ancestors of the race *nanus* of the *cafer* group, which is similar in size and which presently inhabits Nuevo Leon.

The origin of the gilded flicker occurred some time after the mid-Pliocene increase in aridity brought into existence the desert conditions to which it is adapted. A hypothetical history of the gilded flicker follows.

The gilded flicker originated as an offshoot of an early *cafer* population. This population was able to extend its range to the Cape region of Baja California along a woodland connection, probably without the necessity of crossing desert areas. Such an extension occurred in the early Pleistocene and perhaps even during the Wisconsin glaciation (Savage, 1960). Increasing aridity and rising sea level during one of the early interglacial periods caused the isolation of a portion of the population in mountains of the Cape region, while the rest of the population withdrew to the north with the retreating woodland. Several cycles of connection and resumption of isolation may have occurred between the mainland population and its isolate. During isolation the Cape population was exposed

to increasingly arid conditions, to which it was able to adapt. Adaptation to more xeric conditions was followed by an ecological shift, enabling the population to move from the mountain woodlands into surrounding areas which supported cacti suitable for nesting purposes. Such a shift probably took place in a manner similar to that described by Mayr (1954). Once it was able to exist under arid conditions, the population extended its range into the Cape Forest and surrounding deserts. This range extension probably took place before the last period of glaciation. Regardless of when the extension occurred, *chrysoïdes* was probably not able to reach the Sonoran Desert of Arizona and Sonora before the last glacial period. During the glacial maximum, conditions were favorable for an extension of the range of *chrysoïdes* to the north and east. Entering Sonora and Arizona either along the northeastern portion of Baja California or across the land area exposed at the north end of the Gulf of California, *chrysoïdes* spread to the foothills of the Arizona mountains and to the Sierra Madre Occidental of Sonora. Crossing the Sonoran Desert to the south, this form eventually reached the Thorn Forest of southern Sonora and Sinaloa. The Thorn Forest, similar to the Cape Forest of Baja California already occupied by this form, provided suitable habitat and was unoccupied by flickers. Gilded flickers adapted sufficiently to penetrate the Thorn Forest and may still be moving southward in this region.

Contact was established with *cafer* in the isolated mountains of Arizona and probably in the foothills of the Sierra San Pedro Martír of northern Baja California and possibly to some extent in Sonora and Sinaloa. Because reproductive isolation had not been attained, despite the differences between the two forms, interbreeding occurred and is still occurring wherever contacts have formed. The *chrysoïdes* population is maintained in the face of interbreeding with the much more abundant *cafer* because of the following two factors: (1) the contact and resultant hybridization are restricted by areas of unfavorable flicker habitat, resulting in localized hybridization rather than the formation of a continuous hybrid zone; and

(2) the coadapted gene pool of *chrysoïdes*, which has successfully adapted to arid conditions, may suffer disruption from introgression, with the result that selection may act against the entrance of *cafer* genes into the *chrysoïdes* populations. Limited hybridization probably enables the filtering out of genes and gene combinations of *cafer* through selection in gilded-flicker populations. Favorable *cafer* genes may thus be assimilated into the *chrysoïdes* gene pool, while unfavorable ones may be weeded out. Great increase in extent of contacts between the two forms might lead to the swamping of the gene pool of *chrysoïdes* by that of *cafer*.

Various portions of this suggested origin of the gilded flicker can be supported by evidence. Former contacts in Arizona between *cafer* and *chrysoïdes*, if they occurred, would have been more extensive than those at present. The moderate introgression presently occurring suggests that contact and hybridization between the two forms have not existed for a long period, as is the case in the *auratus-cafer* situation.

The apparent southward extension of *chrysoïdes* into the Thorn Forest of Sinaloa suggests that this form is a recent entrant into the area from the north. Since the forest has been in existence for some time (Axelrod, 1948, 1950), and conditions there seem favorable for flickers, there is no apparent reason why *chrysoïdes* has not entered the area previously (see Sinaloan discussion above).

