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OBSERVATIONS ON BREEDING BEHAVIOR IN TRICOLORED RED-WINGS

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The following incomplete observations, made in the Sacramento Valley of California in May, 1939, seem worth publishing since so little is on record of the remarkable behavior of the Tricolored Red-wing, *Agelaius tricolor*. Intensive observations for several hours each day after dawn were made May 13 to 16, 1939, from a high bank overlooking a colony of some 2000 birds in cattails at Willow Slough, near Davis, Yolo County, and this colony and four others near Marysville, Yuba County, were visited at intervals in May and early June.

As a general rule, related species of birds show very similar behavior. The nearest relative of *A. tricolor* is the Red-wing, *A. phoeniceus*. From observations by Allen (1914), Noble and Vogt (1935), Linsdale (1938, pp. 127-156), and the present authors, it is clear that the Red-wing, *phoeniceus*, is territorial. The males of this species arrive before the females and each defends an isolated territory by fighting, by threat display with erected red epaulets (Noble and Vogt) and by "pointing" (personal observation). The male sings from prominent perches and also in aerial song-flight; in either case the epaulets may be erected. Each male frequently has several females, which show no territorial behavior. Courtship includes sexual chases, which often extend beyond the territory (Allen), and singing to the female on the ground with arched wings and erect epaulets (personal observation). Much of the feeding is done far outside the territory, which is the male's display center and within which his females nest.

A. tricolor, by contrast, is perhaps the most colonial of all passerine birds. Neff (1937) found colonies of less than 100 birds rare; most of them consisted of several thousand individuals and some included over 200,000. Dawson (1923) and Neff (1937) adequately describe the amazing density of the nests. We found two adjacent nests with their grasses interwoven, and another occupied nest with a second three inches above it. The species is social from preference, for although potential nesting sites over water are local, the birds are even more local. Under such circumstances, how does the breeding behavior of *tricolor* compare with that of its territorial relative?

Arrival at the nest site.—The Willow Slough colony was established before our observations started, so we have no data on the manner of arrival of the birds. Neff (1937) records cases where both sexes arrived in large numbers together and promptly started to nest. We would guess this to be the usual procedure, and therefore strikingly different from that in *phoeniceus*.

Territory, threat display and song.—Intensive watching in an *uncrowded* portion of the Willow Slough colony showed that each male held a territory some six feet square, to which it usually confined its movements when in the colony, in which it sang and courted, and from which other males were driven out. An immature male was once tolerated in an adult's territory for two minutes, but it was promptly driven out when a female arrived. Fighting never seemed serious and boundary demonstrations, so

common in typical territorial birds, were not seen. At times when another male settled close, or flew low overhead, the owner would draw in its head and partly raise its epaulets—an unmistakable threat display, but rather feeble and not very common. The song, which is similar to that of *phoeniceus* but feebler, was uttered chiefly by males when perched alone. The thousands of songs from the colony blended into a confused babel. Territorial song flights were not seen. (Song also accompanied display to the female, as noted later.) In one instance, when an owner (A) departed for a time, a neighboring male (B) promptly took over his territory, courted a female there and even chased away an immature male. When another adjacent male (C) left, B also paid a short visit to C's territory.

The above observations were made during building and laying, some days after the colony was established. Possibly territorial behavior is more intense earlier, but our general impression is that territory, fighting, threat display and territorial "advertising" song, though definitely present, are feebly developed in *tricolor* as compared with *phoeniceus*, and perhaps are in process of disappearing in the evolution of the species. We were, indeed, unable to distinguish separate territories in the central part of the Willow Slough colony, where the population was denser. Whether this was due to difficulties of observation or to complete suppression of territorial behavior, we cannot say.

Courtship.—On May 13, females were continually flying in with building material. Some were building seriously, while others seemed to have no fixed nesting sites and would fly from one place to another and eventually drop their material. Frequently, on the arrival of a female in a territory, the resident male would expand and arch his wings downward, exposing the epaulets, and spread the tail; sometimes he also raised and lowered his wings or sang. Often, he would then flutter slowly down into the cattails until out of sight. This is a remarkable action for a courting bird, but the female sometimes followed, and his behavior presumably influenced her selection of a nest-site and mate. The arrival of certain females would greatly excite several males, while that of other females (already mated?) did not.

Both male and female often showed similar raising and lowering of expanded wings and tail as a preliminary to copulation. When inviting the male, the female usually arched the body and pointed the beak vertically upward, sometimes quivering the wings or raising and lowering the beak. In many species of birds, other males tend to rush up and disturb copulation if they see it; this was not noted in *A. tricolor*, which is just as well, in view of the proximity of the males. Once, from a tree in the colony, a male flew down in song and with expanded wings to copulate with a female below; this is the only case we observed of an aerial song-flight.

