THE REPRODUCTIVE CYCLE OF AMERICAN COOTS IN CALIFORNIA

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INTRODUCTION

THE American Coot (*Fulica americana*) possesses some peculiarities in breeding behavior that have not been adequately described. During the period from April, 1949, to August, 1950, I made a study of the breeding behavior of this species, some aspects of which have been published previously (Gullion, 1950; 1951*a*, *b*; 1952*a*, *b*, *c*; 1953*a*, *b*). The material presented in this paper constitutes two chapters from a thesis submitted in partial satisfaction of the requirements for the degree of Master of Arts in Zoology in the Graduate Division of the University of California. This completes the publication of the major contributions from the thesis.

This paper discusses the breeding behavior of the coot, in as nearly a chronological order as convenience allows, commencing with pair formation and following through to completion of the nesting cycle and the growth of the young until they are independent and leave their home territory. Two recent papers have dealt in detail with the necessary accessories to actual nesting, *i.e.*, the displays that bring two coots together to form the pair and then the displays and calls that enable the newly formed pair to secure and maintain a territory (Gullion, 1952*b*). The secured territory in turn permits the pair, with a minimum of disturbance, to proceed with the displays and calls which bring both birds into the synchronized physiological condition necessary if fertile matings are to occur and the breeding cycle is to be successfully completed (Gullion, 1953*b*).

The study was conducted in the San Francisco Bay area of western California. Most of the data reported here are the result of observations on five pairs of coots inhabiting two small lakes—Lake Temescal in northeastern Oakland, Alameda County, and Jewel Lake, in Tilden Regional Park, Contra Costa County (for a more complete discussion and maps of these areas see Gullion, 1953*b*).

Many of the coots discussed in this paper were marked with a plastic marker while others were identified by the shape and size of the shield. Sex determination was made mostly on the basis of voice differences, while age determination was made largely by leg color. These techniques have been discussed in previous publications.

The account of development is based upon the average growth of 43 young coots in the eleven broods produced by the five pairs

during the two breeding seasons studied. Young coots were nail-clipped as they hatched. This was found to cause deformation of the nail which served to distinguish the birds until they were 60 to 90 days old and large enough to carry an aluminum leg band. Marking at the time of hatching permitted a close check on the rate of growth of young coots as they were recaptured from time to time.

PAIRING

American Coots are probably exclusively monogamous although various workers have made statements to the contrary (*cf.* Dawson, 1923: 1560; Walker, 1932: 322). In resident pairs with suitable territory the pair bond probably lasts for the life of the respective birds. The territorial behavior of several birds at Lake Merritt, in downtown Oakland, through the winter of 1949–50 suggests that at least some migrant coots may remain paired through the period that they are away from their breeding territory.

Actual pair formation follows a long period of courtship. Prominent among courtship activities are the billing, bowing, and nibbling displays during which two birds touch bills, one then arches its neck and bows its head while the other works its bill through the bowing coot's head, neck, breast, and back feathers (Gullion, 1952*b:* 89). Among winter flocks (as observed among captive coots and at Lake Temescal) these three activities were carried on indiscriminately as regards sex. Generally males initiated the routine, and during the fall and winter another male became the submissive object of display as readily as a female. In fact, the display sequence was observed most frequently between males. Females initiated billing, bowing, and nibbling with males on several occasions, but never with another female.

The readiness with which strange birds participated in bowing and nibbling during the winter was surprising. A bird taken from Lake Merritt and released at Aquatic Park, on the Berkeley waterfront, on November 18, 1949, was bowing with another coot on the following day. Another bird taken from Lake Merritt on the same day and released on Jewel Lake on December 2 was bowing with a resident coot about 12 hours later.

Billing was the initial contact between two coots. If the approached coot billed readily, the other bird attempted to nibble, and if the approached bird was receptive to nibbling, it bowed. With the advancing spring season males submitted to this display less readily and commenced pecking the advancing bird, whereas females began bowing at the approach of another coot. If the approaching coot

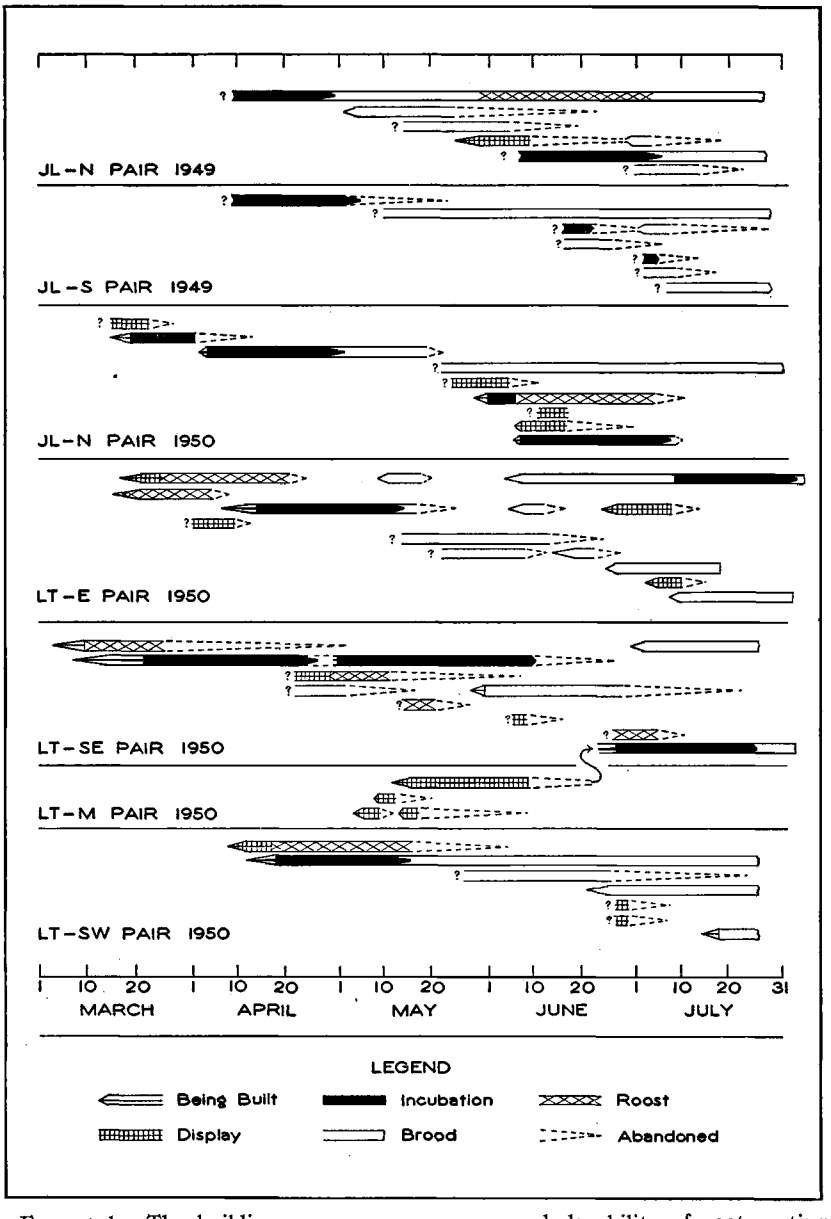


FIGURE 1. The building sequence, use, re-use, and durability of coot nesting structures at Jewel Lake (JL) and Lake Temescal (LT). Each horizontal bar represents a single site.

was another female, she usually pecked the bowing bird, but if the approaching coot was a male, he nibbled on the head and neck of the bowing female and tried to bill with her.

Certain males began advancing to and nibbling upon certain females more frequently, and the beginning of the pair bond became evident. As this behavior became more restricted to members of a pair, the female, though remaining submissive, frequently nibbled on the male when his ardor lagged, stimulating him to further activity. At this stage in the pair formation the female occasionally moved close to the male of her choice and bowed, stimulating him to nibble. Dabbling in the water often accompanied bowing and nibbling behavior, the bowing bird doing the dabbling.

Once the pair bond was fairly well cemented, the pair, with the female leading, began seeking a territory and a nesting site. The success or failure of the pair to secure a territory at this time is the final hurdle in the formation of a permanent pair bond. After territory was secured a *swimming arch* became a frequent display of the female. In this display the female swam immediately ahead of her mate with her neck rigidly arched and her tail broadly fanned to exhibit her white under tail coverts.

NEST STRUCTURES

The American Coot is a prolific builder of structures associated with nesting (figure 1). These structures consist of *display platforms*, *egg nests*, and *brood nests*. It was found that three pairs of coots laying two or more clutches of eggs in a season built nine structures each, while the one pair that laid only one clutch of eggs built seven structures.

Display platforms.—These structures are usually the first to be built in the spring. They are composed of coarse cat-tail stems and leaves and are built upon a foundation such as a floating board or stick (plate 29A) or a heap of broken-down cat-tails (plate 29B). The platform seldom rises more than one inch above the water and is about a foot in diameter. It is usually thoroughly water-soaked, and after the copulation period it is allowed to disintegrate. The non-incubating bird may use the display platform as a roosting site until it disintegrates, and if it is so used, it becomes littered with feces.

Egg nests.—While the display platform is in use the egg nest is built. Often more than one such structure is built before one is finally selected. The remaining nests are either allowed to disintegrate or are put into service as night roosts.

The egg nest, like the display platform, starts on a foundation of some sort with the first materials consisting of the coarse stems of cat-tails. As the nest develops, finer materials are added. A ramp is built on one side of the nest and is worked into the nest structure (plate 29C). This permits birds to enter and leave without tearing the sides of the nest down. Usually the ramp is composed of coarse stems laid lengthwise on the side of the nest.

The egg nest is kept clean of feces, and the cup is composed of fine, dry leaves. The average nest has a rim four to six inches above the water, an overall diameter of about 12 inches, with a ramp about 12 to 15 inches long. The egg cup is usually about one inch deep and six inches in diameter (plate 29D).

Since the egg nest is actually an elaborate raft, it must be added to constantly to keep it from settling below the surface. Materials added to the top of the nest may settle to the water-line in four days, being covered in the meantime with new materials. This results in the accumulation of a great pile of decaying plant material under the nest.

Egg nests may be either new structures or nests used earlier for other purposes. In one instance at Lake Temescal the second egg nest of one pair was built upon a disintegrating display platform of a second pair unable to defend their selected site. The second clutch of another pair was laid in a relined brood nest which had been used by this pair as recently as seven days previously.

Brood nests.—When the eggs hatch, a new nest is usually constructed. This nest, used for brooding young, is like the egg nest but larger, and measures as much as 18 inches across and eight inches high. A cup is frequently lacking, or if present in the original construction, it is soon obscured by the addition of fresh material. A brood nest is readily distinguishable from an egg nest by the wet materials worked into the final lining and the presence of feces in and about the nest (plate 29E). Egg nests are frequently converted to brood nests (plate 29F).

Materials.—The materials used in nest construction were usually those most readily available. The statement made by Grinnell *et al.* (1918: 317) that "the usual material . . . is the green stems of tules or sedges" and that "the drying out of the fresh stems during incubation has led to the popular idea that the birds use dry stalks" was not at all true in my study areas.

Structures built early in the season were composed almost exclusively of dead material since green material was not available.

