

## INTERSPECIFIC RELATIONS OF WOODPECKERS IN TEXAS

BY ROBERT K. SELANDER AND DONALD R. GILLER

CONCRETE information on ecologic relations of closely related species is infrequently reported, especially in this country. A small number of documented cases of interspecific territorialism in birds is known (see review by K. E. L. Simmons, 1951; also, Pitelka, 1951; Legg and Pitelka, 1956; Dixon, 1950, 1954), but many additional data will be needed before the full significance of this phenomenon, with respect to species' distribution, numbers, and evolution, can be evaluated.

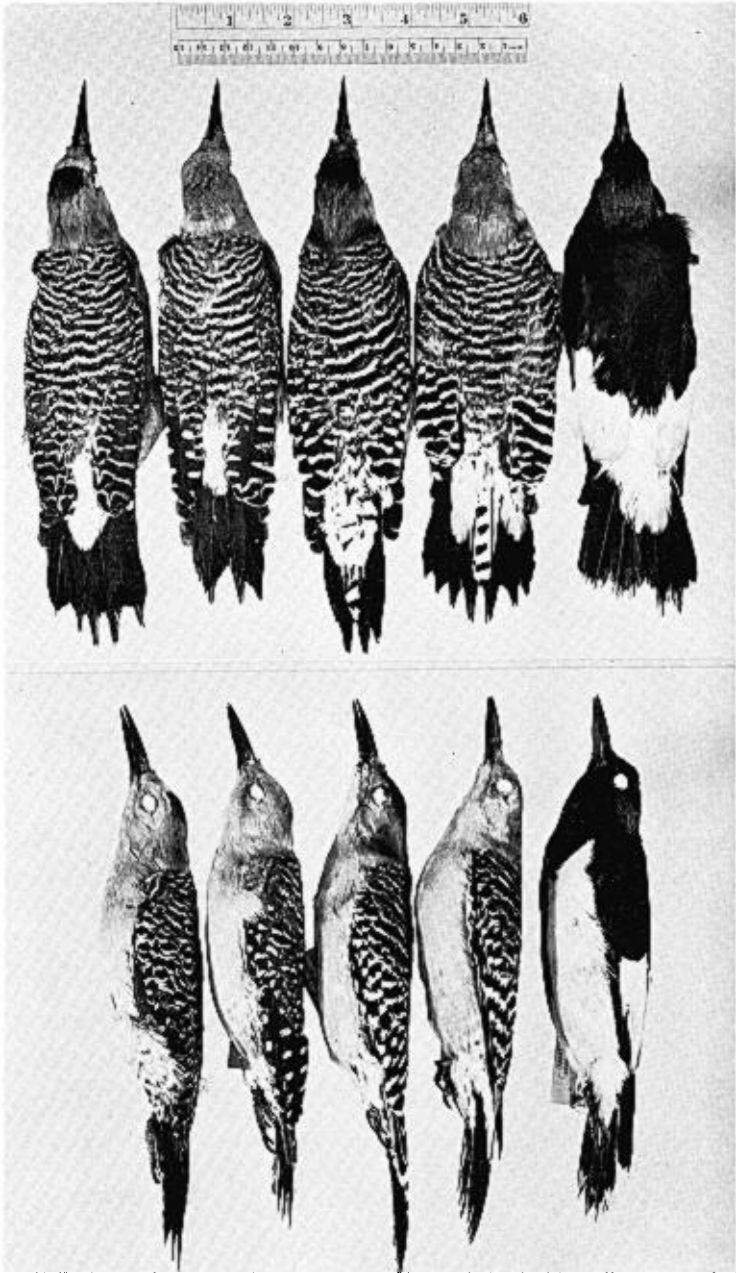
This paper is a preliminary report of studies on territorial and other relations of three woodpeckers in the Austin region, central Texas. The subjects are the Red-bellied Woodpecker (*Centurus carolinus*), Golden-fronted Woodpecker (*Centurus aurifrons*), and Red-headed Woodpecker (*Melanerpes erythrocephalus*). The data herein reported were gathered, more or less irregularly, over a period extending from spring, 1957, to spring, 1958.

### RELATIONS OF *C. carolinus* AND *C. aurifrons*

The following notes on the systematic and ecologic relations of *C. carolinus* and *C. aurifrons* are prompted in part by a recent suggestion (Brodkorb, 1957) that the two may be conspecific. This is not the case, as they are sympatric without interbreeding in central Texas.

*Distribution.*—*Centurus carolinus* ranges west to central Texas and is replaced in the west and in the Panhandle by *C. aurifrons*. Apparently nowhere is there extensive overlap in ranges, but at least locally in south-central Texas they are sympatric. At Austin, Travis County, overlap is limited to a zone not more than 20 miles in width, and the two species may regularly be seen together only within the limits of the city itself. We have little to add at this time to G. F. Simmons' detailed account (1925) of the local distribution of these woodpeckers in the Austin region, which includes all of Travis County and parts of adjacent counties. The reader is also referred to G. F. Simmons' book for accounts of physiography, climate, and vegetation of the region. Climatically, Austin is intermediate between semi-arid regions to the south and west and mesic regions to the east. There is a marked east-west faunal and floral "break" in the Austin region, discussed by Blair (1950). Contact and hybridization between the eastern Tufted Titmouse (*Parus bicolor bicolor*) and a black-crested race (*P. b. atricristatus*) occur in the same region in which ranges of the *Centurus* woodpeckers overlap (Dixon, 1955).

