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## TERRITORIAL BEHAVIOR OF THE AMERICAN COOT

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The American Coot (*Fulica americana*) is an abundant and prolific aquatic game bird, yet relatively little has been published on its breeding behavior. The material presented in this paper was gathered as part of a study of breeding behavior made in the San Francisco Bay area, California, between March, 1949, and August, 1950. Certain additional observations were made in the fall and winter of 1950-51 in the Honey Lake area of northeastern California.

Many of the birds studied were tagged with a neck-tab pinned to the nape of the neck. Others were identified by territorial behavior coupled with size and shape of the frontal shield. Sex determination was made mostly on the basis of voice dimorphism while age determination was made largely by leg color (for details on these subjects see Gullion, 1950, 1951a, 1951b, 1952a).

### STUDY AREAS

The two major study areas were Jewel Lake, a large pond in the north end of Charles Lee Tilden Regional Park, Contra Costa County, and Lake Temescal, which comprises most of Lake Temescal Regional Park at the western base of the Berkeley Hills in Oakland, Alameda County.

Jewel Lake was formed about 1900 by damming Wildcat Creek, an intermittent stream which flows northwesterly between the Berkeley Hills and San Pablo Ridge. This pond has a maximum depth of ten feet; it is 510 feet above sea level and about seven miles from San Francisco Bay as Wildcat Creek flows. About a third of the pond is filled with emergent vegetation, mostly narrow- and broad-leaved cattails (*Typha angustifolia* and *T. latifolia*). Water plantain (*Alisma plantago-aquatica*) and nut-grass (*Cyperus eragrostis*) grow abundantly along the shore. During the summer and fall the open water is choked with sago pondweed (*Potamogeton pectinatus*).

Lake Temescal was formed about 1860 by damming Dingee Creek. It lies about three and one-half miles from San Francisco Bay, at an elevation of 420 feet. There is only about a quarter acre of emergent vegetation, consisting primarily of the same species as at Jewel Lake. The steep shore, which drops quickly to ten or more feet around most of the lake, precludes greater development of marsh vegetation. However, additional cover is supplied by clumps of water iris and weeping willow (*Salix babylonica*) along the shore-line. The sago pondweed is kept in check by chemical means since this lake is heavily used for swimming and boating through the spring and summer.

Supplementary observations were made on Lake Merritt, in downtown Oakland; in the Aquatic Park along Berkeley's waterfront; on Stow Lake and Middle Lake of the Chain of Lakes in San Francisco's Golden Gate Park; in the Suisun Marshes south of Suisun City, Solano County; at the Gray Lodge State Waterfowl Refuge, about eight miles southwest of Gridley, Butte County; and at Honey Lake Waterfowl Management

Marshes are almost entirely migratory. The Middle Chain Lake supports a good breeding population of Pied-billed Grebes (*Podilymbus podiceps*), Mallards (*Anas platyrhynchos*), and coots, while the Gray Lodge and Honey Lake areas normally have some breeding coots as well as many breeders among various species of waterfowl.

The observations made on the several areas will be combined into one generalized account. Most of the data are based on the behavior of coots securing and guarding nine territorial areas. Two of these areas were on Jewel Lake, one at the south end (the JL-S

