

TERRITORIAL RELATIONSHIPS BETWEEN CARDINALS AND PYRRHULOXIAS

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The Check-list committee of the American Ornithologists' Union (1957) and Hellmayr (1938) maintain the Cardinal (*Richmondena cardinalis*) and the Pyrrhuloxia (*Pyrrhuloxia sinuata*) in separate genera. However, others (Mayr and Amadon, 1951) have indicated that these two species may be congeneric. The existence of a second species of Cardinal (*Richmondena phoenicea*), which shows tendencies in bill structure toward the Pyrrhuloxia, further suggests the possibility that the two are congeneric. Ridgway (1901) separates the two genera primarily on the basis of bill structure. Although these differences are valid, the question arises as to whether they may be utilized as so-called "generic" characters in this case. Simpson (1945) points out the basic aspect of the genus as a group of similar species. The concept does not regard the genus as a hierarchical category based on one or few character differences but rather as one which stresses groups of similar characters shared by a natural evolutionary group of species. In the absence of paleontological evidence we must rely on similarities displayed by the present day forms. In this respect, ecology and life history are as important considerations as are morphological characters.

Territory in birds has received much attention in recent years. Hinde's (1956) excellent review shows the great differentiation that exists among species which might be used to throw light on relationships. Our best understanding of the value of territory in this connection should come from a comparison of two closely related species which occur together and utilize the same habitat. Several recent studies have been conducted on the relationships between similar species in areas of overlap. These have shown various degrees of relationship depending on the similarity and/or difference between the two species. Lanyon (1957) found in the very similar and closely related meadowlarks that when both species occur in the same area they hold mutually exclusive territories. The two species of towhees studied by Marshall (1960) are separated by more effective isolating mechanisms, and their territories overlap broadly where the two are found together. This paper summarizes the results of a field study on the Cardinal and Pyrrhuloxia in an area where both occur as abundant residents.

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METHODS AND STUDY SITE

A 42-acre area in the San Xavier Indian Reservation, ten miles south of Tucson, Pima County, Arizona, was selected as a study site. This is the same area utilized by Marshall (1960). The site is situated on the first-step lowlands of the Santa Cruz River, and it contains mesquite (*Prosopis juliflora*) woodland with an understory of gray-thorn (*Condalia lycioides*). Elderberry (*Sambucus*) and hackberry (*Celtis*) are common in hedgerows. Much of the mesquite has been cut out and the fields have been cultivated,

but these have been unused for several years. Varieties of weeds, such as Johnson grass and tumbleweed, have overgrown them. Old irrigation pumps and abandoned Indian houses are scattered through the area.

In and around the study site, birds were banded with aluminum bands and with celluloid color bands. Unfortunately the strong bills of the Cardinals and Pyrrhuloxias allowed the birds to bite off many color bands. This resulted in many unmarked birds within the study area. Trapping and banding were continued throughout the study and resulted in the color marking of 38 Cardinals and 84 Pyrrhuloxias. A total of 95 days, with an average of three and one-half hours per day, was spent in the study area from September 30, 1958, to December 18, 1959.

TABLE 1

POSITION OF MARKED BIRDS WITH REGARD TO THEIR SUMMER TERRITORY IN 1959

Male	Number of Observations			
	Outside of territory		Inside of territory	
	Sept.-April	May-August	Sept.-April	May-August
C-2	22	2	5	17
C-3	1	1	16	42
P-4	5	1	2	12
P-7	0	0	6	19

Territories were determined primarily by noting the positions of singing males and also the points where fighting and chasing occurred. It was found that nesting began sometime in May and lasted until the middle of August. A tabulation of the points where marked individuals were found during this time was used to verify these territorial boundaries (see table 1). Although territorial establishment began in April, this month has been included in the nonbreeding portion of the annual cycle since territorial boundaries were not perfectly defined at that time.

VOICE

Singing is important in the establishment and maintenance of territory in both the Cardinal and the Pyrrhuloxia. Their songs are so similar that they are often indistinguishable. The major difference in their songs lies in the phrasing used during one singing period. Individuals of both species are capable of a wide variety of song types. In the Cardinal one type is used over and over during one singing period, but the Pyrrhuloxia alternates different types. Although the females of both species are capable of singing, the female Pyrrhuloxia is rarely heard to do so. The female Cardinal, on the other hand, sings loudly and often in duets with her mate, but on only one occasion did I observe a female Cardinal singing without her mate. Duet singing is most common during the spring before nesting begins, but it continues throughout the nesting season and probably aids in the maintenance of the pair bond.