*C. carolinus* is common throughout Austin and in the region to the east, especially in forest and woodland on the floodplain of the Colorado River; but, rarely has it been recorded even a few miles west of the city. In Austin, *C. aurifrons* is comparatively uncommon and localized in distribution, but pairs



Specimens of woodpeckers from central Texas in dorsal (above) and lateral (below) view. From left to right, male and female *Centurus aurifrons*, male and female *C. carolinus*, and female *Melanerpes erythrocephalus*.

may regularly be found in several places in the southern and western parts of town, as at Barton Springs; and it occurs in small numbers in central and eastern Austin, as in the City Cemetery a few blocks east of the campus of the University of Texas. West and, especially, south of Austin it is moderately common. At San Antonio, 80 miles south-southwest of Austin, it is common, and there are no records of *carolinus* (Attwater, 1892:235).

Both species are permanent residents in the Austin region. There is probably an influx of *C. carolinus* from the north in the winter, at which time it is more common than in the summer in timber on the floodplain of the Colorado River. However, the local distribution of both species is, by and large, similar in all seasons.

Neither species appears to be in the process of extending its range in Texas. Even the local distribution and relative abundance of these species in the Austin region apparently have not changed to any great extent within the last 33 years. Many of the specific localities for *carolinus* and *aurifrons* mentioned by G. F. Simmons in 1925 are those in which the species are found at the present time. As the city of Austin continues to expand, a decrease in numbers of *aurifrons* may be expected as tracts of mesquite, juniper, and oak are cleared west and south of town.

*Morphologic Differences between Species.*—In central Texas both species of *Centurus* are closely similar in size (Table 1) and in general appearance (frontispiece). The only conspicuous difference is in the color and pattern of the head. In the male *C. carolinus* the entire dorsal surface of the head is red; in the male *C. aurifrons* the nasal region is yellow, the nape is golden yellow, and a coronal patch of red is surrounded by gray. In the female *carolinus* the nasal region and nape are red, whereas these are yellow in *aurifrons*. In females of both species the coronal region is gray. The abdominal region is washed with red in *carolinus*; the belly may or may not have a suffusion of yellowish in specimens from eastern parts of the state (Burleigh and Lowery, 1944). This region is washed with yellow or golden yellow in *aurifrons*. There are also some minor differences in pattern of the upper tail coverts and inner webs of the central rectrices (see frontispiece).

Both species vary geographically in Texas. A series of *C. aurifrons* from the Texas Panhandle and Harmon County, Oklahoma, at the northern limit of the species' range, is considerably larger in all dimensions than birds from central and southern Texas. Specimens from Oklahoma have been referred to *C. a. incanescens* (A. O. U. Check-list, 1957:317), a race named from Brewster County, western Texas, and distinguished from *C. a. aurifrons* of southern Texas and México on the basis of minor color and pattern differences. However, specimens from Brewster County are small like those from central-southern Texas. Variation in size apparently was not considered by Wetmore

(1948) in his review of geographic variation in *Centurus aurifrons*, but it is apparent that there is a north-south cline in size in Texas, which may or may not be concordant with clines of variation in color and pattern.

TABLE I  
MEASUREMENTS (IN MM.) OF WOODPECKERS FROM TEXAS

	No.	Wing	ADULT MALES		Bill	Tarsus
			Tail			
<i>C. aurifrons</i> <sup>1</sup>	8	137.0 (132-140)	82.0 (76-85)	27.06 (24.9-28.8)	24.70 (24.0-26.0)	
<i>C. aurifrons</i> <sup>2</sup>	8	129.7 (128-132)	77.1 (76-79)	25.80 (24.2-27.0)	22.20 (20.2-23.2)	
<i>C. carolinus</i> <sup>3</sup>	6	129.0 (126-132)	76.4 (70-80)	24.35 (23.2-25.3)	21.22 (19.7-21.8)	
<i>M. erythrocephalus</i>	3	140.0 (137-143)	80.0 (78-82)	22.93 (22.1-24.0)	22.10 (21.9-22.3)	
			ADULT FEMALES			
<i>C. aurifrons</i> <sup>1</sup>	1	134	80	27.6	23.2	
<i>C. aurifrons</i> <sup>2</sup>	6	127.8 (125-132)	73.7 (69-77)	23.48 (22.2-25.1)	22.53 (21.7-23.7)	
<i>C. carolinus</i> <sup>3</sup>	4	125.7 (124-128)	73.3 (70-76)	23.30 (22.2-25.3)	19.90 (19.4-20.5)	
<i>M. erythrocephalus</i>	1	141	72	22.5	22.8	

<sup>1</sup> Texas Panhandle and Harmon Co., Oklahoma.

<sup>2</sup> Central-southern Texas from Travis County south.

<sup>3</sup> Central Texas from Travis County east to Anderson County.

Specimens of *C. carolinus* from Austin and Houston southward reportedly are paler than those from northeastern Texas and have been distinguished racially, as *C. a. harpaceus*, by Koelz (1954).

*Habitat Occurrence.*—Throughout its range in Texas, and also extensively in northern México, *C. aurifrons* inhabits xeric vegetation types in which mesquite is often a dominant element. At Uvalde, Uvalde County, and at Pearsall, Frio County, *aurifrons* is a common resident in mesquite woodland. In Palo Duro Canyon, northern Texas, it occurs in riparian cottonwoods and mesquite flats on the floodplain of the Prairie Dog Town Fork of the Red River. Characteristic habitat of this species south and north of Austin is a mixed oak, large mesquite, and juniper formation on gravel ridges extending from the Balcones escarpment for several miles into the black prairie soils east of Austin (see Dixon, 1955, Fig. 9 and p. 169). We have one record of *aurifrons* in this vegetation five miles east of Austin. In this formation *carolinus* is rarely found.

*C. aurifrons* also frequents pecan groves and other open situations on floodplains, and in small numbers it is found in live oaks, elms, and other mesic types in residential districts in Austin, especially where these are adjacent to stands of mesquite, deciduous oak, and juniper.