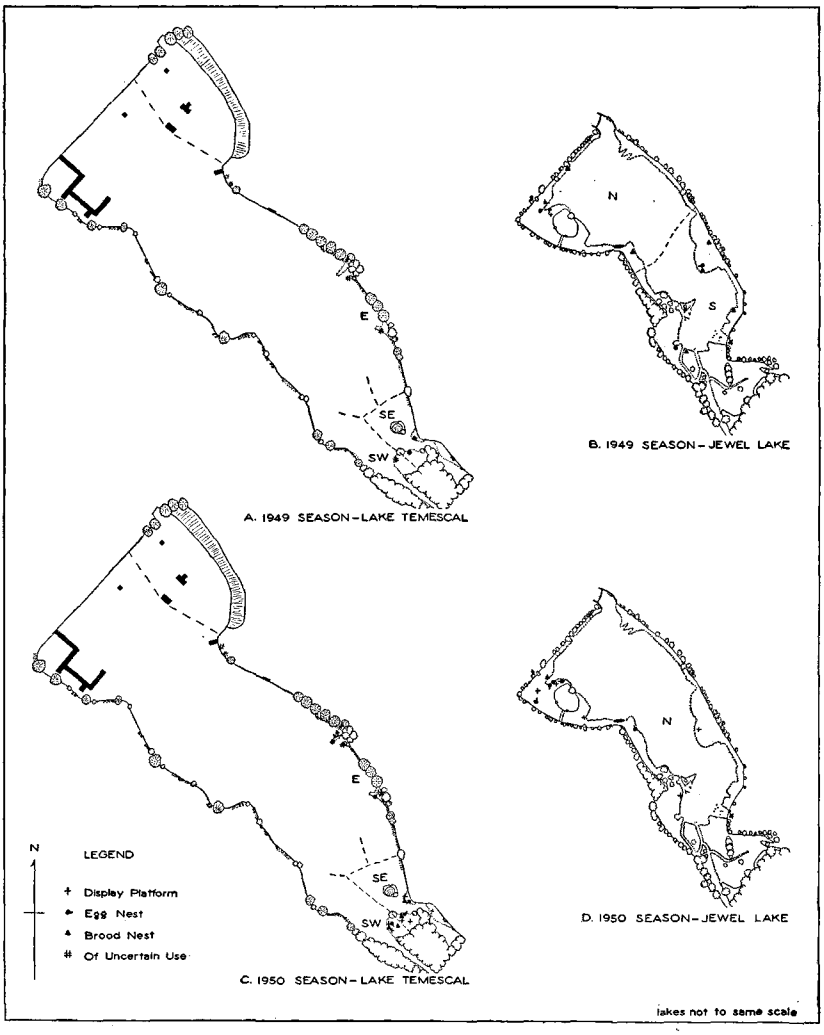


FIGURE 2. Locations of nesting structures, 1949 and 1950.

Later, when coots were feeding exclusively upon the bases of young cat-tail leaves and many loose leaves were floating in the nesting areas, a great deal of greenery appeared in the nest construction. Still later, dried material again predominated as other food became available and the coots ceased feeding upon cat-tail shoots. On several occasions green leaves were pulled down from surrounding cat-tail plants and worked into the nest.

Frequently nests built among broad-leaved cat-tails (*Typha latifolia*)

were composed almost entirely of parts from the narrow-leaved species (*Typha angustifolia*) and vice versa, indicating that materials were secured some distance from the nests. Provost (1947) found evidence that coots in Iowa favored the more buoyant bulrushes (*Scirpus* sp.) and bur-reeds (*Sparganium eurycarpum*) over cat-tail materials for nests. These plants were not available in my study areas.

Though cat-tails were most readily available at Lake Temescal, other materials were used from time to time. One pair used dry willow (*Salix* sp.) leaves in its nest. This and another pair frequently used green stems of the sago-pondweed (*Potamogeton pectinatus*) around the rim of their nests, while the third pair on the lake resorted to small sticks to build up a particularly large brood nest (plate 30E).

Location.—All structures studied in this area were located close to open water (figure 2). Four feet was the maximum distance from open water and two or three feet was the more frequent distance (plate 30A). On three occasions, trails made through the cat-tails by repeated wading on my part, sufficed as open water and nests were built along them.

Certain sites seemed to be favored. For example, the third egg nest of the N pair at Jewel Lake in 1950 was built on the identical site as the second nest of the N pair in 1949 (pair designations refer to territorial pairs discussed in detail elsewhere—see Gullion, 1953*b*: 170–173). It even had its ramp facing in the same direction. Two structures of the E pair at Lake Temescal in 1950 were built on the sites of two of its 1949 structures. One of these, the P16 site (plate 30B), was rebuilt twice before it finally received eggs (figure 1; LT-E pair 1950, first horizontal bar).

Discussion.—Overhead structures were not built by any coots, but nests were invariably located where overhead cover was already present. Observations were infrequent on construction, but they indicated that the female did a large part and probably the major share of this task. However, among a flock of captive birds, held on the Berkeley Campus of the University of California, it was evident that nest building was not entirely the duty of the female since males frequently carried materials to their mates.

Wetmore (1920: 396) believed the male took no part in nest construction, but Walker (1932: 323) was probably more nearly correct when he said, "the female soon took her post on the nest and the male brought reeds to her, some of which she wove into the nest."

The short life of these nests is remarkable (figure 1). The fourth egg nest of the N pair on Jewel Lake in 1950 completely disintegrated within 48 hours of the end of incubation, and many other nests were

little more than accumulations of rotting cat-tail leaves ten days after incubation ended. In direct contrast, a Ruddy Duck (*Oxyura jamaicensis*) made a woven nest of green cat-tail leaves close to a coot nest. Without further additions, this nest lasted to hatch a clutch of duck eggs after 24 days incubation. Following that, coots took it over as a night roost, and it finally collapsed 18 days after the duck clutch had hatched.

Sooter (1942: 127) in an Iowa study, found all of his nests in emergent vegetation with "Narrow lanes of water . . . between the nests and wide channels or large pools." Most other authors likewise record nests as being in emergent vegetation on the water surface. The few records of nests on dry land, in trees or elsewhere, suggest nests built during abnormal water conditions.

COPULATION

Copulation was observed on several occasions and always followed the same general pattern. It is best illustrated by the act observed on April 8, 1950, at Lake Temescal. Both birds of the E pair were swimming and feeding together just north of their platform area (see plate 29B). After a moment of chasing, the female moved into the cat-tails with the male close behind. As she crossed the platform she remained silent but arched and slapped the platform with one foot. Still arched, she settled down on the platform, in a squat with her head under the water. The male mounted her and started giving a closely spaced *kurk, kurk, kurk.* He did not grasp her head but gently mounted squarely on her back, his head lowered and using his wings for balance. She now raised her head out of the water, he reared back, apparently hanging onto her back with his claws as copulation took place. The actual intromission took no longer than two seconds, after which he dismounted and swam away. The hen then stood up and preened for several minutes before leaving.

A copulation observed June 13, 1950, at Jewel Lake differed only in the early stages. On this occasion the male moved to the vicinity of the female from another part of the pond, fed close to her for a moment, and then moved over to her, giving a low cough with his bill open and emitting a barely audible sound. Under his close pursuit she moved away in a *brace* (Gullion, 1952*b:* 89), going directly to a platform at the edge of the cat-tails. Here she assumed the *squat arch* and copulation proceeded as above. The elapsed time between the male's joining the female and resuming normal feeding following copulation was three minutes. The usual notes and displays were involved, *i.e.*, the "coughing" of the male, the chase with

the female bracing, the arch, and post-copulatory displacement-preening. There was, however, no preliminary courtship play, vocal or visual. This has been the pattern of each coot copulation I have observed.

Sooter (1941: 38) agrees that there is no preliminary display but believed that the male grasped the head of the female and that the female gave "some shrill cries . . . during the act." He noted displacement fluffing of the feathers following copulation.

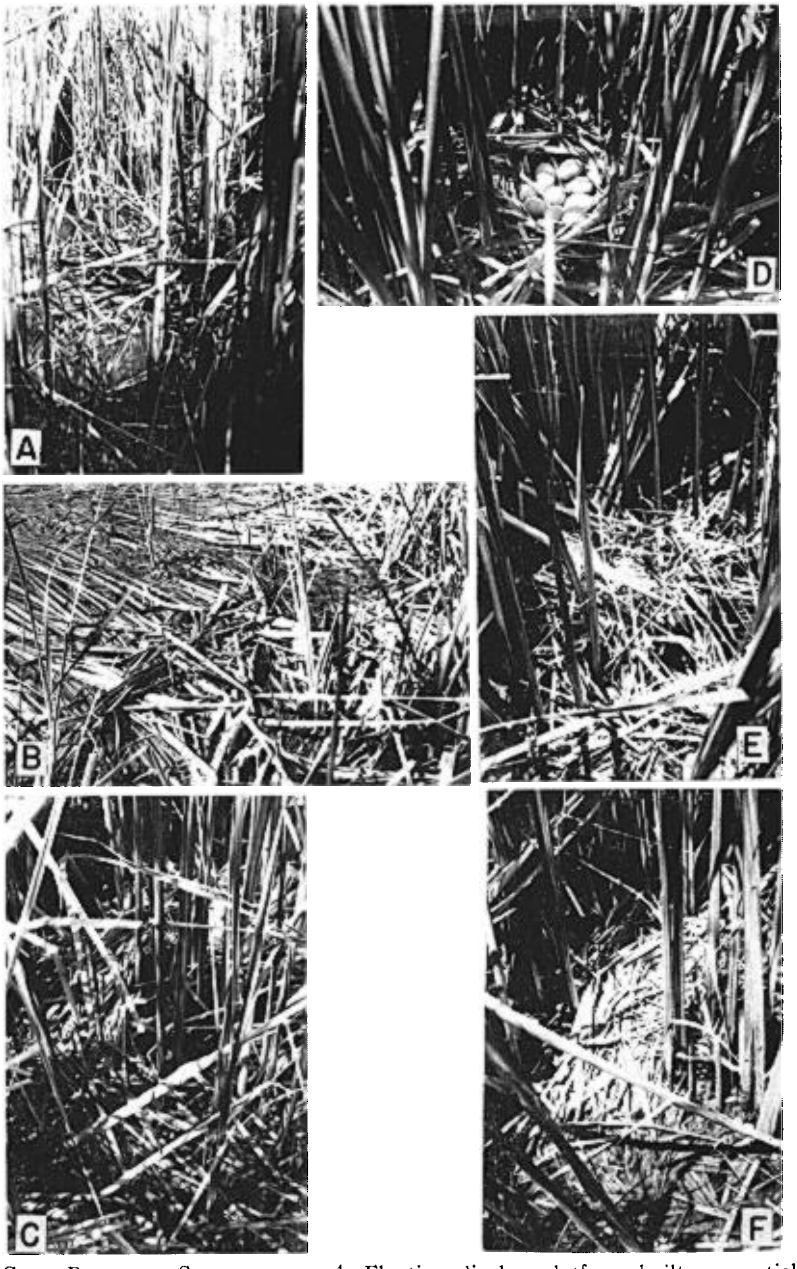
On one occasion an incident was observed that may have been underwater copulation. The M pair at Lake Temescal, without secure territory, was feeding leisurely when the male started chasing the female, giving a low cough as he pursued her. She dived and he followed immediately. When they surfaced about 75 feet away, the male moved off in a brace while the female remained in place, doing displacement-preening. The sequence strongly suggests underwater copulation, but I could not be certain that it did occur. The underwater copulation recorded by several authors may have been misinterpreted fighting (*cf.* Dawson, 1923: 1560; Townsend, 1925: 6).

Copulation after the clutch is complete is probably unusual but was recorded in the SE pair at Lake Temescal in 1950. During this period the M female was established deep in the SE area while the M male was unable to remain close to her. The resulting platform activity of the M female apparently kept the SE male so stimulated that, although he refused to respond physically to her displays, he did chase and try to copulate with his own mate nearly every time they changed incubation shifts, which was hourly. Several times mounting was observed and intromission may have occurred. The seductive behavior on the part of the M female, though evidently disturbing the composure of the SE male, did not do so sufficiently to cause him to be unfaithful or to upset his previous commitments to the regimen of incubation and other family duties.

EGG DEPOSITION

Rate.—It is generally agreed among all who have studied the nesting of the American Coot that one egg is deposited each day until the clutch is complete. In eight nests observed in this study, this was the case.

On the other hand the Lake Temescal SE female delayed 24 hours during the laying of some of the early eggs of her first 1950 set. A 48-hour gap occurred between the deposition of the first and second eggs, since the nest contained two new eggs the third morning, indicating that the second egg was held over to be laid the same day as the third



COOT BREEDING STRUCTURES. *A*. Floating display platform built on a stick. *B*. Display platform on broken-down cat-tails. *C*. Ramp on egg nest. *D*. Egg nest built on foundation of bent-over cat-tails (same nest as *C*.). *E*. Brood nest. *F*. Egg nest converted for brooding (same nest as *C*. and *D*.).

COOT NESTING SITES AND CHICKS. *A*. Minimum nesting cover (site of ♀ nest of the LT-E pair, 1950). *B*. The P16 nest site of the LT-E pair. *C*. Head of a newly hatched coot. *D*. A day-old coot.

egg. A similar gap of at least 48 hours occurred between the laying of the ninth and tenth eggs in the first 1950 nest of the Jewel Lake N pair. Sooter (1941: 41) records two nests with two eggs appearing in one day but believed one was laid by a second female.