Polygamy and promiscuity.—As in *phoeniceus*, polygamy seems the rule. Of three males in contiguous territories with known boundaries, two had three and the other had two building females; laying occurred in seven of the eight nests. Occasionally a male displayed to two females in quick succession. All the females laid at about the same time. The females usually ignored each other, but occasionally chased each other short distances.

At times, two males were seen displaying to the same female, but usually one, the trespasser, was chased away. As already noted, in an owner's absence, his neighbor trespassed and courted one of his females. One female, which was individually distinguishable, returned with building material when her own male was absent; the next-door male postured sexually, whereupon she flew over to his territory and both displayed. Her own male then reappeared, and she returned and displayed with him. In neither case did copulation follow. These incidents suggest that promiscuity may

occur at times, but polygamy, not promiscuity, would seem the rule where we watched; we do not know that this is true for the denser parts of the colony. Allen (1914) saw a female *phoeniceus* copulate with two males in turn.

Immature males.—Males which had dull epaulets, and which we presume were year-old birds, usually showed no restriction to definite territories. As a result they were repeatedly chased away from occupied ground by adult males. These immature birds frequently dashed in and, without preliminary display, tried to copulate with females; the latter usually took to flight, so that vigorous chases resulted. When a taxidermic mount of a female was provided in an adult's territory, an immature male dashed in and copulated, then as hastily retreated.

The sexual chases characteristic of *phoeniceus* are not commonly observed in *tricolor* colonies; they would cause chaos if they occurred. All chases observed at the colony were by immature males save for one instance when an adult male pursued one of his neighbor's females.

Courtship away from the colony.—Occasional song, courtship displays and sexual chases were seen in the large mixed flocks that were feeding in rice fields away from the colony. Also, two males sang, displayed, and pursued females in a grassy field where large numbers of females had assembled to gather nest material eighty yards from a large colony. Dawson (1923) considered that the normal courtship procedure was for the males to gather in trees away from the colony and for the females to visit them there. Males frequented a group of willows and cottonwoods fifty yards from the Willow Slough colony, but we saw no evidence of extensive courtship there. Copulation was once recorded in one of a group of trees on the border of the Willow Slough colony, but this was conceivably on the edge of a male's territory. From present evidence, we consider courtship in the colony to be the rule, outside it the exception. The occurrence of the latter is, however, of great interest, since it bridges the gap between territorial Icteridae and the colonial Boat-tailed Grackle (*Cassidix mexicanus major*) which normally courts away from the nesting colonies, though occasional males show territorial behavior (McIlhenny, 1937).

Building, incubation, and feeding of young.—In *tricolor* only the female builds and incubates. As soon as incubation commences, courtship ceases and almost all the males leave their territories. During much of the day they are well away from the nesting colonies, but, at least at Willow Slough, large numbers returned to roost at dusk, not in their former territories, but together in a group in a nearby part of the slough; this behavior is in marked contrast to that in *phoeniceus*.

Both sexes fed the young, thereby presenting a parallel with the colonial-nesting Rose-colored Pastor (*Pastor roseus*) of Europe, in which males return to the colonies to feed young after an absence during the incubation period (Serebrennikov, 1931). After leaving the nest, young Tricolors gather in large groups and beg from adults indiscriminately; parents presumably feed any young birds. In one colony at this stage, some females were building and laying, presumably for second broods.

The incubation period, determined by comparing the stage of development on various dates through May and early June in each of four colonies, is about eleven days, the fledging period thirteen days.

Simultaneity of breeding.—Dawson (1923) and Neff (1937) have commented on the remarkable simultaneity of breeding in small colonies of *tricolor*, whereas in larger colonies different sections may be in rather different phases of the breeding cycle. One colony examined by Tyler (1907) was most advanced centrally and least advanced peripherally, with intermediate stages in between. At Willow Slough on May 13, almost

every female seemed to be building or laying; on May 16, all were laying or incubating; the young hatched between May 22 and May 27.

Three other colonies were examined on May 16. At one (Hammonton B) all the birds were building, laying, or had just completed clutches. Of a sample of 51 nests here, 19 were partly built, 11 had one egg, 8 two eggs, 10 three eggs, and only 4 had four eggs. At a second colony only 1.3 miles distant (Hammonton A) 35 nests had eggs well advanced in incubation and one held newly hatched young; 16 empty, presumably deserted, nests completed the sample of 52. At a third colony, some 6 miles distant (Reed's Creek), of 44 nests examined, 4 had well incubated eggs, 13 had both eggs and hatching young, 19 had young just hatched, 3 had young two days old, and 5 were empty. Another part of this same colony was rather more advanced. This simultaneity was rechecked on a later visit to all the afore-mentioned colonies on June 2. At the first (Hammonton B), all of 120 nests that were examined either contained young about 2 to 6 days of age or they had been deserted. At the second (Hammonton A), 163 nests had been evacuated by fledglings, one still contained young, 22 had fresh eggs (second broods), and 6 were deserted. At the third colony (Reed's Creek), all young were out of the nest, some being able to fly.

