

THE CONDOR

VOLUME 54

JANUARY-FEBRUARY, 1952

NUMBER 1

BREEDING BEHAVIOR OF THE BREWER BLACKBIRD

By LAIDLAW WILLIAMS

The objective of this paper is to report results of a behavior study of the Brewer Blackbird (*Euphagus cyanocephalus*) in which color bands were used extensively. It principally concerns a nesting colony at the mouth of the Carmel River, Monterey County, California. The work covered six breeding seasons, 1942-1947, and a few supplementary observations were made in the spring of 1948.

The colony is situated at the edge of a marsh. The birds nest principally in Monterey pines (*Pinus radiata*) which, although native to the region, were planted along the streets of a subdivision adjacent to the marsh on what was originally chaparral land. Although the birds forage on lawns, streets, and food trays, they spend a large part of their time on the marsh area, undisturbed in the years of this study. Tules (*Scirpus*), which grow in patches on the edge of the marsh, as well as the pines are used for roosting and day-time resting places. Electric light wires and poles along the streets, as well as the tips of pine branches, are used for display and "guard perches" (fig. 1).

All trapping was done at the river-mouth colony. Three hundred and eighteen birds were color-banded, 158 males and 160 females. The total number of banded birds breeding in the colony over the six years was 117, 47 males and 70 females. In addition, there were eight breeding birds of each sex over the six years that I was unable to trap and band.

I could detect no migration, but found my birds wandering to points as far as 6 miles north, 4½ miles east, 6 miles south, and 4 miles northwest of the banding station at the colony.

At the river-mouth colony most of the birds nested in thick tufts of pine needles, usually at or near the ends of limbs, 7 to 43 feet above the ground. Occasionally planted cypresses (*Cupressus*) were also used. Most of the nests were from 20 to 30 feet up, making close inspection impossible in most cases. This also made the banding of nestlings possible in only a few cases.

The annual cycle of the population studied may be divided into two parts. The *non-breeding period* extends roughly from the end of July to the end of January, and flocks of inconsistent size and membership wander from place to place. However, a nucleus of the colony birds always can be found in the colony area. This period is somewhat interrupted by a fall period of "recrudescence of pairing behavior," weak and irregular, that can be observed at the colony in September and October and occasionally in November. The *breeding period* extends roughly from the end of January through July, and it may be subdivided as follows: *phase 1*, segregation and assortment into pairs—pair formation; *phase 2*, nest-building, copulation and egg-laying; *phase 3*, incubation; *phase 4*, nestling care; and *phase 5*, fledgling care.

In this paper only the breeding period is to be treated in detail. But before its phases are considered in detail, it is necessary to describe calls and displays and to suggest, at least tentatively, interpretations the basis for which will be evident in later sections.

CALLS

1. *Squeee*, uttered by both sexes but more frequently by males; a loud, hoarse whistle with a decided upward inflection. This note and the *tee-uuu* (below) are the loudest in the repertory.

2. *Schl-r-r-r-up*, used by both sexes but more frequently by males; a comparatively subdued, toneless whirring gurgle, aptly described by Mulford (1936) as "a rush of air without vocal accompaniment." This note and the *squeee* are subject to considerable individual variation. Some birds in the colony could be recognized readily by a characteristic variation of one or the other of these two calls.

3. *Kit-tit-tit-tit* (reduced to the simplest form, which is barely suggestive). This is sometimes irregular in delivery, sometimes rhythmic and may sound like *kit-r-r*, *kit-r-r*;



Fig. 1. Marsh and creek area adjacent to breeding colony of Brewer Blackbirds at mouth of Carmel River, Monterey County, California, April 6, 1944. Pines, wires, and poles at the right were used by members of the colony.

it varies in quality of tone and intensity and rapidity of utterance. It is used rarely by males, when bickering over food. Females use it very frequently in quarrels at nest sites and in other situations of aggression. It is regularly used as an accompaniment to the generalized female display (see below). It is also frequently heard accompanying bickerings at the roost when the sexes using it cannot always be identified.

4. *Chug-chug-chug*, or *tucker-tucker-tucker*, or *tit-tit-tit*, etc.; used by males when in the elevated tail display. This sometimes resembles the *kit* notes described above.

5. The female copulatory note, a soft, low, steady series of tapping notes, which are very different from any of the other utterances.

6. *Tschup*, used by both sexes, the "scolding note," uttered when there is a disturbance near the nest or young, or in other situations of excitement.

7. Flocking note, used by both sexes, shorter, higher, less loud and with less *s* sound and more *t* sound than the scolding note.

8. *Tee-uuu*, or *tsee-eur*, or *pit-ee*, a loud, clear, thin whistle, the only *clear* whistled note in the repertory. In each variation the second syllable is lower in pitch than the first. It is used as a warning note, as when a hawk or some other large bird flies over.

9. The *squawk*, a low, scratchy note uttered when two birds make contact during chases (see below); when one bird seizes the other in fights; or when a blackbird is captured by a hawk. It is also given by a blackbird when diving at a hawk. Mulford (*op. cit.*) writes this note as *chaw*.

10. *Tup*, a signal to the young, uttered by the adult when approaching with food for nestlings, but more frequently when approaching fledglings, as well as when flying about accompanied by well-grown but still dependent young.

11. Peeping sounds of young nestlings.

12. Begging notes of older nestlings and fledglings. These notes are quite different from the peeping notes of younger nestlings. They are a low, hoarse, scratchy series of rhythmic notes, *tut-utz-utz*.

13. During intervals between visits of adults, the fledgling utters a note resembling but weaker than the *tschup*; it has a shorter vowel sound and a more nasal quality. This might be called a location note.

DISPLAYS

1. *The ruff-out* (figs. 2-5). This is employed by both sexes, but more often by males. The bird holds the bill almost horizontally, or pointed somewhat upward, and ruffs out many of the contour feathers, especially those of the head and neck, the breast and upper tail coverts (the rump feathers remain flat, as shown in fig. 2). At the same time it partially spreads the wings downward and fans and depresses the tail. As the ruffing and spreading reach a climax, either *squeee* or *schl-r-r-r-up* is uttered and the display immediately subsides. The notes are never uttered without the accompanying display, although the latter varies greatly in the extent of ruffing and spreading. When used by the female it is less pronounced and the utterance is more subdued. The whole display lasts only about a second or two.

The male performs the ruff-out when perched alone. He may perch for some time at one place ruffing out at intervals, sometimes uttering *schl-r-r-r-up*, sometimes *squeee*. Males may display to each other in aggressive threat, perching face to face a few feet apart. Females less frequently ruff out when perched alone. Occasionally, although far less frequently than males, they use this display in threat, also.

2. *Mutual display*.—Members of a pair may perch on wires or pine tips about 18 inches apart and exchange the ruff-out with accompanying notes described above. Further consideration of the behavior of the pair in this situation is found below under "phase 1."

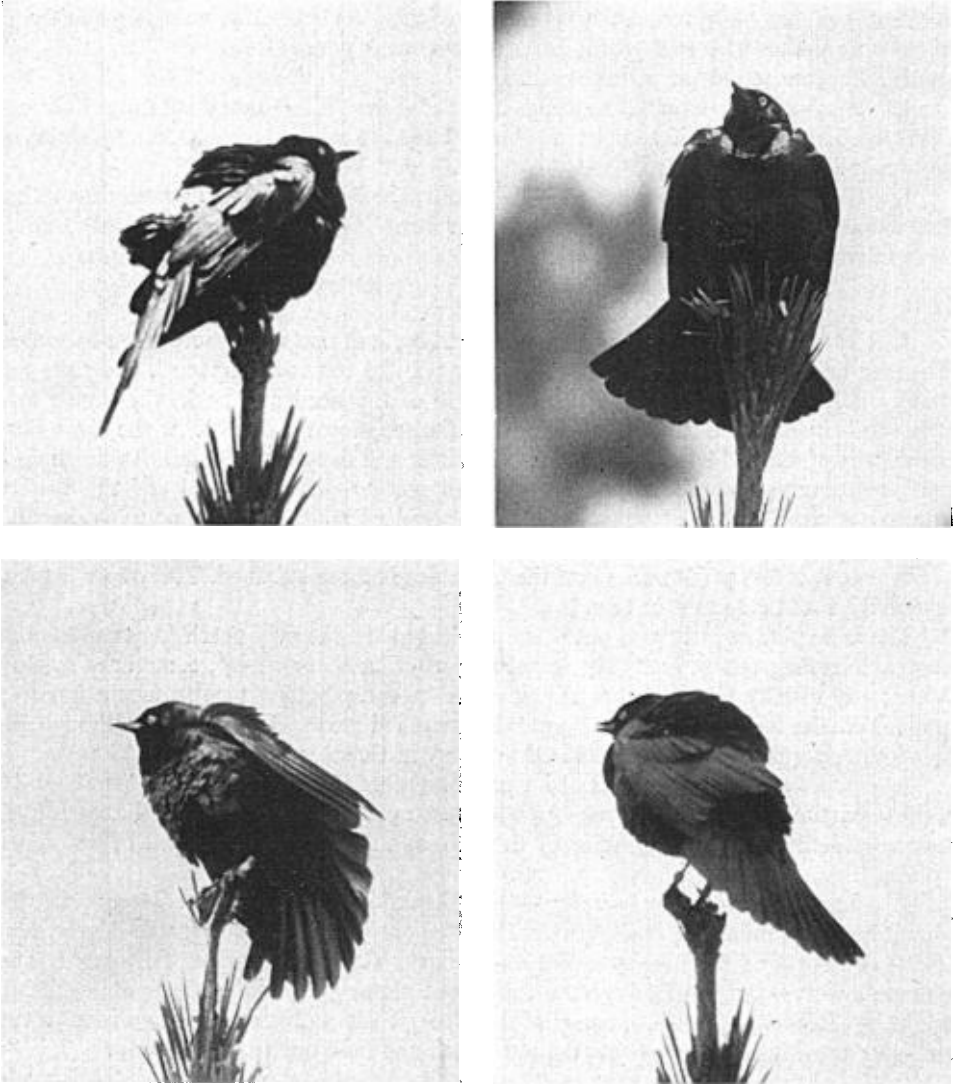
3. *The male pre-coital display*.—This display of the male immediately precedes mounting and copulation. The feathers are ruffed out to a more exaggerated degree than in the ruff-out, and the display is not momentary. The bill is pointed downward. The pale yellow eyes, surrounded by the ruffed out glossy purplish feathers of the head, might be considered an effective part of the display. The tail is more spread than in the ruff-out; the wings are somewhat more drooped and held out from the body.

In this posture the male deliberately approaches the female. If the approach is made on the ground, the feathers of the wings and tail actually scrape it. In approaching the female a half-circle is often made by the strutting male. Sometimes he says *schlr-r-r-up* or *squeee*, but often the approach is silent.

4. *The female generalized display*.—The bill is held upward at a slight angle; no feathers are ruffed; the wings are held somewhat out from the body, drooped and vibrated; the tail is cocked but not spread (fig. 6). This display is always accompanied by the *kit* note (number 3 above).

5. *The female pre-coital display*.—This invitation to copulation is similar to the

generalized display, but the tail is cocked at a steeper angle and the body is tipped forward. There is a very specific series of notes given at this time (number 5 above). Just before the male mounts, the wings of the female become motionless and the body rigid.



Figs. 2-5. Male Brewer Blackbird in ruff-out display.

As the male pre-coital display is an exaggeration of the ruff-out, so too is the female pre-coital an exaggeration of the female generalized display. But the female pre-coital is a necessary prelude to copulation; males do not mount and effect copulation unless the female remains rigid at the climax of the pre-coital display. She attracts the male by posturing and wing-quivering, but copulation does not ensue unless at the male's close approach she stops the wing action and stands rigid. The generalized

display of the female is used long before copulation actually occurs. From the beginning of the breeding period this display and the characteristic *kit-tit-tit* note has a definitely attracting effect on the male and also is part of the female's response to the advances of the male. But the *kit* call is used also by females in pursuit of other females who have trespassed on a nest-site area and in other aggressive situations (see also below under "phase 1").

6. *The male elevated tail display*.—This display is similar to the generalized female display in body appearance, wing action, and tail cocking, but with the tail somewhat



Fig. 6. Female Brewer Blackbird in generalized display.

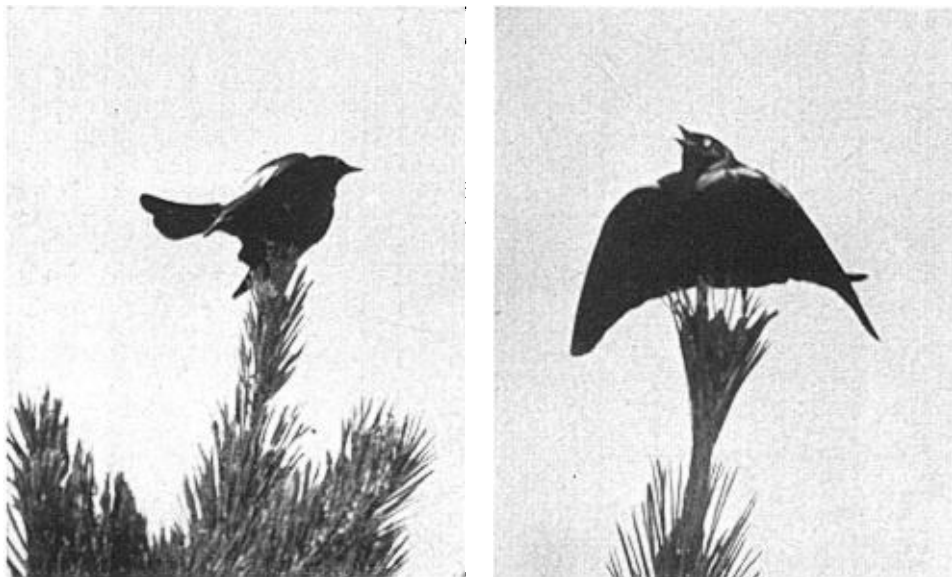
spread and the wings possibly held out a bit wider (figs. 7-8). This is accompanied by the *chug-chug* or *tucker* notes; or the notes *kit-tit-tit*, which resemble the notes uttered principally by females (call number 3 above). This display is used by a male perched alone. It may be performed in alternation with the ruff-out. It is used by a male when a female that has been mutually displaying with him leaves him alone, when his mate is within sight but is not at the moment walking with him or perching within the usual 18 inches (see below), and when a flying female is about to perch beside him. In the last instance, the male may have been displaying the ruff-out while she was absent, but as she approaches he changes to this display. When the female has alighted he changes back to the ruff-out again, and mutual display may result.

The elevated tail display is used by a male on his guard perch as the female comes

and goes past him on the way to the nest. Because it is used when the female is absent and is terminated when she arrives, it is possible that it may function as an invitation or an indication of a receptive state. It is never addressed to another male and has no significance as a threat, unlike the ruff-out, which is used both toward other males and toward females in mutual display.

The similarity of this male display to the generalized female display is very marked.

7. *The head-up display.*—Employed regularly by males, rarely by females. The body is stretched upward, the bill pointing more or less vertically, the tail downward and not spread. No feathers are ruffed and they may even be compressed. The bird's



Figs. 7 and 8. Male Brewer Blackbird in elevated tail display.

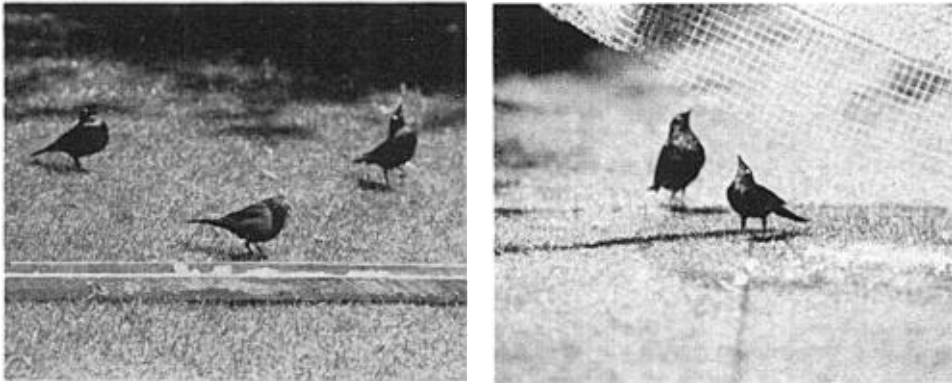
body assumes a very drawn-out, slim appearance. This display is performed chiefly by one male toward another male that is approaching or displaying toward his mate. The intruding male usually responds with the same display and the two birds may stand stiffly in this pose facing each other a few feet apart. They hold this pose for as long as 2 to 4 seconds. If the encounter occurs on the ground the two males often proceed to walk a few feet away from the female, abreast of each other and still maintaining the pose. This display is used also in aggressive situations in general. The rare occasions when a female has been seen in this display concern aggressive situations at a nest site.