Time.—Early in the period of egg deposition the eggs are laid shortly after midnight, apparently about 12:45 a.m. Checks on the third nest of the SE pair at Lake Temescal on June 27–28, 1950, showed an egg deposited between 10 p.m. and 2:15 a.m.; on June 29, a new egg, very much warmer than its nest-mates, was present at 1 a.m.; on June 29–30, a new egg was laid between 11:35 p.m. and 12:50 a.m.; on July 2, the sixth egg was deposited between 12:58 and 1:48 a.m.; and on July 4, the eighth and last egg was deposited after 2 a.m.

The last three or four eggs are probably deposited about 4 or 5 a.m. The first four nights, the female was on the nest each time it was visited, but on July 2 and 4 the male was incubating. Normally he would do so all night, with the female relieving him in the early dawn, and then presumably laying that night's egg. On July 2, however, the male was purposely chased to open water in order to be sure that it was he that had been flushed from the nest. The male did not return to incubate, but the female did and laid the sixth egg at what was probably an unusually early hour. On July 4, the incubating male was not disturbed, and he was still incubating when last checked at 2 a.m. The eighth egg was laid later that morning. Similar data concerning dawn laying of the last eggs in a clutch were obtained from an earlier nest of this pair.

Sooter (1941: 41) records five nests in which eggs were deposited between sunset and 3 a.m. However, he does not indicate the size of the clutches at the time.

Clutch size.—Eight early season nests at Jewel Lake and Lake Temescal contained an average of 9.0 eggs per clutch, ranging from seven to ten. Five late clutches, all second nestings, contained an average of 6.4 eggs, ranging from four to eight eggs per clutch. Sooter (1941: 57), in Iowa, found an average of 8.6 eggs in 224 clutches completed by June 23, 1937, and an average of 6.03 eggs in 1936 and 6.63 eggs in 1937 for clutches completed after June 23. Later, Provost (1947) found an average of 8.8 eggs in early nests in the same general area worked by Sooter. In other words, early season clutches and first clutches average two eggs more than second nestings and late season clutches.

Dump nests.—The use of dump nests by coots or the practice of dropping eggs in the nests of other species seems to be rare or absent. In the literature there are many instances of duck eggs appearing in coot nests but not of coot eggs appearing in duck nests.

Egg shape and size.—The typical coot egg has a slightly roughened texture and a buff ground color with fine purplish-brown spots evenly distributed over the surface. Its shape is what Romanoff and Romanoff (1949: 60) call "conical," though it may vary to "biconical." The American Coot egg seems to be typical for the genus *Fulica* and more or less so for the family Rallidae. Among the genera whose eggs are known, only the Oriental genus *Rallina* with its coarse, chalky eggs and the African genus *Sarothrura* with unspotted white eggs differ from the rest of the family in this respect.

Considering the possibility that small egg size and the consequent reduction in yolk available for the development of the embryo might be correlated with hatching and fledging success, I measured most of the eggs in the 1950 clutches at both lakes.

The average measurements for 49 eggs from nine nests was 49.0 by 33.5 mm., exactly the same average given by Bent (1926: 361). However, there was considerable variation in the size and shape of eggs laid by the different females, as shown in table 1.

TABLE 1
EGG SIZES

Season	*Female*	*Clutch*	*No.*	*Average Size Millimeters*	*No.*	*Average Volume Milliliters*
1949	JL-S	first	1	49.5 × 34.1	1	26.0
1950	JL-N	first	4	47.0 × 31.3	4	21.5
1950	JL-N	second	1	47.1 × 31.7	1	23.2
1950	JL-N	fourth	7	47.1 × 31.7	—	—
1950	JL-N	fifth	2	51.2 × 32.9	2	29.3
1950	LT-E	first	4	50.1 × 34.4	—	—
1950	LT-E	second	4	49.8 × 33.7	—	—
1950	LT-SE	second	10	49.5 × 35.1	5	30.2
1950	LT-SE	third	8	50.5 × 34.8	1	32.5
1950	LT-SW	first	10	50.6 × 34.3	1	27.0

Recovered eggs or shells from several nests were measured for volume by water displacement (table 1). Interestingly, in 1950 the Jewel Lake N female, laying the smallest eggs, had 100 per cent survival of young hatched from five eggs out of a clutch of seven, while the Lake Temescal SE female, laying the largest eggs, hatched only five out of three consecutive clutches totalling 25 eggs, and only one young survived. The Jewel Lake S pair fledged seven out of eight young hatched in 1949, while in 1950 the Lake Temescal E and SW pairs, with slightly larger eggs, each hatched seven eggs, but only fledged one and three immatures respectively. However, small boys throwing stones may have affected the survival of the Lake Temescal birds.

A possible explanation of this inverse correlation might lie in the ages of the adults. The mother of the highly successful 1950 N broods at Jewel Lake was a yearling. Her mate in 1950 was her father, she being a member of his second brood in 1949. Her first eggs were all small, "pullet" sized, compared with the eggs laid by the other females. However, the eggs from her fifth clutch of the season were almost the normal size. On the other hand, at least two of the three 1950 pairs at Lake Temescal were at least two years old and may have been much older.

Egg weights.—Eggs from several nests were weighed at intervals. Four eggs from the first nest of the 1949 S pair at Jewel Lake, weighed 28.9, 26.4, 28.2, and 28.1 grams on May 3. Two days later, in the same order, they weighed 28.6, 26.2, 27.0, and 27.7 grams; the first two were addled and the last two were in the process of hatching. (The wet chick, ten minutes after hatching from the third egg in this series weighed 22.4 grams—table 2). Four fresh eggs from this pair's third 1949 clutch, laid in July, ranged from 29.4 to 31.8 grams. One pipped egg of the 1949 Jewel Lake N pair's second clutch weighed 24.9 grams.

In 1950, seven unincubated eggs of the Jewel Lake N pair's first clutch ranged from 25.6 to 27.0 grams, averaging 26.1 grams. At Lake Temescal in 1950, weights were taken on the first clutch of the SE pair. Three of these eggs on the first day of incubation weighed 33.2, 31.8, and 32.8 grams, while ten days later these same eggs weighed 32.2, 30.7, and 31.7 grams. The last egg, intermediate in weight, was the only fertile egg in the clutch.

INCUBATION

Commencement of incubation.—The incubation of early season clutches may start with the second egg or not until the clutch is complete. Once started, it continues without interruption until hatching occurs. In two Lake Temescal nests in 1950 the two oldest eggs were first pipped within a few hours of each other, while the remainder were pipped at one-day intervals, this indicating that incubation began with deposition of the second egg.

In 1950 the first clutch of the Lake Temescal SE pair and the first clutch of the Jewel Lake N pair were not incubated until the last egg was laid.

In second nestings at Jewel Lake in 1949 and 1950, all eggs hatched at one day intervals, suggesting that incubation began with the first egg, while incubation in a second nesting at Lake Temescal in 1950 is known to have begun with the first egg.

While Rockwell (1912: 121) believed that incubation in the coot normally does not begin until the set is complete, the majority of other workers report findings similar to mine. Sooter (1941: 42) found that commencement of incubation was delayed in the earliest nests and that hatching of the first eggs was delayed accordingly. Provost (1947: 498) states, "in early nests at least, incubation begins anytime between the laying of the first and last egg in a clutch, and it is very likely erratic and discontinuous where it occurs during the egg laying period." Since Provost makes the possible mistake of assuming a 21-day incubation period, which may be incorrect, he may be likewise mistaken in believing that incubation is "erratic and discontinuous . . . during the egg laying period." Provost, perhaps, attributed the delayed hatching of eggs to the discontinuous incubation rather than to the 23 to 25 day incubation period.

The practice of starting incubation with the laying of the first egg, as occurs in the aquatic Rallidae, is a curious behaviorism and does not seem to be general among birds. It is not true of Rallidae that nest in dry locations. In searching through the literature I have found this practice to be most common among those rails building large bulky nests on the water and especially among those forms breeding in tropical areas.

Several times I have torn recently abandoned coot nests apart and each time I was surprised at the heat generated by the decay of the moist plant material in the center of those nests. The question arises as to whether the combination of heat from the "compost pile" under the eggs and the warm air above the eggs is sufficient to initiate embryonic development in the eggs. If that is so, then after one or two days the embryo would develop to such a degree that night chilling through lack of incubation would kill the embryos and result in a number of addled eggs in the clutch. Perhaps coots developed the practice of commencing incubation with the first or second egg so that the eggs do not have a chance to chill, once embryonic development has begun.

Sharing of incubation.—Reviewing the subject of coot incubation, Wetmore (1920: 396) believed that the male took no part in incubation whereas Bent (1926: 361) stated that "it is shared by both sexes and the male often stands guard while his mate is sitting." Sooter (1941: 42) obtained evidence that incubation is shared by both sexes but gave no further information.

After a series of observations on nests at both study lakes during 1950, it became evident that both sexes share in the task of incubation

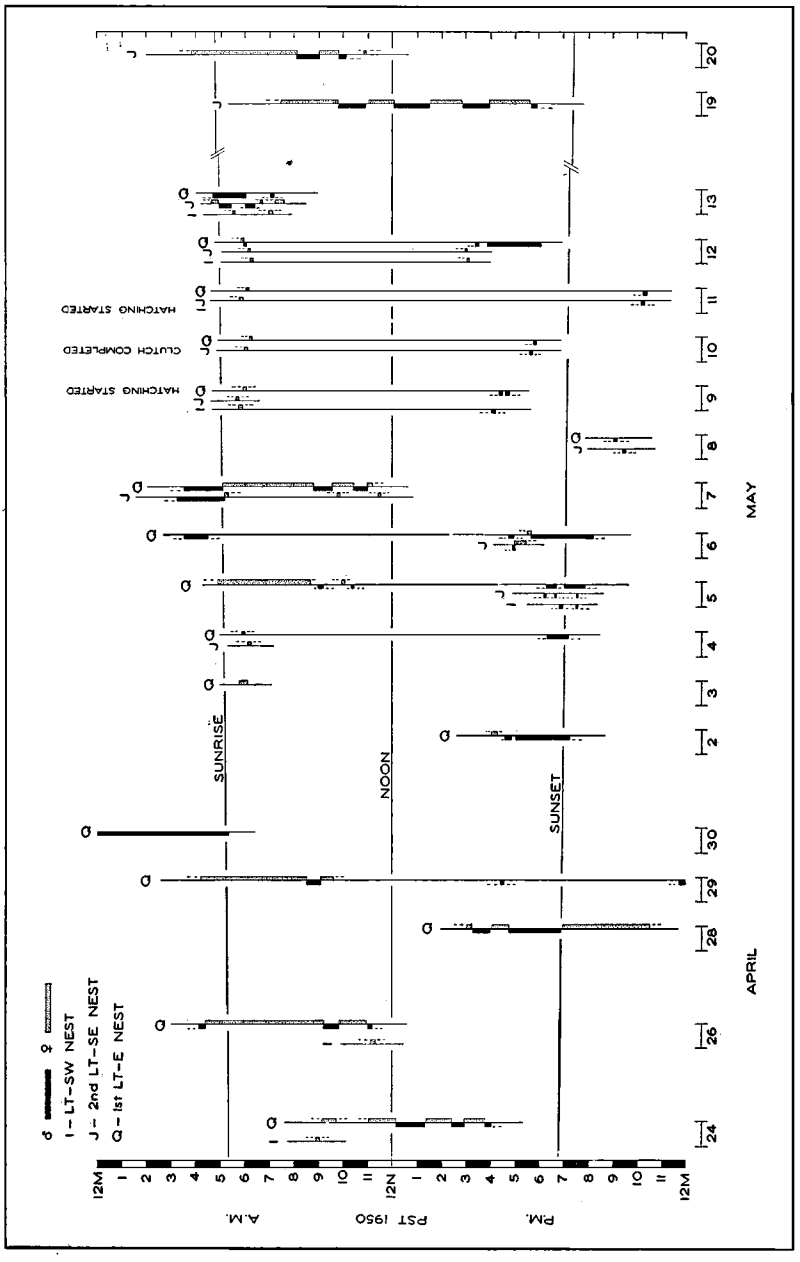


FIGURE 3. Length and pattern of incubation shifts.

and furthermore it seems probable that the male does the major share of it (figure 3). Out of 26 night observations, 23 indicated that the male was on the nest throughout the night. The female relieved the male shortly after daybreak and then took a four-hour shift. Through the rest of the day the shifts were of about one-hour duration until nearly sundown when the male generally took over for the night. Observations on three nests in different stages of incubation at Lake Temescal showed that only males were incubating at night.