*C. carolinus*, in contrast, inhabits mesic formations, frequenting “dead trees, preferably in heavily timbered bottom lands or swampy woods; open deciduous or mixed coniferous woodlands with very large trees [including pecan groves]; heavy woods of oak and elm along rivers and creek bottoms; shade trees and dead trees in town” (G. F. Simmons, 1925:133).

The marked difference between the species in habitat occurrence functions in the overlap zone to limit contact and, at the same time, competition between them. It should be emphasized that these ecologic differences are shown elsewhere than in the zone of overlap. There is no conspicuous narrowing of habitat range in the Austin region. The overlap in habitat occurrence is sufficiently extensive, however, to warrant the hypothesis that either species would, in the absence of the other, occur in greater density in the overlap zone. Considering the fact that populations of *aurifrons* have managed to adapt to mesic and humid habitats in México, it is perhaps surprising that the distribution of the Texas population stops abruptly in the Austin region, unless, of course, the presence of *carolinus* prevents further extension of range.

*Behavioral Differences.*—The two woodpeckers are much alike in behavior, as far as we have determined. *C. aurifrons* is warier than *C. carolinus* and therefore less easily approached and observed; it is decidedly more shy in the vicinity of its nest. Foraging habits seem to be identical in the two species. In the Austin region their breeding seasons coincide (G. F. Simmons, 1925).

The vocalizations are described by G. F. Simmons (*op. cit.*). Both species have the same repertoire of calls, but those of *aurifrons* are louder and harsher, and on this account easily recognized. The pulsed "location" call, used primarily to "advertise" territory in the breeding season, and the common warning *cha* note of the two species are compared in Fig. 1; other calls are equally similar. The "location" call of *aurifrons* is less precisely tuned and slightly higher-pitched than that of *carolinus*, and it ends less abruptly.

*Lack of Interbreeding.*—Considering the ecologic and morphologic similarities of *C. carolinus* and *C. aurifrons*, it is indeed surprising that they do not at least occasionally interbreed. However, in the past two years we have carefully noted the composition of dozens of pairs, and, invariably, the members have been of the same species. Moreover, we have seen no individual evidencing mixed ancestry, although, of course, hybridization in these morphologically similar species might be difficult to detect. The possibility that the color and pattern differences are controlled by a unifactorial genetic mechanism has been considered. If this were the case, interbreeding could occur without intergradation of characters in the hybrids; but it seems unlikely that this same mechanism would control voice and behavioral differences as well. Some specimens of *aurifrons* have one or more red or orange feathers in the nape, but this does not necessarily indicate hybridization. The same character occurs in many (perhaps all) yellow-naped populations of *aurifrons* and is no more marked or frequent in specimens from Travis County than in those from western Texas and northern México.

To sum up, we have found no evidence of cross-pairing or hybridization between members of the two populations, but the nature of the reproductive iso-