Both species have calls that differ greatly. As soon as the young Cardinals are hatched the adults begin using a high, tinkling call that continues until the young have become independent. The Pyrrhuloxia has a harsh chattering call that is used in territorial disputes and as a contact device between members of a pair.

Songs of both species were heard as early as the second week in February. It was not until the middle of March that singing in both species reached its peak. Since nesting began in May, song probably served in mating and pair formation as well as in establishment of territory. Singing subsided during the latter stages of incubation and was rarely heard after the young were hatched. Singing was renewed after the first brood

became independent if a second brood was attempted. Song in September was reduced to only a few scattered half-songs by one or two individuals.

NESTING

Nest building is apparently carried out primarily by the females of both species. Observations on one Cardinal and one Pyrrhuloxia nest under construction showed only the females building, while the males stayed far back in the trees singing. Most nest material, with only one observed exception, was gathered within the established territory. I never saw material gathered within the territory of another pair.

Nests and nest sites of the species were very similar. Eight Cardinal and 20 Pyrrhuloxia nests ranged between 5 and 15 feet above the ground, both averaging 8 feet. In the study area both preferred to nest either in mesquite or gray-thorn. One nest of the Pyrrhuloxia was found in an elderberry. In other areas around Tucson, Cardinals were found to use tamarisk (*Tamarix*) trees, and Pyrrhuloxia nests were not uncommon in palo verde (*Cercidium*). Both species seemed to prefer thick patches of brush or dense hedgerows; however, of the two species, the Pyrrhuloxia utilized more open situations. Cardinals were much more apt to place their nest against a major trunk of a tree than were Pyrrhuloxias, but both usually placed it in the small twigs that occur on the secondary branches. Neither species anchored the nest securely to the twigs or branch on which it was placed.

The nest of the Cardinal was generally constructed of dead material, although green twigs and stems were sometimes added to the outside. The cup was often poorly lined, and it was composed of only a few rootlets, horse hairs, grass stems, or vine tendrils. The bulk of the nest was composed of thin strips of bark and plant fibers, generally supplemented with grass and soft plant stems. In general the nest was loosely built and eggs could often be seen through the sides and bottom. Several nests were found to contain tissue paper and paper napkins either on the outside or woven into the bulk of the nest.

The nest of the Pyrrhuloxia was almost always constructed of dead material. Of 20 nests only one contained green material, and this amounted to only a few mesquite leaves that had been added to the outside. The nature of the material often gives the nest a very decidedly grayish appearance with brownish highlights. The cup was usually well lined with rootlets, and occasionally thin strips of bark, horse hairs, or very small plant stems and fibers were used. The nest was generally smaller and more compactly built than that of the Cardinal, but the difference was not as great as would be expected from the size difference between the two species.

The eggs of the two species are very similar and cannot always be told apart. In the Tucson area Cardinal eggs are somewhat larger and have a more bluish background color than those of the Pyrrhuloxia. The pattern of speckling is identical. Egg laying may occur any time in the months of May, June, July, and early August (see tables 2 and 3). The most active period for both species was the first two weeks in June. Pairs found nesting in August had probably been unsuccessful in earlier nestings. Clutch size of the Cardinal ranged from two to four eggs and averaged three. Clutch size of the Pyrrhuloxia varied between two and three eggs, both numbers being equally common. In one observed case of each species, incubation required 14 days from the laying of the last egg.

Contrary to the statement by Brandt (1951), Cardinals may have a second brood if their first nesting is successful. Two successful broods were noted in each of two color-marked pairs in the study area. In one case, the second brood was started before the first had become fully independent. I have no information on second nesting in the Pyrrhuloxia.

TABLE 2
NESTING RECORDS OF CARDINALS AT SAN XAVIER RESERVATION IN 1959

Pair no.	Building	Eggs	Nestlings	Fledglings
1				June 17
1			Aug. 8	Aug. 13
2	June 5 destroyed			
2	July 4	July 9 destroyed		
3		June 2 destroyed		
3		July 19 destroyed		
3		Aug. 11 destroyed		
5		June 9	June 11	June 24
5		July 25 (1 egg)	Aug. 11	Aug. 25
6				June 18

Young Cardinals are dependent on their parents for almost a month after leaving the nest. In one case, a color-marked young one first left the nest on August 13 and was still being fed by a color-marked adult on September 5. This may account for the presence of begging young of both species as late as September 30 for Cardinals and September 18 for Pyrrhuloxias.