It may seem difficult to account for two such different appearing displays as head-up and ruff-out serving a similar purpose, that is, aggressive threat. The ruff-out may be used as a distant threat, but the head-up display is never used except where males, and rarely females, confront each other at close quarters (see also below under "phase 1").

Most of the calls and displays other than the pre-cotential displays and the female copulatory notes have been noted in rudimentary form during the non-breeding season in flocks resting on wires or at feeding stations. Except in aggressive activities such as occur in roosts or at food, these rudimentary activities and calls seem to have no special meaning in the non-breeding season. The *tschup* may continue to have function throughout the year, as is obviously the case with the flocking note and the warning note.

THE BREEDING PERIOD

Phase 1.—There is no period of male isolation as in typically territorial species. The change from winter flocking to pairing behavior in early spring is gradual. As early as the last of January or early February a difference may be noted. Instead of spending a large part of the day on long foraging expeditions (in the non-breeding period banded birds have been found at the colony in the morning and four miles up Carmel Valley the same afternoon), the birds remain longer in the vicinity of the colony. Some birds spend part of their time together in pairs, but when a number of pairs feeding in an area is flushed they suddenly bunch into a flock. Early in the season there is frequent reversion to flocking behavior, but as the season progresses the birds spend more time in pairs.



Figs. 9 and 10. Male Brewer Blackbirds in incomplete head-up display (bird on the right in each figure). In the completely expressed display, the body is erect and the head held higher than shown here.

Thus, pairs are formed while the birds are in the flock, as mentioned earlier by Lack (1940).

The reassociation of birds paired in previous seasons occurs at this time. Although pairs may breed together in as many as five consecutive seasons (see below), they cannot be considered to remain paired throughout the year. Even if the two members of the pair are in the same flock in the non-breeding season, as they may or may not be, they do not *behave* as a pair at that time, except for occasional and irregular recrudescence of pairing behavior observed from September to November.

At that time there occur temporary instances of segregation into pairs, walking and flying together, with occasional mutual displays. Little of this behavior is seen in January, and then usually not until the third week. In some years none has been observed until February. In March it is usually in full swing.

New pairs are also formed during phase 1. Old pairs show a certain amount of constancy from the beginning. New pairs usually form gradually; considerable time in the early part of this phase is spent in "trial" incidents of pairing behavior with birds that are not the eventual mate.

After the pair is once formed, the members are almost always together, becoming separated only for brief intervals. The male guards his mate from the approaches of other males with increasing constancy. This pair-formation usually comes about at a considerable time before the beginning of phase 2 (nest-building, etc.). The close guard-

ing of the female continues in the second phase. Types of action characteristic of pairing behavior are as follows:

Pairs separate from the flock and walk about together foraging. Or several pairs may be foraging together on the marsh but the two birds of each pair keep a fairly constant distance of about 3 to 6 feet between them, which is generally less than the distance to other pairs in the group.

Pairs perch on wires or on the extreme tips of the higher branches of the pines (sometimes also on concealed perches within the trees). When they perch on wires the usual distance between the members of the pair is about 18 inches. The uniformity of this distance is quite marked and is especially noticeable early in the phase, when a flock containing several pairs is perched on the wires. There will be uneven spacing between the couples on the wire, and perhaps unpaired birds in between, but the spacing between members of a pair is remarkably uniform. When a flock alights on the wires they do not necessarily settle in pairs. But soon some will get up and shift their position until they are sorted out pair by pair, with unmated birds sprinkled between the pairs.

While perched on wires the pair performs mutual displays. Usually the male initiates the activity with the ruff-out and the female replies. When she performs the ruff-out her posturing is much more rudimentary than that of the male, ruffling of the head and neck being less marked and the tail less spread. The male generally utters *schl-r-r-r-up* at this time and the female may or may not reply. Sometimes the male uses the *squeee* note, the female replying with *schl-r-r-r-up* or more rarely *squeee* or not at all. This displaying and calling goes on for several minutes before the pair flies off. Usually the female leads, the male immediately following; sometimes their flight begins almost synchronously.

The classic example of mutual display in the literature is that of *Podiceps cristatus* (Huxley, 1914) which occurs *after* pairing and continues throughout most of the breeding cycle. In the blackbird it is characteristic of the period of pairing (phase 1) and does not continue beyond phase 2.

While perched on the wires, the male sometimes takes a short flight to dart at the female; when the two are perched at the usual 18-inch distance, this amounts to little more than a hop toward the female. The female at this time may be in the generalized display or the dart may cause her to assume it. It is often hard to determine whether the dart or the display comes first. On the other hand, the female may reply to the advances of the male with ruff-out, or she may alternate the two displays.

Sometimes, when the male darts, the female takes a flight of a few feet and re-alights. Or perhaps the male sidles along the wire toward the female and she sidles away. When re-perching or when sidling, the male ruffs out. The posturing of the male is sometimes quite exaggerated at this time and resembles a shortened form of the pre-coital display.

Frequently when the male darts, the female flies rapidly away and the male closely pursues her. A chase ensues. The form of flight is more or less circular, sometimes through the pines of the colony, sometimes out over the adjacent marsh and back again. Sometimes two or three revolutions are made, the course being twisting and with smaller turns within the circumference of the flight. The pace is rapid and the flight broadly undulating. The male utters *squeee* and sometimes *schl-r-r-r-up* while on wing. Sometimes he actually strikes the female in flight; if he does, a *squawk* is heard. Sometimes the flight ends at the place of origin, sometimes at another perch.

Often a third bird joins in the chase, or even a second pair. As many as three pairs have been seen following each other in rough single file. The start of these flights of three or more birds is so sudden, the flight so swift, and the re-perching at such a distance, or in so obscure a place, that the exact sequence and identity of the birds is frequently unobtainable. Sometimes the chase is carried even through the center of the thickest parts of the pines, the birds scrambling after each other, calling loudly and making considerable noise by the brushing of wings against branches.

Copulation and true nest-building have never been observed until April. The majority of the season's first copulations for the first brood occur in the second and third weeks of April (the earliest, April 6, 1945), even though pairing behavior may start in the last week of January. Thus, we may say that phase 1 may extend from the third week of January to the second week in April, a period of twelve weeks. A gradual increase of pairing activity occurs through March, and many pairs are formed by the middle of March.

For second broods, phase 1 is exceedingly brief and can possibly be considered absent, the pair starting off the new cycle with phase 2. In polygamous pairings, also, phase 1 may be brief or absent (see below under "monogamy and polygyny").

Individual pairs vary as to the date when they begin to act as a pair. Also, there is a gradual increase in the amount of time pairs spend as segregated pairs and a corresponding decrease in time spent in the flock. Even in April the birds occasionally join together to form a flock briefly. Constancy in pairing behavior with the same mates is also arrived at gradually. This is much more marked in the case of "new" pairs. "Old" pairs are less frequently involved in chases and their members only occasionally are involved in other types of pairing behavior with individuals other than the "proper" mate. In the course of the formation of a new pair, the members perform pairing behavior with other birds in many instances, until, finally, the "true" pair forms and remains constant through the remainder of phase 1.

It seems, therefore, that activities such as darting and the simple and multiple chases are part of the mechanics of pair formation, since they occur more frequently in pairs forming for the first time and apparently cease when the pair is formed. They occur at a minimum when the pair is held over from the previous season. When a member of an old pair is involved in a dart or a chase, the other bird (or birds) involved is generally unattached, such as a young individual in its first breeding season or one whose mate has not returned. Seldom does such behavior involve members of two old pairs.

Beyond what is suggested above, little is known as to just how pairs are assorted. The following examples show that newly formed pairs become constant only after several trials with other birds, whereas the same pairs which remate in a succeeding year tend to be constant from the beginning. Behavior of two pairs that formed for the first time in 1944 is described here: pair A, M44 (δ) and F67 (♀), and pair B, M20 (δ) and F66 (♀).

Season of 1944.—M44 had a mate F17 in 1943 who did not return in 1944. F67 (his new mate for 1944) was banded as a young of the year on July 10, 1943. Therefore, in 1944, M44 and F67 formed a new pair (A).

M20 was banded in the course of the 1944 season. Since there had been no unbanded males in the colony in 1943, M20 was a "new" male. His eventual mate, F66, was banded as a young of the year on June 27, 1943. Therefore, pair B was also new in 1944.

M44 exhibited pair behavior with five females besides F67 before entering phase 2 with F67 on about April 21. One of these was F66, which later became the mate of M20 and formed pair B. Eight pairing incidents between M44 and F66 were recorded. M44's eventual mate, F67, exhibited pairing behavior with two, possibly three, other males, on one occasion with each. Pair A was first associated on March 10 and pairing behavior was recorded 17 times before the pair entered phase 2 on about April 21. M20 was not banded until April 17. But I feel reasonably certain that the unbanded male who was associating with F66 on March 29 was this bird, as at that time there were only two males in the colony which had not been caught and banded. Eventually all the males were banded in 1944.

Before March 29, F66 showed pairing behavior with two other males besides M44. After March 23 there was no further association between F66 and M44. By that time pair A had become fairly definite, as the majority of incidents of pairing behavior involving M44 and F67 were between themselves only. After March 29, F66 was involved in no further pairing incidents except with the unbanded male and on April 17, F66 was trapped with what was very likely the same unbanded male which was thereafter identified as M20.

Season of 1945.—Both pairs A and B remated with their respective mates of 1944. Members of pair A were seen in pairing behavior with no other birds. They were first seen segregated from the flock on March 10 and were seen together from then on with a few exceptions. One of these was the posturing of M44 to another female and receiving a threat (head-up-display) from that female's mate. Pair A was recorded in only one chase in contrast to the numerous chases and multiple chases in which they had been involved the previous year.

Members of pair B were never recorded in pairing behavior with other birds during the whole course of phase 1 from March 5 until copulation on April 15 and were together on every occasion that they were observed except for two occasions when they were seen separately.

Season of 1946.—Neither member of pair A returned in the season of 1946. Pair B remated for the third consecutive season in 1946.

It is not to be assumed, however, that even after pairs are formed, mated males do not respond to the posturing of a neighbor's female, as indeed they do. The female postures in the generalized display more and more frequently as phase 1 progresses even though actual copulation may still be some time off. The intruding male approaches in ruff-out or even in pre-coital display (although this latter occurs more frequently when the female is in phase 2), or he will just fly or walk toward her. But little progress is made by the intruding male because the mate of the posturing female intervenes, usually walking toward him head-up. Often the mate walks deliberately between the female and the intruder in this posture, and the latter nearly always responds with a head-up display also and both males walk stiffly abreast of each other away from the female, still holding the posture. Sometimes they both shift to ruff-out and may remain for a short time exchanging the ruff-out display, the action being almost identical to that of a pair in mutual display (in which, however, the head-up display never occurs). But the intruder usually does not hold his ground for long. Sometimes, instead of approaching head-up, the mate flies directly at the intruding male. Rarely, the intruder does not retreat and a fight results in which the two birds flutter up, facing each other at close range and pecking or clawing at each other. Actual seizure of one male by the other is rare but it has been seen.

Sometimes the intruding male dives at the posturing female in full flight, whereupon she takes flight; the intruder pursues, the mate pursues, and a multiple chase results. This may rarely happen even in the case of an old pair and a mated male intruder. Even mere juxtaposition of a female near the intruder may bring forth these guarding reactions from her mate whether or not there was an exhibition of displays by either the female or the male intruder. Sometimes, also, two pairs just happen to come together as they walk about. Then, both males may exchange threat displays although there is no apparent cause for this guarding except the presence of one male near the other's female.

In phase 1 there is some toying with nesting material by both sexes and even carrying of it to a site. The male of the pair is sometimes the first to hold nesting material in the bill, but he rarely places it at a site. Actual nest construction is accomplished almost entirely by the female and not until phase 2. Bendire (1895:495) says that "both sexes assist" in nest construction, but at the river-mouth colony the activity of the male with nesting material is almost entirely functionless as far as actual construction is concerned.

In phase 1 there is considerable aggressive behavior, and even fighting, for the possession of nest sites even though nest construction has not begun yet. Females "lay claim" to certain sites to which they occasionally bring nesting material. The aggressive activity for the possession of a nest site is frequently prolonged and often acute and is largely carried on by females. If another female enters a "claimed" tuft, the claimer flies up, uttering *kits*, and often dislodging the intruder. Sometimes the intruding female is not dislodged easily and the two will flutter up or down facing each other, occasionally even seizing each other with bill or claw. The *squawk* is heard as they descend in spirals to the ground.

Such a quarrel over a nesting site usually brings a response from the attacker's mate, which flies into the tree or to some nearby perch. The attacked female's mate also ap-

proaches but the males do not always act belligerently at first. The approach of the males may cause one or both females to assume the generalized display and the males then tend to guard their mates.

However, a male sometimes does initiate the action of driving the intruding male from the nest tree or adjacent "guard perches" and he does drive away other males without the female taking part in the aggressive action. (For a further discussion of the parts taken by each sex in guarding the nest tree and for an analysis of aggressive behavior in general see p. 29.) These activities continue into and reach their height in phase 2.

Phase 2.—This segment of the breeding cycle includes nest-building and egg-laying. It is the period when copulation first occurs and is most frequently performed. (Some copulations also have been recorded in the first few days after the first young has hatched.)

In phase 2 the male, although he takes no part in the actual construction of the nest, usually accompanies the female on each trip as she gathers material and carries it to the nest. At this time they make a long, continuous series of trips in contrast to the toying with and dropping of nest materials, or occasional trips to the nest site, in phase 1. When the female enters the tuft to place the material and mold the nest, the male perches nearby in ruff-out display and utters *schl-r-r-r-up* and *squeee*. His "guard perch" is one of several habitual ones, a wire, a pole, or a branch tip. At times he remains on this guard perch while the female flies off to gather nesting material. At such times the male may drive off trespassing males.

In phase 2 the female exhibits the pre-coital display frequently and other males, as well as her mate, respond; rushes and threat displays between the males are frequent. These advances by intruding males and the guarding actions by the mate which begin in phase 1 reach their height of occurrence in phase 2. In such encounters, except rarely, the mate succeeds in warding off the advances of the rival. However, under unusual circumstances and rarely, promiscuous copulations do occur.

Phase 2, from the beginning of actual nest construction to the completion of the clutch, lasts about 10 days, or two weeks at most.

Phase 3.—This is the period of incubation. Bendire (*op. cit.*) states that the incubation period is 14 days. I. McT. Cowan (MS) gives it as 14 days for two nests in British Columbia. Saunders (1914) says the "eggs hatch in twelve days" in Montana.

Because of the inaccessibility of most nests found in this study (high up and at the end of limber branches), it was possible to look into only a small number of them. Of these it was feasible to make daily inspection of only five. Of these five, three sets were of four eggs, and two were of five eggs each. One set of four hatched in 12 days, all the others in 13 days, reckoning the incubation period from the day the last egg was laid until all were hatched. No thorough study of incubation rhythms was made, but watching females at inspectable nests revealed that they spend time on the eggs before the full set is laid. This correlates with the fact that hatching of the young (except in the set of four, in which all hatched on the 12th day) was spread over as much as three days and indicates that incubation may start before the clutch is complete. The tangible facts ascertained from the few accessible nests coincided with those inferred from parental behavior at other nests.

The male takes no part in incubation. On rare occasions he feeds the incubating female. The male has been definitely seen feeding the female on the nest and the female swallowing the food only twice. Males of 11 other pairs were seen taking food to the female on the nest, but because of thick growths of pine needles it was impossible to see whether the female was presented with the food or not. In most of these instances, the

male emerged from the nest tuft without the food. In three of these 11 pairs, the nests were low enough to be inspected and it was known that the eggs had not yet hatched. In the others it was inferred that the eggs had not hatched judging from incubation and fledging periods and the behavior of the parent birds at these nests.