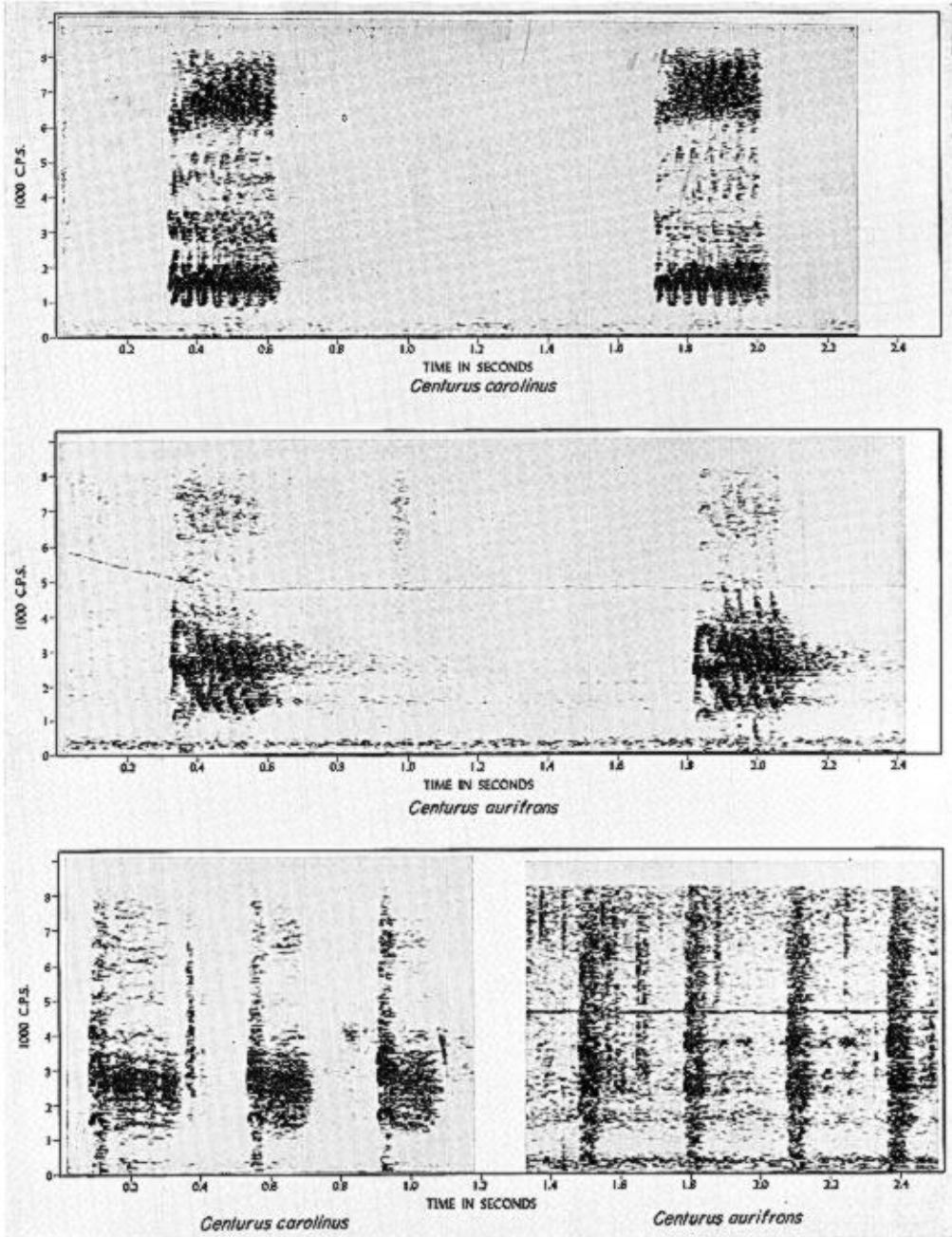


FIG. 1. Sound spectrographs of calls of male *Centurus* woodpeckers from central Texas. Above, "location" calls; below, warning calls. Intensity of markings is proportional to energy involved at the frequency level. (The thin line near 5000 c.p.s. in the graphs of *C. aurifrons* calls results from a signal in the tape recorder itself.)

lating mechanism remains to be determined. Differences in vocalizations seem hardly great enough to function alone as an effective isolating mechanism. At present practically no information concerning sexual behavior in these species, or, for that matter, in any other species of the genus, is available. A thorough study of courtship and mating behavior is indicated, but this might be a difficult undertaking. It appears that in both species many birds remain paired throughout the year. G. F. Simmons (1925:133) notes that *carolinus* "frequently spends the winter about trees where it will nest the following spring. . . ." It is possible that pair bonds are maintained for several years or for life. If so, opportunity to study the critical stage of pair formation will be limited.

It may be noted in passing that these facts bear on the problem of reproductive isolation, since the probability of the occurrence of a "mistake" in pairing, leading to hybridization, depends on the absolute number of pair bonds formed. In species in which pairing occurs each spring, opportunities for "mistakes" are obviously greater than in species in which a bird pairs only once or a few times in its life. Moreover, the formation of lasting pair bonds is usually preceded by long courtship or "engagement" periods, which also tend to reduce the chances for hybridization (Mayr, 1942).

*Territorial Relations.*—Observations by one of us (Selander) on the general spatial relations of the two species and of several interspecific conflicts in 1956 suggested that they held mutually exclusive territories. Subsequent observations confirmed this suspicion, and in the spring of 1957 the territorial relations of two pairs were studied in some detail.

The study area was at the Deep Eddy housing project of the University of Texas in western Austin (Fig. 2). Observations were made almost daily from March 25 to May 11, 1957, and occasionally thereafter through May, 1958. Movements of the woodpeckers were plotted on maps, and the records are summarized in Fig. 3.

The pair of *C. carolinus* nested in a chinaberry tree approximately 75 yards from a deciduous oak tree in which the pair of *C. aurifrons* nested. Both nests were about 15 feet above the ground. The territories of both species extended well beyond the limits of the area shown in Fig. 3.

As observations of movements accumulated, it soon became apparent that a rigid, sharply defined line of division was maintained between territories of the two species. No tree in the study area was frequented at the same time by both species without conflict. Even in the absence of their neighbors, the pairs were reluctant to cross the territorial boundary.

The territorial boundary was well established when our study began, and conflicts were infrequently seen. On March 28, the male *aurifrons* penetrated the *carolinus* territory to point "A" in Fig. 3; immediately he was attacked by the male *carolinus* and driven back to his territory. Again, on April 6, the male *aurifrons* entered the other species' territory.