TERRITORY

Cardinals defend their territories only against trespass by other Cardinals; Pyrrhuloxias defend their areas only against other Pyrrhuloxias. As shown by Hinde (1956), definitions of territory are very numerous. In this paper, territory is defined as that area, within the home range of an individual, which is maintained and defended against members of its own species, and in which the birds sing, nest, raise young, and for the most part restrict their activities. Short excursions are occasionally taken to points outside this area. As seen in table 1, these trips are infrequent and in all instances were made in order to obtain food or water. Territory, therefore, does not include all areas

TABLE 3
NESTING RECORDS OF PYRRHULOXIAS AT SAN XAVIER RESERVATION IN 1959

Pair no.	Building	Eggs	Nestlings	Fledglings
1		July 1 destroyed		
2		June 2	June 9	June 18
3	June 7	June 9 (1 egg)	destroyed	
3	June 24	June 27	July 11	destroyed
3		Aug. 1 (1 egg)	destroyed	
4		June 2 destroyed		
4		June 27	July 4	destroyed
4	July 15	July 19 (1 egg)	destroyed	
7		June 9 destroyed		
7	July 19 destroyed			
8		June 20	?	?
9		Aug. 1	?	?
10				July 29

visited by the birds. Within each territory there is a definite center of activity which is a circular area about the nest. It is here that the birds spend most of their time, especially in the afternoon hours. Here, also, they do most of their singing. Territories are not maintained during the winter. The established adults, however, are always found within a home range which may be much larger than, but always includes, their summer territory.

Of these three types of areas—home range, territory, and center of activity—the territory is the most stable since it is the area most frequently defended. Home range boundaries probably fluctuate greatly and were never observed to be defended. Main-

tenance of a home range helps the birds to become familiar with an area and it also permits individuals to defend the same territory during successive years. One pair of color-marked Cardinals held the same territory in 1960 as they held in 1959. One color-marked male Pyrrhuloxia likewise held the same territory for the two consecutive summers.

By the first of September, most of the young have become independent of the adults. Song has almost ceased and no territorial activity can be detected. At this time loose, non-integrated feeding and roosting flocks are formed which contain Cardinals and Pyrrhuloxias as well as other species. The Pyrrhuloxias always far outnumber the Cardinals in these flocks. This is partly due to the greater number of Pyrrhuloxias in the area and partly to the more gregarious habits of the Pyrrhuloxia.

The roosting behavior, noted on several occasions, may be indicated by summarizing an observation on November 3. At about sunset, 5:50 p.m., Cardinals and Pyrrhuloxias began heading down the hedgerows in large numbers. There was no stopping or backtracking but rather a rapid series of flights. The great majority of both Cardinals and Pyrrhuloxias headed for a section of thick mesquite woodland. There was a lot of calling and moving about in this woodland for approximately five minutes and then everything became quiet for the night.

Establishment.—With the break-up of winter flocks in late February and March, the males of both species became highly pugnacious. This initial activity consisted primarily of individuals chasing each other and it occurred within groups of up to five birds. On April 7 there were five male Cardinals chasing each other in the middle of the study area. No direct conflicts were noticed, but this aggressiveness was in sharp contrast to their winter tolerance. Later in the summer four of these males established territories within the study area, and the point of chasing of April 7 became a boundary between three of their territories. Female Pyrrhuloxias, but never female Cardinals, were noticed to engage in chasing activities, often with the males. These chases apparently establish a dominance order between the individuals so that the most aggressive male succeeds in taking the best territory. This was exemplified by Cardinal male number 3. He was the most vigorous bird in fighting and chasing, and he was most often observed to be the aggressor. He was the first male to completely establish a territory, and this territory contained the best nesting sites and food supply within the study area.

During late April and early May definite territorial boundaries became established. As in the early stages of this process, only the male Cardinal, but both the male and female Pyrrhuloxia were involved. On one occasion a pair of Pyrrhuloxias was noticed moving about an area which eventually became their territory. At one point another pair was encountered and all four birds engaged in a vigorous fight. The intruding pair was driven out and was never noticed to encroach on that area again.