Schmidt (1922) first called attention to Baja California as an area where relict populations occur. He later (1943) compared Baja California and Florida in regard to the accumulation of relict populations. Populations isolated in Baja California were able to diverge to a greater or lesser extent, some even attaining reproductive isolation during isolation (*Toxostoma cinereum*). A review of the avian endemics of the Cape region of Baja California provides evidence for the origin of the the gilded flicker in this area.

Davis (1959) has recently reviewed endemic avian forms in the Cape highlands of Baja California (see also Stager, 1960). Davis considered 17 endemic highland forms in the Cape region. Prior to publication of his paper (*loc. cit.*) I had categorized these, including two species that he did not con-

sider (*Empidonax difficilis* and *Parus inornatus*). Actual forms endemic to the highlands of the Cape region include *Turdus "confinis"* and *Junco "bairdi,"* which may have differentiated to the species level, and endemic races of the following species: *Columba fasciata*, *Glaucidium gnoma*, *Melanerpes formicivorus*, *Empidonax difficilis*, *Contopus sordidulus*, *Parus inornatus*, *Sitta carolinensis*, *Vireo huttoni*, *V. solitarius*, *V. gilvus*, *Pipilo erythrophthalmus*, and *Aimophila ruficeps*.

Populations of other species presently occurring in the highlands and the surrounding country as Cape region endemics may well have entered the highlands from lower areas to the north, at a time when the region was less arid than it is at present. These include races of the following species, all of which are tolerant of somewhat xeric conditions: *Otus asio*, *Aphelocoma coerulescens*, *Psaltiriparus minimus*, and *Pipilo fuscus* (see Davis, 1959, for the occurrence of all but one of these in arid portions of Baja California).

The absence of red-shafted flickers from the list of highland endemics in the Cape region is notable. Other forms that have similar distributions in highlands of other regions of the west, such as *Junco* sp. and *Pipilo erythrophthalmus*, have populations endemic to the Cape highlands and in such places as Guadalupe Island (where a *cafer* population, *rufipileus*, formerly existed). The presence of well-differentiated forms of *Turdus* and *Junco* in the Cape highlands suggests that a *cafer* population could have been isolated there and then diverged to the extent that *chrysoïdes* has. *Hylocharis xantusii* is of interest in regard to the origin of *chrysoïdes*. The form from which *Hylocharis xantusii* is derived almost certainly was ancestral to both *xantusii* and *H. leucotis*. The latter is exclusively a mountain woodland form, while *xantusii* occurs in the deserts of southern Baja California, as well as in the mountains of the Cape region (Grinnell, 1928). This fact suggests that *xantusii* originated as a highland isolate of pre-*leucotis* stock in the mountains of the Cape region, and later became adapted to arid conditions, which permitted it to extend its range out into the deserts. This origin is similar to that described above for *chrysoïdes*. Both forms

(*Hylocharis xantusii* and *Colaptes auratus chrysoides*) presently occur, at least to a limited extent, in the Cape highlands (see Davis, 1959, and Brewster, 1902).

Davis (1959, pp. 75, 83) pointed out that some of the Cape-highland endemics appear to be "non-differentiates," i.e., they have not changed to the degree that other North American populations of the same species have from the condition of the ancestral population, which seems probable in *Junco "bairdi," Hylocharis xantusii*, and certain of the other well-differentiated endemics especially. The gilded flicker also falls into this category, resembling in a number of characters (especially the shape of the breast patch, amount of black on the tail, and crown color) the probable ancestral North American flicker. The *chrysoides* group in these characters is most similar to the Central American *mexicanoïdes* group, which resembles the probable ancestral form even more in other respects, providing further support for the origin of the gilded flicker as a Cape-highland, endemic *cafer* population.