At dawn the females relieved the males between 4:23 and 5:02 a.m. and remained on the nest until about 8:25 to 9:38 a.m., the shortest of three shifts being three hours and 45 minutes, and the longest, four hours and 50 minutes. The length of shifts through the daylight hours varied considerably. The shortest of 21 daylight shifts was 28 minutes while the longest was one hour and 39 minutes.

During four days of observations on the Lake Temescal E pair, the male averaged 47 minutes for seven periods, while the female averaged 56 minutes for five periods. During two days of observations on the Lake Temescal SE pair the male averaged 67 minutes in four periods while the female averaged 71 minutes in four periods. Three short periods of observation in 1950 on the Jewel Lake N pair, incubating its second clutch (fourth 1950 laying), indicated that their shifts varied somewhat from the Lake Temescal pattern, with no changes being observed during observation periods varying from one hour and 42 minutes to three hours and 22 minutes. The Lake Temescal SE pair, on its third clutch during this same period, maintained the same average schedule as on their earlier clutch (67 to 71 minutes).

As noted earlier, observations on the Lake Temescal SE pair in July, 1950, indicate that the female incubates during the nights in which the first three or four eggs are deposited, but with the appearance of either the fourth or fifth egg, the male assumes the role of night incubator which he apparently continues to play until the eggs are hatched.

Dusk shifts by males of up to two hours and ten minutes, followed by the female relieving them for the night, were recorded twice. On all five occasions that nests were checked shortly after sunset and again shortly before daylight the following morning, the same bird was found occupying the nest. If late evening changes were made, they occurred about sunset, otherwise, when the male went on the nest between 4:30 and 5:30 p.m., he remained on the nest until relieved at dawn by his mate. On only one night was the male's assumption of incubation and dawn relief observed; this period totalled 11 hours and 24 minutes.

On two nights that a female coot incubated, it was noted that she also incubated the greater part of her usual early morning shift. On the one occasion that the complete night period for the female was determined, it lasted for 13 hours and 27 minutes.

Incubation behavior.—In 1950 at Lake Temescal 17 nest changes between the E pair and 11 changes between the SE pair were observed. As a rule the males showed an impatience to commence incubation and then a strong desire to leave the nest when their turn was finished. Females were generally less hurried in their actions, remaining away from the nest until called or chased to it and then later not leaving the nest until the male was close by. Whenever the male was off the nest because of disturbance the female would go to the nest and commence incubation even though it was not her turn.

When not disturbed, coots always leave and enter the nest by way of the ramp. The departing bird makes no attempt to cover the eggs, though occasionally a bird forced to depart hastily may accidently scatter nest material over the eggs. The bird coming on the nest invariably spends about one minute preening and drying its breast feathers, standing on the top of the ramp while doing so. At this time the eggs apparently are turned and any needed nest repairs are made. An incubating bird was never seen working with the nest materials unless its mate brought some to the nest, and then the material was hastily placed on the nest rim. I have never observed egg turning by an incubating coot. Some birds slowly rotated on the nest while others always faced in one direction while incubating.

Following relief, each bird covered its territory, seeking out any intruding birds that might have entered while it was incubating. The female usually remained some distance from the nest, feeding and preening. The male, on the other hand, after an inspection of the area, returned to feed and preen in the vicinity of the nest until it was time for him to take his turn at incubation (figure 4).

The *bracing* display that frequently followed a change has been discussed in detail elsewhere (Gullion, 1952*b:* 89). How much of this display exhibited by the Lake Temescal SE pair was normal for the change is unknown, since the SE male was being subjected to the seductive gestures and calls of the interloping M female at this time.

The extent of nest defense against predators by the American Coot is difficult to determine. In the case of repeated nest disturbance on my part the degree of defense seemed to be strongly conditioned by the frequency with which the nest was visited. Nests visited daily were more vigorously defended than those visited less frequently.

Of course, the stage of nesting was important. Although some

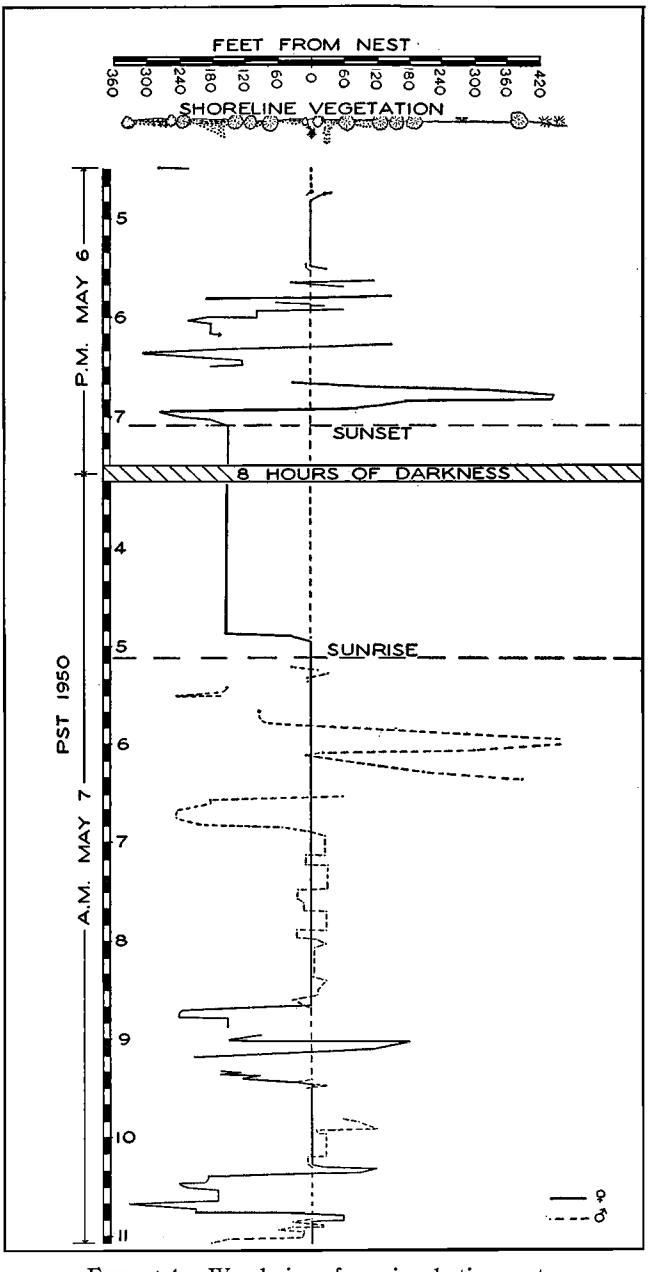


FIGURE 4. Wandering of non-incubating coots.

concern was generally shown when display platforms were disturbed, this generally amounted to no more than a few *poonks* or *puhlks* by the respective birds from some distance away. As the egg nest was built and eggs were laid, the birds came closer and occasionally *swanned* or if very frequently disturbed, they might *churn*. With the advance of incubation, defense became more vigorous, both birds *swanning* almost continually during the period of disturbance, with frequent and prolonged *churning*. When eggs began hatching, nest defense reached a peak, with defending birds actually attacking me. It was during this time that three nesting adults at Lake Temescal were taken by hand and subsequently tagged and banded. In fact, the SE female once climbed on the nest when I was present, and I had to remove her in order to continue my examination of the nest.

On one occasion, a dog waded into the vegetation near the Lake Temescal SE nest and the male quickly and quietly slipped off the nest to hide in the cat-tails. Since neither he nor his mate indicated any desire to defend the nest, it seems probable that little more than *swanning* constitutes nest defense against the larger predators.

Incubation period.—Of the nine successful nests I have studied, four have provided definite data on the period of incubation. The date of laying of each egg was known in three nests and the hatching dates of the fourth were such as to indicate a minimum period corresponding to that determined in the other three nests (figure 5). The five other nests were not located until after the clutch was complete and could not be correlated with other data.

Out of 11 eggs in three nests, marked the day they were laid, none was pipped before the end of the twenty-first day and none hatched before the end of the twenty-second day. Of these 11, five hatched during the twenty-third day, four on the twenty-fourth day, one on the twenty-fifth day, and the last hatched 26 days after deposition but perhaps after only 25 days of incubation (figure 5C and D). Of the eggs in the fourth nest, the last hatched during the twenty-third day after the nest was located, and since all but the first egg hatched at one day intervals previously, it is evident that all but the first egg hatched during at least the twenty-third day after deposition (figure 5A).

Sufficient data were obtained on four eggs to determine that the minimum period of incubation varied from 548 to 558 hours. Since these eggs were among the last deposited in their clutches, it is assumed they were deposited about 4 a.m. and their hatching times ranged from about midnight to after 10 a.m. on the twenty-third day, or between the twentieth hour of the twenty-second day and the sixth hour of the twenty-third day of incubation.

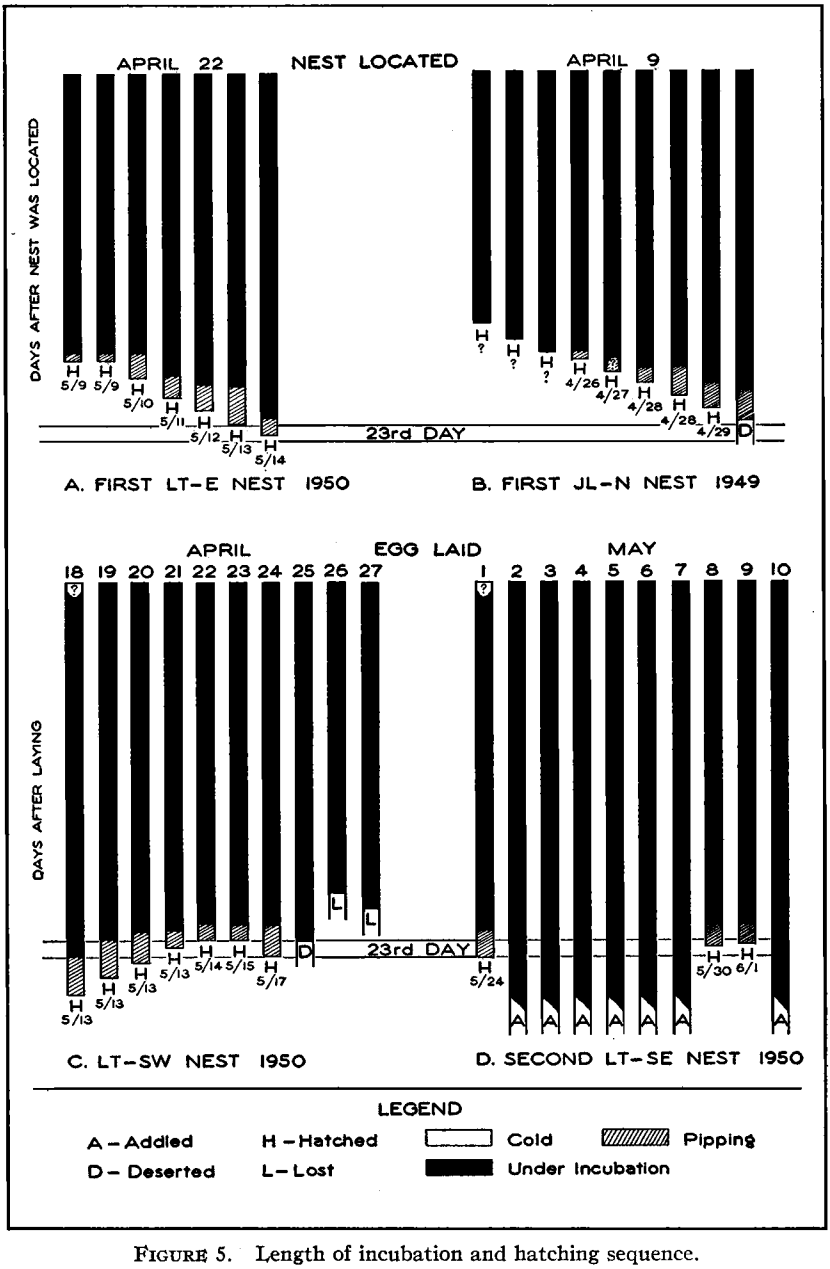


FIGURE 5. Length of incubation and hatching sequence.