Maintenance.—Territories once established were maintained almost entirely by the males of both species. The female assisted in defense only when the nest or young were threatened directly. At times she did not even do this but flew off and left defense completely to the male. In every instance when a Cardinal nest with eggs was being examined, the adults would skulk in the background occasionally uttering high, sharp chips. When young were in the nest, both parents, but more noticeably the male, would hop around excitedly, often quite close to the observer, using the high, tinkling call previously described. When a Pyrrhuloxia nest and eggs were examined the female completely disappeared, but the male often stayed in the same tree and sang vigorously. If young were in the nest, the male, and sometimes the female, would fly around excitedly singing or giving their chatter call.

Territory was maintained in three primary ways: combat, proclamation, and patrolling. Combat, which includes both fighting and chasing, was noticed in both species, but it was much more vigorous in the Pyrrhuloxia. An intruding bird would be met, usually near the boundaries of the territory and either a fight or a chase, and often both, would follow. In all cases the intruder was forced to leave the area. If contact was made well within the territory, the intruder was much more prone to take flight, resulting in a chase. If contact was made near the boundary, then a fight was more likely to occur. For the most part, intrusions were made only by males of adjoining territories. Unmated birds passing through the area were generally tolerated, but an established bird never was. On July 1 an unbanded Cardinal was noticed singing at the northwest boundary of the territory of Cardinal number 1. The latter came up close to the singing male and chipped several times, but no fight ensued. Since this unbanded male was never found to be singing in this area again, it is presumed that he was an unmated bird just passing through the area.

Proclamation of territory consisted of intensive singing on the part of the males of both species. It was most frequent during the early morning, when a chorus of many birds could be heard. At this time singing would usually be from a favored site within the center of activity of the territory. Occasionally during the day competitive singing between males of the same species was heard. This was equally common in the Cardinals and Pyrrhuloxias. The males sang either in unison or alternated with each other. This type of song was most common between males of adjoining territories. Competitive singing between widely separated males was heard on only a few occasions.

Patrolling was noted in both species; however, only the Pyrrhuloxia followed a regular pattern. Cardinals merely wandered irregularly about their territories, singing in many scattered places. Cardinal male 1, for example, sang at scattered spots within his territory throughout the day. His singing on the boundaries of his territory was just as irregular. Some days he would be found singing at the south boundary and then on other days he sang on the northwest boundary. The same trees are used for singing quite frequently through the summer and these points were utilized in delimiting his territory. His flight patterns to and from these singing posts were very regular, and this offered further proof of his territorial limits. All the other male Cardinals in the study area followed the same pattern. The Pyrrhuloxia, as exemplified by male number 7, made a regular circuit of his territorial boundary. After the initial singing in the morning the male would make his rounds, singing a few songs in one bush and then in the next, until a complete circuit had been made. He was never observed outside of the area just described.

Once the young are out of the nest, territorial defense and maintenance were reduced, and they stopped entirely if it was late in the season. If a nest was destroyed, territorial activity increased although it never reached the peak of the initial activity. Individual pairs of both species were seen to make as many as three attempts at reneating, with a recurrence of high territorial activity, if their nests were abandoned or destroyed.

Composition.—Within the limits of the study area, territories of six Cardinals and ten Pyrrhuloxias were established (see figs. 1, 2). The total portion of the study area occupied by Cardinals was 54.5 per cent, whereas that occupied by the Pyrrhuloxias was 60 per cent. Both species required a suitable amount of woodland within each territory. An average of 45 per cent of the territory of each pair of Cardinals and 43 per cent of the territory of each pair of Pyrrhuloxias included mesquite woodland (see table 4). Cardinals appeared to require denser woodland in which to nest than did Pyrrhuloxias. An example of this was the fact that, although Cardinals were occasionally

seen and heard to sing from an open mesquite patch, none established a territory there. One pair of Pyrrhuloxias (pair 2), however, was able to establish a territory at this spot and raise one family. This patch consisted of small and widely spaced mesquite trees with much open, weed-covered ground between them. In other areas near Tucson, Car-

