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## AUTUMNAL BREEDING IN THE TRICOLORED BLACKBIRD

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IN temperate climates most birds breed in the spring or summer. But in many resident species there is a period of active sexual behavior in the autumn, during which time the gonads may attain full breeding size and some individuals may achieve spermatogenesis (Marshall, 1952a, 1959). This is followed by a period of winter inactivity, succeeded by rapid spring recovery and breeding. There are, however, exceptions to this general picture. In some species such as the Anna's Hummingbird, *Calypte anna*, and Horned Owl, *Bubo virginianus*, the breeding period begins in the early or middle part of the winter. In others (e.g., the Mourning Dove, *Zenaidura macroura*) the breeding period may extend from early spring well into the autumn without a break. The only temperate-zone species known to me that may breed throughout the year are the Rock Dove, *Columba livia*, and House Sparrow, *Passer domesticus*, in Britain (Lees, 1946; Summers-Smith, 1958), and the Red Crossbill, *Loxia curvirostra*, which has bred at all times of the year in North America (Griscom, 1937; Bailey, 1953). This may also prove to be the case in certain Australian desert birds (Keast, 1959), but this picture is as yet poorly worked out. Some of these species may even come into breeding condition while molting (Keast, 1959; Kemper, 1959).

In some species sporadic out-of-season breeding occurs. The unusually mild weather of November and December 1953, induced several species to breed in Britain (Snow, 1955), and some were successful in fledging young. Autumnal breeding regularly occurs in parts of Australia (Keast, 1958, 1959). In California, where mild temperatures prevail well into the autumn, regular autumnal breeding might be expected, but I have found references to autumnal breeding in only 11 species, although I have doubtless overlooked others. In some of

these such as the Mourning Dove (Howell, 1912); Band-tailed Pigeon, *Columba fasciata* (Willard, 1913; Abbott, 1927a; Grinnell, 1928; Jewett, 1941); Acorn Woodpecker, *Melanerpes formicivorus* (Michael, 1936); and Abert's Towhee, *Pipilo aberti* (Cardiff and Cardiff, 1950), this may merely represent delayed termination of a breeding season normally extending late into the summer as found by Pitelka (1950) on Santa Cruz Island in early September 1948. However, in other cases it appears to represent a definite second nesting period, separated from the spring breeding by molt and gonadal regression. Following violent summer rains, Gambel Quail, *Lophortyx gambelii*, bred in the fall of 1950, a year when spring rains failed in the Mojave and Colorado deserts (Macgregor and Inlay, 1951). In coastal California fall breeding has been noted in the California Thrasher, *Toxostoma redivivum* (Grinnell, 1900; Sargent, 1940; Davis, 1952; Dyer, unpubl.); Scrub Jay, *Aphelocoma coerulescens*, and California Quail, *Lophortyx californicus* (fide Mewaldt, 1959); Western Meadowlark, *Sturnella neglecta* (Abbott, 1927b); Lesser Goldfinch, *Spinus psaltria* (Sharp, 1908; Chambers, 1921; Abbott, 1927b); and House Finch, *Carpodacus mexicanus* (Smith, 1930; Howell and Burns, 1955). Some of these isolated nestings were correlated with the heavy rains of 1925 in southern California, but others did not accompany unusual climatic conditions. Thus, while the potential for autumnal breeding appears to be widespread in many Californian species, success apparently has not been great enough from those fall attempts to have given the habit selective advantage and thus to spread it through the population.

In the tropics, however, double breeding seasons, correlated with the double rainy seasons of many areas, are common (Moreau, 1950a; Miller, 1959a), although it has only recently been demonstrated that the same individuals may have two breeding periods within a year (Miller, 1959a). In other areas of the tropics single breeding seasons are the rule as in temperate regions. Such is the case in Central America (Skutch, 1950), Indonesia (Voous, 1950), and among Hawaiian (Richardson, 1957) and African sea birds (Moreau, 1950b). Year-round breeding is rare and is confined to those regions in which rainfall fluctuations are minimal (Miller, 1954).

#### AUTUMNAL COLONIES OF TRICOLORED BLACKBIRDS

Fall breeding was unknown in the Tricolored Blackbird, *Agelaius tricolor*, until I discovered a large breeding colony in Colusa County, California, on 16 October 1959. Search of many other areas in the Sacramento Valley revealed two additional colonies in Yuba County.