Table 1  
The Study Areas

Areas	Acres	Number of coots		Origin	Type of water	Notes
		Breed- ing	Winter- ing			
Jewel Lake	2.7	4	10-12	impoundment	fresh	pH 8.5 (see text).
Lake Temescal	12.0	6	20-25	impoundment	fresh	(see text).
Lake Merritt	155	0	300-500	natural	saline	No emergent or floating vegetation in water. Level controlled by flood-gates. Badly polluted.
Aquatic Park	95	0	100-110	impoundment	saline	Vegetation same as Lake Merritt. Level controlled by valves. Badly polluted.
Stow Lake	47.1	0-2	50-70	impoundment	fresh	No emergent vegetation and floating vegetation scarce. Subject to much disturbance from human activities.
Middle Chain Lake	2.2	4	?	impoundment	fresh	1/3 filled with emergent vegetation. Good food and cover situation.
Suisun Marshes	58,700	0-?	to 50,000	natural	brackish	Well supplied with natural emergent vegetation. Some parts subject to inundation by ocean tides. Water subject to variation in level and in salinity.
Gray Lodge Refuge	2,500	?	to 5,000	improved natural	fresh	Intensively managed for breeding and wintering waterfowl. Cover and food conditions excellent.
Honey Lake Refuge	2,000	?	0-500	improved natural	alkaline	Intensively managed for breeding and wintering waterfowl. Cover and food conditions excellent.

area guarded by the JL-S pair) and one at the north end (the JL-N area), both of which are normally permanent coot territories (see fig. 1). Of the seven territories on Lake Temescal, three are permanent, these being the one centered about the east inlet (the LT-E area), one at the mouth of Dingee Creek (the LT-SW area) and one in the area southeast of the island (the LT-SE area; see fig. 2). The other four territories on Lake Temescal were all temporary, that is, they were established in late winter and

fourth along the west shore (the LT-W area), including mostly the northern part of the SW area. It is believed that temporary territories were maintained mostly by wintering migrants, although some of those established during late spring may have belonged to local young of the previous season.

#### BEHAVIOR

The American Coot, in its behavior, seems to be as completely territorial as any species of bird. Among resident coots territorial behavior lasts throughout the year. Moreover, during parts of the breeding period coots indulge in aggressive behavior against other species of birds and also against some non-avian vertebrates. Since territorial activity is at its lowest ebb during the winter, it seems logical to begin the discussion with that season and to follow chronologically the seasonal development and decline of territorialism.

*Winter.*—By the middle of October resident coots seem to have retired to the area they intend to defend as winter territory. This nucleus area, centered about the previous season's nesting sites, is referred to as the "core" area (see figs. 1 and 2). Core areas are defended throughout the winter by resident coots, except when physical conditions such as altered water levels or extensive ice coverage force them to do otherwise.

Two pairs at Lake Temescal were forced to abandon core areas when the water level dropped to a minus 13 foot stage and the nearest shoreline was over 250 feet from the previous outer limits of these two core areas. A third pair (LT-E), whose territory was along a steep shore, defended a laterally displaced core area of approximately the same size as their normal area. With restoration of the normal water level, the pairs returned to defend their former areas.

At Honey Lake, despite a considerable influx of wintering migrants, territorial areas were successfully defended through the winter. Even during brief periods of extreme cold when all but small areas of water surface were frozen, territorial birds remained on or close to their core areas, quickly resuming active defense as soon as the ice melted.

Throughout the winter a few pairs of migrant coots at Lake Merritt indulged in poorly developed territorial activity and by mid-December some of the 18 migrant birds had established territories at Lake Temescal. In addition to the migrant coots on Lake Temescal, seven taken at Lake Merritt ( $\delta$  632,  $\delta$  633,  $\delta$  637,  $\delta$  639,  $\delta$  650,  $\text{♀}$  635,  $\text{♀}$  643) were released there on December 9 and 16, 1949; these were sexed by laparotomy, tagged, and the primaries of one wing clipped. On Jewel Lake the JL-N $\delta$  was paired with one of his 1949 second brood daughters and was defending a core area. A recently arrived pair was defending a core in the JL-S area and there were about 12 other migrant coots on the lake.

Through January the sizes of the defended areas remained relatively stable, but new pairs commenced to defend previously unused areas on Lake Temescal from time to time. Up until the end of February the winter condition prevailed, core areas being defended by resident birds and new similarly sized areas being established and guarded by either newly formed or migrant pairs.