Lack (1933) has discussed some of the psychological factors affecting breeding time in birds. The above data show that social behavior must be added to these. With three colonies only a few miles apart, the differences in breeding time (synchronous, however, at each colony) cannot possibly be due solely to physical factors acting on the birds' physiological state. Such synchronous breeding also corroborates Darling's observations on *Larus* (1938) that breeding time is most closely synchronized in large colonies. *A. tricolor* does not show the "contagious" courtship behavior described in *Larus argentatus* by Goethe (1937) and Richter (1939). Linsdale (1938) and McIlhenney (1937) give evidence for simultaneity of nesting in the colonial icterids, *Xanthocephalus xanthocephalus* and *Cassidix mexicanus*, respectively, but, as is to be expected, it seems absent in the more closely related, but non-colonial *Agelaius phoeniceus* (Allen, *et al.*).

Mass destruction of eggs.—One colony near Marysville was reported to contain about 60,000 birds up to May 12. At the time of our first visit on May 16 only a few hundred were left. An examination of about one hundred nests revealed that more than three-fourths contained freshly broken eggs or minute shell chips; only a few were undisturbed and these latter contained freshly laid eggs. On June 2 no adult birds were seen in the vicinity; of 114 nests examined, 62 contained shell chips, 46 others were empty and 6 contained newly-hatched, but dead, young. Some of the nests showed small holes in the lining, as if made by birds' beaks.

Another instance of mass desertion and egg destruction occurred at the Willow Slough colony. Some 2000 birds were present there from May 10 to 16; on May 25 there were only about 250, and on May 30 only about 40; these were carrying food to young. Examination of nests in the colony on this latter date showed that many of them had been disturbed; the eggs were broken and the linings deranged.

Neff (1937) has reported several instances of wholesale desertions in Tricolor colonies, but no egg destruction. A colony described by Evermann (1919) was suddenly and almost completely deserted shortly after laying had occurred. Many of the nests were left with bits of broken egg shell much as we observed them at the Marysville colony; the destruction was attributed to skunks. Mailliard (1900) has described a colony which contained many abandoned nests, some with broken eggs. He suggests that the rapid growth of the tules in which the nests were situated may have caused

desertion of early (low) nests in favor of higher building sites. The destruction of exposed nests he attributed to Swainson Hawks (*Buteo swainsoni*) which abounded in the neighborhood. Neither predators nor signs of predator activity were apparent at either of the disrupted colonies under our observation. The egg destruction appeared to be bird work, probably of some moderately small species, and all available evidence seems to indicate that the members of the colony deserted en masse, first eating their own eggs. McIlhenny (1937) reports that adult males of *Cassidix* will occasionally eat nestlings in the colonies of their own species.

Sex ratio.—Males appear to predominate in the colonies during nest building and laying because they perch higher and because many females are away collecting building material. However, actual counts at Willow Slough showed at least equal numbers of the sexes, and sometimes up to two females per male. During incubation, the males disappear, and counts at various colonies revealed around twenty females to each male. Neither stage is satisfactory for estimating the true sex ratio. Perhaps a better time is when the young have hatched and the males are helping to feed. Counts in one colony (Reed's Creek) with newly hatched young on May 16 gave 149 males to 315 females, that is, 47 males per 100 females; on June 2, counts of adults flying in to feed fledglings gave 200 males to 427 females, the same ratio as above.

These counts probably indicate a real surplus of females, as was found by McIlhenny (1937) for the Boat-tailed Grackle. Some of the apparent surplus, however, may be due to the fact that females apparently mature and nest in one year, whereas at least some males do not breed the first year. A similar condition is suggested by Linsdale (1938) for *Xanthocephalus*. Species of birds with a marked preponderance of females are rare (Mayr, 1939).

Relations of A. tricolor with A. phoeniceus.—Many nests of *A. phoeniceus* were found in colonies of *tricolor*, although it is doubtful whether the former will take up territories after the latter have arrived. A male *phoeniceus* occasionally will chase a male *tricolor*; the reverse was not observed.

SUMMARY

1. The Tricolored Red-wing, *Agelaius tricolor*, is extremely colonial whereas the Red-wing, *A. phoeniceus*, is territorial.
2. In less dense parts of a Tricolor colony each male defends a few square feet from other males, and here it sings and its females nest. Territorial song, fighting and threat display are rather feeble and possibly are absent in crowded areas.
3. Polygamy is the rule; promiscuity possibly occurs at times. The best counts, made during the fledging period, show about 47 males to each 100 females.
4. Males desert their territories during incubation, but return to feed the young.
5. The members of each colony show a marked simultaneity in breeding, whereas neighboring colonies may be in different phases of the reproductive cycle.
6. Mass desertion of nests with destruction of eggs was observed in two instances.

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