Breeding was successfully carried out in two of these colonies, but the birds in the third never progressed beyond the stage of manipulating nest material. Other areas in which breeding had occurred in spring had no fall colonies, and a general survey of the valley showed that breeding, although perhaps not confined to the two colonies I discovered, was not widespread.

Details of the unusual social organization in the Tricolored Blackbird will be given elsewhere, but it is necessary, for comparative purposes, to summarize the main features of spring breeding. Although morphologically very similar to the Red-winged Blackbird, *Agelaius phoeniceus*, the Tricolored Blackbird differs strikingly in its social organization, being the most highly colonial of North American passerines. Breeding colonies, seldom smaller than 100 nests, are sometimes as large as 100,000 to 200,000 nests. The males defend territories that average about 35 square feet, within which one to three nests are built by females. Nest building and incubation are performed exclusively by the female, but the male takes an active role in feeding the young. Most colonies are located in emergent aquatic vegetation, but they may be situated in trees along streams, weed patches, and even grain and alfalfa fields. From the nesting areas the adults fly as far as four miles to obtain food for the young. While the great concentration of birds in a small area is the most conspicuous feature of these colonies, the degree of synchrony among members of the colony is no less important, since, in most colonies, all the nests are built and eggs laid within the period of about one week.

The Colusa colony of October, five miles west of the city of Colusa in the heart of an extensive rice-growing district, was situated in a large duck-hunting club on which the cattails had been kept green by pumping water on them throughout the dry season. The nesting area occupied approximately 972,000 square feet, and assuming an average of one nest per 50 square feet, an estimate based on wading through most parts of the colony several times, approximately 19,500 nests were constructed. The Haskell Ranch colony of October, eight miles southeast of Marysville, was likewise located on a duck-hunting club, but here the water was supplied by runoff from the irrigated pastures that largely surrounded it. This colony occupied about 110,000 square feet, and approximately 2,150 nests were built.

The timing of major events in both colonies is shown in Table 1. In marked contrast to the synchrony of spring colonies, nest building in both autumnal colonies was protracted, especially at Colusa, and these later nestings did not solely represent growth on the periphery of the colony but were constructed throughout the colony area. Inasmuch

TABLE 1  
TIMING OF EVENTS — AUTUMN COLONIES OF TRICOLORED BLACKBIRDS  
1959

<i>Event</i>	<i>Duration</i>	
	<i>Colusa colony</i>	<i>Marysville colony</i>
Rainfall	18 Sept.	18 Sept.
Nest building	3 Oct. — 6 Nov.	3 Oct. — 21 Oct.
Egg laying	7 Oct. — 5 Nov.	7 Oct. — 18 Oct.
Incubation	11 Oct. — 11 Nov.	11 Oct. — 1 Nov.
Nestlings	23 Oct. — 25 Nov.	23 Oct. — 15 Nov.

as no individuals were color banded, it is not known whether these later nestings represented first attempts of new individuals or repeats of individuals having failed in their first try. However, in the Colusa colony, the number of birds involved in the breeding effort appeared to increase throughout the month of October, so that it is likely that later nestings represented, at least in part, first attempts of birds stimulated to breed by the reproductive behavior of other individuals.

In spite of the uniform density of cattail growth, particularly at Colusa, the nests were neither as densely nor as uniformly spaced as is typical of spring colonies, although there were regions of nest density in both colonies that compared favorably with that of spring. No instances of nests in actual contact were discovered. Clutch size was the same as in spring, clutches of three being most common with many of four and fewer of two. Many nests were deserted during building, but far more were deserted after the eggs had been deposited. Eggs were hatched in no more than one fourth of the nests in which they were laid. By breaking eggs in hundreds of deserted nests, I determined that desertion took place either immediately following laying or soon thereafter. No deserted eggs that were well incubated were found. The role of infertility in nest desertion is not known, but mass desertion at this particular phase of the breeding cycle may also occur in the spring when it is not due to infertility, but can be correlated with food availability in the surrounding environment.

Nestling survival was also poor in both colonies, few surviving past four days of age. In most instances only one nestling fledged per nest, but two young were fledged in at least several nests, and two nests were known to have fledged three young each. By repeated visits to both colonies during the time in which young were in the nests, I estimated that only about 50 young were fledged at the Haskell Ranch and 200–300 at Colusa. Nestling survival was poorer the first week of November, a period of very strong winds, than the following week.