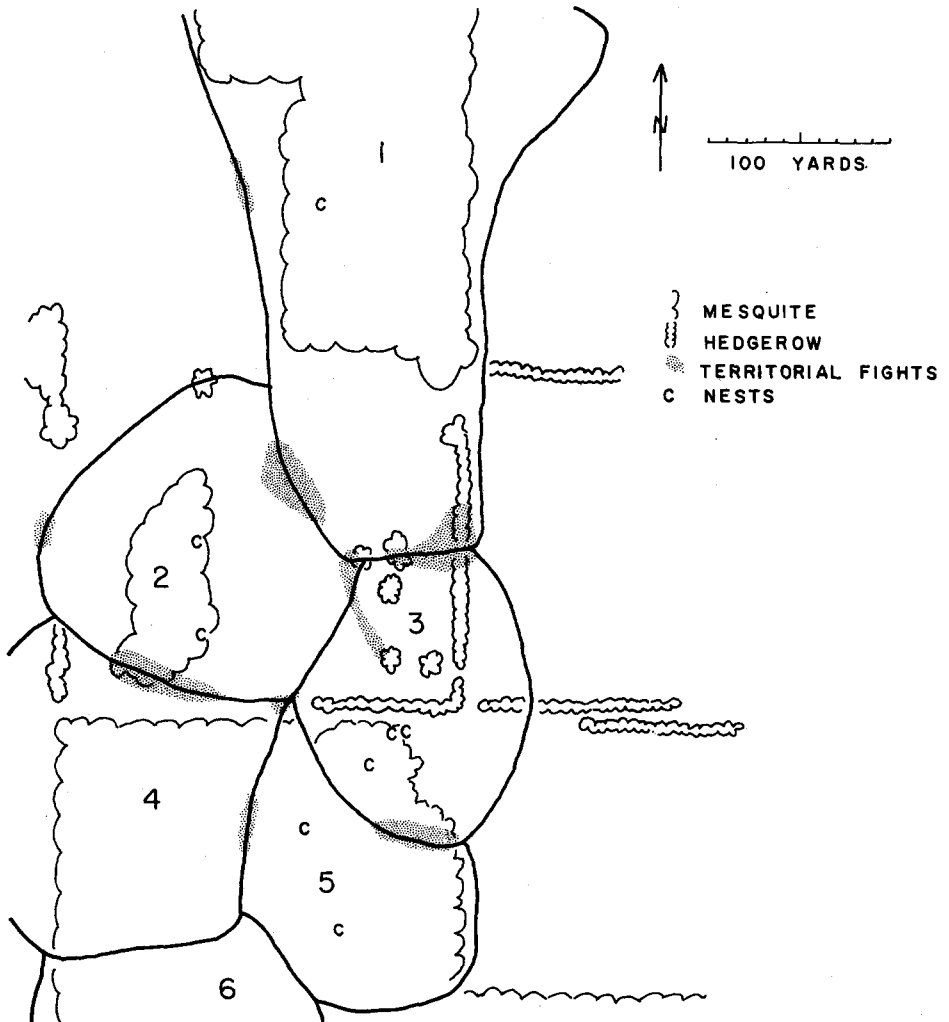


Fig. 1. Diagram showing six territories of Cardinals (*Richmondia cardinalis*) within the study area.

dinals were found nesting in hedgerows between open fields, but these were always fairly dense and contained large trees. In these same areas the Pyrrhuloxias were often found nesting in trees with little or no vegetation around them.

Both Cardinals and Pyrrhuloxias appear to prefer an open field within the limits of their territory. This is not too surprising because, as shown by McAtee (1908), their diet consists of weed seeds. The fact that one territory did not include such an area shows that this is not absolutely necessary. Food supply apparently plays only a minor role in the territorialism of these birds, but this paper offers no direct evidence on this

long-debated point. Even though most territories included a considerable area of open fields, these fields were not exploited to their maximum. Often birds of both species were seen feeding together in groups outside of their territories. No conflicts were noticed on these occasions, indicating that these feeding areas were not part of established terri-