One male was seen bringing food to his mate who was incubating five eggs at an inspectable nest. The presentation was not seen, but the female was heard uttering notes very much resembling those of a begging nestling. At another nest that was too high for inspection, the female was seen taking food from the male and settling back down into the nest without apparently passing it on to any possible young. It was believed that she was still incubating. Lack (1940a:177) says that feeding of the female by the male has not been recorded for any of the Icteridae.

Phase 4.—Data in the literature on the length of the nestling period is scant. Saunders (1914) says that "the young leaves the nest when ten days old." I was able to ascertain the nestling period definitely in only three instances in the colony and elsewhere. In each of these the period was 13 days, calculating it from the day the last egg had hatched until all the young had left the nest under natural conditions. As in determination of the incubation period, the information obtained at these three nests corroborated the observations at many inaccessible nests. The male assists in feeding the nestlings (see also below under "monogamy and polygyny").

Nestlings that died were sometimes removed by their parents. On six occasions nestlings too undeveloped to have left the nest by their own effort were found on the ground 50 or more feet from the nearest nest. These bore no apparent marks of having been carried by a predator. Two of these dead nestlings were actually seen being carried by the parents in flight and deposited. One of these young, which was carried by the male, was newly hatched and weighed 8.3 grams. Others that were found on the ground were larger. The places of deposition were those regularly used to drop excreta taken from the nest, a pathway, pavement of the street, and the edge of a creek.

As the fledging period progresses the parent birds become more and more demonstrative toward the observer, hovering overhead and uttering *tschup* notes and even swooping at the watcher's head. Although I, myself, have never been actually touched by the birds, I have seen passersby being brushed by swooping parent birds from a colony in the Carmel business district. Such reactions made observation of the feeding rate difficult, and sometimes impossible, within a few days of fledging time. The male generally exhibits greater disturbance, although sometimes both birds seem equally disturbed, and less frequently the female was more demonstrative; but usually nervousness did not disturb feeding rhythm in the female as much as in the male.

Initial flights by fledglings of three, four, and seven feet from the nest have been seen. According to Fautin (1941:225), young Yellow-headed Blackbirds "are unable to fly at the time they leave the nest but they are very adept at making their way through the vegetation." No young Brewer Blackbirds have been noted leaving the nest later than July 7 (1943) at the river-mouth colony.

Phase 5.—The period of fledging care may last more than three weeks. Juvenal Brewer Blackbirds at the river-mouth colony have been fed by the male up to the 26th, and by the female to the 25th, day after leaving the nest.

Second broods are usually attempted if the first is unsuccessful. There have been as many as three attempts by a pair in one season. A second brood is sometimes raised even when the first brood is fledged. Two broods are frequently raised in Oregon (Gabrielson and Jewett, 1940:529), and one or two broods are raised in Washington (Dawson and Bowles, 1909:45). According to Saunders (1914:136), however, Brewer Blackbirds "do not raise a second brood" to his knowledge in Teton and northern Lewis and Clark counties in Montana.

Two females at the river-mouth colony have been seen carrying nesting material for a second brood nest on the same day that they were still feeding fledglings. One female even fed a fledgling three days after the day that she was first noted placing material for a second nest.

Discussion.—The foregoing summary of the five phases is an attempt to describe the behavior traits characteristic of each. It is not to be construed that each phase is definitely set apart from the next. It was not believed that observations were complete enough to say precisely on what days, for instance, phase 1 started and ended, and phase 2 began. With "new" birds it was often impossible to set a time when pairing behavior started because many new birds did not become banded until a season was

Table 1
Duration of Phase 1 of Some "Old Pairs"

Year	Pair	First observed date of pairing behavior between members of the pair	Approximate date for beginning of phase 2	Approximate length of phase (in weeks)
1944	M1-F1	Jan. 21	Apr. 9	11-12
	M2-F11	Jan. 21	Apr. 10	11-12
	M3-F19	Feb. 25	Apr. 9	6-7
	M4-F18	Feb. 25	Apr. 10	6-7
	M11-F4	Feb. 25	Apr. 4	5-6
1945	M1-F1	Mar. 1	Apr. 12	6
	M2-F11	Feb. 27	Apr. 12	6-7
	M11-F4	Feb. 27	Apr. 4	5-6
	M20-F66	Mar. 5	Apr. 9	5
1946	M2-F11	Feb. 25	Apr. 18	7-8
	M6-F2	Feb. 28	Apr. 22	7-8
	M23-F21	Jan. 25	Apr. 19	12
	M24-F36	Jan. 28	Apr. 8	10

well along. It was also thought possible that some of these might have started their pairing activity before joining the colony. But old birds were more dependable, being seen almost daily. For some of these the long period of pairing activity in phase 1 for first broods could be fairly well timed and the change of behavior of the female when she began to engage in actual nest construction and copulation could be noted (see table 1).

Each phase graded into the next one. Phase 1 was considered a matter of weeks; phase 2 was a matter of days and was reckoned from its first manifestation (either copulation or actual nest construction) until the completion of the clutch in those cases where the nest was inspectable. Where nests were not inspectable the completion of the clutch was reckoned back from the fledging date. This was correlated with the dates of nestling feeding, and a theoretical date of the laying of the last egg was thus obtained. Then this was further correlated with the observation of nest construction and copulation. The time occupied by phase 2 was found to be about 10 days; in no case did the period exceed 14 days.

Length of phases 3 and 4 is based on incubation and nestling periods of 13 days each (see above). The length of phase 5, fledgling care, was not adequately studied to determine its precise length (see above).

The activities of the male do not necessarily follow a sequence or pattern of behavior paralleling that of the female throughout the entire cycle. The male may perform on the same day activities characteristic of more than one phase. Nevertheless the phase in which a female may happen to be has a bearing on the male's behavior.

MONOGAMY AND POLYGYNY

Males are both monogamous and polygynous, which is male polygamy as distinguished from polyandry, or female polygamy. Individual males have been monogamous one year and polygynous the next (table 2). There was little or no indication that any individual male showed a consistent tendency toward either monogamy or polygyny.

The longer the period of survival, the greater the likelihood that a male would change his status. Of the total of 55 males that bred in the colony in the six years of the study,

Table 2

	Pair Relationships											
	1942		1943		1944		1945		1946		1947	
	M	F	M	F	M	F	M	F	M	F	M	F
Monogamous	11	15	12	14	14	23	12	27	24	37	6	36
Polygamous	2	1	5	8	7	12
Number of mates per polygynous male	2		2		2		2		6 with 2 1 with 3		7 with 2 4 with 3 1 with 4	
Total	13	15	13	14	19	23	20	27	31	37	18	36
Females per 100 males	115		107		121		135		119		200	

Table 3

Monogamy, Polygyny, and Changes in Pair Relationships Correlated with Survival

Years of survival*	1	2	3	4	5	6	Totals
Total numbers of males	26	13	7	5	3	1	55
Constantly monogamous	21	4	2	0	0	0	27
Constantly polygynous	5	1	0	0	0	0	6**
Experienced change	8	5	5	3	1	22**

* Some records, particularly of younger birds, may refer merely to occurrence as breeders in the study colony rather than to survival. See text.

** In this table, the eight unbanded males which were part of the breeding population were arbitrarily relegated to the one-year group. Seven of these were monogamous. Their occurrence was as follows: 1942, 4; 1943, 0; 1944, 0; 1945, 2; 1946, 1; 1947, 0. The eighth such male was polygynous and was present in 1947.

29 survived for two or more years (table 3). Six of these were constantly monogamous and one was constantly polygynous, whereas 22 changed their status. There were nine males that survived four or more years, all of which fluctuated between monogamy and polygyny (see tables 3 and 4).

Throughout the six years of study there was a trend toward increase in the proportion of females to males, with a corresponding increase in polygyny (table 2). But not all males followed the trend toward polygyny (table 4). A male (no. 2 in table 4) after being monogamous in the first two years when there was only a slight female excess (1942-43), became polygynous in 1944 (sex ratio, 19:23). But he returned to monogamy in the year of a still higher ratio, 1945 (20:27) and continued as a monogamous male in the year 1946 when the sex ratio (31:37) was near to that in 1944, his only polygynous year. Also, number 5, who survived through all six years, was polygynous only in 1946 (ratio, 31:37), but monogamous in 1947, the year of the lowest male proportion (18:36). Likewise, number 14 started monogamously (1944 and 1945), became polygynous in 1946, but was monogamous in 1947.

Although no thorough studies of dominance or peck-order were made, certain males at the feeding station were obviously dominant to others. But this dominance was not always consistent with polygyny. A male considered to be dominant (number 6 in table 4), although polygynous in 1945 and 1946 (he was the only male in 1946 to have three

Table 4
Changes in Pairing Relations of Individual Males in Successive Years*

Sex ratio (M:F)	1942	1943	1944	1945	1946	1947
	13:15	13:14	19:23	20:27	31:37	18:36
Male number						
1	mo	mo	p(2)	p(2)	mo
2	mo	mo	p(2)	mo	mo
3	p(2)	mo	mo
4	p(2)	p(2)	mo
5	mo	mo	mo	mo	p(2)	mo
6	mo	mo	p(2)	p(3)
7	mo	mo	p(2)	mo
8	mo	mo	p(2)
9	mo	p(2)	mo	mo	p(3)
10	p(2)
11	p(2)	mo	mo
12	mo	p(2)	mo	mo
13	mo	p(2)	mo	p(2)
14	mo	mo	p(2)	mo
15	p(2)	p(2)
16	p(2)	mo
17	mo	p(2)	p(3)
18	mo	p(2)
19	mo	p(2)
20	mo	p(3)
21	mo	p(2)
22	p(2)
23	p(2)
24	mo	p(4)
25	mo	p(3)
26	mo	p(2)
27	p(2)
28	p(2)
Remaining males, monogamous only**	8	4	5	6	9	3
Total monogamous	11	12	14	12	24	6
Total polygynous	2	1	5	8	7	12
Total males	13	13	19	20	31	18

* Key: M, male; F, female; mo, monogamous; p, polygynous; numbers in parentheses indicate numbers of mates.
** Total monogamous males occurring one year only or without change of status, 27.

females), had only one mate in 1944; whereas another (number 1) who seemed below him in peck-order had two females in 1944, and a third male (number 2), who was usually driven away by number 1 and number 6 and so evidently subordinate to them, was also polygynous in 1944. Male number 4, who seemed dominant to numbers 1, 2

and also to number 6, was polygynous in 1942 and 1943 (the only polygynous male in 1943); but he had only one mate in 1944, in contrast to numbers 1 and 2.

However, there were four cases of loss of a female to another male which might possibly involve dominance. These will be considered beyond in the discussion.

When polygyny occurs, it usually comes about in the following manner: When the female is incubating (phase 3), the male does not guard her constantly as he does in phases 1 and 2, and he takes no part in incubation. Therefore, he pays less attention to his mate and he notices other females more. If an unmated female, or more rarely, a female whose mate does not seem to be aggressive enough to guard her, is present at this time, the unoccupied male may take this female polygamously as a "secondary" female.

In most cases the male guards the secondary female while she is in phase 2 as assiduously as he did his primary female. In most cases I did not become aware of the new attachment until the secondary female had already started actual nest construction and copulation was being performed. As in second cycles, phase 1 may be extremely short, a matter of only a few days, or may be passed over entirely (see above).

Antagonism between primary and secondary females has sometimes been noted. When this has occurred at or near the nest site of the primary female, the antagonism has been attributed to nest site competition rather than rivalry between females attended by the same male.

At about the time the secondary female starts to incubate, the primary female's eggs have usually hatched and the male assists in feeding the nestlings. Sometimes these events coincide quite closely. For instance, in 1944, a male mated with a secondary female the day his primary female began to incubate, April 19. On April 23 he accompanied the secondary female as she built her nest. On April 28, this female laid the first of a set of four eggs, and the set was complete on May 1. On May 2, the primary female hatched her young and the male helped to feed them. More than one secondary female may be acquired successively in this fashion. In some instances, however, two of the mates may be acquired almost simultaneously.

The entire attention of a male is not necessarily taken from the incubating female. Monogamous males spend much time on their guard perches near the nest at this time. Polygynous males have been known to guard at two nests if the incubation periods overlap. But if one female is in phase 2 while the other is in phase 3 (incubation), the male gives more attention to the former and guards her with greater zeal.

The polygynous male M13 divided his time to a certain extent between his two mates. On May 12; even though he was assisting his female in feeding nestlings, he would occasionally fly over to the guard perch near the nest of the secondary female, 220 feet away, where incubation was in progress. From this perch he would swoop low over me as I inspected the nest.

Polygynous males are capable of performing in a single day activities which might be considered characteristic of more than one phase of the breeding cycle. For instance, M24, on May 10, 1946, fed nestlings of his primary female on the same day that he copulated with the secondary female. On May 27, 1946, M24 fed fledglings of his primary female's first brood (they had been fledged about two weeks), visited the guard perch at his secondary female's nest, as well as visiting at the second nest of his primary female, who was in the early days of incubating a second set.

In the year 1947, when the ratio of males to females was 1 to 2 (table 2), polygyny was most frequent. There were certain cases of polygyny in which it was difficult to determine whether the customary attention was paid to the secondary females. In other

cases (M40, M47, UM8), it was questionable which, if any, of the females should be considered the primary one because their cycles were very nearly parallel, or because the precise timing was not ascertained. In these cases all females were classified as secondary and the pairings designated as "multiple." With M38, who had three mates, F38 was designated as the primary female, possibly rather arbitrarily, because she was definitely his primary in the year before, but timing of the cycles of the three mates in 1947 seemed to be more or less parallel.

Among three females attended by M24, two of them seemed to begin incubation at about the same time, but the third female's activities were spaced at about the usual interval behind the first two. One of the two early females, F36, was definitely a primary in the year before, and she was classified as a primary female in 1947.

In 34 of a total of 35 cases of polygyny, the male fed nestlings of at least one female. In 23 cases he fed at least one brood of nestlings of *all* his females. This number might have been higher but for the fact that in certain nestlings, the young died before time could be spent watching the nest to prove or disprove male attention. There were 17 cases in which parts of two nestling periods overlapped; in seven of these the male was

Table 5
Feeding of Nestlings by Polygynous Males

Number of ♀ ♀ per polygynous ♂	2	3	4	Totals
Number of cases	29	5	1	35
Cases of ♂ feeding nestlings at nests of				
(1) All his ♀ ♀	20	2	1	23
(2) Some of his ♀ ♀	9	2	11
Cases of overlapping nestling periods, not more than two broods at one time	11	5	1	17
Cases of ♂ feeding at two nests on the same day	5	1	1	7
Cases of ♂ feeding at nest of one ♀ and fledgling of another on the same day	6	1	0	7
Cases of ♂ feeding at none	0	1	0	1

observed feeding at the two nests on the same day (table 5). There were also seven cases of the male feeding nestlings of one female and fledglings of another on the same day (table 5). The nestling periods never overlapped at any one time in more than two nests of one male.

Although I was unable to carry out extended periods of watching at any one nest, periods varying from one to three hours at various nests throughout the fledging period indicate that although the female usually exceeds the male in the number of trips per hour with food, the reverse is sometimes true, particularly early in the nestling period when the female is brooding the young. In the seven cases of feeding at two nests on the same day by polygynous males, the combined rate for both nests might equal the maximum rate for a male feeding at only one. But it was not observed to exceed this rate which was found to be 14 feedings per hour. Summaries of these records follow.

M2 (designated as individual number 1 in table 4): Overlap in nestling periods at least eight days; distance between nests about 45 feet. On May 16, 1945 (observation period of three hours, 6:36-9:36 a.m.), male feeds nestlings of primary female 8 times, nestlings of secondary female 7 times. Total, 15 feedings for entire period; average rate, 5 feedings per hour.

M19 (designated as individual number 13 in table 4): Overlap in nestling periods at least two days; distance between nests about 80 feet. It was impossible to observe the two nests simultane-

ously. On June 14, 1945, at several nests watched simultaneously for two hours and 15 minutes (7:10-9:25 a.m.) in the vicinity of the secondary female, M19 definitely fed at this nest once (at 8:42) and flew to the same nest site at 8:55, but feeding could not be seen on the latter occasion. In the afternoon of this day, in 35 minutes of continuous watching, the male fed twice at the nest of the primary female.

M44 (designated as individual number 8 in table 4): Overlap in nestling periods at least eight days; distance between nests 270 feet. On June 6, 1945, the male was seen to deliver food to the secondary female's nest at 7:30 a.m. and to that of the primary female at 11:11 a.m. These two nests also could not be observed simultaneously.