In January, 1950, at Gray Lodge Refuge and in the period from October, 1950, to March, 1951, at Honey Lake Refuge, coots were observed to be in the same stage of territorial behavior as in the San Francisco Bay area. The core areas at Gray Lodge and Honey Lake seemed to be similar in size to those at the south end of Lake Temescal. In January, 1952, migrant coots were seen engaging in definite territorial behavior on Lake Mohave, a few miles south of Hoover Dam in southern Nevada.

*Spring.*—During early March an upsurge in territorial activity became evident (fig. 3). Resident coots commenced protecting areas adjacent to their winter core areas and generally expanding their domains, with antisocial displays (Gullion, 1952*b*) be-

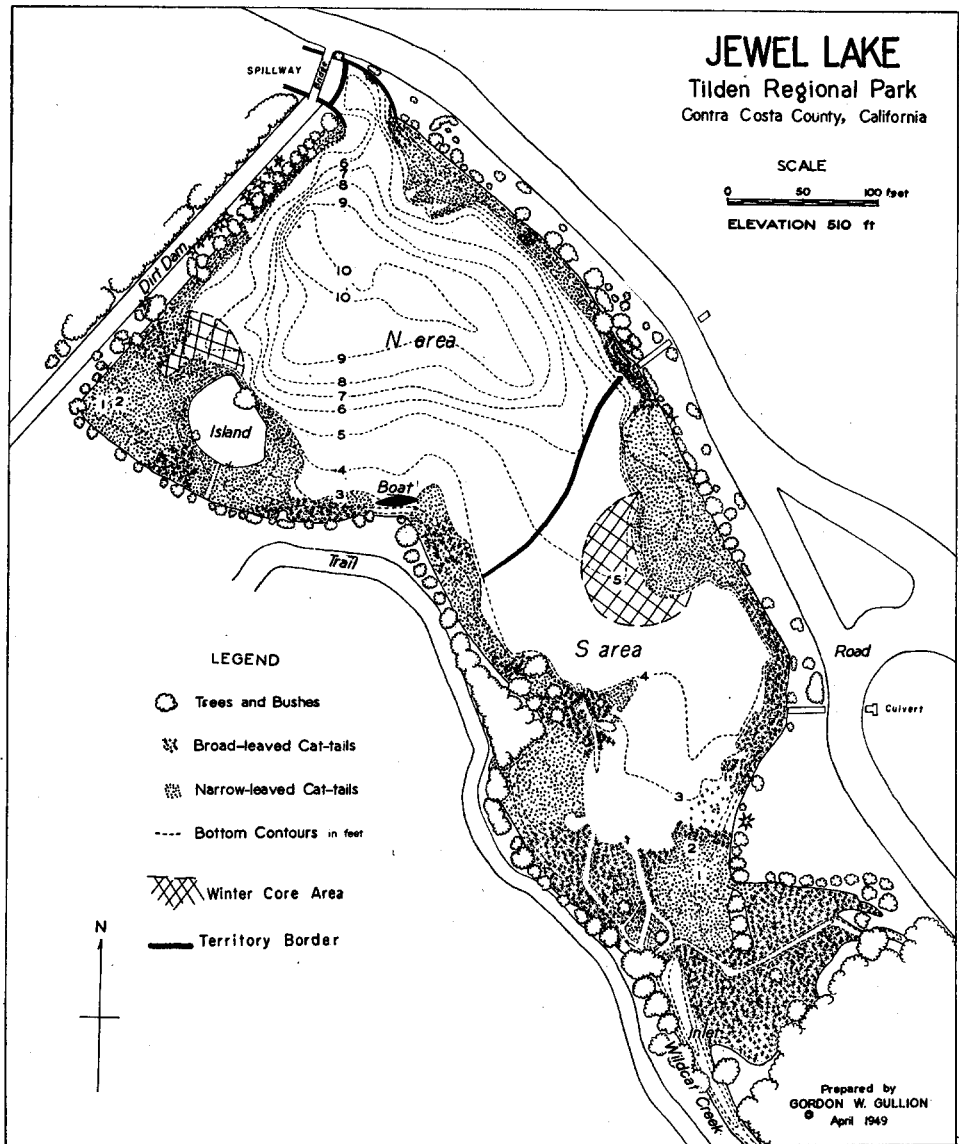


Fig. 1. Territorial areas of American Coots on Jewel Lake.

coming increasingly frequent and severe. At both Jewel Lake and Lake Temescal resident coots were building nest structures in mid-March and were laying eggs by the end of the month.