TABLE 2  
CLIMATIC SUMMARY, SACRAMENTO, CALIFORNIA (1905-1958)

<i>Month</i>	<i>Mean temperature °F.</i>	<i>Mean precipitation in.</i>	<i>Mean wind velocity m. p. h.</i>
April	58.9	1.51	9.9
May	64.0	0.70	10.4
June	70.1	0.13	11.2
September	70.5	0.24	8.8
October	63.2	0.81	7.9
November	53.8	1.82	7.6

which was calm and sunny. Since the days at this time of year are very short and the parents were forced to bring adult rather than larval insects to the nestlings, the rate at which protein could be delivered was doubtless low, and starvation is the most probable cause of the high rate of nestling mortality.

Because of the large nonbreeding populations of blackbirds of several species in the vicinity of the nesting colonies, it was difficult to determine the extent of the areas exploited for food for the young. At the Haskell Ranch food was apparently gathered only on irrigated pastures, and I had no evidence that any adults flew farther than one mile to get it. At Colusa food was gathered in the shallow water of rice fields, which had been flooded after harvesting to attract ducks. Here also the adults did not appear to fly farther than one mile.

The Sacramento Valley experiences mild spring and autumn temperatures (Table 2), although cold nights are regular in November. Autumnal precipitation is most erratic, and means are misleading. In 1959 the only rain prior to late December fell in one storm on 18-19 September (Table 3). The sky then remained nearly cloudless for the duration of the breeding period. Both colonies started 15 days after the heavy rain, a point to be discussed later.

The drastic changes in the ecology of the Sacramento Valley produced by agriculture profoundly influence all the breeding activities of the Tricolored Blackbird. The large rice-growing areas are the center of abundance of the species in the valley today. The crop is harvested in late September and early October, and normally the stubble is burned shortly thereafter. If possible, the fields are plowed and the checks reformed before the rains; they offer neither cover nor insects unless they are flooded for hunting. Autumnal conditions are equally unfavorable for breeding in the dry farming areas and the rangeland, the latter being grazed to the ground early in the summer. The annual

TABLE 3  
SUMMARY OF WEATHER AT SACRAMENTO, CALIFORNIA—1959

<i>Month</i>	<i>Temperature</i>	
	<i>Mean temperature °F.</i>	<i>Departure from normal °F.</i>
April	63.8	+5.6
May	64.6	+0.6
June	74.2	+3.9
September	69.7	-0.6
October	66.3	+3.6
November	54.5	+1.4

  

<i>Month</i>	<i>Precipitation</i>	
	<i>Amount in.</i>	<i>Departure from normal in.</i>
April	0.21	-1.30
May	Trace	-0.70
June	0.00	-0.13
September	1.61	+1.37
October	0.00	-0.81
November	0.02	-1.80

grasses do not sprout until after the first heavy rains, and, normally, autumn and winter growth is slow, although occasionally, if early rains are followed by hot weather, there may be rapid growth and some plants may set seed. The irrigated pastures, which are restricted to certain parts of the valley, remain green and productive throughout the summer and early autumn. They and the duck-hunting areas are thus the only places in the valley capable of supporting any fall blackbird breeding.

#### MOLT AND GONADAL CYCLES IN THE TRICOLORED BLACKBIRD

Molt and gonadal cycles have never been studied in the Tricolored Blackbird, and our knowledge is based upon field observations and specimens collected during the fall breeding period. In the males, the feathers acquired in the postnuptial molt are strongly edged with brown, making an individual that has undergone the molt conspicuous at great distances in the field. All the males observed in the breeding colonies had undergone the normal summer molt and were breeding in the typical brown fall plumage. Fifty breeding birds that I collected had also completed the molt. Molt stage in females cannot be determined in the

field, but all of 34 breeding specimens taken in the colonies had also molted. Since males do not normally breed until they are two years old, it was not expected that immatures would be involved in the autumnal breeding, but participation by immature females was more likely. The sample of 88 birds collected contained only three immature males and one immature female. This suggests that six-month-old individuals were not involved in the breeding effort and were absent from the marsh during the day. None of the immatures had enlarged gonads, and although the female had completed her molt, the males had not. Gonads were not enlarged in any of the 35 male or 13 female Redwings collected.