M16 (designated as individual number 15 in table 4): Overlapping in nestling periods at least 7 days; distance between nests 282 feet. On May 22, 1946, each nest was observed twice for short periods between 8:08 and 11:42 a.m., totalling an hour and 17 minutes at each nest. It was impossible to watch the two nests simultaneously. The male fed three times at the primary female's nest and five times at the secondary female's nest.

M40 (designated as number 26 in table 4): Overlap in nestling periods, at least 7 days; distance between nests 205 feet. On May 20, 1947, in an observation period of one-half hour, the male fed once at each nest.

M47 (designated as number 24 in table 4): There were three overlapping nestling periods among the six cycles of the four females attended by this male. Feeding at two nests on one day was observed on June 17, 1947. The two nests were 105 feet apart. In two hours (8:17-10:17 a.m.), the male fed at one nest four times, at the second 11 times, giving a combined rate of 7.5 feedings per hour. The principal events in the history of M47 and his four females in 1947 before June 17 are summarized here. The four females and their nests are referred to as A, B, C, and D.

April 25, M47 accompanies A while she builds. May 11, feeds nestlings at B. May 20, brings food to the nest of A (to the incubating female?) and also feeds nestlings of C. May 21, accompanies A, who reverted to phase 2 through an accident to the nestlings of her first brood. May 23, accompanies separately A and D, both building nests for their second broods and also later on feeds nestlings at C. May 27, accompanies B in phase 2 of a new cycle, her first brood having become almost independent. June 3, feeds D on her nest while she incubates. June 17, feeds nestlings of A's new brood and also those of D.

M24 (designated as number 17 in table 4): Overlap in nestling periods 13 days; nests located on opposite sides of one tree, 35 feet apart. Feeding of nestlings was observed at two nests on one day as follows:

Date	Length of observation period	Number of feedings by male at primary nest	Number of feedings by male at secondary nest	Total	Average hourly rate
May 12, 1947	½ hr. (2:02-2:32 p.m.)	4	1	5	10
May 13, 1947	1 hr. (3:26-4:26 p.m.)	1	2	3	3
May 16, 1947	½ hr. (9:31-10:01 a.m.)	1	5	6	12

Because of the special significance of the simultaneous attention of M24 to his three females, a full record of the events recorded from April 11 to June 24, 1947, is given here. The primary female, F36, nested in pine A; secondary female 1, F51, nested in the same tree 35 feet north of the nest of the primary female; secondary female 2, F18, nested in pine E, 85 feet to the northwest of the nest of F51. The first two could be watched simultaneously. The record of all the activities of M24 during periods of continuous observation is believed to be complete. It was not possible to record all the activities of the females, nor to be certain, sometimes, whether they carried food in their bills. "♂" refers to M24 unless otherwise noted. "♀" refers to the female of each column unless otherwise noted. "Pair" refers to M24 and the respective female of each column. Asterisks in the hour column indicate isolated observations.

Date	Hour	Activities at nest of F36	Activities at nest of F51	Activities at nest of F18
April 11	7:15 a.m.	♂ accompanies ♀, who carries nesting material site.		
	8:10 a.m.		♂ accompanies ♀ to wires near her nest site.	
April 14	6:30 p.m.	♂ perches with ♀ on wire near nest site.		
April 19	*	Pair walks about together, another pair present, many <i>kit</i> notes. Later: pair copulates.		
April 28	*	♀ incubating.	♀ incubating.	Pair seen together twice.
April 29		♀ incubating.	♀ incubating.	Pair seen together in vicinity of nest site; ♀ has nesting material. Later: ♂ accompanies ♀ as she carries material to site.
April 30	*	♀ incubating.	♀ incubating.	Pair flies to ground; alight near another pair. ♂♂ display "heads up."
May 4	7:06 a.m.	♂ flies from pine E, alights on wires in vicinity of nest, ruffs out and utters <i>schl-r-r-r-up</i> notes at another ♂ whose mate is nesting in same tree.		♂ perches on tip of nest tree (pine E), then flies over to vicinity of pine A.
	Later		♂ brings food to nestlings (one trip observed).	♀ incubating.
May 5	*	♀ brings food to nestlings (observed once).	♂ and ♀ bring food to nestlings (observed once).	♀ drinks, forages, returns to nest; ♂ not with her.
May 6	12:05 to 1:05 p.m.	♀ made 8 trips to nest; on at least 5 of these she fed nestlings. ♂ did not feed nestlings but at 1:04 p.m. he alighted on wire near this nest with food, looked toward the nest, but delivered at the nest of F51.	♀ made 6 trips to nest and fed nestlings on each trip. ♂ fed nestlings 4 times and removed excreta twice.	
May 10	1:08 to 2:08 p.m.	♀ made 11 trips to nest; on at least 7 of these she fed the nestlings. ♂ fed the nestlings 9 times.	♀ made at least 11 trips to the nest. On some of these she had food. ♂ did not feed nestlings.	
May 12	2:02 p.m.	Observation starts.		
	2:07	♂ feeds nestlings.		
	2:12	♀ at nest first, feeds nestlings; ♂ arrives and feeds nestlings with ♀ present.		
	2:17	♀ feeds nestlings.		
	2:18	♂ feeds nestlings.		
	2:21		♀ feeds nestlings.	
	2:22	♀ feeds nestlings.	♀ feeds nestlings.	
	2:24		♀ feeds nestlings, and removes excreta.	
	2:25	♀ feeds nestlings, leaves just before ♂ comes to feed nestlings.		
	2:30	♀ feeds nestlings.		
	2:31		♀ feeds nestlings.	
	2:31½		♂ feeds nestlings.	

Date	Hour	Activities at nest of F36	Activities at nest of F51	Activities at nest of F18
May 12	2:32	Summary: ♀ made 5 trips to nest and fed nestlings each time; ♂ fed nestlings 4 times.	♀ feeds nestlings. Summary: ♀ made 5 trips to nest and fed nestlings each time; ♂ fed nestlings once.	
May 13	*	♂ feeds nestlings.		♀ incubating. Another ♀ in pre-coital posture on edge of creek. ♂ approaches her but at same time another ♂ approaches also. ♂ goes to this other ♂ in "head-up" posture, terminating the incident. Later: ♂ seen on wires near nest.
	3:26 p.m.	♀ feeds nestlings.		
	3:35		♀ goes to nest, removes excreta.	
	3:40		♂ goes to nest, feeds nestlings; while he is there ♀ comes and feeds nestlings. First ♂, then ♀ leaves nest.	
	3:44	♀ feeds nestlings, removes excreta.		
	3:45		♀ feeds nestlings.	
	3:50	♀ feeds nestlings,		
	3:54	♀ feeds nestlings,	♀ feeds nestlings.	
	4:00	♀ feeds nestlings, removes excreta.		
	4:01	♂, with food, alights on wires near nest, flies toward the nest, hovers in front of it, then out toward the observer, then toward the nest, then alights on a branch half-way between the two nests, then to the wire, then delivers at the other nest	♂ feeds nestlings.	
	4:02		♀ feeds nestlings.	
	4:05	♀ feeds nestlings, removes excreta.		
	4:09		♀ feeds nestlings, eats excreta.	
	4:12	♀ feeds nestlings.		
	4:17	♀ feeds nestlings.		
	4:18	♂ feeds nestlings.		
	4:20		♀ feeds nestlings, removes excreta.	
	4:26	♀ goes to nest. Summary: ♀ made 9 trips to the nest and fed the nestlings on at least 8 of these; ♂ fed nestlings once.	Summary: ♀ made 7 trips to the nest and fed the nestlings on at least 6 of these; ♂ fed nestlings twice.	
May 14	*	♂ seen feeding nestlings once.		
May 16	9:31 a.m.	♀ goes to nest.		
	9:32		♂ drives another ♂ from nest tuft.	
	9:34	♀ goes to nest.	♂ feeds nestlings, removes excreta.	

Date	Hour	Activities at nest of F36	Activities at nest of F51	Activities at nest of F18
May 16	9:37		♂ feeds nestlings.	
	9:40		♂ feeds nestlings.	
	9:41		♀ feeds nestlings, remains at nest.	
	9:43		As ♂ comes to feed nestlings ♀ leaves.	
	9:44	♀ feeds nestlings, removes excreta.		
	9:46		♀ feeds nestlings.	
	9:48	♀ feeds nestlings.		
	9:49	♀ feeds nestlings.		
	9:50	♀ feeds nestlings.		
	9:57	♀ feeds nestlings, removes excreta; ♂ feeds nestlings immediately after ♀ leaves.		
	9:59		♀ feeds nestlings.	
	10:00	♂ drives two male Red-wings from beneath nest. Summary: ♀ made 7 trips to nest and fed nestlings on at least 5 of these; ♂ fed nestlings once.	♂ feeds nestlings. Summary: ♀ fed nestlings 3 times; ♂ fed nestlings 5 times.	
May 17	11:06 a.m. to 12:06 p.m.			One hour of observation divided with several other nests in this vicinity revealed this ♀ feeding nestlings; ♂ was not seen.
	12:26 to 1:26 p.m.	♀ made 24 trips to nest and fed nestlings on at least 22 of these; ♂ did not feed nestlings.	♀ made 20 trips to nest and fed nestlings on at least 11 of these; ♂ fed nestlings 6 times.	
May 19	*	♀ still feeding nestlings; possible to see at least 2 young in nest; ♀ removes excreta.	♀ fed a fledgling in pine B; ♂ twice fed a fledgling in pine A.	
May 20	*	♀ fed a fledgling; later, ♀ fed fledgling again.		♂ seen in the vicinity of this nest.
May 22	*	♂ feeds fledglings of either or both these ♀ ♀.		♀ and ♂ feed nestlings; ♂ alights near this nest but flies off to pine B and gives food to a fledgling.
May 23	*	♀ feeds fledglings on ground beneath pine A.		♂ and ♀ feed nestlings.
May 24	*	♀ feeds fledglings in tules not far from pine A.		
May 30	9:54 a.m.		♀ at beginning of phase 2; ♂ accompanies ♀ who takes nesting material to site of first nest.	♀ feeds nestlings twice.
	11:00	♂ feeds a fledgling; ♀ also feeds a fledgling.		
May 31	*		♀ moulding nest.	
June 3	*			♂ and ♀ feed a fledgling; ♂ in partial pre-coital posture approaches ♀.
June 6	*		♂, with food; goes toward nest but comes away and feeds a fledgling (fledgling of which ♀?).	
June 24	*		♂ feeds nestlings of second brood.	

Sometimes, in the case of a male with two females, the disruption of the cycle of one of the females—the loss of eggs or death of nestlings—will throw her back from phase 3 or 4 into phase 2, ready for the beginning of a new cycle, earlier than if she had fledged her young. In two such instances, this has led to transfer to a new mate. In 1944, a female (F22), reverting to phase 2, found her mate (M45) occupied with a secondary female that was starting the nesting cycle. Thus, F22 was available to another male (M2) who took her as his secondary female, since his primary female was incubating.

In 1945, two pairs returned intact from 1944 (M11–F4 and M19–F25) and with them a third female (UF5) which was the only female remaining unbanded in the colony in 1945. M11 took UF5 as a secondary female in the usual way. Her nestlings died, causing her to revert to phase 2 a day or two before the primary female, F4, had finished caring for her fledglings and was ready to commence a new cycle. Usually under such circumstances the primary pair recommences the second cycle together. But in this instance, the male (M11) had already had his attention focused on the reverting secondary female. This made the primary female (F4) available to another male (M19) whose own primary female was incubating at the time. Thus, F4 became the secondary female of M19 for her second brood. M19 fed the nestlings of this brood as well as those

Table 6

Years of survival	Breeding Status of Females at the Colony								Totals
	1			2	3	4	5	6	
	Banded	Unbanded	Total						
Always primary	12	5	17	10	7	3	2	0	39
Changing	1	1	7	2	3	1	1	15
Always secondary	17	3	20	2	1	0	0	0	23
Unknown	1	0	1	0	0	0	0	0	1
	—	—	—	—	—	—	—	—	—
	31	8	39	19	10	6	3	1	78

of his primary female, F25. The following season, 1946, both primary pairs M11–F4 and M19–F25 remated for the third consecutive season, and all were monogamous.

Promiscuous copulations, that is, copulation between un-paired individuals, was rare. It was indicated, however, in 1947, the year of the highest preponderance of females, on at least two occasions. But because observations were incomplete, the status of the birds concerned was not clearly known at the time. In 1946, a “stolen” copulation occurred: a male (M2) whose own mate (F11) was incubating copulated with another female (F32) whose young had just died (or had been destroyed) while her own mate (M16) had his attention centered on his secondary female (F54) who was in phase 2. But on the following day M16 exchanged ruff-outs with M2 and was later found to have reestablished relations with F32, while still maintaining those with F54.

THE PAIR BOND

A monogamous male's mate is considered a “primary female.” The first seasonal mate of a polygynous male is also considered a primary female. Secondary females are those that mate with a polygynous male subsequently in the same year. However, the females of the polygynous birds M40, M47 and UM8 in the season of 1947 were all considered secondary, and were exceptions to this definition. The females of M38 and M24 in the same season were also exceptions.

Some females remained in primary relations throughout their years in the colony; others were always secondary. Some changed their status from year to year; while a few shifted from primary to secondary status for a second brood within one season.

There were 34 banded females that were always primary, 20 banded females that were secondary, and 15 that changed their status. One female in 1947 (F65) fledged a brood of young without my ever being able to determine her status (table 6).

Among the 15 that changed their status, there were five which changed from primary status for the first brood to secondary for the second brood in the same year (individual females nos. 1, 2, 8, 12 and 15 in table 7). In three of these (nos. 1, 8 and 12), the original mate disappeared during the season. The other two (nos. 2 and 15) became the secondary mates of other males although their own mates were still present. The circumstances explaining these latter two cases of "cycle disruption" are related on page 24 (females F4 and F22).

There were 9 instances of change from primary status in one year to secondary in the subsequent year. These occurred in females numbered 4, 5, 6, 7, 10, 11, 13 and 14 in table 7. The change came about in the second year of occurrence in the colony for numbers 4-7; in the third year for number 10; and in the fourth year for number 13. Female 14 changed this way twice, in her third and fifth years.

In all of these instances, except number 6 (F57), the changes came about when the primary mate of the preceding year failed to return. In 1947, the second year of occurrence of number 6 (F57), her primary mate (M40), who returned also, did not pair with her. Instead, he mated polygynously with two other females, both of these in secondary status, while number 6 (F57) became one of the four secondary females of M47 (see above). This constituted one of the three "primary divorces" from the total of 45 primary pairings.

There were 6 instances of change from secondary to primary in the subsequent year (table 7). These occurred in numbers 2, 3, 9 and 11 in their second year; number 14 in her fourth and number 15 in her fifth year. In two of these (2 and 15), the female had first changed from primary to secondary within one season and before becoming primary in the subsequent year. In all of these cases the mate of the secondary pairing returned. All, therefore, with the exception of number 11, were involved in "secondary divorces." (Number 2 was involved in both a primary and a secondary divorce.)

Only two females became primaries to the *same* male whose secondary mates they had been at an earlier time. Number 11 was the secondary mate of M45 in 1944 and his primary in 1945 and 1946. Number 15 maintained a primary bond for four years (1943-1946) with M11. Her one secondary mating occurred because of "cycle disruption" in her fourth year, 1945. In 1947, when M11 failed to return, she became the primary of M19 to whom she had been secondary for her second brood in 1945, two years before.

Out of a total of 20 banded females that were always secondary, there were only 3 (F33, F54 and F70) which returned for two or more years (see table 6). In each of these returning secondaries, their mate of the previous year did not return. Because there were only three unbanded females in secondary status in the six years of study, two in 1942 and one in 1945, there is the possibility that either the number of returning secondaries might be higher, or that some of these three might have, on a subsequent year, become primary and been additions to the group of females of shifting status.

Because 15 females individually varied in pairing relations over the years of their survival, it is believed that had the 20 banded females which were in the "always secondary" group survived longer (only two survived for two years and one for three), they too might have changed and become primaries in some years. It will be noted in table 6 that while less than half of the banded one-year birds were primaries, about 90 per cent of the two- and three-year birds were primaries at some time.

In the six years of study 115 pairings were recorded, 70 primary pairings and 45

secondary ones. In 45 of the total of 70 primary pairings, both members of a primary pair returned in the following year. From these 45 possibilities for remating (table 8) there were 42 rematings (93.3 per cent) and only three divorces (6.6 per cent).