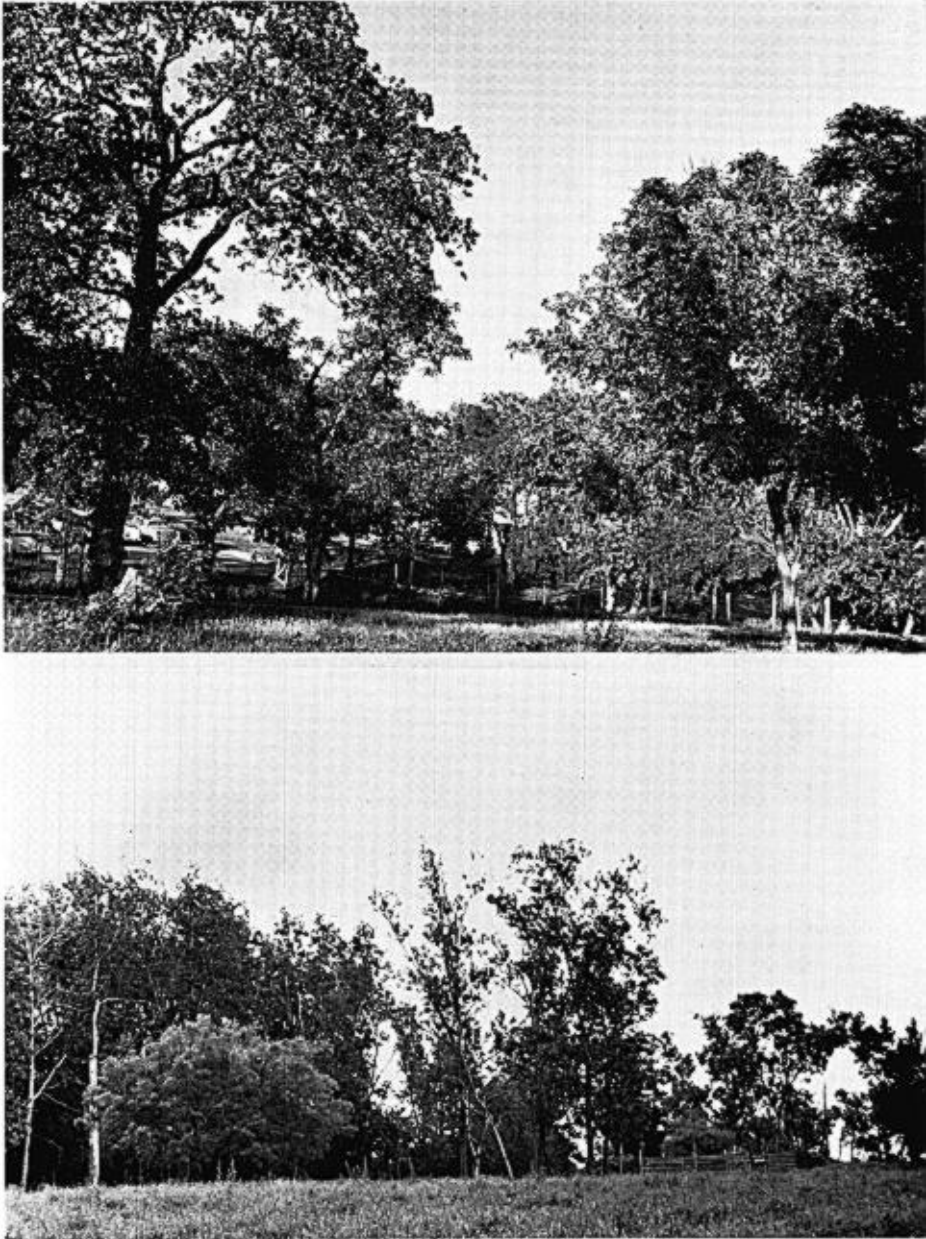


FIG. 2. Above: View of territory of *C. carolinus* at Deep Eddy study area, taken facing north from position "A" in Fig. 3. Below: Study area at Walker Ranch. Nest-tree of *M. erythrocephalus* is just left of large mesquite; that of *C. carolinus* is on the far right.



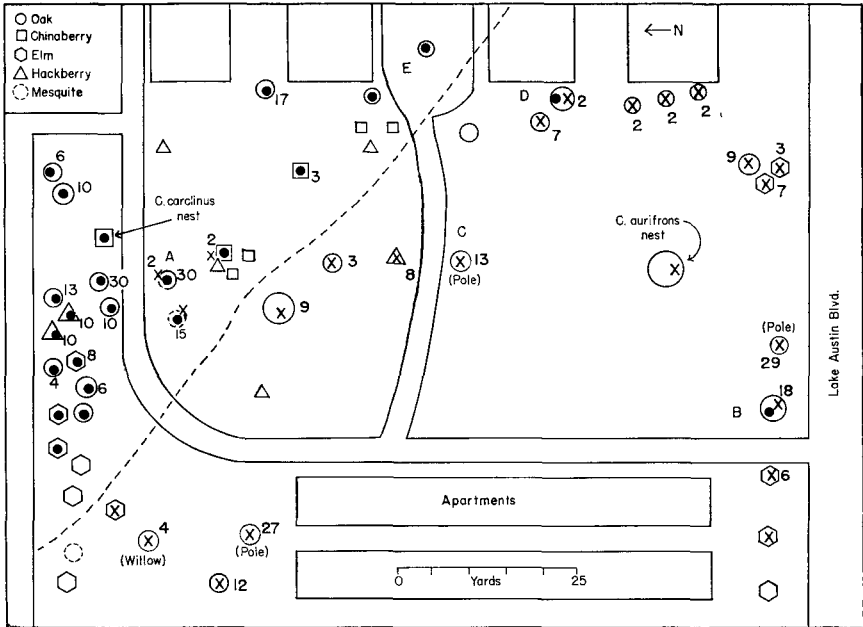


FIG. 3. Study area at Deep Eddy housing project, Austin, showing interspecific territorialism in *Centurus*. X's indicate records of *C. aurifrons*; dots represent records of *C. carolinus*; where there is more than one record for a location, the number is indicated. The territorial boundary is indicated by the dashed line.

The two males fought in three different trees near point "A," and the *aurifrons* finally retreated to his territory, flying to the nest-tree.

On April 25, the female *aurifrons* entered *carolinus* territory. This time the female *carolinus* responded, a fight ensued, and the female *carolinus* chased the female *aurifrons* back across the territorial boundary.

*C. carolinus* less frequently trespassed on *C. aurifrons* territory. On May 11, however, the male *carolinus* flew very near to the ground from his nest-tree to the tree at position "B." It "hid" behind the tree for two minutes, peeked around one side or the other at the nest-tree of *aurifrons*, then flew toward the *aurifrons* nest-tree, where the male and female were perched. Both the male and female *aurifrons* attacked the male *carolinus* as he flew toward the tree. The female soon returned to the nest-tree, but the male continued to attack, driving the male *carolinus* to position "C," at which point he circled back and returned to the nest-tree. The retreating male *carolinus* continued on to his own nest-tree.

On March 29, the male *carolinus* entered *aurifrons* territory, where he fought with another male *carolinus* at position "D," and again within his own territory at position "E." The latter individual held a territory east of the study area. The pair of *aurifrons* was foraging off the study area at the time of this invasion.

Displays and calls used in interspecific territorial defense did not differ in any way from those employed in intraspecific encounters of the same type.

In the spring of 1958, the territory of the pair of *aurifrons* at Deep Eddy was

expanded to include that part of the territory of *carolinus* shown in Fig. 3. On April 19, the two males engaged in a vigorous fight in the *carolinus* nest-tree, following which *carolinus* retreated from the area. Subsequently, the pair of *aurifrons* raised a brood in the same hole used by *carolinus* in the previous year.