Twelve nestlings were taken from nests and hand reared. The 10 that survived began their postjuvinal molt in late December, completing it in early February. They are being kept for observations on future molts and gonadal cycles.

In an attempt to determine whether any adults involved in the autumnal breeding had also bred in the spring, I sectioned ovaries from 25 females, hoping to find follicle scars indicating spring activity. Unfortunately, it has not been possible to distinguish ruptured from atretic follicles in the material sectioned, although this may be possible when a collection of ovaries made through the summer period has been obtained and studied. In any event, double breeding seems likely in view of the large number of birds involved and since large and successful colonies nested in spring close to the sites of the fall colonies. More precise information on this point is highly desirable.

#### FACTORS INITIATING FALL BREEDING

Perhaps because of the stimulus provided by Rowan's (1925) important experiments on the role of light in influencing reproductive cycles in birds, there is more experimental evidence for its influence on avian gonadal cycles than any other factor (Farner, 1959; Wolfson, 1959a). Most species that have been investigated have responded in some way to gross changes in the duration of photoperiod. Since no fall breeding bird has been investigated experimentally, decreasing day lengths are not known to stimulate any bird, but there is suggestive evidence that mammals (Bissonnette, 1941; Yeates, 1947) and fish (Hoover and Hubbard, 1937) do respond to decreasing photoperiod. Particularly in mammals where, because of long gestation periods or delayed implantation, mating regularly occurs in the autumn, response to decreasing day length may be widespread.

Wolfson (1959a and b) has argued that short days are necessary

before the preparatory phase of the avian testis can be completed. Since thousands of Tricolored Blackbirds came into breeding condition in September 1959, without having experienced short day lengths, it is clear that such a stimulus is not necessary to terminate a refractory period in this species, if indeed, it even has one. Wolfson has informed me that he is unable to detect any refractory period in the tropical African weaver, *Quelea quelea*, and this may be widespread among tropical and nomadic species. Refractory periods, in those species possessing them, are doubtless an adaptation preventing the species from responding to environmental conditions at a time of year when attempted reproduction would not be successful enough to carry selective advantage (Miller, 1959b).

As far as the Tricolored Blackbird is concerned, fall breeding does not exclude the operation of photoperiodic stimulation (Farner, 1959). However, even if the birds did prepare gonadally on the long photoperiods of summer immediately following the molt, it seems unlikely that this alone could have produced the timing of actual breeding observed this autumn, and a consideration of additional environmental influences seems warranted.

It is becoming increasingly apparent that biological clocks of high accuracy are possessed by many species (Brown, 1957; Pittendrigh, 1958a; Blake, 1959), and the tenacity with which some tropical and southern hemisphere species cling to their normal breeding periods when kept in the north-temperate zone (Baker and Ranson, 1938; Bedford and Marshall, 1945; Davis, 1954) is suggestive of their importance in birds. However, there is no evidence on this point for the Tricolored Blackbird.

The accelerating influence of warmth and the inhibiting influence of cold is well known in most north-temperate species (Marshall, 1959) in spite of Rowan's demonstration that Slate-colored Juncos (*Junco hyemalis*) came into breeding condition in the middle of the winter in Alberta when subjected to photoperiod manipulation. In California temperatures are mild both in spring and fall, although increasing in the spring and decreasing in the fall. Whereas suitable temperatures are probably necessary for both spring and fall breeding in the Tricolored Blackbird, temperature is unlikely to have been influential either in preparing the birds for autumnal breeding or triggering them to breed.

Many experiments and field observations suggest that rainfall is important in stimulating birds to breed, but normally it is difficult, if not impossible, to distinguish rainfall *per se* from the effects it produces

upon the vegetation. In an experiment designed to test this, Marshall and Disney (1957) showed in *Quelea quelea* that immatures breeding for the first time responded to the green grass whereas the adults responded directly to the rainfall. Change of response to rainfall with age may be widespread among tropical and desert species, and its investigation would be an important line of study. Captive Galapagos finches in California were stimulated to sing when rain fell on the cages (Orr, 1945), but recent observations on the Galapagos Islands have shown that many of the species breed prior to the rains (R. I. Bowman, pers. comm.) in apparent anticipation of them (see also Moreau, 1950), so that caution in the interpretation of results with caged birds is necessary. Also, gonadal cycles are poorly known in species that respond suddenly to rain, and, hence, the state of the gonads at the time of rainfall is unknown. Allen Keast informs me that he has gathered evidence showing that many Australian desert birds have enlarged gonads long before the rain actually falls so that ovulation can be completed within two weeks of the first fall of rain.