Examining the literature, I have not found any published reference to an incubation period of over 22 days in this species. Some workers apparently calculated the incubation period as that period from the time the last egg was laid until the time the first egg hatched (which might have been as short as 11 days in the nests I studied). This may explain the 14 day incubation period published by Burns (1915: 282) and repeated by Bergtold (1917: 89). Bent (1926: 361) is most nearly correct when he states: "The period of incubation is 21 or 22 days." He does not indicate the source of his data. Subsequent authors have almost universally accepted Bent's statement, most of them giving the 21 day incubation period.

The suggestion is made by both Burns (1915: 281) and Bergtold (1917: 41–42) that climate might affect the length of incubation. Considering this possibility it might be worth noting that while the study areas in the San Francisco Bay area have a July average temperature of about 62° F (U.S.D.A., 1941: 783) the area studied by Sooter in Iowa (1941) has an average July temperature of about 75° F (U.S.D.A., 1941: 862). This temperature difference may account for the apparent difference in incubation periods between these two areas.

HATCHING

Sequence of hatching.—Since the eggs are generally under continuous incubation from the time they are laid until they hatch, the hatching is usually in the same one-a-day sequence as the laying.

As pointed out earlier, incubation in early nests is often delayed, with a consequent bunching-up of the hatching of the first eggs, but once hatching commences it proceeds at a fairly uniform rate (figure 5A, B, C).

Sooter (1941: 42) states, "hatching began 21 days after the first egg was laid, except in the earliest nests. The first nests required one or two days longer to start hatching." In the early nests I watched, hatching was delayed one to three days. In one nest four eggs hatched on one day, hatching during their twenty-third, twenty-fourth, twenty-fifth, and possibly twenty-sixth days respectively (figure 5C).

The commencement of pipping was hard to determine, but data on 33 eggs indicated that pipping begins from 12 to 76 hours before the chick frees itself from the egg-shell and is hatched. The average time seems to be about 36 hours. The duration of pipping does not seem to be correlated with individual pairs or with an egg's position

in the sequence of laying of the clutch. In other words, the length of time it took a full-term embryo to free itself from its egg-shell and egg-membranes seemed to be dependent upon the strength or determination of each chick and not upon possible hereditary influences of its parents or its position in the sequence of egg deposition.

Hatching failures.—Egg desertion, particularly of the last eggs in a clutch, appears to be frequent among coots. A stimulus to brood seems to operate after a certain number of chicks have hatched, and in brooding, the desire to incubate is overcome, thus limiting the number of eggs hatched from any one nest. Regardless of the size of the clutch, no more than eight eggs were hatched in any of the nests I had under observation. In one nest two eggs were dumped into the water and the nest converted for brooding purposes after the seventh egg hatched (figure 5C). The eighth egg was later recovered and found to contain a full-term embryo that should have been pipping the egg within hours of the time it was jettisoned. In another nest the ninth egg was deserted after it was pipped and although the young hatched, it soon died from neglect (figure 5B).

A survey of the literature reveals that broods of more than eight young coots are uncommon and normally there are fewer, this in spite of frequent clutches of more than eight eggs. Hendrickson (1936: 216) reports five as the largest brood he studied in Iowa and later Friley *et al.* (1938: 84) repeated the observation in the same area, but they noted that the "hatching of larger broods was common." Sooter (1941: 45–46) presents tabular data that may support my observations, though he does not draw the same conclusions. In 1937, he recorded an average hatch of 8.22 eggs per nest out of an average clutch of 8.45 eggs. Miller (1946: 12) indicates that few broods of more than eight birds occur in the Black Gallinule (*Gallinula chloropus*). While these data are not conclusive, they do point to a problem that should be investigated further.

It is my belief that the calls of young coots stimulate the parents to brood rather than incubate. So long as there are few young moving or calling from under the incubating adult, the stimulus to incubate remains predominant and one bird sticks close to the eggs. However, the activity of seven or eight young coots causes sufficient stimulus of a different nature to initiate brooding and feeding behavior and to terminate incubation. The activity of a single young has little effect upon the desire to incubate and is unable to excite a strong feeding stimulus in the parents. In the case of the consistent failures of the three nests of the Lake Temescal SE pair in 1950, the feeble activities of the single chick were not sufficient to excite con-

sistent care by the adults, and it perished before the hatching of another egg could initiate additional brooding stimulus. The nearly full clutch of eggs remaining retained control of the parents' instincts to incubate. On the other hand, in more successful nests, the stimulus provided by the activity of an increasing number of chicks not only stimulated the parents to care for the first hatched before it perished but also to provide adequate care for the chicks subsequently hatched. As the motionless eggs turn to active, noisy chicks, the incubation instinct becomes overwhelmed by the desire to brood and feed, and the adult birds cease incubation of the remaining eggs and turn their full attention to caring for the young.

If this behavior is as general as it appears to be, it means that a coot brood of about eight is the maximum usually hatched even though the nest may contain more than eight eggs. This would definitely limit the productivity of the species and illustrates a disadvantage of staggered hatching. In waterfowl and gallinaceous birds having large clutches, a simultaneous hatch insures full-term incubation for most or all of the eggs and parental care for the young once they have hatched.

A second factor preventing the hatching of eggs is, of course, sterility. The SE pair at Lake Temescal laid more sterile eggs than fertile ones. In 1950, they laid their first clutch in late March and did not commence incubating until the eighth and last egg was laid on March 29. Only the last egg of this clutch hatched, after 23 days of incubation, on April 21. On this date six eggs remained in the nest, and two of these were found to be rotten.

A second clutch was commenced in this same nest on May 1, while eggs of the first clutch still remained. On May 5 there were five new eggs and one old egg, all under incubation. A fresh egg replaced the old egg on May 6. The hatch of the second clutch was extremely irregular, the first, eighth, and ninth eggs hatching from a clutch of ten (figure 5D). The stimulus provided by the last two young was sufficient to start parental care, though the first chick was allowed to die. Despite two constantly begging young, incubation of the six remaining addled eggs continued for about eight days after the last egg hatched.

Twenty-six days after the hatching of the second clutch the SE pair started its third clutch. This clutch was under incubation from the first egg, but only the sixth egg of the clutch of seven hatched (an eighth egg was lost from the nest earlier).

It seems possible that the partial sterility in this pair resulted from senility in one or both birds. This pair fledged at least three young

in 1949, but only one young was fledged out of three nesting attempts in 1950. Romanoff and Romanoff (1949: 12) indicate that egg productivity in domestic chickens decreases with advancing age, and "the period during which their eggs are fertile is even shorter." They further indicate that reproductive capacity in the male fowl declines at a faster rate than in females. This perhaps may not be true of the American Coot, but it does present a possible explanation for the erratic hatch of the eggs of the SE pair at Lake Temescal in 1950.

The ages of the SE birds are not known, but the male did possess yellow-orange legs like those found on an eleven-year-old banded female at Lake Merritt. It seems possible that the male was the senile individual in this pair, since the reproductive capabilities of the female seemed to be unimpaired, as she deposited three clutches totalling 26 eggs in a period of 105 days.

The eggs that became addled in other nests apparently had been laid consecutively, since the hatch, once begun, normally proceeded uninterrupted. Unfortunately, none of these nests was found early enough in its history to determine at which end of deposition the addled eggs were laid. Although the hatching pattern in one nest indicated that the fourth and sixth eggs of a clutch of seven became addled, it is possible that it was the earliest eggs that became addled in other nests. If so, these data suggest a possibility that delayed incubation allowed the earliest eggs to be killed by chilling, as discussed earlier.

CESSATION OF INCUBATION

In four nests incubation ceased quite promptly when eggs failed to hatch on schedule. In 1949 and 1950 at Jewel Lake, nests were deserted the day the last fertile egg hatched, leaving two or three addled eggs behind. Even the three LT-SE nests, carrying nearly full clutches of addled eggs through the normal incubation period, were incubated for only seven or eight days after the last egg hatched or was due to hatch.

Leopold (1933: 367) indicates that some gallinaceous birds incubate addled clutches for many days after the hatch should have occurred (up to 56 days in Bobwhites, *Colinus virginianus*). I believe this is also true of many ducks.

LARGE CLUTCHES

The carry-over of eggs, as it occurred in the first LT-SE nest, might explain the clutches of over a dozen eggs that frequently are reported for this species. The idea of two females depositing eggs in one nest

is hardly compatible with the extreme territorialism exhibited by the American Coot (Gullion, 1953*b*). Also, since a bird is normally on the nest continually from the time the first or second egg is laid, a strange female would have little chance to slip in and deposit one egg, much less six or seven. Hence, clutches of more than 12 to 14 eggs probably represent telescoped cycles of egg deposition by one female. Sooter (1941: 41) indicates this in his study of coots in Iowa, and Alley and Boyd (1947: 199) record instances of this sort in the Black Coot (*Fulica atra*). However, Alley and Boyd also record a certain amount of promiscuous laying.

CARE AND DEVELOPMENT OF THE YOUNG COOT

The first five days.—The newly hatched American Coot is a grotesque little creature. Its body is covered with dense black down, tipped with brightly colored plumes. On the dorsal surface and wings, these plumes are long and orange, but on the ventral surface they are short and yellow. A ruff of wire-like filoplumes encircles the neck. The bald pate lacks any sort of covering, and there is light blue skin over the eyes. A number of orange, waxy, club-shaped structures tip the down at the base of the bill and around the eyes. The tip of the bill is black; the egg tooth is white, grading into the orange that extends back to the front edge of the nares. The bill and frontal shield from the nares back are fleshy and a deep blood red (plate 30C). The legs and feet are a transparent greenish-gray, and a claw one millimeter long tips the pollex. The young coot's eyes are open when it emerges from the shell, and it holds its head steadily erect at the age of 15 minutes. The newly hatched coot weighs between 19 and 22 grams wet, and the yolk stalk is sealed across about 10 minutes after hatching. The feet are perhaps its most prominent feature. They are about one-third of the adult size, and the swimming lobes are well developed (table 2). The young coot gives a characteristic *whewr* note from the time it first pips the egg.

By the time the young coot is six hours old it has dried out and lost a gram or two of weight. It is quite buoyant and can climb in and out of the nest and swim to cover once it is on the water (plate 30D). However, in undisturbed nests, it is probable that young coots do not leave the shelter of the incubating parent for many hours after hatching, perhaps even for a day or two.

When nests are disturbed, every young goes over the side, except those that are less than 15 to 20 minutes old. Those young that go out of the nest before they are dry and fluffy generally drown. They are not yet buoyant, and they lack sufficient strength to keep on the surface of the water for more than two or three minutes.

TABLE 2

SIZE COMPARISONS BETWEEN DIFFERENT AGE CLASSES OF AMERICAN COOTS (ALL DATA FROM LIVING BIRDS OF UNKNOWN SEX)

Age	*Bird*	*Weight (grams)*	*Tip of bill to top of frontal shield (millimeters)*	*Middle toe length (millimeters)*	*Tarsal length (millimeters)*	*Hallux length (millimeters)*	*Pollex claw length (millimeters)*
At hatching	—	—	14.8	25	20	8.5	1
At hatching	—	22.4 (wet)	—	—	—	—	—
At hatching	R-3	17.4 (dry)	—	—	—	—	—
At hatching	L-3	19.6 (wet)	—	—	—	—	—
6 hours+	—	22.1	—	—	—	—	—
3 days	R-2	25.9	—	—	—	—	—
9 days	R-3	51.2	18	28[1]	21	11	1.5
10 days	R-2	34.1	16	25[1]	18	10	—
19 days	R-2	55.9	20.5	34	21	11	2
28 days	607	166.9	28	54	36	18	2
36 days	608	223.1	28	60	41	19	—
64 days	040	392	35	64	44	18	3
71 days	035	492[1]	39	65	49	19	—
73 days	034	447[1]	40	67	48	21	4
78 days	035	498	—	—	—	—	3
82 days	034	404	40	68	50	—	—
Adult female*	033	432	45	60	42	20	—
Adult male*	037	656	48	73	54	24	—

[1] Apparent discrepancies are probably due to sexual differences (see Gullion, 1952*a*).
* Parent pair of birds R-2, R-3, L-3, 034, 607 and 608—Jewel Lake N broods, 1949.