Other forms may have originated in Baja California and later moved northward. The occurrence of species pairs such as *Lophortyx californica* and *L. gambelii*, *Pipilo fuscus* and *P. aberti*, and *Toxostoma cinereum* and *T. bendirei* suggests separation of the original populations of these forms into Baja California and Mexican isolates, followed by divergence and later extension northward of the populations. *Calypte costae* and *Poliophtila melanura* are other forms that probably originated in isolation in Baja California. At any rate a Baja Californian origin of the gilded flicker appears not to have been a unique event.

Bogert and Oliver (1945) provided an excellent discussion of the herpetofauna of Sonora, offering corroborative evidence for a Baja Californian origin of the gilded flicker. These authors conclude (p. 333) that the

origin of the fauna of Sonora involved: "(1) Pleistocene climatic changes; (2) southward withdrawals of populations on the peninsula of Baja California and on the mainland as a result of the most recent glacial period; (3) partial or complete differentiation during isolation; and (4) subsequent migrations or secondary dispersals by way of five main dispersal routes." Among the dispersal routes to which they referred is entry into Sonora by way of the Colorado Desert of northwestern Sonora and northeastern Baja California. Regarding forms entering Sonora from the Colorado Desert, Bogert and Oliver stated (p. 331): "Many elements now in this desert are believed to have survived the Pleistocene cold in Baja California." The gilded flickers probably entered Arizona and Sonora from this area.

A number of lizards and several snakes have distributions similar to the distribution of the gilded flicker. Among them are *Dipsosaurus dorsalis*, *Coleonyx variegatus*, *Calisaurus draconoides*, *Sauromalus* sp., *Lichanura* sp., *Chilomeniscus cinctus*, and *Phyllorhynchus decurtatus*. Some of these reach Sinaloa; others do not. According to Bogert and Oliver (1945, p. 330), the first four forms represent "stocks that survived the last glacial period isolated in Baja California." The present ranges of these forms in Sonora are attributed to postglacial dispersals. *Lichanura*, with one form in Baja California, one in the Mohave-Colorado Desert region, and one in Sonora, probably also originated in Baja California. Bogert and Oliver listed (p. 324) a postglacial entrance for the Sonoran form.

This type of evidence suggests that the origin of the gilded flicker, as proposed above, is generally correct. Conclusive evidence is not likely to be found by zoogeographical studies. Fossil evidence might demonstrate the former occurrence of *cafer*-like flickers in the mountains of the Cape region.

#### THE EVOLUTIONARY IMPORTANCE OF INTROGRESSION

Mayr (1957b, p. 371) wrote: "When an ornithologist speaks of 'species' he has a phenomenon in mind in which hybridization. . . [is] . . . of no consequence." This extreme view is unwarranted at this time.

New situations of hybridization are being discovered and studied yearly, and it appears likely that hybridization and introgression have played a role in the evolution of some species of birds. The constantly increasing

number of studies of this nature should soon permit a thorough evaluation of the relative importance of hybridization in avian evolution.

The effects of introgressive hybridization on populations have been discussed by Anderson (1949, 1953) and Stebbins (1959), using mostly botanical evidence. Similar effects in animal populations were suggested by Stebbins (*loc. cit.*). A number of comments can be offered concerning such effects in situations of allopatric hybridization (see Anderson, 1953, p. 294).

The role of introgressive hybridization in relation to man's activities has been adequately emphasized by Anderson (1953) and Stebbins (1950). Anderson also pointed out that conditions in the past may have favored introgression. In particular he noted (1953, p. 297) that in the past introgression was apparently favored in the southwest. Axelrod (1957, pp. 42-43) discussed the role of hybridization and introgression in the west during glacial and pluvial times. He stressed the part played by hybridization in "establishing new variants" which could have produced "scores of adaptive types."