Some pairs without suitable territory began to invade territorial waters frequently, seeking possible nesting sites, while others departed for other regions. The last non-territorial coot left Jewel Lake on the night of March 26, and the non-territorial population on Lake Temescal consisted of only seven coots (including four tagged birds) on April 5.

Elsewhere in the Bay area the departure of migrant coots was apparent. The winter population of 103 coots on Berkeley's Aquatic Park had dropped to 81 by March 10;

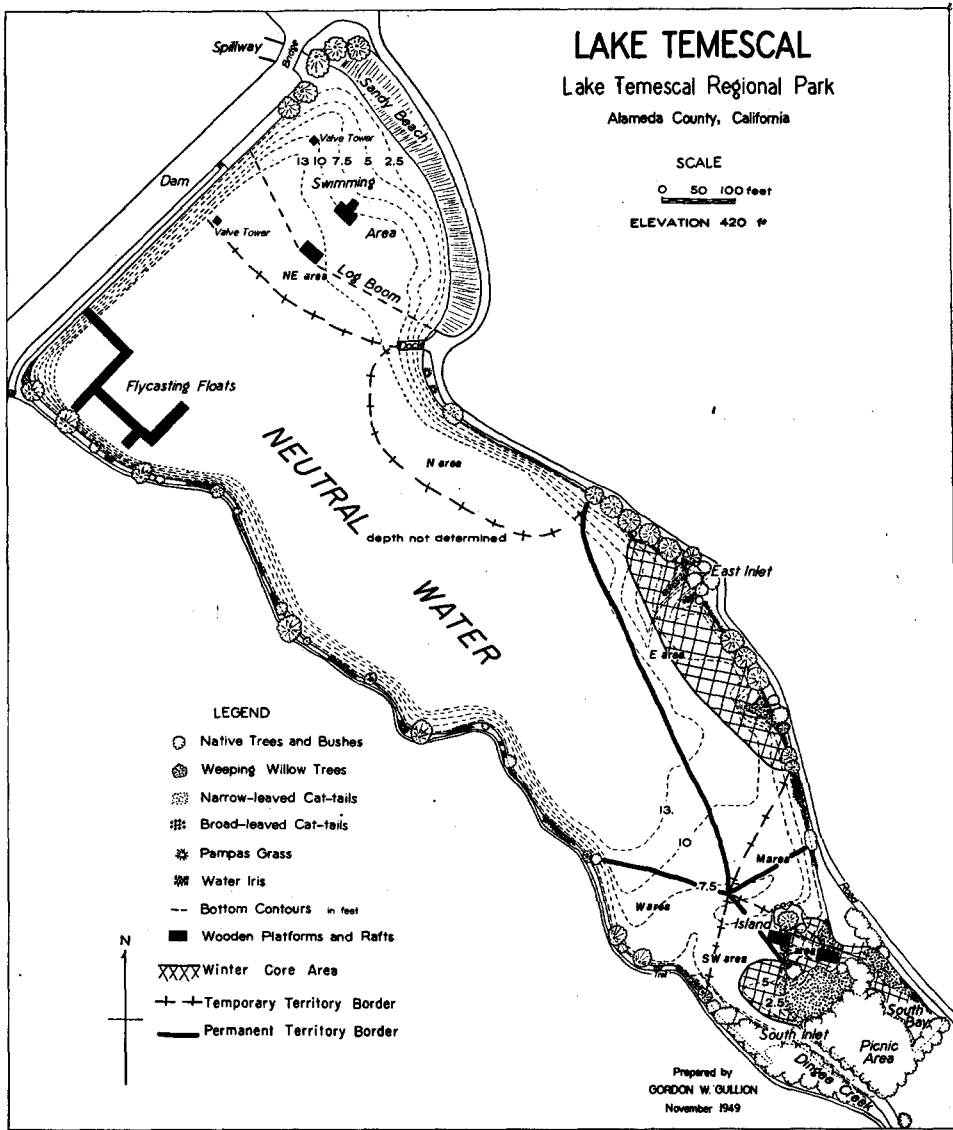


Fig. 2. Territorial areas on Lake Temescal.

to 43 on March 24; to 16 on March 29; to ten on April 8; to seven on April 12; and to none by April 21. A similar drop was noted on Lake Merritt but it was not so readily documented because of the size of this lake.

Territorial affairs at Gray Lodge and Honey Lake in March, 1950, and March, 1951, respectively, were in the same state of flux as in the Bay area during the same seasonal period. Core areas observed in midwinter at both areas had been much expanded and the wintering flocks, at least at Gray Lodge, were much reduced in size.

During a late evening hour on March 31, 1950, I observed what seemed to be the peak of territorial expansion on Lake Temescal. A pair was trying to establish a new

territory between the LT-E and LT-SE areas (the LT-M area). The LT-W pair was trying to obtain control of a cattail area within the LT-SW area while the LT-N pair sought control of some cattails near the center of the LT-E area (see fig. 2). The urge to nest was becoming powerful and three resident pairs, with fully expanded territories, controlled all the good nesting sites. The several other territorial pairs found themselves without suitable nesting sites and were trying to secure them.

The resulting vicious melee was desperate. For 53 minutes I watched a continual conflict centering just northwest of the island. At times as many as seven birds were in simultaneous paired display, on several occasions four birds were engaged in one scrap and at least three times excitement became so intense that coots coming to the aid of their beleaguered mates attacked and thoroughly mauled their own mates before realizing their mistake.