In addition, there were six cases in which a returning banded bird had been mated to an unbanded one in the previous year. Some of these unbanded birds may, of course, have returned the following year and might have added to the total of either the rematings or divorce.

Table 7
Changes in Pairing Relations of Females*

Number of female	Year of occurrence					
	First	Second	Third	Fourth	Fifth	Sixth
1(F52)	P, 2nd. b. SW
2(F22)	P, 2nd. b. SCd	P(PD)(SD)
3(F32)	S	P(SD)
4(F44)	P	SNM
5(F50)	P	SNM
6(F57)	P	S(PD)
7(F51)	P	SNM
8(F49)	P	PR, 2nd. b. SW
9(F38)	S	P(SD)	PR
10(F41)	P	PR	SNM
11(F31)	S	P (with first year's mate)	PR	SNM
12(F66)	P	PR	PR, 2nd. b. SW	SNM(SD)
13(F20)	P	P(PD)	PR	SNM
14(F18)	P	PR	SNM	P(SD)	SNM
15(F4)	P	PNM	PR	PR, 2nd. b. SCD	PR(SD)	PNM (fourth year's secondary)

* Explanation:
P, primary status.
PR, primary status, remating with primary mate of previous year.
PNM, primary status with new mate, mate of previous year not returning.
PD, primary divorce, primary mate of previous year returning but mating with another female.
S, secondary status.
SNM, secondary status with new mate, primary mate of previous year not returning.
SD, secondary divorce, secondary mate of previous year returning but mating with another female.
2nd. b. SW, secondary status for second brood, the primary mate for first brood disappearing (the female "widowed in season").
2nd. b. SCd, secondary status for second brood (primary mate still present) due to "cycle disruption."

Not considered as divorces are three cases in which one member of a primary pair returned to the study colony while the other deserted to another place and survived to complete at least one breeding season. The deserting individuals are included in that group of 11 males and 9 females which shifted to or from the study colony. In each case of desertion, the pairs were broken after one season in the study colony, and the deserting individual never returned.

Two of the three cases of primary divorce are mentioned above (no. 2 and no. 6, table 7). One of these (no. 6) was detailed above. The details of the other (no. 2) are as follows: The female (F22), whose case of "cycle disruption" in 1944 is explained on page 24, returned in 1945 as did her primary mate, M45, and her secondary mate, M2. Because she mated with neither her primary nor secondary previous mates in 1945, she was credited with both a primary and a secondary divorce.

The third primary divorce occurred when a female (no. 13, table 7) divorced M12

in 1945, her second year of occurrence. Although M12, her mate of the previous year, 1944, returned, he mated instead with another female (F19, an "always primary," see table 6). The mate of F19 of the previous year had failed to return. Number 13 paired with M14, a male whose mate of 1944 also did not return in 1945. Thus, although both of these returning females made new matings, each with a returning male, only one divorce occurred.

Table 8
Remating and Divorce in Primary Pairs

	1943	1944	1945	1946	1947	Total	Per cent
Cases in which both members of a primary pair returned from the preceding year	4	8	10	13	10	45	
Case of remating	4	8	8	13	9	42	93
Cases of divorce	0	0	2	0	1	3	7
Undetermined cases possibly of remating or divorce	1	2	0	1	2	6	

Table 9
Duration of the Bond in 70 Primary Pairs

	Years					
	1	2	3	4	5	6
Pairs established in 1942 and perhaps in existence before 1942	+1	+1	+1	+1	+1	0
Pairs formed and dissolved in 1943-1947	29	9	3	1	0	0
Pairs formed in 1944-1947, intact in 1947, and perhaps in existence after 1947	6+	5+	3+	1+	0	0
Totals	44	15	7	3	1	0

Some primary pairs maintained their pair bond for a number of years. This is detailed in table 9.

M6, who survived for all six seasons, had but two primary females; one, F6, was his mate in the years 1942-1944; and when F6 did not return in 1945, he mated with F2, with whom he continued for the remaining three years of the study period.

M14, who survived for four years (1943-1946) had F10 as primary female for the first two years and F20 for the last two. Pair M2-F11 remained intact as a primary pair for all five years that each bird occurred (1942-1946). Likewise pair M17-F24 survived intact for all the four years (1944-1947) that each occurred, as did M24-F36 for the three years (1945-1947) of their occurrence.

Of the total of 45 secondary pairs, there were only six in which both members returned in the following year. In all six there was a secondary divorce; that is, none of the secondary matings occurred twice. Two females (nos. 11 and 15, table 7) moved from a secondary relation in one year to a primary one in a subsequent year with the same male.

COLONIAL NESTING

In the area within about a 12-mile diameter around the colony at the mouth of the Carmel River, I found nine other colonies and no pairs nesting singly, although it is possible that a single pair might have been overlooked. Some nests on the peripheries

of the colonies were considerably more isolated than the majority of nests toward the centers. The river-mouth colony was a quarter mile west of the nearest other colony, the second nearest being a mile to the north.

In no year did the river-mouth colony exceed an area covering nine acres. Every year the greatest density of nests was confined to the center area of one acre. Considering only the first nesting for the season of each female in the years 1944-1946, the density for the whole colony varied from 4.1 nests per acre in 1944 to 6.7 in 1946, whereas in the center acre alone the density varied from 14 in 1944 to 23 in 1945. La Rivers (1944) found that on a 15-acre tract 14 miles northwest of Reno, Nevada, during the period May 17 to June 16, 1934, there were 107 nests of this species, a density of "slightly more than 7 nests per acre."

Three of four pines in the center acre of the river-mouth colony were particularly attractive to the birds. One pair of these trees, with trunks four feet apart and branches intermingling, but separated from the other trees, had a height of 45 feet and a combined spread of about 48 feet. This pair of trees (considered as one unit and referred to as pine E) contained seven nests in simultaneous use in 1945. The nests varied from 21 to 42 feet above the ground; no two nests were closer together than about nine feet, nor farther apart than about 37. This represents the maximum crowding in the colony. Possibly such crowding was partly due to the fact that the trees were not evenly distributed over the nine acres.

The arrangement of nests of polygynous males does not suggest a territory embracing them all as is the case in some polygynous species, such as the Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Fautin, 1940), or the bishop-bird, *Euplectes hordeacea* (Lack, 1935). Although the nests of a polygynous male may be in the same tree, one of the nests may be as near or even nearer to the nest of another male than to its own second nest. But frequently the nests of a polygynous male were in different trees, often considerably farther separated than the nests of different males, with one or more other nests in between.

In 1944, the nests of the two females of M2 were 40 feet apart in trees on opposite sides of a street. M13 had two females, the primary having a nest 10 feet away in the same tree from the secondary of M2, and placed near the end of a limb almost over the center of the street and in a rough line between the secondary and primary females of M2. The secondary nest of M13 was 220 feet away from the primary one, at the other end of the colony, with the nest of still another male in between.

In 1946, M16 had the nests of his primary and secondary females separated by 282 feet. Nesting about 15 feet away on the other side of the same pine in which the primary female was situated was the nest of a monogamous pair, while 20 feet from the secondary nest in the latter's tree was the secondary nest of still another male. All the breeding cycles of these females mentioned overlapped, at least in part, especially from the beginning of phase 2 through phase 4.

Sometimes nests of a polygynous male may be situated in the same tree. The primary and first secondary females of M24, the male with a primary and two secondaries in 1947 referred to previously, were about 35 feet apart at opposite sides of pine A, but another polygynous male concurrently had the nests of his two females in the same tree. The cycles of the four females more or less coincided. The longest distances separated primary and secondary nests of each male, and not the nests of the two different males. The nest of the third female of M24 was in a different tree, 85 feet from the nearest nest in pine A and with the nest of another polygynous blackbird in between.

The nests of the four females of M47, in 1947, possibly suggest a territory in that three of the females had nests in pine N. The fourth female had a nest in the next pine to the north (pine M). This nest was 105 feet from the nearest nest of M47 in concurrent use in pine N with no other nest in between. But here again there were nests of other pairs in concurrent use in pine N about as near (10 feet) to one of the two nests of M47 as these two nests were to each other, and considerably nearer than the nest of the third female of M47 in pine M.

AGGRESSIVE BEHAVIOR

By aggressive behavior is meant (1) the flying of one bird at another and forcing it to fly away, and (2) posturing with the ruff-out or the head-up display.

If an attack occurs on the ground, the attacked bird usually re-aliases a short way off. If the attack occurs on a fence post, power wire, or pole, the attacked bird is displaced from the perch. If it occurs in a nest tree, the attacked bird usually leaves the tree altogether. But the attack is usually not followed with further pursuit beyond displacement from the perch or nest tree. If immediate displacement is not effected by the attack there may be contact between the two birds.

Aggressive behavior of the male is only partially restricted to a limited area. This area includes the nest tree and adjacent guard perches. But such localized aggression does not begin to take place until after the pairs are formed during phase 1. From the latter portion of phase 1 through phase 4, there is a certain amount of aggressive behavior by the male centering in this area. This activity reaches its height in phase 2. There is also considerable aggression between females and between pairs centered in the nest tree. But other pairs eventually settle in the nest tree. Apparently a tolerance is developed between these pairs. How this is brought about is not understood.

Birds of other species are also driven from the nest tree and the immediate vicinity. Attacks have been observed on the Redwing (*Agelaius phoeniceus*), the Cowbird (*Molothrus ater*), the House Finch (*Carpodacus mexicanus*), and others.

The greatest portion of the male's aggressive activity is directly concerned with guarding his female, as outlined on page 9, as part of the activities characteristic of phases 1 and 2. This reaches its height in the latter phase, but extends somewhat into subsequent phases. The action is not limited to any area and may occur wherever the female may be, in any part of the colony and at any distance from the nest tree.

In attempting to evaluate the role of the sexes in guarding the nest site and nest tree, with its adjacent guard perches, and to compare the extent of localized male aggression versus non-localized aggression directly connected with a sexual situation, the histories of 14 males and their mates were selected for extensive analysis (see table 10). Not each seasonal record of each male and his mate (or mates) was selected but only those seasonal histories were utilized which were considered to be both sufficiently studied and fairly representative of aggressive behavior in general. The histories included both monogamous and polygynous behavior in any given year and those of males in different years where change in pairing status occurred.

In these histories a total of 426 incidents of aggression were recorded. (table 10).

Table 10
Classification of Records of Aggressive Behavior

Column designation	By ♂ without ♀ taking part			Total	By ♀ alone	By pair together			Totals	
	♀ absent	♀ present				♂ initiates action	♀ initiates action	Equal initiation	Total	Total
	A	Not definitely sexual	Sexual	C	D					
1. At nest tree and vicinity	78	32	49	159	48	18	46	22	86	293
2. Away from nest tree and vicinity	12	4	92	108	12	0	13	0	13	133
Totals	90	36	141	267	60	18	59	22	99	426

These concerned only acts between Brewer Blackbirds and not between a blackbird and some other species. Acts of aggression which obviously concerned food, or roosts, are omitted. Aggressive actions away from the defended area admittedly might concern a source of food not apparent to the observer but certainly in most cases they did not. The result of observations of aggression over food at the feeding station, which unfortunately are scanty, will be discussed in connection with individual dominance.

A total of 293 incidents of aggression were recorded at the nest tree and vicinity (line 1, column J in table 10). By nest tree and vicinity is meant the tree in which the nest is located, the shrubbery immediately below it, the ground in the umbrage of the tree, and the guard perches used by the male. Precise boundaries of the defended area were not obvious, if any really existed at all. No boundaries of aggression for the males whose mates had nests in the two adjacent pines (referred to above under "colonial nesting" as pine E) could be plotted beyond the fact that localized aggression occurred in these two trees and on the power wires (guard perches) on the opposite side of the street, 15 to 50 feet from the nests. Other nest trees in the colony were smaller and might contain as few as one or two nests.

It was noted that both male and female were more vigorous in repulsing trespassing birds when these birds were in that part of the tree near the nest site, or in the nesting branch, or tuft, itself.

The guard perch was used by males as a vantage point to watch the activities of other males and the coming and going of his female to and from the nest. Often his uttering of the *schl-r-r-up* notes from the guard perch were answered with the same note by the female on the nest. Ryves and Ryves (1934) describe similar "song perches" for the polygamous Corn Bunting (*Emberiza calandra*) in England which were used by the male to watch the nest site and the activities of the female passing to and from it.

M2, in 1944, used as guard perch the top of a power pole which was within a few feet of the trunk of the nest tree. The branches of the tree partly surrounded the pole, but the top of it was in the open and at a slightly higher elevation than the nest, which was about eight feet away. This bird also used the wires which stretched in both directions from the pole. His points of rest on the wires were indefinite and seemed to extend about 10 to 20 feet from the pole.

M9, in 1944, used as guard perch any of five parallel wires that passed along his nest tree. The point at which the bird perched was more or less opposite to the nest and about 10 or 15 feet away. Along these wires this bird drove and postured aggressively at the other two males which also nested in the tree. One of these males used the highest branch tip of the tree, as well as the wire; the third male's perch was usually on the wire at a point also opposite his nest which was about 15 feet west of the nest of M9. But I could not see that any of these males seemed definite as to the exact point of perching.

In 1946 M21 used principally the tips of two upsweeping branches, about 15 feet apart and about 35 feet southeast of the nest (second brood) of his primary female and about 100 feet northeast of that of his secondary female. From these perches, where he could watch both nest sites, he postured in elevated-tail display as his primary female passed by on trips with food for the nestlings. On June 1 (both females in phase 4), he repeatedly flew from these perches to drive House Finches from the nest of his primary female. He also flew from his primary's nest tree to dislodge a male Brewer Blackbird from the nest tree of his secondary female, returning to the tree of the former female. On June 6, another male Brewer Blackbird alighted on a branch tip of the primary's tree while M21 was at her nest feeding nestlings. M21 immediately flew out from the nest and dashed at this intruder, forcing him off the tree.

Of the total of 293 cases of aggression in the nest tree and vicinity (line 1, table 10), 159 or 54 per cent concerned action by the male without the female of the pair taking part; 48 or 16 per cent concerned action by the female alone; and 86 or 30 per cent by the pair acting together.

Because of the influence of the female's presence on the action of the male's behavior in general, the 159 cases of male action without the female taking part in aggressive behavior have been broken down into two categories (table 10): "female absent" (line 1, column A) and "female present" (line 1, columns B and C).

The cases of aggression at the nest tree by the male of the pair without the female taking part but where the female is nonetheless present have been further broken down into situations not definitely sexual (line 1, column B), and others definitely concerned with sex (line 1, column C). By sexual situation is meant (1) action of the other male toward the female of the pair (walking toward, flying to, and alighting in close proximity of the female); (2) pre-coital display by the other male to the female; (3) action of the female toward the other male (walking toward, flying to and alighting in close proximity of, the other male); and (4) generalized female and pre-coital displays, or utterances of the copulatory notes by the female in the presence of the other male. When the other male is merely present in the nest tree without these actions or displays being exhibited, no definite sexual situation is considered to have occurred and the aggressive actions of the male of the pair are relegated to column B. There were 32 cases "not definitely sexual" in the nest tree and 49 that were considered sexual (20 per cent and 31 per cent of male aggression at nest tree, respectively).

Aggression by the female alone in the nest tree occurred 48 times, as mentioned above. Although only occasionally extending her aggression to adjacent wires or the area immediately beneath the nest tree, the vigor of her attack seemed greater than that of the male alone. There are occasional cases of seizure of female by female in the nest tree (see description of phase 1), especially at the nest site. Concerning aggression at the nest site, Chapman (1928:138) states that in the Wagler Oropendola (*Zarhynchus wagleri*), it is only the females that fight.

Pairs also act together in defense of the nest tree. This team action is based on 86 records also mentioned above. In 22 of these, or 26 per cent, the initiative seems to be equally shared by male and female of the attacking pair. In only 18, or 21 per cent, the attack was initiated by the male. But in 46, or 53 per cent, it was initiated by the female.

When the male takes the initiative, he usually drives at a lone male, or the male of a pair. When the female takes the initiative, it is usually another female that is driven away. There are three cases, however, in which the female of the pair attacked a male which was trespassing, while her mate, who was present, did not assist. In 17 cases, when two pairs were present, however, the male mates of either attacking or defending females merely followed their females in flights to the nest tree and did not attack each other.