Fluctuating environmental conditions of the Pleistocene probably resulted in many situations of hybridization and introgression. Retention of the ability to interbreed during periods of drastic environmental changes is probably more advantageous than full speciation for geographically isolated populations. In the Pleistocene such isolates of a formerly united population possessed less genetic variability than when they were originally connected. These isolates were therefore more likely to become extinct during rapid environmental shifts. The ones that survived extinction underwent divergence. Some of these probably evolved isolating mechanisms during their divergence. Secondary contacts between reproductively isolated populations resulted in reinforcement of the isolating mechanisms and competition between the newly formed species (Sibley, 1957). The effects of selection from reinforcement and competition placed additional stress on the formerly isolated populations, which were already being subjected to considerable environmental changes. Other isolated populations

failed to achieve reproductive isolation during their divergence. Some of these populations probably became extinct, while others survived until secondary contacts were established with the populations from which they were originally separated. Hybridization and introgression resulting from the formation of such contacts preserved the genetic variability of both forms for utilization in the future evolution of the combined population. In addition, the genetic variability of the populations acquired in isolation was made available to the combined gene pool of the reunited population. Recombination from hybridization and introgression made available new gene combinations for selection to act upon. The importance of recombination effects of hybridization and introgression has been indicated by Anderson and Stebbins (1954) and Stebbins (1959). Those populations that failed to develop isolating mechanisms while geographically isolated probably became extinct less frequently than those that achieved full reproductive isolation.

Probably the genetic contact between the *auratus* group and the *cafer* group benefited both forms and enhanced their chances for survival in the Pleistocene. Hybridization between *cafer* and *chrysoides* has probably also been of mutual benefit to these forms. Populations of *chrysoides* are adapted to arid conditions; gene flow between this form and *cafer* may result in the ability of the latter to extend its range into more arid regions, as perhaps in parts of Mexico. Probably also introgressive hybridization has continued to be a major factor in the evolution of the forms in which it occurs. Such forms were "preadapted" by virtue of introgressive hybridization to the extensive environmental changes caused by man in the past several thousand years. It seems more than coincidental that species undergoing introgressive hybridization, such as *Junco* sp. *Quiscalus quiscula*, *Colaptes auratus*, *Pipilo erythrophthalmus*, and *Icterus galbula*, are among the most successful of North American species in terms of their widespread distribution and abundance.

Continuous or recurrent hybridization and introgression probably result in a genetic response of the gene pools to a repeated infusion of alien genes. Genes and gene com-

binations best able to function under conditions of this sort will be favored in such populations; such genes are called "good mixers" by Mayr (1954). Through selection for genes that do well in a variety of genetic backgrounds under conditions of introgression, the populations involved might be said to become genetically adapted to such a condition. Retention of such genes to some extent in populations that again were isolated, may have acted to retard the development of isolating mechanisms, facilitating interbreeding between the forms when contact was resumed. Genetic adaptation to introgression during past times may be a factor in maintaining genetic links between two forms, even if partial isolating mechanisms are present when contact is again resumed. Since there have been four major glacial periods, plus frequent minor fluctuations of environmental conditions, it seems likely that such genetic adaptation would occur.

Topographical conditions and ecological factors are important in the effects of introgressive hybridization. The presence of the Black Hills east of the Rocky Mountains allowed an apparently isolated *cafer* population to exist during the last glaciation in an area far to the east of other such populations. The result is that the present situation of introgression reflects the eastern extension of *cafer* influence in the area. Environmental conditions in the area of contact between two forms may directly determine the effects of hybridization on the populations. If favorable conditions exist for the formation of a large, continuous area of contact, swamping may occur should the populations lack reproductive isolating mechanisms. A situation approaching swamping is occurring in the *cafer* group of *Colaptes auratus*, exposed to the larger *auratus* gene pool in British Columbia. The presence of partial reproductive isolating mechanisms in populations allowed to form an extensive contact usually