The following day the new boundaries seemed to be established. The LT-W pair succeeded in holding the LT-SW pair at the new border, but the LT-M pair, though occupying its new area, was impotent against the furious attacks of the LT-SE and LT-E males. The LT-M birds were able to repulse the irregular invasions of the migrant birds and the LT-W pair. Only the attention required by nesting duties prevented the LT-SE and LT-E coots from driving the LT-M pair out of its newly acquired area.

The LT-M pair, by being able to remain in its area, gradually developed a determination to defend it and confidence in its ability to do so. Although under constant pressure from the LT-SE pair, the LT-M pair remained in possession of a more or less secure territory.

Through early April the non-resident birds (including migrants and possibly some immatures of the 1949 season) continued to maintain their territories but as the season wore on they gradually gave up their futile efforts to secure adequate nesting areas and left the lakes. The LT-N pair gave up about April 5 and moved out shortly afterward. About April 8, the LT-M ♂, possibly discouraged over the repeated attacks of the LT-SE ♂, deserted his mate and territory and disappeared from the lake. Following her mate's disappearance, the LT-M ♀ abandoned the M area, which was then promptly absorbed by the LT-W pair. On April 17, a marked male (♂ 633—previously a member of the gregarious non-territorial flock consisting of migrants and other marked coots) and his newly acquired mate (M ♀) regained the LT-M area from the LT-W pair's control. About April 20, the LT-W ♂ deserted his mate and area, to be almost immediately replaced by another marked male (♀ 650) from the flock.

At Jewel Lake the JL-S ♀ disappeared in late April, 1950, and after about two weeks of nonterritorial behavior, the JL-S ♂ left the pond with only the JL-N pair present. At the same date in 1949 the summer territories on Jewel Lake had been fully determined (see fig. 1).