#### RELATIONS OF *C. carolinus* AND *M. erythrocephalus*

In April, 1958, an unexpected opportunity to study ecologic relations of *C. carolinus* and a third species of similar size (Table 1), *Melanerpes erythrocephalus*, was provided. This woodpecker, like *C. carolinus*, with which it is sympatric in southeastern Canada and the eastern United States, reaches its southwestern distributional limit in central Texas at Austin. Formerly a fairly common summer resident in the Austin region (G. F. Simmons, 1925:131), it is now rare. There have been no more than a half-dozen records of this species in Travis County in the last 10 years. It is possible that withdrawal of *M. erythrocephalus* from central Texas was related to the long drought that ended in the spring of 1957 (Blair, 1958). Now that environmental conditions are again "normal" in this region, it will be interesting to see if it returns in any numbers.

On April 17, we were directed by Mr. Wyle Hord to the territory of a pair of *erythrocephalus* on the Walker Ranch, along the Colorado River about two miles east of Austin (Fig. 4). According to Mr. Hord, the pair was first seen by him in the spring of 1957. The birds nested successfully in 1957 and wintered there in 1957-58. A fledgling was seen near the nest-hole on August 7 by Mr. Fred S. Webster and Dr. C. H. Brownlee. Webster, who has been one of the most active observers in the central Texas region for the past six years, informs us that this is the only breeding record of this woodpecker in the Austin region that has come to his attention. He suspects, however, that a few additional pairs may be found along the Colorado River between Austin and Bastrop. Occasionally, lone birds have been seen in winter along Onion Creek, a few miles southeast of Austin, and along the Colorado River.

Fortunately, a nesting pair of *carolinus* was located in the same area, permitting study of the territorial relations of the two species (Fig. 4). Observations were made at the Walker Ranch from April 17 to 23 and on May 1.

Activities of the *erythrocephalus* centered about a small, dead cottonwood tree adjacent to a small corral and a mesquite tree in a grassy meadow (Fig. 2). Several holes had been drilled in the cottonwood, including one "active" hole about 15 feet above the ground which the birds occasionally entered and in which at least one roosted at night. They were not incubating at the time of our study, but we saw some courtship behavior and it was obvious that they were preparing to breed; copulation was noted on May 1. On the same day a third individual of *erythrocephalus* appeared and was attacked and driven from the territory by the pair. Apparently this species breeds somewhat later, on the average, than does *C. carolinus* (Bent, 1939).

Movements of the birds were recorded and mapped (Fig. 4) over a period of about eight hours on three different days. The birds often visited the nest-tree and also spent a good deal of time in the adjacent grove of tall cottonwoods, to which they almost invariably retreated as we approached the nest-tree. They also visited cottonwoods and hackberry trees along the river; and on April 18 the pair fed for one-half hour in a large cottonwood

only 25 yards from the nest of *carolinus*. The pair of the latter species nested in a dead limb of a cottonwood which was larger than that used by *erythrocephalus*. The nest-hole was 15 feet above the ground, and the opening faced north. The nests of the two species were 80 yards apart.

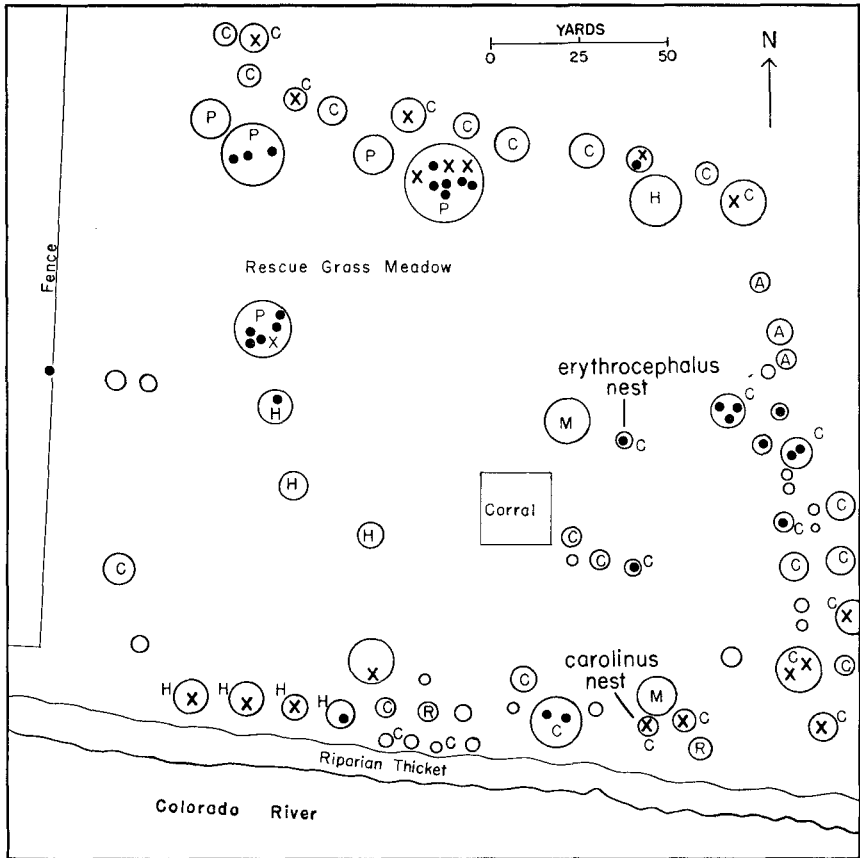


FIG. 4. Study area at Walker Ranch, showing overlap in territories of *C. carolinus* and *M. erythrocephalus*. X's indicate records of *carolinus*; dots represent records of *erythrocephalus*. Letters identify trees, as follows: A, ash; C, cottonwood; H, hackberry; M, mesquite; P, pecan; R, retama.