results in the reinforcement of isolating mechanisms to prevent the destruction of the genetic systems of the species through the effects of swamping. A small contact, such as that occurring between *cafer* and *chrysoides*, may result in lessened introgression whether or not isolating mechanisms are present. In the case of partially reproductively isolated populations forming a small contact, reinforcement may or may not occur. If some recombination products resulting from hybridization are valuable to the populations involved, continuous gene exchange may be maintained despite the action of partial isolating mechanisms (see Dobzhansky, 1950, p. 416). The action of topographical and ecological factors in limiting gene flow between interbreeding populations that lack isolating mechanisms may permit "filtration" of genes across the barrier under control of natural selection, thus acting in much the same manner as when reproductive isolating factors permit selection to operate in situations that involve large-scale contact. Thus, a contact between freely interbreeding populations that is small enough to preclude widespread swamping may bestow upon the interbreeding populations some advantages usually accruing from evolution of isolating mechanisms. Other factors such as the genetic adaptation of the populations to introgression and the size of the populations may be important in determining the effects of introgression that result from the formation of secondary contacts.

Evidently introgressive hybridization has been a factor of importance in the evolution of flickers and other animal species, as well as in the evolution of plants. Recombination and increased variability through introgression probably enhanced the ability of some forms to cope with changing conditions in the Pleistocene. A fuller assessment of the role of introgressive hybridization in animal evolution is not possible at present.

#### INTROGRESSIVE HYBRIDIZATION AND THE SPECIES PROBLEM

The essential property of a species is its reproductive isolation from other populations (Mayr, 1963). However, a rigid adherence to the use of this property as the most

important criterion in the determination of species status inevitably results in the "lumping" of all forms that are interfertile to any degree. Such species have been designated as

"cenospecies" (Ripley, 1945). Situations of allopatric hybridization are among the borderline cases in which it is difficult to draw a line between the status of species and that of subspecies for the forms involved.

A major objection to past attempts at determining the status of forms involved in hybridization is the overemphasis on morphological differences between them. The taxonomist who deals with allopatric hybridization, in which the forms may show considerable morphological divergence, is, in Mayr's (1957a, p. 376) words, "reluctant to unite them into a single species" when the differences appear to be great. However, as Mayr pointed out (1948, p. 210), "Most of the morphological characters studied by the taxonomist are neutral in regard to the maintenance of isolating mechanisms." Clearly, morphological differences are in themselves of no value in the determining of the status of hybridizing forms; only when they are demonstrated to relate to the maintenance of reproductive isolation are they important.

The critical fact determining the status of hybridizing forms is whether or not isolating mechanisms are in operation. The presence of some kinds of isolating mechanisms may be easily detected, especially if no F<sub>2</sub> or backcross individuals are found. Care should be exercised to ascertain the presence of F<sub>2</sub> and backcross hybrids when one is studying hybrid situations. Variation of F<sub>1</sub> individuals may be considerable (see Hinde, 1956); such variation may be mistaken for that commonly found when backcrossing is occurring. The greatest difficulty occurs when backcrossing is observed and interbreeding is apparently taking place freely.

If hybrid individuals are for any reason (hybrid inviability, hybrid breakdown, and so on) less adapted than individuals of the parental forms, selection may operate to reduce the frequency of hybridization. The action of selection against the hybrids produced indicates that isolating mechanisms are in operation. Sibley (1957, 1961) stressed the importance of determining the presence or absence of selection against hybrids. He suggested that selection operating on the hybrids determines whether the forms involved will merge owing to the effects of swamping,

or continue to diverge through the reinforcement of isolating mechanisms until complete isolation is attained. It is often impossible, however, to determine whether selection is acting against the hybrids when interbreeding is occurring rather freely. The studies of the Mexican towhees by Sibley (1950, 1954) indicated that the nature of the selective forces that act on hybrids may differ in various areas of contact between forms.

There seems to be no assurance that lack of selection against hybrids, as apparently occurs between the flicker groups *auratus* and *cafer*, will necessarily result in the merging of the parental populations and the swamping out of their differences. Rather, there is evidence that some populations are able to maintain their identities despite considerable introgression (Dice, 1940; Blair, 1947; Baker, 1953; Knight *et al.*, 1956).