In early May, hatching was occurring or was just completed and the vigor of territorial defense surged to a new high peak (fig. 3). The few nonresident birds still holding sections of the permanent territories were soon driven out of those areas and left the lakes. By late May, 1950, at Lake Temescal, except for a small sector of the LT-SE area still held by the LT-M pair (in which three display platforms had been built), the limits of the several territories were the same as they were in July, 1949.

*Summer.*—By the first of June, the establishment and expansion of territory had ceased and all the successful coots were busily engaged in family duties and in protecting the territorial areas they had secured.

Interspecific aggression was severe. A Ruddy Duck (*Oxyura jamaicensis*) trying to nest in the SE area at Lake Temescal seemed to be encountering a good deal of opposition from the LT-SE pair. Before this pair of coots had young, another Ruddy Duck

was able to bring off a brood from a nest very close to the LT-SE pair's first egg nest with very little opposition.

During mid-June the LT-M pair at Lake Temescal was slowly losing control of its area and by the last of June the LT-M area had been completely reclaimed by the LT-SE pair. This was possible because the LT-SE pair had finally hatched some young after a previously unsuccessful attempt and were no longer concerned with the restrictive duties of incubation.

On June 21, 1950, the power of the LT-E pair was demonstrated. A passerby threw several slices of bread into the water near the east inlet of Lake Temescal, deep in the LT-E territory. Although several Mallards and coots came over to participate in the feast, the presence of the LT-E ♂ in the area discouraged their approach and they re-

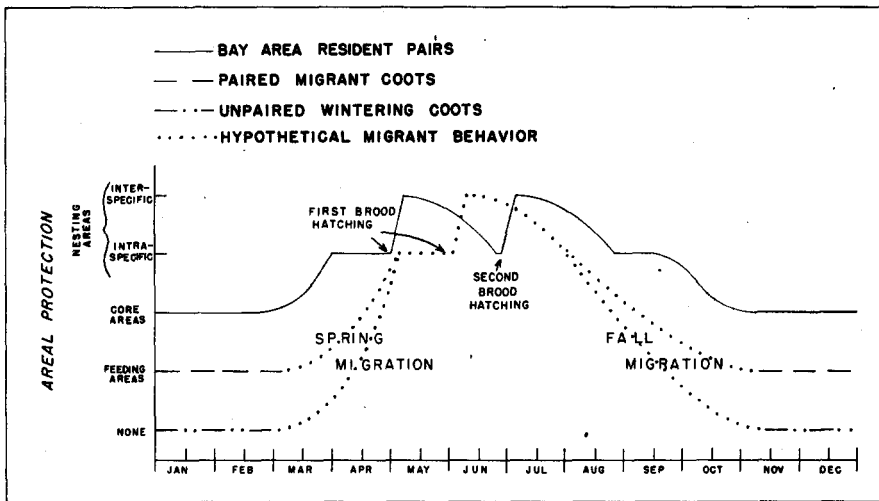


Fig. 3. Levels of territorial activity in American Coots resident in San Francisco Bay area and the hypothetical levels in migrant coots wintering in the same area.

mained at the border of the LT-E area for about 15 minutes while the LT-E pair carried all of the bread to their young. Finally the would-be trespassers departed, without any of them coming closer than about 50 feet to the owners of the area.

By late June interspecific strife was waning. The immatures of the first broods were large enough to care for themselves and several pairs were incubating second clutches and had either little time or inclination to engage in territorial disputes (fig. 3). However, by mid-July, second clutches were hatching and territorial pugnacity rose to its second peak of the season. Those pairs with second broods not only attacked other adult coots and other species, but they also drove the immatures of their previous brood from their home areas.

This behavior was particularly well documented in the summer of 1949 at Jewel Lake and seems worth describing in detail. On the first of June the JL-N pair had six one-month-old young and the JL-S pair had seven young about three weeks old. By June 20, both pairs had second sets under incubation and border disputes had become infrequent and not particularly vigorous.