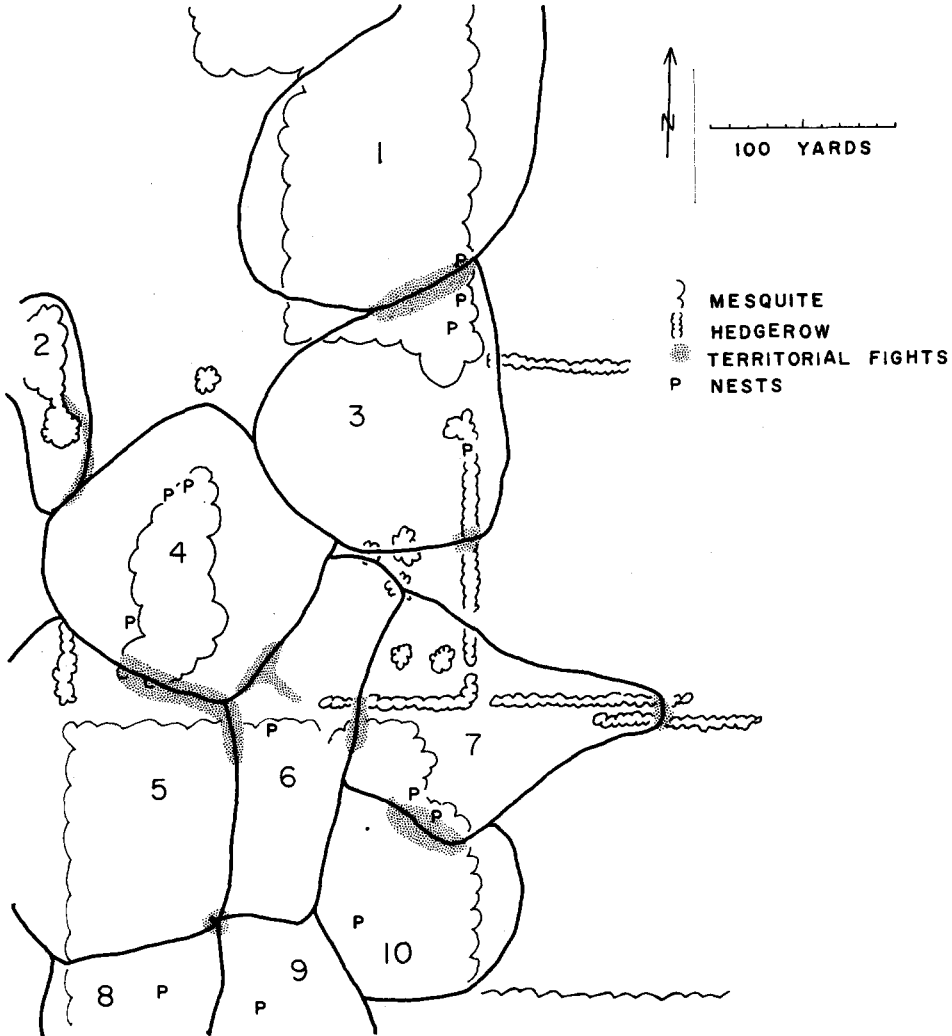


Fig. 2. Diagram showing ten territories of *Pyrrhuloxias* (*Pyrrhuloxia sinuata*) within the study area.

tories. During the height of the breeding season, two color-marked Cardinals (numbers 2 and 3) were seen fighting near the border of the territory of one of them. A chase ensued and continued to the boundary between their respective territories. At this point the chase stopped and both birds fed within a foot of each other. Although this may have been an example of "substitute activity" (Tinbergen, 1939), it is thought by the author that if food were of major importance in territoriality, the mere act of feeding in close proximity, regardless of the cause, would have aroused aggressive behavior rather than suppressing or displacing it.

Size and shape.—The size of the territories within the study area is given in table 4. Territorial fights of Cardinals and Pyrrhuloxias are summarized in figures 1 and 2. Other disputes that were not as well documented are not included. It will be seen from these figures that the territorial boundaries are not thin lines but often bands of perhaps five or ten yards in width. In these areas the boundary lines are drawn through the area where the fighting was most intense or along the major flight path during the chasing. Two territorial fights between Cardinals 2 and 4, and one between Pyrrhuloxias

TABLE 4
SIZE OF TERRITORIES AND AMOUNT OF MESQUITE WOODLAND WITHIN EACH

Cardinal			Pyrrhuloxia		
Pair no.	Territory	Per cent of mesquite	Pair no.	Territory	Per cent of mesquite
2	3.9 acres	19	2	1.3 acres	27
3	3.9	16	3	2.9	25
4	4.1	51	4	3.5	50
5	3.5	94	5	3.3	52
			6	2.2	54
			7	2.2	18
			10	2.3	78
Average	3.7 acres	45	Average	2.5 acres	43

4 and 5, were almost identical with regard to the place where fighting was most intense and as to the pattern of the chase. In all three cases it was the northernmost male who chased the other male in a southeastern arc. Similarly the fights between Cardinals 3 and 5, and Pyrrhuloxias 7 and 10, were almost identical.