Since the first eggs in a coot clutch are often hatched a week before the last, one parent takes over the major share of incubation while the other seeks food for the young already hatched. Usually the male incubates during this period, also brooding those young not feeding with the female. Although the female occasionally relieves the male on the nest, she probably does not incubate for more than one or two hours a day.

If the nest is disturbed during the hatching period, the female takes the older members of the brood away from the nest to safety while the male stays to defend the nest and the young and eggs remaining in it.

The female frequently comes to the nest with food for the young, which is exclusively animal matter for the first few days after hatching. At Jewel Lake, in 1950, the female was observed collecting large numbers of freshly emerged dragon-fly (Anisoptera) and damsel-fly (Zygoptera) imagoes for her young. The two- and three-day-old young got off the nest and swam several feet to await the approach of the food-laden hen. After being fed several times they returned to the nest and the protection of the incubating male.

A brood nest is contructed as soon as the eggs start hatching, and

after three or four days the female broods the older, more active chicks at night on this nest while the male incubates the remaining eggs and the newly hatched young on the egg nest.

When a sufficient number of young has hatched (about eight), both parents turn their attention to care of the young and desert the remaining eggs or dump them out of the nest, as discussed above. When about five days old, the young begin to spend the major share of the day-time following their parents on foraging excursions in the emergent vegetation. At this stage the alarm notes of their parents are enough to send the chicks scurrying into hiding.

Six to fifteen days.—During this interval there is a general loss of ventral body plumes, and the dorsal plumes bleach (see table 3). Growth is rapid, and young coots quickly develop proficiency in swimming, diving, and fighting.

Frequently some of the young are left in dense cover while both parents forage with other young. For example, in one 1949 brood at Jewel Lake, on ten occasions on seven different days, both parents were seen feeding with two to five young from a brood of six. In fact, this brood was 21 days old before all six young were seen at one time. During the greater part of the first three weeks, only one to four young were seen at any one time. This characteristic of coot behavior precludes reliable counts of broods.

By the time they are eight days old, young coots are consuming considerable quantities of vegetable matter. Among the earliest vegetable food observed to be taken were the white, starchy bases of cat-tail leaves and fine bits of sago-pondweed.

The time spent brooding decreases considerably by the end of the first week, and by the end of the second week the young are seldom, if ever, brooded during daylight hours. At night both parents probably share in brooding, since two brood nests are in constant use through this period.

Sixteen to thirty days.—During this period the growing coot undergoes a striking plumage change. At an age of about 25 days the breast becomes whitish, contrasting sharply with the otherwise very dark plumage of the young bird. Juvenile feathers are generally replacing the natal down everywhere except on the wings and tail.

There is quite a bit of variation in the rates of growth of different young coots. Although this variation was usually least within broods, in at least one instance one young lagged 11 days behind its brood-mates in getting its distinctive white breast.

The duration of the brooding period is not known definitely, but

TABLE 3

GROWTH AND DEVELOPMENT OF THE YOUNG COOT

Age in days	*Weight in grams*	*Plumage and soft parts*	*Voice*	*Activity*
2		Same as newly hatched young (see plate 30D and text).	*whewr*	Swims well and assumes begging display.
4	25–30	All colored body plumes gone from ventral surface and many lost from back; club feathers and filoplumes becoming prominent on head.		
6		The few remaining body plumes bleached white.		Dives and assumes the fighting posture of the adults.
10	35–55	Body covered with dense black down tipped with white bleached plumes. Wing plumes and head filoplumes still orange, and club feathers prominent. Bald pate present and looks sunburned.	A *peep* when in trouble.	Can swim under water readily and fights proficiently.
15		All body plumes lost but plumes remain concealed on wings. Head filoplumes faded, giving hoary appearance to head; few club-feathers remain. Bill a bright red-orange.		Dives for vegetable food and begins to preen and to move independently of parents.
20	60–80	Dorsal body surface covered with dense black down; and ventral surface with dense brown down. Some colored filoplumes remain around edge of pate, but all the rest are bleached white; a few club-feathers remain. Skin over eyes still blue, and pate is bald and "sunburned," with two rows of black feathers becoming apparent. Bill still has black tip; white egg tooth grades rapidly into red-orange portion distal to nares. Base of bill and frontal shield a bluish-red; shield shows definite development. Iris dark gray-brown; legs dark gray-green.		Chases insects and feeds by tipping and diving.

TABLE 3—(*continued*)

Age in days	*Weight in grams*	*Plumage and soft parts*	*Voice*	*Activity*
25		Two white spots appear laterally on breast at water-line and spread so that only narrow stripe of black separates them the next day. On 27th day white has extended to throat and head. Head filoplumes all bleached; bill has turned pale orange.		
28	160	Dorsal body surface covered with very long black down. Natal down and a few faded plumes remain on wings. Breast and throat covered with dark gray, light tipped feathers; side of neck and cheeks covered with very light gray feathers with black tips. Narrow black stripe splits light breast and belly plumage. Flanks have medium gray feathers. Pate covered with light gray, black tipped feathers, forming *halo;* rectrices and remiges show no development. Oil-gland developed and tufted. Egg tooth has disappeared, and bill is encircled by broad black band just distal to nares. Tip of bill an orange-gray-green with base grading from light flesh color around nares to deep blood-red on shield. Iris very dark, opaque, gray-green.		Dives and tips for food; one dive of 15 seconds noted. Young seldom fed by parents.
36	200–225	Dorsal body surface covered with dark gray; ventral surface with light gray teleoptiles. Natal down still covers wings; few faded filoplumes remain on head. Under-tail coverts formed but still concealed. Bill has greenish tip, followed by black band, and from nares back, grades from yellow-green thru flesh color to blood-red on shield where blood capillaries are visible. Whole of bill streaked with narrow, dark pencil-like streaks. Iris and legs gray-green.	A dimorphism is apparent—calls *pzeep* and *pweep* in addition to the natal *whewr*.	Feeds in brood flocks.
40		"Halo" fully developed, forming dark skull cap. Back of neck becoming medium gray with some dark feathers appearing among lighter feathers on side of neck resulting in a speckled effect. Breast remains light gray.		

TABLE 3—(*continued*)

Age in days	*Weight in grams*	*Plumage and soft parts*	*Voice*	*Activity*
42–44		Breast darker, and tail developed with under tail coverts becoming visible. Bill becoming very dark.		Feeds independently with brood-mates in loose flocks but still heeds calls and warnings of the parents.
45–55		Body generally medium gray. Bill, after being dark, begins to turn light again.		Feeds without parents.
60		Two dark gray spots become apparent laterally on breast at water-line. Rectrices developing rapidly, but remiges not yet apparent.	A poorly developed adult *poonk* and the natal *whewr*.	
70	Average adult (♂♂, 498; ♀♀, 495)	Top of head dark gray, back gray-brown, rump reddish-brown, throat medium gray. Rectrices ¼ sheathed; remiges still ½ sheathed. Bill light, mottled ivory distal to nares, base smooth medium gray. Frontal shield flesh colored; iris grayish on perimeter becoming reddish-brown towards pupil; legs gray-green.		
75		Remiges fully unsheathed, bill uniform grayish-ivory, iris reddish, frontal shield reddish.		Beginning to fly.
80		Immature resembles adults in all characters except for grayish bills and gray-green feet and legs.		Leaves home territory.
120		Bill begins to look adult; from this time on immatures can be separated from adults only on basis of leg color (see text).		

one hen on Lake Temescal was still occupying a brood nest with her three young 46 days after the last had hatched. It is believed, however, that she was sharing a night roosting place with them rather than actually brooding them. On several subsequent nights these young occupied the nest by themselves while their parents roosted on floating debris nearby.

Hollister (1919), watching captive American Coots at the National Zoological Park, noted that the young were brooded by the female at night for about 20 days following hatching. Ward (1953: 323) reports a general abandonment of family duties by males during the rearing period. These coots were summer residents in Manitoba and presumably without the strong ties to a local area that permanent-resident coots exhibit.

By 16 to 20 days the young coots feed themselves to a large extent and by 30 days are independent, though still often feeding in company with their parents. By this time brood counts become more reliable, since the immatures of each brood tend to become a closely knit group.

Thirty-one to fifty-five days.—The young coots enter this period with the whitish breast and most of the body down replaced by definitive feathers. The light breast is soon replaced by a medium-gray breast, the white undertail coverts appear, and the top of the head develops a dark haloed appearance.

At the end of this period, the bird has its full juvenile plumage and has assumed the body proportions of the adult. A coot of this age responds to aggressive displays of outside adults by evasive action and frequently chases immature ducks out of its home territory.

In one instance a juvenile was 60 days old before it showed the white under-tail coverts. The variation in growth between broods was most noticeable. One Lake Temescal brood developed so slowly that its parents failed to renest in 1950, while all other pairs in the area were bringing off second broods.

When 40 to 45 days old the juvenile coots are foraging almost entirely without their parents but usually in company with one or more brood-mates.

Fifty-six to eighty days.—At about 60 days the first dark adult plumage appears as two black spots laterally and just above the waterline on the breast. This dark plumage rapidly spreads over the entire body. The remiges and rectrices develop almost entirely during this period and the immature coot flies at about 75 days of age. The first indication of an adult voice becomes apparent.

Even as late as 70 days after hatching, immatures occasionally are seen to assume the begging display and to receive food from their

parents as a result. Normally at this age, begging results in being pecked rather than receiving food, so the immatures are hesitant about approaching the adults closely.

The immatures closely resemble adults by the time they are 80 days old, and their parents have generally driven them from their home territory, perhaps regarding them as territorial invaders. They differ from the adults in possessing a darker, grayish bill and gray-green feet and legs. They are as heavy as the average adult.

Development after eighty days.—At about four months of age the bill of the immature resembles that of the adult sufficiently that age identification cannot always be certain, though some immatures retain a mottled bill in excess of five months. Once the bill is like that of the adult, only the gray- or blue-green feet and legs serve to separate the birds of the year from adults. The frontal shield on immature coots is characteristically flat, but this cannot be used as an age criterion since adults in non-territorial, non-breeding condition will also have flat shields (Gullion, 1951*b*). Leg color remains diagnostic until the following spring when the legs become greenish-yellow.

By the second year, the legs have become clear bright yellow, and each season thereafter the coot's legs apparently become progressively darker yellow, tending towards orange. This darkening was accomplished by the shedding of leg scutes, one at a time, during the spring season by birds held captive during this study (Gullion, 1953*a*).

An American Coot that is ten or eleven years old will have reddish-orange legs, but otherwise the plumage is much the same as in a five-months-old immature coot.

The age at which American Coots commence breeding is not known definitely. However, it is known that at least some females may breed during their first year. As noted above, one year-old female on Jewel Lake, mated to her father, proved very prolific in 1950, having laid five clutches of eggs (37 in all) during the season. Territorial activity probably has more control over the breeding age of coots than has physiological maturity.

RENESTING

The American Coot, like many other birds, renests if its early nests are destroyed and, unlike most game birds, it also may raise a second brood following the successful rearing of one brood. This is at least true in the San Francisco Bay area, although Sooter (in correspondence) is quite certain that this was not the case in his study area in Iowa.

During this study four nests were lost: two deserted apparently due to my activities, one lost to a predator (raccoon suspected), and a fourth to uncertain causes. The two deserted nests were the second and third clutches of the JL-S pair in 1949 while the last two were the first and third nests of the JL-N pair in 1950.

The third clutch of the 1949 S pair was started not later than seven days following desertion of their second nest, and the second clutch of the 1950 N pair at Jewel Lake followed no later than four days after the destruction of their first nest. Following the successful rearing of a brood from its second clutch, the JL-N pair laid a third clutch, which mysteriously disappeared while still being deposited, and the fourth clutch was commenced not over four days following its loss.

In both of the 1950 nest losses the clutch was either still being deposited or had just been completed, so the female probably was still in the physiological state necessary for continued egg production. This fact is not known for the two 1949 nests. Sooter (1941: 47) by removing eggs from nests during the deposition period was able to get females to lay from 14 to 18 eggs. The JL-N pair in 1950 almost equalled this by laying 17 eggs in 23 days.

In all three instances the renesting required the selection of a new nest site and building a new nest. In at least the last case a new display platform also was built.