The rainfall cycle is an important seasonal variable in lowland California. The summer drought is extreme and constant in the Sacramento Valley, there being no measurable mean precipitation for either July or August. The spring breeding season comes at the end of the rainy period, and there is no evidence that rains in any way influence initiation of spring nesting. It is difficult to think of any selective advantage that might be achieved by responding to rains at this time. In the autumn, however, rain might be more influential. In the absence of irrigation, rainfall would be necessary to produce grass growth, and even in 1959 in the irrigated country, both colonies started (as dated from the time of hatching of the first eggs) 15 days after the heavy rain of 18 September. This is strong circumstantial evidence that the heavy rain was important in causing fall breeding, but experimental work is needed on this point.

Since the breeding seasons of most birds are timed so that the young are being fed when the food supply is most readily available, direct influence of food might be expected to be important in stimulating breeding. No experimental evidence on this point is available, but there is some indirect evidence (Marshall, 1951, 1952b). Reduced food intake is known to depress gonadal activity in domestic fowl (Breneman, 1955), and out-of-season breeding in Starlings, *Sturnus vulgaris*, has been thought to be due to man-provided food (Marshall, 1952a). Clutch size of predators varies in response to lemming population density, and if lemmings are too scarce, breeding may be altogether inhibited (Pitelka *et al.*, 1955). Other references are given in Lack

(1954). In all these cases the mechanisms for the response are unknown.

When fall breeding began in the Tricolored Blackbird, the adults were subsisting largely on rice, which is found in great abundance in the stubble fields after harvesting. Clearly breeding could not have been attempted if the adults were not able to supply their own needs in a short period of time each day, but this condition is present in many areas of the valley where breeding did not occur, and many other species that do not breed in the autumn have equally abundant food resources available to them at this season of the year. It is possible that the adults may perceive the insects in the irrigated pastures and freshly flooded stubble fields, but this does not appear likely.

Another category of factors known to influence some bird species can be termed general ecological conditions. Again, there is a wealth of scattered observational evidence but a scarcity of experimental results. In the Tricolored Blackbird these conditions may be of prime importance as the timing of spring breeding in northern California varies several weeks in response to agricultural practices (Orians, MS). The unique fall habitat conditions at both colonies have already been noted. Thus, both the green cattail growth in which all nests were placed as well as the pastures and flooded fields in which food was gathered were irrigation products of restricted distribution in the valley. Such ecological conditions, as a stimulating mechanism, or at least as a permissive factor, are probably important for both fall and spring breeding and, perhaps combined with the early rain, were responsible for triggering fall breeding. Unfortunately, however, I do not know whether the birds had prepared gonadally prior to the rain, and future collecting will be necessary to clarify the role of photoperiod in the Tricolored Blackbird breeding cycle.

In any event, timing mechanisms in avian reproductive biology must be considered in the perspective of adaptational and evolutionary explanations (Farner, 1958; Pittendrigh, 1958b). The great variability between bird species in their response to photoperiod manipulation in the laboratory, in their reproductive cycles when transplanted to another hemisphere, in their possession of a refractory period, speed of gonad maturation, length of time of maintenance of active gonads, variation in clutch size in response to ecological conditions, variability of breeding periods in desert regions, all point to great evolutionary flexibility in the mechanisms behind them. Hence, Wolfson's (1959a) claim that breeding periods in transequatorial breeders, the small tropical clutch sizes in most birds, and supposed smaller size differences between inactive and active testes in tropical species (Moreau, Wilk and Rowan,