The females often attacked each other vigorously. At such times, the males seem to watch each other. If, in her aggressive actions, one female happens to perch near the other male, or if she responds to the presence of the males by exhibiting the generalized female display, the mate will fly toward them and intercede with the head-up display. Up to this moment males may exchange ruff-out display with appropriate calls, but motion towards the other male often is not elicited until the latter is near the female or responds to her posturing. Three examples of aggression in a nest tree by a pair in which the female took the initiative follow:

On April 14, 1944, F24 was repeatedly driving F66 who was trespassing in pine M, where F24 had her nest. On one of these occasions F24 followed up the attack on the street beneath the nest, whereupon the two males came as F66 went into the pre-coital display; both males did head-up display.

On April 2, 1944, two pairs (pair A, M9 and F2, and pair B, M11 and F4) contend for a nest site in pine I. Pair B is perched on wire near nest site. Soon F2 (of pair A3, uttering the aggressive *kit*

notes, alights on wire near them. Immediately M9 (of pair A) alights between F2 and pair B, does head-up display, to which M11 replies with like display. F2 flies to one of the branch tips of pine I, whereupon F4 dashes at her.

Pair A of the above example was involved in another nest-site contention in pine E on April 28, 1944. Pair B in this example, however, refers to M14 and F10. Pair B was on the wires opposite pine E when pair A flew across to the nest site. Pair B flew after them, the female going inside the nest tuft. There was an utterance of excited *kit* notes, a *squawk* from inside the tuft and the two females tumbled out of the nesting tuft, fluttering down toward the ground in close contact. Although both males were in the nest tree, there was no record of aggression beyond their accompanying their mates to the nest tree.

The largest number of aggressive actions of any one type away from the nest tree is that of the directly sexual type (92). The motivating causes of the aggressive behavior in some of the other categories of action away from the nest tree (line 2) were not clear. It was believed possible that some of the 12 cases in column A may have occurred when the female was present but not visible to the observer. Some of the actions of lone females (line 2, column E) and of females in the presence of their mates (line 2, column G) obviously concerned a source of nesting material, and all the actions in these two categories may have had the same motivation.

No thorough studies of dominance were made, but some evidence was obtained indicating dominance in a social situation at the feeding station. But in sexual situations, that is, the aggression of male in defense of his mate, dominance seemed to have little or no influence. When one of these dominant males approached the female of a less dominant male, the latter did not hesitate to defend his mate. M1, who was driven by most males, including M14, at the feeding station, nevertheless was aggressive in defending his mate against advances by this dominant bird. M1, on March 23, 1944, flew to M14, and displayed the head-up when the latter had alighted near the primary female of M1. On May 4, 1944, two other males gathered around the secondary female of M1 as she displayed the pre-coital. One of these was M14, and M1 did not hesitate to attack him.

The records of M14 and M2 at the feeding station indicate that the former was dominant over the latter, also. As might be expected, M14 guarded his female against advances of M2. On March 31, 1944, the two pairs, M14-F10 and M2-F11, were on the marsh. M2-F11 was rather close to F10. M2 walked to F10 and displayed in pre-coital. M14 flew over to them, M2 stopped the display and the two males flew at one another. After this the pairs reassorted themselves and M2-F11 flew off together. But the less dominant (at the feeding station) M2 had defended his female two days previous to the above incident. Pair M2-F11 was at the edge of the creek. F11, after a while, became separated. M14 flew down and alighted near her but M2 walked toward them in head-up display. Soon all three flew up, M2-F11 to their nest tree and M14 to his.

Because of the influence that the female has upon the male's aggressive actions, it was thought better, in table 10, to insert actions "not definitely sexual" (column B) between those definitely sexual (C) and those in absence of the female (A) as an indication that although no actual sexual situation was present it is still possible that the defending male was aggressive because his mate was there also and *not* merely because another male was present.

It would seem, therefore, that the female has a decided influence on the aggressive behavior of this species. Although there is some aggression by a lone male which is influenced by an area, this localized activity does not occur prior to pair formation. More positive aggressive response is aroused in defense of the female during the process of

pair formation and afterward. Moreover, this defense may occur at any place. At the nest tree the female is more vigorous and is more apt to take the initiative in aggressive behavior of pair against pair, the males usually being more inclined to guard their mates rather than attack each other.

DISCUSSION

Although the Brewer Blackbird, as indicated in the present study, has certain aspects of behavior which are similar to, and have their counterparts in, the behavior patterns of other members of the family Icteridae, some elements of behavior are unlike those in published accounts of the other species. The Brewer Blackbird's combination of both monogamous and polygynous pair relationship, coupled with a strong pair bond, including male cooperation in nestling care, apparently differs from the other species in the family, as indicated by information now available. The strength of the bond and the extent of male nestling care in polygynous cases of the Brewer Blackbird seems to exceed that of most other non-icterine passerines which have been described as polygynous.

Displays compared to those of other icterids.—There is a similarity in the displays of the Brewer Blackbird to some of those of the other icterids. The ruff-out may be considered basically similar to the "courtship display" of the Cowbird (Friedmann, 1929: figured on plates 7 and 8), to the display accompanying the song of the Yellow-headed Blackbird (Fautin, 1940:79), and to the "song display" of the Red-wing (Beer and Tibbitts, 1950:67 and fig. 2c). It lacks the forward and downward head motions of the Cowbird ("bowing") and the Yellow-headed Blackbird, and does not end in the same manner as does the display of the latter species which is climaxed with the bill "almost pointing skyward" (Fautin, *loc. cit.*). In the Cowbird the erection of the feathers of the hind-neck stands out more in proportion to the other feathers than in the Brewer Blackbird and there is much more spreading of the wings in the former species. In the Yellow-headed Blackbird the white wing patches become very conspicuous and in the Red-wing the red shoulder patches are exhibited and become a prominent feature of the display. There are no such contrasting color features in the plumage of the Brewer Blackbird and such striking special effects as created in the other two species are lacking. However, it may be that the iridescent purple feathers of the head and neck in the Brewer Blackbird are possibly shown off to greater advantage through their being ruffed out. Also the effect of greater overall size may be obtained by the erection of these feathers as well as those of most of the body. The heightened effect of the pale yellow irides when set off by the surrounding ruffed-out feathers in the male pre-coital display was commented on on page 5.

A counterpart to the head-up display is found in the Red-wing, the Boat-tailed Grackle (*Cassidix mexicanus*) and the Cowbird. It is called the "stretch" in the case of the Red-wing by Beer and Tibbitts (1950:67 and fig. 3c) and, as in the head-up of the Brewer Blackbird, it is used as a "threat" when two males confront each other at close quarters. The Boat-tailed Grackle's display of this type as witnessed in Louisiana seemed to me very much like those of both of the above two species (unpublished personal observations). This is probably the same display described by McIlhenny (1937: 276-277) as being used by this grackle: "They compress their feathers tightly over the entire body, depress the tail, extend the neck straight up, with beak pointing skyward, and remain in this position for minutes without moving a muscle."

The similar display used by the Cowbird is called "bill pointing" by Laskey (1950) and was previously noted by Friedmann (1929:175). Laskey considers it "the commonest intimidation gesture used by the male" of this species (p. 158).

The Red-wing uses the "stretch" as a threat in territorial guarding: "When one

male approaches the edge of his territory, the male in the adjacent territory will often fly to a position opposite the first male and light in the low vegetation. Both birds then draw their feathers tightly to the body and point the bills upward." (Beer and Tibbitts, *loc. cit.*).

Like the Brewer Blackbird, the Red-wing has two very dissimilar threat displays. In addition to the "stretch" Beer and Tibbitts describe a "directional display" which "in some respects is very similar to the basic song display" and it "was observed to be used in two different situations: The first as a threat and the second to attract the female . . . This same display was observed to be used as part of the regular courtship of the females [by the males] and as a part of the [male's] pre-copulatory display" (1950:67 and fig. 2d). There is, then, a further analogy to the Red-wing in that the ruff-out of the Brewer Blackbird also is used both as a threat and in mutual display.

Aggression and territoriality.—The Yellow-headed Blackbird and the Red-wing are strongly territorial species. In this study of the male Brewer Blackbird, aggressive action was only partially associated with a limited area. The more positive and frequent aggressive responses were elicited in defending the female wherever she might be. This was correlated with the lack of a territorial outline embracing the locations of the nests of males behaving polygynously. Polygynous males of the Yellow-headed Blackbird and the Red-wing, on the other hand, mate with females who build within one area, the boundaries of which are well defended by the male (Fautin, 1940; Mayr, 1941; Beer and Tibbitts, 1950).

Lack of territorial defense by either male or female Bobolink (*Dolichonyx oryzivorus*) after the young were hatched was reported by Kendeigh (1941). Laskey (*op. cit.*) believes that in the Cowbird "intimidation gestures and fighting were not in defense of a piece of ground as in territorial behavior, but were purely sexual" (p. 168). She "witnessed no sustained effort to keep males or females out of a pre-empted area" (p. 166). Aggressive behavior influenced by the tendency to defend the female rather than an area was also observed in the Rosy Finch (*Leucosticte tephrocotis*) by Twinning (1938).

Sex ratio of breeding populations and polygyny in some icterids.—The family Icteridae is probably the most "interesting family for a study of sex ratios," writes Mayr (1939), "because it contains some genera with an equal sex ratio, some with a surplus of males and some with a surplus of females. An equal sex ratio probably occurs in the majority of the species; there is evidence to support it in the case of the Bronzed Grackle (*Quiscalus aeneus*)" (Snyder, 1937) and in the Baltimore Oriole (*Icterus galbula*) (Mayr's own observations). Surplus of males in the family occurs rarely, writes Mayr, and cites the Cowbird as an example (Friedmann, 1929:170, 173).

An excess of females has been correlated with polygyny in the Wagler Oropendola (*Zarhynchus wagleri*). It was determined by Chapman (1928:165) that the "females outnumbered the males six to one." Kendeigh (1941) writes concerning the Bobolink breeding on 50 acres of "restored prairie" in Iowa: "There were ten females here, but evidence for no more than six males, with polygyny strongly indicated" (p. 169). The Yellow-headed Blackbird has been found to have an excess of females in Utah (Fautin, 1940). The total breeding population at one colony was found to consist of 12 males and 40 females (a ratio of 1 to 3.33).

Allen (1914) suggests that polygyny occurs in the Red-wing. Both polygyny and monogamy were found to occur in this species in Nevada by Linsdale (1938). The number of females obtained by males seemed to depend on the suitability of the habitat where the male's territory was located: "A male with a thickly grown stand of strong, upright cattail stems would have as many as six females all actively nesting. Another in

a less suitable part of the same marsh might have only one female. At least one male kept a territory throughout a season where the sites for nesting were few, there being no tall vegetation, and not a single female settled there" (pp. 140-141). Mayr (1941) also recorded sex unbalance in favor of females in the Red-wing in the breeding populations of two small swamps in New Jersey. In one of these there were three males to five females. One male was monogamous, the other two polygynous, with two females each. What seems to be possibly the most precise study of actual numbers of each sex of an icterid hatched at a breeding colony is furnished by J. F. Williams (1940). By sample dissection, measuring and marking of nestlings this writer was able to come to the conclusion that among 94 young Red-wings which were successfully fledged, 47 were males and 47 were females.

That the sex ratio of the breeding population of the Brewer Blackbird may be unbalanced and may vary at one colony from year to year was established in the present study. Whether the sex ratio is more balanced in other icterids in which polygyny occurs regularly remains to be determined by population studies based on marked birds.

Wright and Wright (1944) have shown that although some first-year male Red-wings breed, others, because they come into active spermatogenesis later than do the fully adult males, are unsuccessful in obtaining territories and therefore mates. These authors write: "Perhaps the smaller testes of the year-old bird are producing less male hormone which in turn would render the bird less aggressive and less able successfully to compete with adult males in maintaining a territory" (p. 56). Beer and Tibbitts (*op. cit.*) also state that yearling Red-wings do not "usually have the drive to establish territories for themselves" (p. 65). First-year Yellow-headed Blackbirds, also, fail to establish territories (Fautin, 1940:78). It has been suggested that the female Yellow-headed Blackbird breeds in its first year but that the male does not breed until its second year, thus creating a disparity of males in the nesting colony which is not due to an actually uneven sex ratio (Linsdale, *op. cit.*: 135).

If the sex ratio of the Red-wing at fledging is 50:50, as demonstrated by Williams (*op. cit.*), further study may prove that some of the other icterids in addition to the Bronzed Grackle and Baltimore Oriole have an even sex ratio at fledging. Thus, the greater number of females in a breeding population may be due to a factor, or factors, other than the *actual* sex ratio of the species. One of these factors may be the differing time of maturity between the sexes. In this regard, the evidence in the present study of the Brewer Blackbird is not conclusive, but it indicates at least that the non-breeding of first-year males is not the only factor.

Maintenance and replacement of populations.—It will be seen from figure 11 that whereas there was a build up of the total breeding population from the year 1944 to the year 1946, there was a drop in 1947. In each of the years 1944-1946 there was an increase in both sexes of the returning populations. But whereas in 1947 the returning female population increased to 26 from 18 in 1946, the returning male population dropped to 13 from 16 in 1946. Replacements in the male population in the year 1944 and 1945 were the same, eight, but increased in 1946 to 15. But in 1947 they dropped considerably, to five. Replacements in the female population dropped slightly from 1944 to 1945, but increased in 1946 from 12 to 19 and although there was a drop in replacements again in 1947, from 19 to 10, the drop was not as marked as that of the males (15 to 5). In this discussion an assumption has been made that all the unbanded birds of each sex were new to the colony.

Whereas there was a drop in total population in 1947 from the 1946 population (from 68 to 54) there was a far greater drop in the number of males compared to that of females. The female population was only reduced by one (37 to 36) but the male

number dropped from 31 to 18. The proportion of replacements to returning birds in the 1947 population of females was less than in the 1946 population, but the difference was not as great as in the male population for the same years. Thus the low male population in 1947, which dropped from 31 to 18, although partly due to a lack of returning birds, was due principally to a lack of replacements. This was the lowest number of replacements for either sex in any of the six years of study. The indications, therefore, seem to be that some factor or factors reduced the male population by 42 per cent, the female population by only 2.7 per cent, between the seasons of 1946 and 1947.

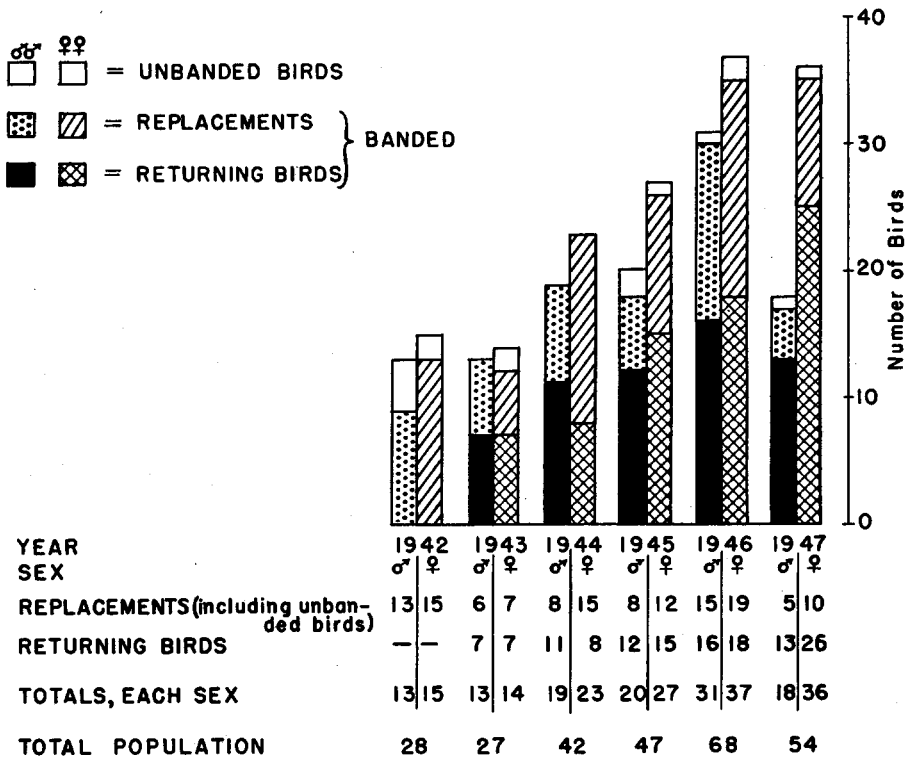


Fig. 11. Population data for the breeding colony of Brewer Blackbirds studied.