The pair members of *carolinus* were feeding young, making repeated visits to the nest with insects. They foraged over a much larger area than did the *erythrocephalus*. It will be seen in Fig. 4 that *carolinus* visited the large pecan tree to the north of the *erythrocephalus* nest-tree and also the southern part of the grove of cottonwoods and a line of hackberry trees along the river. Sometimes they flew south across the river to forage in trees located several hundred yards from their nest. On three occasions the male *carolinus* passed within a few feet of the nest-tree of the other species, while one or both of the latter were present,

but no interspecific conflict was seen. We noted, however, that *carolinus* did not forage in the grove of cottonwoods east of the *erythrocephalus* nest-tree, although several times they flew through the grove on their way to forage in trees beyond the study area to the north.

In summary, it seemed evident even from our limited series of observations that the territorial relations of *C. carolinus* and *M. erythrocephalus* were decidedly different from those of the former species and *C. aurifrons*. Their territories overlapped broadly and no interspecific conflict was noted.

*Experiments with Dummies.*—In an attempt to investigate factors involved in species recognition, we have performed a series of experiments in which dummy woodpeckers (study skins) were placed at various points in the territories of pairs of woodpeckers and the ensuing responses recorded. Not all of these throw light on the problem of interspecific territorialism, but they are none the less of some interest.

On May 8, 1957, a male dummy *C. aurifrons* was wired to a limb one foot below the nest-hole of the pair of *C. carolinus* that was being studied at Deep Eddy. Immediately the female *carolinus* attacked the dummy, striking it repeatedly with her bill for a period of 45 minutes. The great majority of her blows were directed at the head, particularly the eye region. Her attack stopped only when we approached the tree to retrieve the dummy, which was by then all but torn to pieces. The male made only a few passes at the dummy and left the tree a few minutes after it was placed in position.

The next day, May 9, we attached both male and female dummies of *carolinus* to the nest-tree of the pair of *aurifrons*, placing them within two or three feet of the nest-hole. At once both male and female *aurifrons* attacked the dummies, with the first blows being directed male to male and female to female. In this particular case, the male was much more aggressive than the female. The latter seemed apprehensive and alternately pecked at the dummy and retreated. After 15 minutes the head of the male dummy was detached and fell to the ground. Nonetheless, the male continued his attack on the headless dummy for another five minutes and then directed his response toward the female dummy; but he continued to make occasional passes at the headless dummy. Again the majority of blows were directed at the dummies' heads.

Ten minutes after the head was knocked from the male dummy, both dummies were removed from the nest-tree and placed on a telephone pole 40 yards from the nest-tree. The dummies were attacked in their new positions, but with lessened intensity, and the attacks were not so long sustained. The same type of experiment was performed by placing a dummy male *aurifrons* on a post within the territory of the *carolinus*. As in the previous experiment, the dummy was attacked with less intensity than when it was placed on the nest-tree.

The results of our work with dummies were not unexpected in view of our previous observations on territorial behavior. Subsequent tests with other pairs of *carolinus* have shown that the female of this species takes a more active part in defense of the nest-hole area against the dummies than does the male. The same pattern of behavior may be seen when one approaches the nest-tree of a pair of *carolinus* in which eggs or young are present. The female usually remains in the nest-tree calling excitedly, whereas the male almost invariably flies to a distant tree, returning only when the intruder has departed.

A second test with *aurifrons* also confirmed our first, to the effect that in this species the male is more aggressive in encounters at the nest-hole than is the female; but additional testing is needed.

The fact that attacks were usually directed at the heads of the dummies suggested that this part of the body alone supplies at least the important sign stimuli releasing aggressive behavior. This was confirmed by wiring the head of a dummy female *carolinus* two feet above the nest-hole of a pair of *carolinus* in a mesquite tree on the University of Texas campus on April 6, 1958. The female came to the nest-tree, suddenly flew to an adjacent stand of cottonwoods, and returned in company with the male. The male flew to the head and pecked it violently (Fig. 5), and the female soon joined him in the attack. After about 10 minutes, the forepart of the dummy's head, including the bill, came loose, and the male flew off with it in his bill. To our surprise, the female continued her attack on the remnants of the head, a ball of cotton used to stuff the dummy and a tuft of red feathers on the coronal and occipital regions. Her attack continued for several minutes but ceased abruptly when her blows dislodged the few remaining feathers. Shortly thereafter, the male returned and investigated the "remains"; then he entered the nest-hole, presumably to incubate, and the female foraged in the nest-tree. These observations suggest that the red feathers of the head are of paramount importance in releasing aggressive behavior. We have not pursued the problem further, but it is clear that the response to the head alone is fully as strong as to the entire dummy.

Despite the fact that the pair of *M. erythrocephalus* did not behave aggressively toward *C. carolinus*, even when the male of the latter species flew within a few feet of their nest-tree, they readily attacked dummies of that species placed near their nest-hole (Fig. 6). When presented simultaneously with dummies of *carolinus* and their own species, they usually directed their initial attack at the latter, but the defense of the nest-tree against the *carolinus* dummy was vigorous. These tests help account for the fact that the pair of *carolinus* avoided perching in the vicinity of the nest-tree of *erythrocephalus*.

#### DISCUSSION

In a recent review of interspecific territorialism in birds, K. E. L. Simmons (1951:407) has suggested that the term be confined to cases in which "a territory holder of one species exhibits persistent aggressive behaviour to an intruding bird of a second species, showing to it some, if not all, of the reactions usually forthcoming in intraspecific encounters." Further, he suggests that the aggression should be related to the territory as a whole and not merely to a particular part of it, thus excluding contests between hole-nesters at nest-sites. We are in general agreement with Simmons in this regard. Conflicts between hole-nesting species competing for roosting or nesting sites frequently involve



FIG. 5. Male *C. carolinus* attacking head of male dummy *C. carolinus* near nest-hole.

species which do not hold exclusive territories. The relations of *C. aurifrons* and *C. carolinus*, however, satisfy all criteria for interspecific territorialism. The case is unusual in that the territories are mutually exclusive; in their ter-

ritorial relations, the two woodpeckers behave as if they were a single-species population.