Both pairs at Jewel Lake in 1949, the one pair at Jewel Lake in 1950, and two of the three pairs at Lake Temescal in 1950 laid clutches following the successful rearing of an earlier brood. In 1949, at Jewel Lake, the S pair laid its second clutch not over 40 days after hatching their first brood while the second clutch of the N pair appeared 38 days after hatching their first brood. In 1950, the third clutch of the JL-N pair appeared not over 30 days after the successful hatch of its second clutch. At Lake Temescal in 1950, the SE pair began laying its third clutch 26 days after a partially successful hatch of its second clutch while the E pair commenced laying its second clutch 56 days after the hatch of its first clutch. In each case a different, though not necessarily new, nest was used for clutches following successful rearings.

The stimulus that determines when a new clutch is to be laid is unknown. The variation in intervals cannot be related definitely to brood size or age, to the size of clutches laid previously that season, or to the success of earlier layings (see table 4).

The American Coot appears to show great variation in the length of time between the hatching of the first clutch and the laying of

TABLE 4

CLUTCH SIZE AND BREEDING SUCCESS

		Clutch Number														
		1			*2*			*3*			*4*			*5*		
Season and pair	*Interval between broods (days)*	*Eggs*	*Hatched*	*Reared*	*Eggs*	*Hatched*	*Reared*	*Eggs*	*Hatched*	*Reared*	*Eggs*	*Hatched*	*Reared*	*Eggs*	*Hatched*	*Reared*
1949																
JL-S	40	10	8	7	6	deserted		4	deserted							
JL-N	38	9	8	6	6	6	4									
1950																
JL-N	30	10 destroyed			7	5	5	7+?	destroyed?		8	4	0	5+?	3+?	3+?
LT-E	56	7	7	1	4	4	1									
LT-SE	26	8	1	0	10	3	1	8	1	0						
LT-SW	—	10	7	3												

the second. Sooter (1941: 41) records one nest that hatched two broods, with the eggs of the second clutch appearing within 48 hours following the successful hatch of the previous clutch. He believed the second clutch was the product of a different pair but gives no evidence to support his belief. In view of the strong territorial behavior displayed by breeding coots, this would be very unlikely in the area I have studied, and I doubt that the territorial behavior of Iowa coots differs that much from the birds in western California. He makes the statement (p. 41), "On several occasions eggs were laid in nests while they were hatching or shortly before the hatching period began."

HATCHING AND FLEDGING SUCCESS

During this study, a total of 119 eggs was laid in 16 nests by six pairs of coots (table 4). Of these, 57 eggs (48 per cent) hatched, 27 eggs (23 per cent) were addled, 17 eggs (14.5 per cent) were taken by predators, 10 eggs (8.5 per cent) were deserted, 4 eggs (3 per cent) were lost to unknown causes (knocked out or buried ?), and 4 full-term embryos (3 per cent) were left to die in the nest or jettisoned at about the time they were due to hatch. Thirty-one young fledged, representing 54 per cent of the eggs hatched or 26 per cent of the eggs laid.

In 1949, the season's productivity at Jewel Lake amounted to 8.5 young per pair, while in 1950 the single pair produced eight young. At Lake Temescal in 1949, the season's productivity was at least 3.3 young per pair while in 1950 it was 2.0 young per pair.

Sooter (1941: 71) in his Iowa study, estimated a fledging success of 1.9 young per pair. Kiel and Hawkins (1953: 320) found a 97 per cent successful hatch among 380 nests studied in southwestern Manitoba, with a 99 per cent hatch among "1,394 eggs in successful nests with complete clutch counts." The overall productivity in the Bay Area study in 1949 was 5.4 young per pair, in 1950 about 3.5 young per pair, with a total survival for the two years of about 5.1 young per pair. Survival per successful clutch amounted to about 3.4 immature coots.

PARENT-YOUNG RECOGNITION

As discussed above and noted in table 3, the developing young coot goes through quite an array of abrupt plumage changes. Since there may be a week's difference between the age of the oldest and youngest bird in the brood, the oldest bird may have become almost

wholly white-fronted before the birds in the middle of the brood begin changing. Similarly, the youngest bird may still retain the solid black natal down while all its brood-mates are turning much lighter.

Since the parents seem to recognize their brood by the color pattern of the majority, the oldest birds become subject to occasional attacks when they start turning light. As more young progressively turn light, the parents accept the light-fronted birds as theirs, and the attacks are directed at the younger birds, still in their natal down. Sometimes these parental attacks are quite severe, and it is conceivable that young might occasionally be killed by their parents during this transition period.

The parent coots are obviously confused by this change in the appearance of their young, since they frequently will bill an odd-colored young, feed it, and then severely attack it, only to resume feeding it immediately afterwards.

Alley and Boyd (1950: 46), in a study of parent-young recognition in the Black Coot, have noted that "parent Coot will attack and drive away chicks conspicuously older or younger than their own." They did not note the same reaction to the plumage differences of birds at the extreme ends of large broods. No experiments were made in the Bay area concerning brood mixing, but Alley and Boyd noted that if strange young of the same age were placed in Black Coot broods less than 14 days old, they would be accepted by the parents.

During this period it would seem that only strict territorial defense and aggressiveness would prevent a great deal of mixing of young broods in areas where many pairs breed. Hence, one function of increased pugnacity following the hatching period might be the maintenance of brood integrity (see Gullion, 1953*b*: 179–180).

BREEDING BEHAVIOR OF OTHER RALLIDAE

Among members of the family Rallidae, only the Black Coot and Black Gallinule in Europe seem to have been investigated along the lines reported in this paper. Details of the nesting habits of most members of the rail family are apparently little known. However, a review of what is known will permit some interesting comparisons with behavior of the American Coot.

Pairing.—Monogamy in the Rallidae is probably quite general. It seems probable that monogamy would be necessary in those species in which both sexes incubate. The genera *Rallus*, *Rallina*, *Porzana*, and *Gallinula* in addition to *Fulica* show this shared incubation be-

havior, and monogamy is probably general in at least these genera (see table 5). The Corn-Crake (*Crex crex*) however is polygamous (Mason, 1947: 192), and correlated with this, only the female incubates. On the other hand, the Blue Reed-Hen (*Porphyrio poliocephalus*) is apparently also polygamous, the male incubating the eggs of two to six hens in one nest (Oliver, 1930: 348).

Stuart Baker (1929: 35) believes the Black Coot in India pairs for life, and Oliver (1930: 330) says the same is usually true of the Weka Woodhen (*Gallirallus australis*).

Nesting.—Nesting behavior in the Black Coot (Witherby *et al.*, 1947: 205), Red-knobbed Coot (*Fulica cristata*—Priest, 1934: 30), and the Red-gartered (*F. armillata*), White-winged (*F. leucoptera*) and Red-fronted coots (*F. rufifrons*—Gibson, 1920) seems closely to resemble that of the American Coot. The members of the several genera more or less closely related to *Fulica* usually build their nests of marsh vegetation, either floating on the water or on shore immediately adjacent to water. This includes the genera *Porphyrio*, *Porphyrula*, *Gallicrex*, and *Gallinula*.

Nest locations of other Rallidae are highly variable. The extinct Chatham Island Rail (*Cabalus modestus*) nested in holes in the ground (Oliver, 1930: 327), and this may also be true of the Island Hen (*Atlantisia rogersi*—Lowe, 1928: 102), but this is perhaps unique for the family. Most genera have nests located in marsh vegetation or in rank grass closely adjacent to water. However, some exceptions are the Australian *Eulabeornis*, which builds a nest of sticks on the roots of mangroves (Mathews and Iredale, 1921: 196) and the Palearctic *Crex*, which regularly nests in grain or hay fields or pastures, as does also the North American *Coturnicops*. The Oriental genera *Rallina* and *Amaurornis* generally nest in forested or bushy areas far removed from water and often above the ground. The White-breasted Water-Hen (*Amaurornis phoenicurus*), for example, often builds its nests "in thick bushes many feet above the ground" (Stuart Baker, 1929: 24). The highly adaptable Woodhens (*Gallirallus*) of the Australian region nest wherever food is abundant. The nest may be (according to Oliver, 1930) in the forest or scrub, under a leaning tree trunk, under a clump of rushes, in a flax bush, or under rocks. Smith (1952: 400) says of the recently rediscovered Takahe (*Notornis mantellii*), "The three- to four-month nesting season begins . . . when every pair prepares a number of nests, each consisting of a grass bowl with at least two entrances, set between thick snow grass tussocks . . . . The last to be made is apparently chosen for actual egg laying."

The rails as a group use whatever vegetation is most readily available—usually grasses and aquatic plants but occasionally sticks and other materials. Nests are usually lined, and a ramp by which the incubating bird enters and leaves the nest is constructed by rails of several species (table 5).

The Black Coot builds nests which it uses for brooding its young (Kirkman, 1912: 453), and the Red-knobbed Coot apparently builds platforms and other structures much like those of the American Coot (*cf.* Jackson, 1938: 308–309). The Black Gallinule builds both display platforms and brood nests (Howard, 1940). Walkinshaw (1937: 471) suggests that brood nests are built by the Virginia Rail (*Rallus limicola*), and it seems probable that the "three to four empty nests in the vicinity for every occupied one" (Bent, 1926: 350) of the Purple Gallinule (*Porphyrula martinica*) represent display platforms and brood nests. The extra nests of the Clapper Rail (*Rallus longirostris*) mentioned by Grinnell *et al.* (1918) may also represent brood nests. The Green-backed Reed-Hen (*Porphyrio madagascariensis*) of East Africa is known to build excess nests that are used at least for roosting (Jackson, 1938: 320).

Copulation.—Höhn (1949: 209) studying the Black Coot in England, reported a sequence of events and displays similar to that elaborated for the American Coot above. The brace, arch, and mounting proceed as in the American Coot, with the male not taking hold of the female's head but maintaining balance with his wings and feet. He recorded a high-pitched call but did not know which sex gave it and observed post-coital preening in only one instance. However, this sequence differed in that, "The plumage is held as in the common aggressive pose," apparently the swimming arch, preceding movement to the platform.

Nylund (1945: 121) speaking of the Black Coot in Finland, says, "The first mating takes place about one day before the laying of the first egg, the last at the time of the laying of the last egg."

Egg deposition and clutch size.—Apparently many Rallidae deposit one egg a day until the clutch is complete (see table 5).

A survey of the literature reveals that the clutches of six to ten eggs of Bay area coots are about normal for the species. However, as pointed out by Lack (1948: 27) the tropical Rallidae tend to have smaller clutches than the more temperate species. The Rallidae of England, for example the Black Gallinule, have clutches of from five to eleven eggs (Witherby *et al.*, 1947: 200). The same species in the Phillipines, however, averages four eggs (McGregor, 1909: 78), and the clutches of the tropical Rallidae range from the minimum of

TABLE 5

BREEDING BEHAVIOR OF THE RALLIDAE[1]

Species	*Pairing*	*Nest ramp*	*Brood nests*	*Eggs deposited*	*Clutch size*	*Incubation*			*Number broods*	*Authority*
						Commences	*Sex*	*Period*		
Clapper Rail (*Rallus longirostris*)			used		8–9					Grinnell *et al.*, 1918
							both			Bent, 1926
									2	Forbush and May, 1939
				daily		last egg	both	22–23?		Kozicky and Schmidt, 1949
King Rail (*Rallus elegans*)	monog.				6–14		both?			Trautman, 1940
				daily	8–14	late eggs	both	21–24		Meanley, 1953
Virginia Rail (*Rallus limicola*)					5–12					Grinnell *et al.*, 1918
					7–12	1st eggs				Bent, 1926
			used	daily			both			Walkinshaw, 1940
								19–20		Mousley, 1940
Water Rail (*Rallus aquaticus*)				daily	6–11	last egg	both	19–20		Witherby *et al.*, 1947
Slate-breasted Rail (*Rallus pectoralis*)		used			4–6					Mathews and Iredale, 1921
Argentine Rail (*Ortygonax rytirhynchos*)					4–5		both?			Gibson, 1920
					6–8					Schmidt, 1948
Spotted Rail (*Pardirallus maculatus*)		used			7					Sclater and Hudson, 1889
Red-legged Banded Rail (*Rallina fasciata*)					5–6		both			Riley, 1938
Ypacha Rail (*Aramides ypecaha*)								21		Bergtold, 1917
					4–7					Schmidt, 1948
Weka Woodhen (*Gallirallus australis*)	monog.				4			20		Oliver, 1930
Black Woodhen (*Gallirallus troglodytes*)	monog.				2–3		both	27	2	Oliver, 1930

TABLE 5 (cont.)