TABLE 4  
BREEDING SEASONS OF AUSTRALIAN PARROTS IN BRITISH ZOOS\*

<i>Species</i>	<i>Range</i>
<i>I. Species breeding in spring or summer in both hemispheres.</i>	
<i>Polytelis swainsoni</i>	Inland parts of New South Wales, Victoria and South Australia.
<i>Platycercus caledonicus flaveolus</i>	Western New South Wales and adjacent parts of Victoria and South Australia.
<i>Platycercus icterotis</i>	Southwestern Australia.
<i>Platycercus zonarius barnardi</i>	Southwestern Queensland, interior of New South Wales, mallee of South Australia and adjacent portions of Victoria.
<i>Psephotus haemonotus</i>	Southeastern Australia.
<i>Psephotus varius</i>	Interior of South Australia and New South Wales.
<i>Neophema elegans</i>	Southwestern Australia, South Australia and adjacent parts of New South Wales and Victoria.
<i>II. Species retaining their southern hemisphere rhythm.</i>	
<i>Trichoglossus haematod</i>	Northern Australia.
<i>Platycercus venustus</i>	Northwestern Australia and Northern Territory.
<i>Melopsittacus undulatus</i>	Nomadic over most of Australia.
<i>Psephotus chrysopterygius</i>	Northern Territory.

\* Breeding data from Baker and Ranson (1938). Ranges after Peters (1937).

1947) are indications of the influence of photoperiod is not likely to be true. All three of these suggestions demand that the species are unable to escape from the depressing influence of an inadequate photoperiod and, hence, are ecologically hindered. Even Wolfson's temperate Slate-colored Juncos prepare well on constant photoperiods of 12 hours' duration, and it seems unreasonable to postulate that tropical species are not reproducing at their ecological optimum. This does not mean, however, that photoperiod is totally without influence, because, as Wolfson has pointed out, it cannot be eliminated merely because of its constancy.

With respect to species retaining their normal calendar month for breeding after hemisphere transplantation, Wolfson offers the alternative hypothesis that "the day length requirement of these species is such that the time of the breeding season in relation to the calendar year is not altered." I find it difficult to devise a scheme by which the drastically altered photoperiod could produce the timing reported in these cases. The facts suggest to me that day length requirements in these species are such that almost anything can be done within wide

limits without altering the normal internal sexual rhythm. Further analysis of the data on Australian parrots in Baker and Ranson's paper reveals an interesting fact. All those species that change over to the northern spring are from southern Australia, while all those retaining their ancestral breeding season are from northern, *i.e.*, tropical, Australia (Table 4). The one exception is a nomadic species (*Melopsittacus*), which is known to breed independently of season in the Australian deserts. Thus, as might have been expected, photoperiod seems to be less important to the tropical than to the temperate parrots.

#### THE ANTIQUITY OF FALL BREEDING

In the spring, when all blackbird species other than the Tricolor are widely dispersed, a dense aggregation of blackbirds always means a Tricolor colony in action. In the fall, however, not only are all the species of blackbirds highly aggregated, but their numbers are also swollen by the influx of millions of birds from elsewhere in western North America. All marshes harbor large roosting flocks of birds, which spend much of the day resting, preening, and singing in the cattails. Nesting material is readily available within a few feet of the nest site and need not be conspicuously carried for great distances as often happens in the spring. The adult insects brought to the nestlings are smaller than the larvae brought in the spring so that adult blackbirds flying to the colonies with food are easily overlooked unless closely examined with binoculars. The Haskell Ranch marsh was visited weekly by university-trained biologists in the fall of 1959, and none of them noticed the colony until it was pointed out to them. Thus, breeding could have been going on, at least sporadically, in the fall for some time without having been observed.

In many respects the climate of the Sacramento Valley in the autumn is suitable for breeding. Low mean wind velocities combined with warm weather help to make this period favorable (Table 2). Clearly, the critical factor is the frequency of occurrence of sufficient rains to initiate and maintain adequate vegetative growth to produce the insects necessary to support breeding. I have therefore examined the weather records for Sacramento for the last 60 years to determine the pattern of autumnal rains. If we assume that rain is necessary to trigger autumnal breeding and that the 15 days elapsing between the rain and the start of breeding in the fall of 1959 is representative of the time necessary to come into final breeding condition, a total of 50 days would be required from the first rain until the first young fledge. If we further assume that fledging after 1 December is not likely to be suc-

cessful enough to give selective advantage to late fall breeders, it follows that the first rain must fall before 11 October. If only one-half inch of rain need fall to initiate breeding and another one-half inch in the following month to sustain plant growth, it would have been possible for Tricolors to have bred 18 times in the past 60 years. However, if one inch is needed to initiate, and another inch to maintain breeding, there could have been only seven successful nestings during that period. Heavy September rains with follow-up precipitation have occurred only twice.