The shape of the territories of both species tended to be roughly circular. They were, however, modified by the landscaping and other factors. Territories were modified, where possible, to cover both mesquite woodland and open fields. Hedgerows afforded greater penetration into open areas by providing trees and bushes from which advertisement could be made. Pyrrhuloxia territory number 7 was an example of this. Pyrrhuloxia territory number 6 was very compressed by the other territories around it. This resulted in a long, thin territory which included both mesquite woodland and an open field.

The size, shape, and position of territories of Cardinals and Pyrrhuloxias were remarkably similar. This was so striking that if a person viewing the maps of them were not aware that two species were involved, he might think they represented the same species during different breeding seasons. The similarity is even more striking when these territories are compared with the dissimilar territories of Brown and Abert towhees as described by Marshall (1960) from the same area. Such differences as exist between territories of Cardinals and Pyrrhuloxias are due to the greater number of Pyrrhuloxias in the area. For example, Cardinal territory 1 was roughly equivalent to Pyrrhuloxia territory 1 plus 3. Territories of Cardinal 2 and Pyrrhuloxia 4 were almost identical, as were those of Cardinal 3 and Pyrrhuloxia 7. Pyrrhuloxia number 6 was squeezed in between many others as shown by the greater number of territorial fights engaged in by this pair. In the study area, the ratio of number of territories of Cardinals to territories of Pyrrhuloxias was 1 to 1.6. The ratio of territory size was 1.5 to 1. Results of netting and trapping, which were not selectively different between the two species, showed that the Pyrrhuloxias outnumbered the Cardinals in the area by about 2 to 1. Therefore, the differences in size and shape between territories of Cardinals and Pyrrhuloxias was due to the greater density of the Pyrrhuloxias.

The size and shape of the territories remained fairly stable during the summer.

However, a few minor fluctuations were noted. These were primarily the result of the shifting of the center of activity when a new nest was built. If the new nest was built on the opposite end of the territory from the old one, then the region of the old nest was not defended as often nor as vigorously as before. This allowed a neighboring pair to gain control of the vacated area. The nest of Pyrrhuloxia 1 was destroyed and this pair moved farther north. When the nest of pair 3 was destroyed, they re-nested near the boundary of the territory of pair 1. Several fights between these two pairs occurred at this time. No further fights occurred after the initial few and pair 3 successfully held part of the territory of pair 1 for the rest of the summer.

Nest sites were placed without regard to the size or shape of the territory. Some were in the middle and others were at the edge (see figs. 1, 2). Similarly there was much randomness with regard to placement in relation to the mesquite woodland, although Cardinals did not nest in hedgerows as did a few pairs of Pyrrhuloxias. Cardinals and Pyrrhuloxias tended not to nest near each other. The fact, however, that Cardinal 5 and Pyrrhuloxia 6 had concurrent nests only three yards apart, shows that proximity may not be critical. Since both species utilize the same type of place to build the nest, and since the nests and eggs are so similar, this tendency not to nest near each other may be a result of some form of competition.

SUMMARY AND CONCLUSIONS

Territorial behavior and other aspects of the life of the Cardinal and the Pyrrhuloxia in southern Arizona are basically very similar. Their songs are homologous and at times they are indistinguishable. These songs are of prime importance in the establishment and maintenance of territories. They may also aid in pair formation, but only in the Cardinal are they involved in a definite ritualistic duet, which strengthens the pair bond. The female Pyrrhuloxia is rarely heard in the field. A second type of vocalization is present in both species, but these calls are not homologous. Both species begin singing in the middle of February, and by September, singing is almost nonexistent.

The nesting cycle and habits are almost identical. Such differences as smaller egg- and nest-size of the Pyrrhuloxia are most likely a function of its smaller body size. The ability of the Pyrrhuloxia to nest in more open situations suggests a mechanism for reducing competition between the two species.

The territories of these two species are not mutually exclusive. On the contrary, they are often coincident. This suggests that the difference in the average size and in the shape of their territories is a function of local density. Food supply is considered of only minor importance in the territorialism of these birds.

The size, shape, and position of territories, along with the almost identical amount of woodland within each, and the basic similarities in the breeding behavior and cycle, suggest that the ecological requirements of these two species are extremely similar. Differences in ecology which cause a different geographic distribution of the two are not evident on the study area, where they both occur and utilize the same environment in the same way. The considerable similarity between the two species in life history supports the hypothesis that they are congeneric.

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