There was evidence of some slight shifting from one breeding colony to the other; that is, it was known that certain birds lived for one or more complete breeding season at some place other than the study colony either before or after entering the breeding population under discussion. In the six years of the study, there were 11 males and 9 females that shifted in this way (see below, also table 11). As far as the study colony was concerned, as indicated by banded individuals, each bird made only one change. Thus, after coming to the colony it remained there until its final disappearance (presumed death); or after leaving the colony, it did not breed there again. But the number of each sex which came to or left the colony had no effect on the sex ratio in any one year because the additions and subtractions cancelled each other except in the year 1945, when the number of females in proportion to males was reduced by one by such a shift, and in 1947 when the male population was likewise reduced by one.

Age of breeding males.—The constituents of the new population of males in each

year are shown in table 11. The ages of a large part of the newly banded male population were necessarily unknown. This was due to the fact that I felt that I had not sufficiently studied plumages to distinguish adults from first-year birds after the postjuvinal molt. In the Red-wing and the Yellow-headed Blackbird, there is apparently little difficulty in identifying a first-year bird. Therefore, those males of each year's new population which were banded for the first time in the preceding fall, winter, and during the course of the breeding season, must remain of unknown age. However, there were four males banded before the completion of the postjuvinal molt that bred in their first year.

There were certain males which were known to enter the breeding population of the colony not sooner than their second year of age (line B and C, table 11). Because of their date of banding they were known to have lived through at least one breeding season before entering the breeding population of the study colony. There was evidence that three of these bred at some other place the year before joining the study colony because

Table 11
Analysis of Composition of Annual Groups of Males in Breeding Colony

Line		1942	1943	1944	1945	1946	1947	
A	Returning males, at least two years old	7	11	12	16	13	
B	Entering, bred elsewhere in previous year	1	1	1	
C	Entering, breeding in previous year not ascertained	1	1	1	1	
D	Total number of males at least two years old	9	12	13	18	14	
E	First-year males, banded as juveniles	2	2	
F	Banded males of unknown age	9	2	5	5	12	3
G	Unbanded males	4	0	0	2	1	1
H	Total number of males of unknown age	13	2	5	7	13	4

they had been observed feeding free-flying young in that year (line B, table 11). One of these three was M47. This bird, a son of the pair M2-F11 and hatched at the colony in 1944, was seen feeding young, presumably his own, in 1945. But this male was not a member of the breeding population at the study colony until 1946.

The exact ages of the four males in line C, table 11, were unknown except in the case of M22. This bird was banded in juvenal plumage in 1944. He began but did not successfully conclude a breeding cycle in the study colony in 1945, his first year, but did so in 1946. (The history of his apparent eviction from the colony is related beyond.)

From data in lines D, E, H, table 11, little can be deduced as to the breeding of first-year males beyond the definite fact that four bred in the colony and one (M47) apparently outside of the study colony. There is, of course, the possibility that there may have been more first-year males in the group of individuals of unknown ages.

Factors leading to polygyny.—The failure of yearling males to compete with fully adult males, as outlined for the Red-wing by Wright and Wright (*op. cit.*), is indicated in the failure of M22 to complete a breeding cycle in his first year, and his success in the following year. The situation is not entirely parallel in that the Brewer Blackbird shows little territorial behavior, but it suggests a lack of drive on the part of the yearling to defend his mate or mates.

In 1945 M22 seemed at first to be carrying out the usual pattern of a polygynous male by taking on a secondary female, F33, while his primary, F32, was incubating. But something disrupted the breeding cycle of F32, apparently destruction of the eggs. At the time of her reversion to phase 2, an old (at least four-year) male, M2, whose mate, F11, was incubating at the time, was observed in "pairing behavior" with F32 and was observed to be apparently successful in an aggressive situation

with M22. Thus M2 took over F32 as a secondary for a second brood, and later fed nestlings at the nests of both his primary (F11) and F32. In the meantime M22 lost his secondary, F33, also to another old (three-year) male, M44, who made a secondary pairing with her while his own primary female was incubating. M44 completed the breeding cycle with F33.

After losing both his primary and secondary mates in this way M22 ceased his efforts to breed in the study colony in 1945. In 1946, however, he was successful in polygynous breeding, completing a cycle with a new primary female and carrying a secondary at least as far as phase 3.

This withdrawal of M22 from the scene in 1945 subtracted one male from the total count of males. Although M22 started out polygynously but withdrew, two cases of polygyny remained (M2 with his primary, F11, and F32 as secondary, plus M44 with his primary and F33 as secondary). Had M22 maintained himself and repelled the other males from his primary and secondary females, only one case of polygyny would have existed. Thus, the failure of a first-year male may contribute to the lower breeding population figures of males and add to the cases of polygyny.

Another simpler case was indicated in 1943, when a first-year male seemed to have been excluded as a breeder and his possible female taken from him by an old male who acquired her as a secondary mate. Two other usurpations occurred, one in 1944 and one in 1945, each leading to polygyny, but in the first of these the deposed male was an adult, and in the second the ages of both the successful and unsuccessful males were not known. Thus, there is indication that some immatures cannot compete with adults. It is possible that some of these ousted birds may have bred at other colonies (this was not indicated for M22, however).

It seems correct to assume, however, that individuals that established themselves in the colony, with the exception of those which were known to shift their locations, permanently maintained their breeding status at the colony, and that the reduction in returning males in 1947, for instance, indicates that these males died rather than that they went to another colony to breed.

There were some cases of polygyny upon which the sex ratio had no bearing. In the two cases of "cycle disruption," one in 1944 and one in 1945 (see page 24), one case of polygyny was added without an additional female being present.

Unbalance in the numbers of males to females was evidently not a factor in the three cases of polygyny resulting when a female was widowed in mid-season and then was acquired as a secondary by another male with whom she had a second brood. This interpretation rests on the fact that the original male in each case had already functioned in the breeding population and was included in the male count for the year concerned.

Thus, polygyny may arise without any additional female being added to the population from "cycle disruption" or the widowing of females within a season. But the chief cause of polygyny is the excess of breeding females. This may be in part (probably a small part) due to the non-breeding of first-year males and in part (at least as indicated in the year 1947) to a reduction of the male population as compared to that of the female. The cause of this differential rate of maintenance and replacement between the sexes of the breeding population is unknown. The actual extent of the effect of non-breeding first-year males on the sex ratio is also unknown. Since it is known that *some* first-year males breed, the non-breeding of other yearlings may not be of great importance. But the data at hand are too meager to evaluate this importance.

Nestling feeding by polygynous males in the Icteridae.—With a possible exception in the case of the Tricolored Red-wing, nestling care by the male seems more fully developed in the Brewer Blackbird than in other icterids in which polygyny has been reported. In those reports which have come to my attention in which male care has been stated, none has mentioned male feeding at the nests of more than one of the mates.

Chapman (*op. cit.*) describes the male *Oropendola* courting several females, one at a time, but the association between mates covers "only the period when the ova are ready for fertilization" (p. 165). The male takes no part in the care of the young.

In the case of the Bobolink in which polygyny was indicated "all attempts to prove that the same male was simultaneously associated with two or more nests by capturing them at each nest were unsuccessful. Failure resulted because the young were fed regularly by a male at only one nest and because of the high nest mortality" (Kendeigh, 1941:170).

The Yellow-headed Blackbird aids "very little in caring for the nestlings. Only two males [in a study of 128 nests] were observed to make any attempt to feed the young" (Fautin, 1941:224).

Care of the nestling Red-wing is largely carried on by the female (Allen, *op. cit.*). The female of this species "takes care of the young by herself with but little help from the male," write Beer and Tibbitts (*op. cit.*: 73). On occasion the latter authors have observed adult males carrying food in the vicinity of the nest and assumed that they were feeding the young. But "as soon as the young fledge, there is a noticeable increase in activity by the male in feeding the young" (p. 73). No special consideration is given to the male Red-wing's attention to young in polygynous cases in the work of Allen (*op. cit.*) or Linsdale (*op. cit.*). Mayr's observations (1941) did not cover the fledging period and Beer and Tibbitts (*op. cit.*) make no mention of polygyny at all.

In the polygynous Tricolored Red-wing, both sexes feed the young (Lack and Emlen, 1939:227). But these authors give no details as to whether a male may feed the young of one or of more than one female.

Nestling feeding by polygynous males in other passerines.—Only those papers that have come to my attention in which there is mention, either positive or negative, of male nestling care will be considered here.

In a four-year color-band study of the Winter Wren (*Troglodytes troglodytes*), Kluijver *et al.* (1940) found that 50 per cent of the males were polygynous. On three occasions a male had three mates at once, and once one male (no. 42) had 5 at one time (pp. 37-38). The male is a "nest-building specialist" and may construct many nests in the course of a season. This specialization in nest building, the authors believe, may have given rise to the polygynous habit because when the female begins incubation the male makes more nests and by this means attracts other females and thus obtains additional mates. Many males do not feed young in nests. Both parents accompany the fledglings but some males do not feed them. No comparisons are made by the authors between monogamous and polygynous males as to the extent of care of the young. However, it is clear that at least one polygynous male (no. 42), in the year 1936, did feed nestlings of two of his mates, devoting himself to each brood successively.

Welter (1935) states that in the case of the Long-billed Marsh Wren (*Telmatodytes palustris*) the male, which, as in the case of the Winter Wren, also builds extra nests, is polygynous. "Between one-fourth and one-third of the territories, which were carefully studied in this investigation, were inhabited by two females and one male" (pp. 14-15). The male does not feed nestlings but "in contrast to the period in the nest, both parents care for the fledglings" (p. 29).

A bigamous male Black Redstart (*Phoenicurus ochrurus*), which was banded, had two mates whose nests were 100 meters apart. The male fed the young in both nests alternately; second nests were started at the same time by both females and again the male fed both broods (Hoehl, 1941).

In a banded population of the Pied Flycatcher (*Muscicapa hypoleuca*) studied in Finland, four cases of bigamy occurred (Haartman, 1945). As in the Brewer Blackbird,

it could be demonstrated that the same male was in one year monogamous and in the next polygynous. "A tendency to bigamy in certain individuals is not considered as probable" (from English summary, p. 32). In all cases studied the bigamous male took part in feeding the young of the first female with which he paired, but not those of the second.

In the territorial, polygynous Bishop-bird (*Euplectes hordeacea*), "each male has a succession of females, courting with and building [a nest in the territory] for one at a time" (Lack, 1935:833). But the females alone feed the young.

Ryves and Ryves (1934) found the Corn Bunting to be both monogamous and polygynous as a result of their studies in North Cornwall, England, covering the breeding seasons of 1932-1934. In 1932, four out of 16 males were polygynous. In 1933, 15 out of 24 were polygynous (there were at least 45 females). In 1934, all 15 males studied were polygynous (there were 51 females). It was indicated that a pair bond existed for the season, at least, and that a polygynous male may pay attention to more than one female at a time. In regard to male care of the young the authors write that the female "practically alone, undertakes the work of rearing the young." However, the male "does, on occasion rare enough to merit specially noting, help to feed his progeny" (p. 16). When the young "have attained a fair size" the male helps the female for short periods during the day. At this time he may feed at the rate of 20 trips in 30 minutes. "When the young are out of the nest, he may help the hen a little more frequently, though the latter still takes the lion's share of the work" (p. 17). Although comparisons of the extent of care of the young given by polygynous as opposed to monogamous males are not made, it is clear that polygynous individuals do assist the female. How many mates of each male were thus assisted is not stated for the years 1932 and 1933. In 1934, however, the authors state that one male with seven mates was observed to help feed nestlings at the nest of one of these but not at the nests of any of the other six. In regard to the higher proportion of females in 1934, the authors comment that "either there had been a failure to establish the existence of a good many breeding hens [in previous years], or hens in 1934 were actually in greater numerical strength" (p. 155). Thus, it is possible that the degree of excess of females may vary in different years, as in the present study of the Brewer Blackbird.

Bigamy may occur in territorial passerine species when a female, widowed in the breeding season, is taken on as a second mate by a neighboring male. In five years of study of the White-crowned Sparrow (*Zonotrichia leucophrys*), Blanchard (1941 and *in litt.*) recorded four cases of bigamy of this sort occurring among 24 color-banded pairs watched. Pairs were found to remain intact throughout the winter (Blanchard, 1936). One bigamous male (male I) maintained contact with both his first and second mates throughout the winter and remated the following spring with the second female (Blanchard, 1936). One instance (in 1937) is recorded of a bigamous male which fed nestlings of two females. This male (IV) had, in the beginning, two mates, females II and IVb, and he fed nestlings of female II first (Blanchard *in litt.*). A neighboring male (VII) who owned the adjacent territory, although at first driven off by male IV, finally succeeded in pairing with female IVb for her second brood (which was subsequently destroyed). His success was probably due to the preoccupation of male IV with female II. The first two nests of female IVb had been on, or close to, the common boundary between the territories of the two males. Her third nest, however, built when she was paired with male VII, was definitely inside the boundary of the area belonging to male VII. But some sort of bond between male IV and female IVb seems to have persisted to the nestling period of this third brood because, although attacked by male VII, male IV was seen to deliver food to the young of this, his former second mate's third brood. Of the

relations of male IV and VII to female IVb, Blanchard writes: "In this triangle two males became interested in one female. One male, her original mate, whether on account of the marginal location of the nest or the dividing and weakening of his defensive instinct by polygamy, was unable to retain possession. Yet his interests were still sufficiently persistent to extend through the lost female to her brood in another territory and doubtless by another male." (Blanchard, 1941:37).

Polygynous behavior occurs in the territorial Song Sparrow (*Melospiza melodia*) under circumstances similar to those described for the White-crowned Sparrow. However, polygyny seems to be less frequent in the Song Sparrow. In the course of her eight-

Table 12
Broods Fledged per Monogamous and Polygynous Male

	1942	1943	1944	1945	1946	1947	Totals
Monogamous males	11	12	14	12	24	6	79
Polygynous males	2	1	5	8	7	12	35
Monogamous broods							
Total nests	14	14	17	16	31	7	99
Nestlings hatched in	13	14	14	13	27	7	88
Young died in	3	2	1	6
Unknown results in	4	1	3	0	9	1	18
Young fledged in	9	13	11	10	16	5	64
Polygynous broods							
Total nests	4	2	12	24	24	43	109
Nestlings hatched in	4	1	11	23	21	41	101
Young died in	2	13	14	12	41
Unknown results in	3	0	0	1	0	3	7
Young fledged in	1	1	9	9	7	26	53
Broods fledged per male							
Known results only							
Monogamous	.81	1.08	.78	.83	.66	.83	.81
Polygynous	.50	1.00	1.80	1.12	1.00	2.16	1.54
Presuming unknown broods fledged							
Monogamous	1.18	1.16	1.00	.83	1.04	1.00	1.04
Polygynous	2.00	1.00	1.80	1.25	1.00	2.41	1.71

year study of 438 breeding Song Sparrows (the number of males ranging from 25 to 66 per year), Nice (1937) found only four cases of polygyny. These were bigamous males, each bigamy occurring in a different year. The cases apparently arose "from the situation where a female with a nest of eggs has lost her mate and rather than desert them, attaches herself to a neighboring male, in spite of the fact that he is already mated" (Nice, 1937:91). Disaster overtook nestlings in two of these cases before nestling feeding by the male at both nests could be proved or disproved; one nest was too far away to be watched to determine the extent of male attention. But it was definitely determined that one male actually fed nestlings at both nests.

Unlike the White-crowned and Song sparrows, the Brewer Blackbird is not held to a rigid territorial system and therefore the acquisition of extra mates is not restricted to neighbors nor is the necessity of patrolling an enlarged area a complicating factor.

Polygyny and nesting success.—Polygyny in the Brewer Blackbird resulted in a greater number of broods fledged *per male* than did monogamy (table 12). This occurred in most years of the study and the total result favored polygyny. Greater success per

polygynous male resulted even though the number of broods fledged was greater in monogamy than in polygyny. Thus, success *per broods attempted* was greater in monogamy.