Other considerations suggest that the above requirements are too liberal. In other regions out-of-season breeding only occurs after much heavier rains than ever fall in California in the early autumn (Serventy and Marshall, 1957), and although lesser amounts may stimulate gonadal activity, it is not enough to sustain breeding (Keast and Marshall, 1954). Interpretation, however, is hindered by our scanty knowledge of the original vegetation of the Sacramento Valley and its probable response to autumn rains. Before the arrival of European man, valley vegetation probably consisted of a mixture of perennial bunchgrass-oak parkland, ephemeral pools, alkaline flats, extensive marshes, and dense riparian jungles. Virtually none of these vegetation types remain today. Largely gone also is the extensive late winter flooding formerly characteristic of the valley. Early explorers repeatedly reported the Sacramento-San Joaquin Valley as being a huge lake 40 miles wide and 300 miles long.

The response of the current annual vegetation to autumnal rains is usually slow, rapid growth not occurring normally until early spring. The response of perennial grasses was probably slower both because of the growth characteristics of perennials and the retarding influence of mulch. The reflooding of the marshes and alkaline flats probably did not occur until late in the fall or perhaps not until winter in dry years. Thus, the presence of emergent vegetation and production of insect populations are likely to have been rare if not absent.

Agriculture has changed the Sacramento Valley in many ways. The draining of the marshes and establishment of flood-control measures have been among the most important for blackbirds. Such changes resulted in a deterioration of blackbird habitat, but this was in part compensated for by the development of irrigation, particularly rice culture and irrigated pastures, which succeeded the wheat raising of the 1800's. Extensive irrigation began in California at the turn of the century, grew rapidly during the 1920's, 1930's, and 1940's, until in 1956 about seven million acres were under irrigation, over one million of these being in the Sacramento Valley and over three million in the

TABLE 5  
CALIFORNIA RICE ACREAGES

<i>Year</i>	<i>Acres</i>
1912	1,600
1915	30,000
1920	162,000
1925	103,000
1930	110,000
1935	100,000
1940	118,000
1945	230,000
1948	236,000

San Joaquin Valley (Farrell, 1958). Rice became an important crop about 1920, and today approximately 250,000 acres are planted to this grass (U.S. Dept. Agric. Prod. and Market. Admin., 1949), current acreage being limited by governmental restrictions (Table 5). Following the development of irrigation was the establishment of duck-hunting clubs. Clubs are of many types, from a small pothole used by a farmer and a few of his friends to large, managed marshes with permanent caretakers and elaborate buildings. The effect, so far as blackbirds are concerned, is to provide green cattail growth at a time of year when it is otherwise unavailable, and to provide extensive feeding areas in the stubble fields flooded for hunting. Today about 31,500 acres of land are in duck clubs in the Sacramento Valley (P. L. Arend, unpubl.).

Evidence that favors the view that fall breeding has been taking place, at least sporadically, for a long time is provided by the suitable temperature and wind conditions in the valley in the autumn. Heavy rains do occur occasionally in the early autumn, and there is suggestive evidence that the fall breeding of 1959 was triggered by rain. Also, the possibility of more suitable conditions in the original vegetation cannot be ruled out.

Set against this, however, is evidence suggesting that breeding in the autumn may have a recent origin. The response of the original vegetation to fall rains was probably insufficiently rapid to provide the insect population needed to support breeding. The breeding of 1959, although apparently stimulated by natural rainfall, was completely dependent upon nesting sites and feeding areas provided by irrigation, and, since no additional rain fell during the breeding period, nesting would have been a complete failure under natural conditions. The poor synchrony and lack of good colony structure, which characterized both fall colonies, suggest that fall breeding is of such recent origin that time has

not been available for the species to have evolved a good response to autumnal conditions. Furthermore, if breeding had been going on for a long time, one might have expected the species to have evolved a smaller autumnal clutch size because feeding conditions would always be poorer than in spring due to short day lengths and lower insect populations. Yet clutch size was the same in fall and spring colonies. Suggestive evidence is also provided by the failure of any other Californian birds to show regular fall breeding. If environmental conditions had been suitable in the past, it is likely that a number of species would have been able to capitalize upon them. In western Australia, where fall breeding occurs following heavy, unseasonal, late summer rains, many species respond in large numbers (Serventy and Marshall, 1957). In 1953, following heavy late March rains, 22 species were found breeding or showing signs of it, and 16 others were shown histologically to have been stimulated. Heavy rains in February 1955 were followed by breeding in at least 40 species, and an additional seven species were influenced. In all cases there had been normal breeding the previous spring.