There is likewise no evidence that selection against hybrids must always result in reinforcement of isolating mechanisms. The work of Stebbins and Daly (1961) suggests that isolating mechanisms may even break down as hybridization between two forms continues over a period of time. Whether or not reinforcement will occur appears to depend on three factors: (1) the nature of the contact between the hybridizing populations; (2) the advantages accruing to hybridizing populations by virtue of their genetic contact; and (3) the extent and seriousness of the disruption in the gene pools of the interbreeding populations caused by gene exchange between them. Gene wastage occurring through hybridization when selection operates against the hybrids may be insignificant compared with the advantages offered to populations able to partake of each other's genetic variability.

Another attempt to deal with the taxonomic status of interbreeding populations stresses the importance of gene exchange. This is contained in a paper by Mainland (1942), who presented the following modified species definition for situations involving hybridization: "A species is an actually or potentially interbreeding array of forms whose net mutation rate is greater than the actual or potential gene exchange with other arrays of forms." Difficulties arise in applying

these ideas to actual situations. The ascertaining of mutation rates of hybridizing forms is impossible to accomplish in natural situations. The determination of introgression may be difficult, especially when few characters are available, as in the crows *Corvus cornix* and *C. corone* (Meise, 1928). Little work has been done on the disruptive effects of gene flow in natural populations. Despite these difficulties, it is evident that the genetic contact between hybridizing forms must be taken into account in any consideration of the taxonomic status of the forms.

It should be recognized that the ability to exchange genes is not the important consideration in regard to the status of the forms. It is rather the exercising of control over the amount of gene exchange by natural selection that is of importance. Once selection is able to regulate gene flow, the possibility exists for the eventual elimination of the genetic contact between hybridizing populations. Control of interbreeding by selection depends on the presence of isolating mechanisms. Clearly any attempt to determine the status of such forms should depend on evidence regarding the presence or absence of isolating mechanisms.

The taxonomist confronted with a situation of hybridization in a secondary contact is thus in a dilemma. Basically he must determine whether isolating mechanisms are present in the interbreeding populations. Isolating mechanisms vary in effectiveness; reproductive isolation may be complete, lacking, or partially effective. Furthermore, other variable factors may operate to reduce, enhance, or obscure the effects of isolating mechanisms, or even to simulate the effects of such mechanisms when they are absent.

As Dobzhansky has indicated (1950, p. 416), "not only the presence but also the degree of reproductive isolation between species will be determined by the exigencies of adaptive evolution." Thus, gene exchange between partially reproductively isolated populations may have a disruptive effect upon the populations' gene pools, resulting in reinforcement. On the other hand, if the disruption caused is minor (as when the area of contact is small) and there is a premium on increased variability resulting from gene exchange, selection may cease perfecting or

even reverse reproductive isolating mechanisms. Given a large contact and the absence of effective isolating mechanisms, swamping will result. If effective isolating mechanisms are present, reinforcement should occur. If weak isolating mechanisms are present, the sudden opening of a large contact, with widespread interbreeding, may reverse the isolating mechanisms, since extreme swamping will place a premium on genes able to mix with alien genes (Mayr, 1954). Reversal is more apt to occur if the populations have previously been exposed to introgression, as the gene pools are probably "adapted" somewhat to this situation. We have seen that with small contacts a great variety of possibilities exist. With this array of possibilities the situation at best is difficult, though not impossible.

In dealing with hybrid situations, the taxonomist must concentrate on available information in attempting to ascertain whether isolating mechanisms are present. The available information should include (1) the nature of the contact—its size and the actual amount of contact between individuals of the two forms; (2) information as to the presence of F<sub>2</sub> or backcross individuals; and (3) the distance from the contact in which introgression is detected. When the contact is large, reinforcement of isolating mechanisms should be detectable in the contact area if such mechanisms are present and effective. When the contact is large and reinforcement is not detectable, analysis of the nature of the hybrid zone should give a clue as to what is occurring. Two occurrences are most common. In one, there is a hybrid zone that contains individuals of both parental types as well as hybrids; no introgression can be detected beyond the limits of the hybrid zone. In the other, introgression can usually be detected, and the hybrid zone contains only hybrid individuals. In the first case it seems probable that some isolating mechanisms are operating, although they are not fully effective. The populations involved may be considered species. In the second case swamping may ultimately occur. The populations may be considered conspecific, as isolating mechanisms are either absent or so ineffective as probably to result in their eventual elimination.