Actual figures for young fledged per pair are lacking. As mentioned earlier, most nests were inaccessible for inspection and so actual numbers of young in each brood could not be ascertained. Success in fledging a brood was determined by observing the female feeding young out of a nest in which she had been feeding nestlings just previously. Observing a polygynous male feeding young out of a nest could not be used as a criterion for fledging at any particular nest unless it was known that fledging on, or immediately preceding, the date of observation could be referred to only one of the male's mates. In some cases designation of the nest from which the fledgling came could be corroborated by the fact that both male and female fed the same fledgling. But in no case could either proportion of fledged young per eggs laid, or the actual number of fledglings be obtained with any accuracy, except at the negligible number of nests inspected and from which fledging occurred.

Likewise, it was occasionally difficult to determine whether a brood of nestlings on, or near, the expected date of departure actually left the nest, or died therein, or had been destroyed. Fledglings scatter soon after leaving and feeding by parents could be undetected. Death or destruction of nestlings at an earlier date in phase 4 is more readily determined by the behavior of the parents. These undetermined cases are marked "unknown results" in table 12.

I had no reason to believe that there was any differential in the number of young per fledged brood between monogamy and polygyny. The figures herewith are presented for what they may be worth and only as a basis for comparison between productivity of males in monogamy as against polygyny. Claim cannot be made that they are an indicator of actual nesting success of the species.

A greater number of broods per polygynous male than monogamous male were fledged in 1944, 1945 and 1947 (table 12). This is also shown by the total figures. If all the broods with "unknown results" are added to the fledged broods of monogamous males, productivity of polygynous males remains higher.

Higher number of fledgings per polygynous male was not indicated in the years 1942 and 1943. Too little information was obtained in 1942 to suggest any explanation. In 1943, polygyny was insignificant (only one case, a male with two females). In 1946, when the addition of the "unknown results" to fledging in the monogamous cases were made, fledgings per monogamous male were but 4 per cent greater than those per polygynous male.

Thus, it may be possible that polygyny is of advantage to the species in that when an excess of females occurs, the proportionately fewer breeding males may be able to accommodate these extra females, and even if the actual nesting success *per broods attempted* is lower in polygyny than in monogamy, more broods per male are produced in this way than if each male remained monogamous and the extra females unpaired.

The cause of the greater failure in the fledging of polygynous broods is unknown. It might be thought possible that the polygynous male's care of nestlings of all broods of each mate was not always sufficient to insure fledging. It might be that the maximum rate of 14 trips per hour per male, which was noted for nestling feeding at one nest and which was not exceeded in the cases of the polygynous males at two nests simultaneously, was inadequate in the case of polygyny. But it is believed that sufficient observation of the rates of feeding in a sufficient number of cases of polygyny are lacking to draw any true conclusions on this point, even presupposing that the extent of male feeding was of ultimate importance.

The percentage of monogamous nestings which reached at least the nestling stage at which monogamous males were observed to have taken any part in feeding nestlings is only slighter higher than in the case of polygyny (table 13). There were 16 broods in monogamy and 25 in polygyny in which male feeding of nestlings was not proved because the male either disappeared or the young died before male behavior could be watched; or there was not sufficient observation to prove or disprove male attention.

The difference in percentage of fledging between the two groups is greater than the difference in percentage of male attention (table 13).

That it is not entirely impossible for the female to fledge young without the assistance of the male might be indicated in the case of F21 in 1946, whose monogamous mate disappeared during incubation and was never seen again. F21 fledged her young alone and continue to feed the fledglings for at least 13 days. Fledging occurred in at

Table 13
Fledging Success in Relation to Pairing Status of Males

	Males monogamous		Males polygynous	
	Numbers	Per cent	Numbers	Per cent
Total number of nests	99		109	
Nests with young	88		101	
Nests with young fed by males	72	81.8	76	75.2
Results of nests with young fed by males				
Young fledged	57	79.1	46	60.5
Young died	5	6.9	25	32.8
Unknown	10	13.8	5	6.5
Per cent fledged with unknowns included		93.0		67.1
Per cent died with unknowns included		20.8		39.4

least 6 of the 15 monogamous broods and in 6 of the 19 polygynous broods in which observation was insufficient to prove or disprove male attention.

Monogamy, polygyny and the pair bond.—There were more cases of monogamy (80) than cases of polygyny (35) in the six years of the study. For that reason, possibly, the Brewer Blackbird should be considered to have a greater tendency to monogamy. But as we have seen, there was a certain proportion of both sexes which were sometimes in a monogamous relationship and sometimes in a polygynous one. It seems well indicated that there is nothing inherent in the individual male which tends to make him polygynous rather than monogamous. Polygyny was brought about by circumstance. It is believed that the factors which lead a female into a secondary pairing are not necessarily all, or even partly, inherent.

The seasonal bond between the male and his mate is strong in both monogamy and polygyny. Once a primary pairing has been formed, and if both members return the next season, the chances are remote (6.6 per cent) that it will be broken by divorce. The new female entering the breeding population for the first time would tend to make a primary pairing if a new male were available. If such is not available a secondary pairing is made. If the secondary female survives to subsequent seasons she has the chance of making a primary pairing at some time.

In the Song Sparrow, Nice (1937) records only eight cases of remating from year to year in something over 200 possible cases (4 per cent). "I believe it is a comparatively rare occurrence with my birds because of the many chances a male has to get a mate before his former [migratory] mate returns, the presence of the resident females being a complicating factor. I do not have any certain case of a female joining a new mate when the old one was available; either the former mate was dead or was already mated,

or, in one or two cases, returned later than she did." No such complicating factors apply to the Brewer Blackbird. It does not maintain a bond throughout the non-breeding period. But there is a tendency for flocks of birds of the study colony to visit, and roost, at the colony area throughout the non-breeding period. As the breeding season starts the colony birds tend to remain for longer daily periods at the colony area. In this way members of a "returning" pair may readily find each other.

Lack (1940*b*), in his review of pair formation, distinguishes between cases of remating of the pair from year to year and true life-pairing in which the members of a pair remain together all the time. In the case of the Brewer Blackbird, however, I feel that one may say that there is some sort of personal attachment or bond between primary pairs, which may be maintained for some time, not impossibly for life. It is only rarely broken by divorce but is periodically *interrupted* in the non-breeding season.

In regard to the co-existence of polygyny and a pair bond, Heinroth (1928) goes so far as to say that he would abolish the question of monogamy and polygamy in birds because, he states that, "There is either marriage, and then that is always monogamous, or else there are casual matings where the partners may change and then there is no marriage" (translation). The careful guarding of more than one female, the feeding of the young in the nest of the several females, and the continuation of the pairing with the primary female in the following year, or years, in the Brewer Blackbird, does not support Heinroth's statement.

SUMMARY

A population of Brewer Blackbirds (*Euphagus cyanocephalus*) was studied at a breeding colony at Carmel, Monterey County, California, for six breeding seasons. Color bands were used.

The breeding season is divided into five phases, with certain types of behavior characteristic of each: (1) segregation from the flock and assortment into pairs, or pair formation; (2) nest-building, copulation and egg-laying; (3) incubation; (4) nestling care; (5) fledgling care.

Thirteen call notes were distinguished and found to be associated with certain types of activities. Most of the seven distinct displays were accompanied by one or two specific call notes and were associated with aggression (threat), pairing behavior, or the preliminaries to coition. One of these was performed by the pair together as a mutual display.

There is no period of male isolation. Pair formation starts while the birds are still in flocks. New pairs tend to form gradually; pairs of the previous season tend to re-associate at the start of the breeding period (their identity as a pair having been lost during flocking in the non-breeding period).

Types of behavior characteristic of birds in phase 1 are their walking and perching together in pairs, mutual display, darting of the male at the female, the chase, and the multiple chase. Phase 1 may last as long as 12 weeks. After the pair is formed the members are almost always together and remain so until phase 3. The female exhibits the generalized display as phase 1 progresses, and the male guards her against the approaches of other males.

Phase 2, which has not been observed to occur before April, lasts about 10 days or two weeks. Response by intruding males to the displaying female and the consequent aggressive guarding by her mate reach their height in phase 2. Promiscuous copulations were only rarely observed.

In phase 3, incubation is performed by the female alone. On rare occasions the male feeds the incubating female on the nest. Because his attention is not entirely focused on his mate (the "primary female") in phase 3, as it was in phase 2, a male may become

polygynous by mating with an extra unguarded female which becomes the "secondary." There was little to indicate a tendency toward either monogamy or polygyny in any particular male. The greater the length of survival the more apt was the male to vary his pairing status.

The sex ratio of the breeding population trended toward an increase in the proportion of females until, in 1947, females outnumbered males two to one; as a corollary polygyny also increased. In the exceptional year, 1947, polygyny expanded to as many as four mates per male and the acquisition of some of the females was not typical.

The polygynous male guards his "secondary" female as he did his "primary" female. When the "primary's" eggs hatch he assists the female in feeding her nestlings as he later may do also at the nest of the "secondary." In all but one case of polygyny the male has been observed feeding nestlings of at least one of the females. In 23 cases he fed some of the broods of nestlings of *all* the mates. In 17 cases the duration of two nestling periods overlapped at least in part. In seven of these the male fed at two nests on the same day. The combined rate of feeding at the two nests in such cases might equal the maximum rate of a male feeding at only one nest (that is, 14 trips with food per hour) but was not known to exceed this rate.

Thirty-four banded females were always "primary" (lone or first mates of a season) throughout their years of occurrence; 20 banded females were always "secondary" and 15 shifted or varied their status.

Less than half of the females surviving only one year were primary. On the other hand, only three banded secondary females survived for two or more years, whereas the primary females and those of changing status survived five and six years. Longer survival apparently increased the possibility of a bird changing status.

There were 80 cases of monogamy and 35 cases of polygyny; there were 70 primary pairings and 45 secondary pairings. From 45 of the 70 "primary" pairings both members of a pair returned in the following year. All of these returning "primary" pairs remated with the exception of three cases in which there was a divorce. The primary pair bond may be maintained for as long as five years.

The locations of the nests of polygynous males were not arranged within a territory embracing all of them but the nests were interspersed among those of other males. Although there was a certain amount of aggression by the male near the nest-site and his guard perch, far greater aggression was shown by the male in guarding his mate wherever she might be and thus with little or no relation to any particular area or territory. Such localized aggression did not occur prior to pair formation. Females were often more belligerent in defending the actual nest site against trespassers than were males. The pair together sometimes acted as a team in repelling other pairs at or near the nest site.

A more or less constant trend of replacement occurred in the females of the population, but there was a sudden drop in numbers of both returns and replacements among the males between the last two seasons of the study. This caused a 1:2 sex ratio, the highest recorded proportion of females in the population studied.

Factors leading to polygyny were believed to be (1) an excess of females which might be caused by a depression in the male population or possibly by non-breeding of some yearling males; (2) death of males or destruction of nests in monogamous matings.

There are few detailed examples of nestling feeding among icterids in which polygyny occurs. The polygynous males of the Brewer Blackbird appear to be exceptional in the degree to which they participate in feeding of nestlings. Polygynous males of other passerines are recorded as assisting at nestling feeding only in a small degree.

More broods per male were fledged in polygyny than in monogamy, but the propor-

tion of fledged broods to nests containing young was higher in monogamy than in polygyny. The available, limited data suggest that nestling feeding by the male in polygyny was slightly lower than in monogamy and that the death rate of nestlings was appreciably higher.

More cases of monogamy than polygyny were recorded. The seasonal pair bond between the polygynous male and his mates is strong. The chance for "divorce" in succeeding years in primary pairings is remote, and the non-maintenance of the primary bond in the non-breeding season is considered to be only an "interruption" and indeed may be only apparent.

LITERATURE CITED

- Allen, A. A.
1914. The red-winged blackbird: a study in the ecology of a cat-tail marsh. *Abs. Proc. Linn. Soc. N. Y.*, 24-25:43-128.
- Beer, J. R., and Tibbitts, D.
1950. Nesting behavior of the red-winged blackbird. *Flicker*, 22:61-77.
- Bendire, C.
1895. Life histories of North American birds. Part 2. *Smithsonian Inst. Spec. Bull.*, 3:ix+518 pp.
- Blanchard, B. D.
1936. Continuity of behavior in the Nuttall white-crowned sparrow. *Condor*, 38:145-150.
1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.*, 46:1-178.
- Chapman, F. M.
1928. The nesting habits of Wagler's oropendola (*Zarhynchus wagleri*) on Barro Colorado Island. *Bull. Amer. Mus. Nat. Hist.*, 58:123-166.
- Dawson, W. L., and Bowles, J. H.
1909. The birds of Washington. Vol. 1 (Seattle, Wash., Occidental).
- Fautin, R. W.
1940. The establishment and maintenance of territories by the yellow-headed blackbird in Utah. *Great Basin Nat.*, 1:75-91.
1941. Development of nestling yellow-headed blackbirds. *Auk*, 58:215-232.
- Friedmann, H.
1929. The cowbirds (Springfield, Ill., and Baltimore, Md., Charles C. Thomas).
- Gabrielson, I. N., and Jewett, S. C.
1940. Birds of Oregon (Corvallis, Oregon, Oregon State College).
- Haartman, L. V.
1945. Några fall av polygami hos svart och vita flugsnapparen (*Muscicapa h. hypoleuca* Pall.). *Vår Fågelvärld*, 4:27-32.
- Heinroth, O.
1928. Ehigkeit oder Keinehigkeit. *Beitr. z. Fortpflanzungsbil. der Vögel*, 14:1-3.
- Hoehl, O.
1941. Bigamie beim Hausrotschwanz. *Beitr. z. Fortpflanzungsbil. der Vögel*, 17:30-31. (As reviewed by M. M. Nice, *Bird-Banding*, 19, 1948:177.)
- Kendeigh, S. C.
1941. Birds of a prairie community. *Condor*, 43:165-174.
- Huxley, J. S.
1914. The courtship habits of the great crested grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proc. Zool. Soc. London*, 1914:491-562.
- Kluijver, H. N., et al.
1940. De levenswijze van den winterkoning *Troglodytes tr. troglodytes* (L.). *Limosa*, 13:1-51.
- Lack, D.
1935. Territory and polygamy in a bishop bird, *Hordeacea hordeacea* (Linn.). *Ibis*, 1935:817-836.
1940a. Courtship feeding in birds. *Auk*, 57:169-178.
1940b. Pair-formation in birds. *Condor*, 42:269-286.

- Lack, D., and Emlen, J. T., Jr.
1939. Observations on breeding behavior in tricolored red-wings. *Condor*, 41:225-230.
- La Rivers, I.
1944. Observations on the nesting mortality of the Brewer blackbird, *Euphagus cyanocephalus*. *Amer. Midl. Nat.*, 32:417-437.
- Laskey, A. R.
1950. Cowbird behavior. *Wilson Bull.*, 62:157-174.
- Linsdale, J. M.
1938. Environmental responses of vertebrates in the Great Basin. *Amer. Midl. Nat.*, 19:1-206.
- McIlhenny, E. A.
1937. Life history of the boat-tailed grackle in Louisiana. *Auk*, 54:274-295.
- Mayr, E.
1939. The sex ratio in wild birds. *Amer. Nat.*, 73:156-179.
1941. Red-wing observations of 1940. *Proc. Linn. Soc. N. Y.*, 52-53:75-83.
- Mulford, A. S.
1936. Ecological relations of the Brewer blackbird (Unpublished thesis for the degree of Master of Arts, University of California, Berkeley).
- Nice, M. M.
1937. Studies in the life history of the song sparrow. I. *Trans. Linn. Soc. N. Y.*, 4:vii+1-247.
- Ryves, Lieut.-Col. B. H., and Ryves, Mrs. B. H.
1934. The breeding habits of the corn-bunting as observed in North Cornwall: with special reference to its polygamous habit. *Brit. Birds*, 28:2-26, 154-164.
- Saunders, A. A.
1914. Birds of Teton and northern Lewis and Clarke counties, Montana. *Condor*, 16:124-144.
- Snyder, L. L.
1937. Some measurements and observations from bronzed grackles. *Can. Field Nat.*, 51:37-39.
- Twining, H.
1938. The significance of combat in male rosy finches. *Condor*, 40:246-247.
- Welter, W. A.
1935. The natural history of the long-billed marsh wren. *Wilson Bull.*, 47:3-34.
- Williams, J. F.
1940. The sex ratio in nestling eastern red-wings. *Wilson Bull.*, 52:267-277.
- Wright, P. L., and Wright, M. H.
1944. The reproductive cycle of the male red-winged blackbird. *Condor*, 46:46-59.

Carmel, California, April 20, 1951.