Where the two species of *Centurus* occur together, competition for space and nesting sites is manifested in interspecific territorialism. Lack of significant differences in feeding and nesting habits and in timing of events of the annual cycle would seem to preclude the possibility of their coexistence, except in a narrow contact zone where there is complex inter-digitation of vegetation types. Reproductive isolation is complete, but the species have so far failed to evolve ecologic adjustments that would permit extensive sympatry.

In the case of *Centurus carolinus* and *Melanerpes erythrocephalus*, sympatry is possible because the necessary ecologic adjustments have been made, and it appears that they do not show interspecific territorialism. There are obvious differences between these species in foraging habits and habitat occurrence. Our observations show that *erythrocephalus* feeds regularly not in the manner of "typical" woodpeckers but by "flycatching." The relatively longer wing and tail of this species (Table 1) may be related to this trait, which has also been noted by several other writers, including G. F. Simmons (1925:132), Skinner (*vide* Bent, 1939:201), and Nauman (1930). Studies of stomach contents by Beal (1911) reflect differences in foraging habits in the two woodpeckers. He notes that *erythrocephalus* "eats very few beetle larvae or other grubs, or ants that live in wood or other places of concealment. Apparently it is not so fond of pecking wood as are the other species [of woodpeckers] . . ." In our experience, *carolinus* "flycatches" only occasionally, and all lines of evidence point to the conclusion that *erythrocephalus* obtains significantly less of its food by foraging over trunks, branches, and leaves than does the other species. In the course of our studies in April, we rarely saw *erythrocephalus* dig or probe into bark, whereas *carolinus* fed almost exclusively in this fashion. Typically, *erythrocephalus* fed by perching in exposed positions atop large pecan or cottonwood trees and darting out some 20 to 40 yards to catch large flying insects, some of which were beetles. We watched one or both individuals repeat this action for periods of up to an hour, and Nauman (1930) calculated that one bird, which was feeding a fledgling, made five to seven sallies per minute, catching a calculated 600 flying insects in the course of an hour. Between sallies, the birds often perch crosswise in the manner of passerines, and the head is turned from side to side as they peer about for insects. Some insects are swallowed immediately after a bird returns to its "lookout" perch, but larger ones are usually wedged in crevices (typically in stumps), smashed, and picked apart.

This discussion is not intended to suggest that *erythrocephalus* feeds exclusively in this manner. The species also drills into wood and, especially in the fall and winter, feeds on beechnuts, berries, acorns, seeds, and other vege-



FIG. 6. *M. erythrocephalus* attacking male dummies of its own species (above) and *C. carolinus* (below).



table food (Beal, 1911); in addition, it reportedly (Bent, 1939:199) takes both eggs and young of some small passerines.

The fact that *erythrocephalus* tends to frequent more open situations than does *carolinus* may be related to differences in feeding habits. In any event, it is probably important in permitting the two species to coexist. Bent (1939:195) regarded *erythrocephalus* as "essentially a bird of open country and not in any sense a forest dweller," and other naturalists quoted by Bent have noted its preference for open groves, "old burns," and other similar situations. Our observations and those of G. F. Simmons (1925:131) in Texas agree fully with these reports. Simmons noted the preference of *erythrocephalus* for edges of woodlands, orchards, groves, and clearings in open woods, and that of *carolinus* for heavily wooded bottomlands. At the Engeling Wildlife Management Area, Anderson County, Texas, in November, 1956, we found *erythrocephalus* somewhat less numerous than *carolinus* and confined to a partly burned stand of trees bordering a meadow, whereas *carolinus* was generally distributed throughout the oak forest. Even in the study area at Walker Ranch, a preference of *erythrocephalus* for open situations was apparent, as evidenced, for example, by the location of the nests of the two species (see Fig. 4).

Since the foregoing was written, Kilham (1958a, 1958b, and 1958c) has published three important articles dealing with the biology of *C. carolinus* and *M. erythrocephalus* in Maryland. Among his significant findings are the following: Pairs of *C. carolinus* disband in late summer, and nesting, which begins in April, is preceded by a long period of courtship and pair bond reinforcement beginning in January. Individuals of *M. erythrocephalus* holding small winter territories in woodland defended their areas and acorn stores against *C. carolinus* and a variety of other species of birds.

#### SUMMARY

Interspecific relations of three woodpeckers of approximately equal size were studied in central Texas. The closely related, morphologically similar Red-bellied Woodpecker (*Centurus carolinus*) and Golden-fronted Woodpecker (*Centurus aurifrons*) are sympatric in a narrow zone in the Austin region. Within this overlap zone, differences in habitat occurrence limit contact and competition; but both species occur in the city of Austin, where they hold mutually exclusive territories. Feeding and nesting habits are similar in the two species, as are vocalizations and displays. Reproductive isolating mechanisms, the nature of which are unknown, have evolved, but the species have not made ecologic adjustments which would permit extensive sympatry.

The territorial relations of a pair of *C. carolinus* and a pair of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) were studied. Their territories overlapped broadly, and interspecific antagonism was not observed. It is suggested that differences in foraging habits and habitat occurrence are important factors permitting extensive sympatry of these species.

The reactions of nesting woodpeckers to dummies were tested. Both *carolinus* and *aurifrons* attacked dummies of their own or of other species placed in their nest-trees or elsewhere in their territories. The head of a *carolinus* dummy was as effective in releasing aggressive behavior in *carolinus* as was the entire dummy. Dummies of *carolinus* and *erythrocephalus* placed near the nest-hole of *erythrocephalus* were attacked with approximately equal vigor.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TEXAS, AUSTIN, TEXAS, MAY 26, 1958