I therefore conclude that fall breeding in the Tricolored Blackbird, although it may well have taken place prior to 1959, is most probably a man-induced phenomenon, which postdates widespread irrigation in the valleys of California. Furthermore, its future would seem to depend upon the continuance of agricultural and hunting practices that provide nesting and feeding sites at this time of the year. At first it might seem unlikely that an additional breeding season could be created by agricultural modification of the country, but Belcher (1930) noticed grass warblers breeding out of season in Nyasaland when banana plantations were flooded, resulting in a rank growth of vegetation. As irrigation continues to modify the vegetation in many parts of the earth, it may well be that many species will respond in a similar manner.

#### NATURAL SELECTION AND AUTUMNAL BREEDING

Whether or not a double breeding season in the Tricolored Blackbird will confer selective advantage to those individuals responding to autumn conditions will depend upon a delicate balance between the advantages of the increased productivity and the increased mortality. Mortality among adults undertaking autumnal breeding may be expected to be greater than among nonbreeders, because there may be increased susceptibility to predation or increased winter mortality resulting from the birds having entered the winter in poorer physical condition as a result of the metabolic strain of breeding. If the survival of fall-

produced young is great enough to offset this increased mortality, advantage will accrue to fall breeders, and the proportion of the population responding to suitable fall conditions will increase.

The increase in productivity made possible by autumnal breeding varies greatly depending upon the breeding pattern of the individuals within the population. The intrinsic rate of natural increase for the species would be most greatly increased if fall breeding made possible reproduction by six-month-old individuals, since the age at which first offspring are produced has the greatest influence upon this population parameter (Cole, 1954). As we have seen, however, breeding by immature birds does not seem to have been the case, although it cannot definitely be excluded. The increase in productivity made possible by breeding twice each year once the age of one year has been reached is less pronounced than in the above situation, but it is nonetheless significant. It is nearly equivalent to doubling the number of fledglings reared if survival is the same in spring and fall, and if fall-hatched young are able to breed the following spring. However, we have seen that nestling survival in the fall was very poor, and we do not know whether fall-hatched females will be able to breed the following spring. Males most surely will not, but they may breed when they are one and one-half years old, which is earlier than spring-hatched individuals do. If, in addition, fall breeders were unable to breed the following spring, the reproductive rate would be further lowered, in fact lowered below what it would be if only spring breeding were attempted. If, however, we assume that adults are capable of breeding twice annually, the most likely situation based upon present evidence, even low success among autumnal breeders is likely to carry selective advantage, because mortality among adults due to predators in the Sacramento Valley seems to be very low. Accipitrine hawks are very scarce, and the easy feeding conditions for adult blackbirds in the fall make it likely that they could rapidly make good the physical strain incurred through breeding, so that their winter mortality should be little affected if at all. However, the spread of genotypes with low thresholds of response to fall conditions will not necessarily cause widespread fall breeding because agricultural practices insure that threshold stimuli will occur only in restricted areas. If the use of irrigated pastures and the practice of flooding the rice fields in the autumn continue, fall breeding should persist as a minor but interesting part of the breeding cycle of the Tricolored Blackbird.

## SUMMARY

Thousands of Tricolored Blackbirds bred in at least two colonies in the Sacramento Valley of California in October and November 1959. Nesting success was low, but some young were fledged from both colonies. Breeding was entirely dependent upon agricultural and duck-hunting practices, and it is likely that fall breeding is of recent origin, postdating irrigation in that area. Rainfall seems to be the most likely factor inducing fall nesting, but the population may have been physiologically prepared some time before the rains came. Because of favorable conditions for adult blackbirds, fall breeding is likely to confer selective advantage upon those individuals responding to autumnal conditions in spite of low breeding success such as was observed in 1959.

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