Species	*Pairing*	*Nest ramp*	*Brood nests*	*Eggs deposited*	*Clutch size*	*Incubation* — *Commences*	*Incubation* — *Sex*	*Incubation* — *Period*	*Number broods*	*Authority*
African Crake (*Crecopsis egregia*)					5		both?			Jackson, 1938
Corn-Crake (*Crex crex*)									2	Morris, 1892
							♀	17?		Kirkman, 1912
								19		Niethammer, 1942
	polyg.									Mason, 1947
				daily	8–12	last egg	♀	?	1–2	Witherby *et al.*, 1947
Little Crake (*Porzana parva*)								21–24		Evans, 1891
					7–8	1st egg	both		2	Witherby *et al.*, 1947
Marsh Crake (*Porzana pusilla*)					4–8					Mathews and Iredale, 1921
				daily	6–8		both	20–21		Witherby *et al.*, 1947
Spotted Crake (*Porzana porzana*)					8–12	1st egg	both	18–21	2	Witherby *et al.*, 1947
Sora Rail (*Porzana carolina*)					10–12	1st eggs				Grinnell *et al.*, 1918
					10–12		both			Bent, 1926
		used		daily			both	16–19	1	Walkinshaw, 1940
Spotless Crake (*Porzana tabuensis*)					4–6					Lucas and LeSouëf, 1911
					3–4					Mathews and Iredale, 1921
	monog.		used		3		♀			Oliver, 1930
Water-Cock (*Gallicrex cinerea*)					4–5					Hume, 1890
	monog.								2	Stuart Baker, 1929
Black Gallinule (*Gallinula chloropus*)					4					McGregor, 1909
					10–12		both			Bent, 1926
	monog.		used				both			Howard, 1940
		used		daily				19–21		Miller, 1946
				daily	5–11	1st egg	both	19–22	2–3	Witherby *et al.*, 1947

TABLE 5 (cont.)

Species	*Pairing*	*Nest ramp*	*Brood nests*	*Eggs deposited*	*Clutch size*	*Incubation* — *Commences*	*Incubation* — *Sex*	*Incubation* — *Period*	*Number broods*	*Authority*
Purple Gallinule (*Porphyrula martinica*)			used		6–8					Bent, 1926
Purple Reed-Hen (*Porphyrio porphyrio*)					3 3–5			23–25		Whitaker, 1899 Dresser, 1903
Green-backed Reed-Hen (*Porphyrio madagascariensis*)			used		6–10					Dresser, 1903 Jackson, 1938
Blue Reed-Hen (*Porphyrio poliocephalus*)	polyg.				7–10 5–7		♂			Hume, 1890 Oliver, 1930
Takahe (*Notornis mantellii*)	monog. monog. used				1–2 1–2	last egg last egg?	♀ ♀	?	1	Smith, 1952 Williams, 1950
Black Coot (*Fulica atra*)	monog.		used	daily daily	6–9	1st egg 1st egg	both both	23–24 21–24	2–3	Kirkman, 1912 Stuart Baker, 1929 Ruthke, 1939 Nylund, 1945 Witherby *et al.*, 1947
Red-knobbed Coot (*Fulica cristata*)			used	daily	8–9 3–7			21		Priest, 1934 Jackson, 1938
American Coot (*Fulica americana*)	monog.	used	used	daily	4–10	1st egg	both	23–25	2	Present study
Red-gartered Coot (*Fulica armillata*)	monog.				6–7	early				Gibson, 1920 Schmidt, 1948

[1] This table does not attempt to give a complete review of the literature concerning the breeding behavior of all the rails in the world, but it does attempt to show some aspects of the behavior of a wide range of species within the family from widely separated parts of the world.

two to four eggs of the Green-backed Reed-Hen (Jackson, 1938: 301) to a more usual number of four to seven eggs. A notable exception is the nearly extinct Takahe of temperate New Zealand, with its normal clutch of one or two eggs (Williams, 1950: 219). The South American tropical Fulicinae have clutches of five to seven eggs while the Red-knobbed Coot, of more temperate Africa, has a clutch of eight or nine eggs (Priest, 1934: 30).

The slight amount of data available suggests that rail eggs generally may be deposited in the early morning. Ruthke (1939: 143) says that eggs of the Black Coot are always laid in the morning. Walkinshaw (1937: 470) found that Virginia Rail eggs were laid between 4 and 8 a.m., and he says (1940: 176) that Sora (*Porzana carolina*) eggs are "laid during the very early hours of daylight."

Incubation.—The sharing of incubation seems to be general among many forms related to the American Coot (see table 5). However, shared incubation is not universal throughout the rail family.

Although little information is available on the length of incubation periods by each mate, Nylund (1945) found that female Black Coots devoted more time to incubation than the males did. Among the other Rallidae, only the Black Gallinule seems to have had its length of incubation shifts recorded. Howard (1940: 56) gives this period as 38 minutes, apparently for both birds, and indicates that it was of uniform duration, which is certainly not the case in the American Coot.

Observations on the incubation behavior of any of the Rallidae seem to be rare. Howard's study (1940) of the Black Gallinule relates how one mate climbed on the nest to preen and then gently forced the incubating bird off. The ceremony that the gallinules perform during a change of shifts resembles their platform activity, just as the similar activity often results in a pre-copulatory display in the American Coot.

A review of the literature on incubation in the Rallidae indicates that the 23 to 25 day period of the American Coot is about average for the Fulicinae and gallinule groups, but a little longer than most of the less aquatic rallids (see table 5).

Care and development of young.—The Black Coot parents, like those of the American Coot, divide their brood for foraging excursions and night brooding (Witherby *et al.*, 1947: 206), and prolonged parental care of young seems to be general among Rallidae. The Water-Hen or Black Gallinule parents care for their young assiduously for about 20 days but are attacking them by the time a second clutch is started on the thirty-first day (Howard, 1940: 60). Walkinshaw indicates

that young Virginia Rails (1937: 471) and young Soras (1940: 162) are brooded on the nests for several days following hatching. The hen alone cares for young Corn-Crakes early in their life, not allowing the male to assist until the fourth day, which he does continually from that time on (Kirkman, 1912: 572). Witherby *et al.* (1947) indicate that both sexes share in caring for the young for an extended period of time in the Water-Rail (*Rallus aquaticus*), Little Crake (*Porzana parva*), and Spotted Crake (*Porzana porzana*). This, according to Oliver (1930), is also true of the Spotless Crake (*Porzana tabuensis*), Weka Woodhen, Black Woodhen (*Gallirallus troglodytes*), and Blue Reed-Hen.

The Rallidae in general seem to have black downy young. The nestlings of most of the true rails are all black without any of the colorful adornments of the more coot-like forms.

Ridgway and Friedmann (1941) describe the downy young of the North American Rallidae. They note (p. 185) that the young Black Gallinule is mostly black but that the down on the chin and throat has "whitish, curly tips." The natal down of the Purple Gallinule is a step closer to the natal down of the American Coot with its head and chin "ornamented by fine hairlike filaments of silvery white" (p. 197). The downy chick of the Caribbean Coot (*Fulica caribaea*) is evidently similar to that of the American Coot (p. 222).

The young of the Black Coot develops at a rate comparable with that of the American species, and immatures of that species depart from their home areas when about 70 days of age (Cramp, 1947: 196). The downy young of the Black Coot closely resembles the young American Coot, except that it possesses slate-black tarsi and toes as compared with the greenish-gray tarsi and toes of *F. americana* (Ridgway and Friedmann, 1941: 208).

Renesting.—The Black Coot seems to renest with much the same readiness that the American Coot does. Alley and Boyd (1947: 199) record a nest in which three eggs were deposited while the first clutch was still hatching.

While few data are available, it seems probable that many of the Rallidae are double-brooded, at least among those members of the family nesting in the warmer parts of the world. If a pair of American Coots, with an incubation period about as long as any rail, can raise two broods in about 150 days, it seems reasonable to suppose that many of the species with shorter incubation periods probably do likewise. Several forms are known to do so (see table 5).

Hatching and fledging success.—Alley and Boyd (1947) give data for the Black Coot in England that compare closely with data on the

American Coot presented earlier in this paper. They studied 14 pairs of coots with a total deposition of 121 eggs. Of those, 34.7 per cent hatched and the 28 young believed to have fledged represented 23.1 per cent of the total eggs laid, or 66.7 per cent of the eggs hatched. Only 5 per cent of their eggs were infertile and only 4 per cent were abandoned. Predators, including man, took 57 per cent of the eggs while 34 per cent were lost to miscellaneous causes (swamping, knocking-out, burying, and undetermined). They indicated a final fledging success of 1.8 young per adult pair.

SUMMARY

The American Coot is probably always monogamous in its sexual behavior. Pair formation in the early spring is gradual, following a series of mutual displays. However, if one mate disappears during the nesting season, a second mate may be accepted within 48 hours. Among the resident coots with secure territories, pairing seems to be as permanent as the life of the birds or their ability to maintain a territory.

Coots breed in a habitat which contains abundant nesting material, and they use this material freely in constructing floating structures associated with breeding. These structures are bulky, and since materials seldom present a procurement problem, they are not built for permanence but must be added to repeatedly while in use. Eggs are seldom laid in more than two of the eight or nine structures usually built by a pair in the Bay area. The other structures are utilized for resting, roosting, and brooding sites.

The three types of structures built by coots—a display platform, the egg nest, and a brood nest—follow one another in a definite sequence, and breeding events can be reliably predicted by their appearance. Certain modes of construction permit the identification of a nest type even before it is placed in use.

Copulation normally, and perhaps always, takes place on a display platform. There is little or no precopulatory display or chase, and the two birds resume normal activity within two or three minutes following copulation. Copulation has been observed from 19 days preceding the laying of the first egg to the day of laying the second egg in a clutch of eight. Copulation following completion of the clutch has been observed, but it was apparently the result of abnormal circumstances.

Eggs may appear before the nest is completed and are laid daily in the very early hours of the morning. The nest is completed and lined by the time the clutch is complete. Early season clutches

averaged 9.0 eggs while second successful clutches averaged 6.4 eggs. Nine renesting attempts, either following a successful hatch or following a nest loss, averaged 7.8 eggs per clutch, ranging from four to ten eggs per clutch.

Incubation in the earliest clutches of the season may not begin until the last egg is laid, but later clutches, both first and second layings, are incubated beginning with the first or second egg. Incubation is continuous and is shared by both sexes, the male probably doing the greater share of it.

When deposition of the clutch is just beginning the female incubates all night, but otherwise the male incubates from dusk to dawn; the female always takes about a four-hour shift at dawn and then shifts of about one hour duration follow until sunset. There is, however, a great deal of variation in shift lengths from pair to pair and from day to day. The only rigid phase of the daily schedule seems to be the female's dawn shift and even that may vary as much as one-half hour in length.

The shortest incubation period recorded was in excess of 22 days and 20 hours, the longest between 25 and 26 days. The normal incubation period is about 553 hours from time of deposition until the time the chick is completely free of the egg shell and its membranes. Eggs are pipped for an average of about 36 hours preceding the hatch, and the hatch usually follows the staggered one day interval of deposition.

Young coots are quite helpless until a day or so old and require prolonged parental care. The male parent does most of the brooding during the staggered hatching period while the female brings food to the nestlings and takes the older young away to feed and brood. Later, the parents divide the brood during feeding and brooding. The parents forage with the young until they are from 20 to 30 days old. From then on the young are largely on their own.

During the first 45 days of development the young coot goes through several contrasting and conspicuous plumage changes that make it possible to date events in the breeding cycle of its parents quite accurately.

Most pairs of coots show a surprising persistence to renest. If nests are destroyed or eggs fail to hatch, a subsequent clutch is started in very short order. Renesting following nest destruction took about four days, while renesting following a successful hatch began from 20 to 56 days later.

The nesting behavior of the American Coot apparently differs very little in any respect from that of the other Fulicinae and the generally aquatic genera of gallinules. Variations from the general rallid nesting

behavior pattern are restricted to those necessitated by the physical properties of the primarily aquatic habitat of the American Coot.

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