Small contacts provide a greater difficulty.

The chief reason is that the effects of interbreeding over a small area rarely cause disruption of a large gene pool. If isolating mechanisms are absent, introgression may be detected. Considerable introgression should be viewed as evidence for conspecificity of interbreeding populations. However, if the contact is very small, introgression may not be detected even when isolating mechanisms are absent. If strong isolating mechanisms are present, slight reinforcement may occur, or there may be evidence of hybrid inviability, hybrid breakdown, or other isolating mechanisms. Weak or partial isolating mechanisms may be impossible to detect in small contacts. In such cases I suggest that the situation be resolved on the basis of the width of the hybrid zone and the composition of the hybrid population. Lack of individuals of the parental types in a hybrid zone of this nature provides sufficient indication of gene exchange between the populations to enable them to be considered conspecific. The presence of a large proportion of individuals of the parental types in the hybrid population may be construed as sufficient grounds for one's considering the populations as separate species, unless the contact is very small.

The last situation to be considered is "hybrid swarms," hybrid populations more or less cut off from genetic contact with parental populations. Local selective pressures are of fundamental importance in such cases. Ordinary hybrid swarms tell the taxonomist little, other than that viable hybrids can be produced. One cannot be sure of the circumstances under which the swarm originated, but can only sample and describe the swarm and its variability. If the hybrid swarm originated from a limited number of individuals of the two forms invading the area, isolating mechanisms may have broken down because of a limited choice of mates, much as experimental hybridization can induce interbreed-

ing of species not known to hybridize in the wild. Should the swarm originate in the above manner, and its variability be great, the taxonomist then has little information with which to determine the status of the two forms. It is thereby demonstrated only that they show potential for interbreeding under certain circumstances. When analysis of a hybrid swarm shows reduced variability in one or more characters by which the two parental forms differ, some basis is provided for a taxonomic decision. In such cases, the interbreeding populations have demonstrated considerable genetic compatibility, so that selection may fashion from the hybrid products a less variable, integrated gene pool, adapted to the local environment. When two forms exhibit genetic compatibility capable of permitting initial hybridization, backcrossing, and stabilization of a hybrid swarm, they may be considered conspecific.

In all other instances in which the evidence offers no conclusive indication as to what the status of interbreeding populations may be, I suggest that the populations be considered conspecific until proved otherwise. Hybridization between two populations in secondary contact, in a situation in which no conclusive evidence is available by which to determine the status of the forms, is bound to involve some interaction between the gene systems of the populations involved. While hybridization occurs, the gene combinations of both populations are available to each population, even in areas away from the zone of contact and interbreeding. As long as gene exchange occurs, the evolution of the populations will be directly affected by the interbreeding. The policy of recognizing hybridizing populations as conspecific pending the determination of the presence or absence of isolating mechanisms is as valid as, or more so than, the assigning of specific status to such forms; the latter implies that the populations have achieved reproductive isolation.

#### TAXONOMIC STATUS OF THE FLICKERS

The various North American flickers, excluding *Colaptes fernandinae* of Cuba and including the Central American *mexicanoides* group, should be recognized as comprising one species, *Colaptes auratus*.

The five subspecies groups that comprise

the species *C. auratus* are allopatric. Those groups (*chrysocaulosus* and *mexicanoides*) that are completely allopatric do not differ from the other groups in a manner suggesting the attainment of reproductive isolating mechanisms. The *chrysocaulosus* and *mexicanoides*



groups have in the past been considered within "*Colaptes auratus*" and "*C. cafer*," respectively, and studies to be reported upon elsewhere indicate that their patterns of variation ally them with these forms. Mayr, Linsley, and Usinger (1953) recommended that doubtful allopatric populations be treated as subspecies, and this suggestion is followed.

Wherever the groups have come into contact, interbreeding has resulted. Hybridization between *auratus* and *cafer* has produced considerable introgression. Gene flow between these two forms is sufficient to make available to each population the mutations and gene combinations of the other. Hybridization between *cafer* and *chrysoïdes*, although not so widespread as that occurring between *auratus* and *cafer*, has nevertheless resulted

in considerable introgression. There is evidence that genes originating in the *auratus* population are ultimately able to reach southwestern *chrysoïdes* populations through the intervening *cafer* population. Such introgression is, and has been, of fundamental importance in the evolution of the flickers and argues for the merging of *cafer* and *chrysoïdes* with *auratus*. There is little doubt that the present hybridization and introgression will continue. It is likely that evolution will continue to operate on the complex of populations as an evolutionary unit. Eventually, the populations may be isolated again, perhaps to undergo speciation. However, at this time the evolutionary unit comprised of populations of the groups *auratus*, *cafer*, *chrysoïdes*, *mexicanoïdes*, and *chrysocaulosus* should be considered one species.

## SUMMARY

1. INFORMATION IS PRESENTED concerning the relationships, ecology, and behavior of North American flickers, *Colaptes auratus*, including the subspecies groups *auratus*, *cafer*, *chrysoïdes*, *chrysocaulosus*, and *mexicanoides*.

2. The situation of hybridization between the *auratus* and *cafer* groups of *Colaptes auratus* is analyzed, with the use of color and mensural characters. The hybrid zone, including the area in which 95 per cent or more of the flickers are hybrids, is a broad band of variable width extending from British Columbia eastward to Alberta and southward and eastward from there to Texas.

3. Evidence is presented for the occurrence of introgression in populations of *auratus* and *cafer*. Diminishing effects of hybridization are detectable in populations of *auratus* to the Atlantic Ocean, and *cafer* to the Pacific Ocean and Mexico.

4. Color characters used in the study were found to be somewhat correlated in hybrids but not to an extent invalidating their use as separate characters. No evidence for assortative mating was found in a study of the mating patterns of a limited number of hybrid pairs.

5. Localized hybridization occurs between the *cafer* and *chrysoïdes* groups. Considerable introgression has occurred, although the hybrids are found largely in hybrid swarms, more or less geographically isolated from parental populations. Some hybrid swarms have undergone partial stabilization. Evidence is offered that indicates that genes from eastern *auratus* populations, introgressing into the western *cafer* populations, are able to enter the *chrysoïdes* population as a result

of the hybridization between *cafer* and *chrysoïdes*.

6. An attempt is made to trace the history of the hybrid situations in North American flickers. The hypothesis is developed that *chrysoïdes* originated in Baja California as an isolated *cafer* population. Hybridization between *auratus* and *cafer* has apparently occurred over a long period. Hybridization between *cafer* and *chrysoïdes* is thought to be of more recent occurrence.

7. Introgression was probably of major importance for the survival of some animal species in the Pleistocene and is probably a factor in their present success under conditions of constant human modification of the environment.

8. Selection, isolating mechanisms, and reinforcement are discussed in terms of the advantages of gene exchange between populations. Criteria are discussed for determination of the taxonomic status of hybridizing populations, including (a) hybridization along a broad area of contact between populations with strongly developed and those with poorly developed, or nondeveloped, isolating mechanisms; (b) hybridization along narrow contacts, involving populations exhibiting strongly and weakly developed isolating mechanisms; and (c) both ordinary and stabilized hybrid swarms, geographically isolated from their parental populations.

9. The North American flickers are considered to be conspecific. Five subspecies groups of the species *Colaptes auratus* are recognized. These are *auratus*, *cafer*, *chrysoïdes*, *mexicanoides*, and *chrysocaulosus*.

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