However, too much disturbance of the LT-S nest resulted in its being deserted on June 21 and the JL-S ♂ suddenly became very antagonistic, attacking Red-winged

Blackbirds (*Agelaius phoeniceus*) and one of his own immatures and finally engaging in three short fights with the JL-N ♂ in the border zone.

Throughout late June the JL-S pair was seen repeatedly attacking birds of their own brood although such antagonism was not occurring in the JL-N territory. However, on July 1, as the second JL-N brood commenced hatching, the JL-N pair's tolerance ceased and the immatures of the first brood became subject to repeated attacks by their parents. Within a few days these immatures were concentrated in a zone adjacent to the territorial border zone (fig. 1) and even there they occasionally were attacked.

The JL-S pair had begun a third nesting and subsequently deserted it by July 4. During the period from July 6 to 15, trapping operations were carried out on Jewel Lake and in this period, perhaps due to the pressure of trapping, the JL-S pair gave up its territory and left the pond.

On July 19 the JL-N pair was penetrating the old JL-S area. It gradually took over more and more of that area, driving the immatures south before it and finally reaching and defending the southernmost reach of open water by July 21. On this date an attack against a Black Phoebe (*Sayornis nigricans*) was recorded, the JL-N ♂ actually jumping out of the water after the flycatcher. By the end of July, the JL-N pair was going into the cattails at the south end of the pond and chasing the immatures out.

The pressure exerted by the JL-N pair against the immatures of both broods caused them to leave the pond as soon as they were able, their departures commencing about July 12 and continuing at regular intervals, as the immatures became capable of flight, until about August 5. In 1950, the attacks of the JL-N adults upon their first brood progressed along the same pattern as in 1949. In 1949 all the first JL-N brood had left the pond by July 25 and in 1950 they had all departed by July 28. Since the hatching dates of both the first and second broods in both years were identical, that is, the last week in April and the first week in July, this close similarity in departure dates is of interest. It was felt that the trapping pressure in 1949 might have driven the immatures from the pond, but there was a minimum of disturbance in the area in 1950, and yet they departed at about the same time.

*Fall.*—Observations on the decline from the peak of summer territorial behavior were restricted to Lake Temescal.

In mid-September of 1949, the three resident pairs were defending the full extent of their areas but doing so intraspecifically only. It was noticed that the LT-SE pair seemed to avoid contact with Mallards deep in its territory, although a month earlier the ducks would have been relentlessly driven from that area. Immature coots, however, were not tolerated within this area. Several times immature birds that seemed to be of the LT-SE brood were attacked and repelled when they entered the area that was previously their home. Disputes between adults, especially the LT-SE and LT-SW pairs, were frequent and vicious.

Subsequent observations in late September and early October indicated a gradual decrease in territorial areas. However, even as late as October 7, the LT-SE pair seemed to be defending most of its area, although the LT-E and LT-SW pairs were defending somewhat reduced areas. By mid-October, most of the pairs were principally concerned only with core areas.

#### HOMING

In connection with winter territorial behavior and the possibility that migrant coots might return to the same winter territory year after year, an experiment was conducted to determine whether or not winter homing occurred. Thirteen coots trapped at Lake Merritt and seven coots from the Gray Lodge Refuge were used in this study. All were birds of the season.



The Lake Merritt birds were tagged and released as soon as possible after trapping. Four were placed on Lake Temescal, four on the Aquatic Park, three on Stow Lake and two were released in the Suisun Marshes near Suisun City.

Within five days three of the four birds released on Lake Temescal had returned over the three miles of metropolitan Oakland to Lake Merritt and all four had returned within two and one-half months. Three weeks after their release on Aquatic Park, two of the four coots had returned across four miles of industrial developments to Lake Merritt and although only two were recorded at Lake Merritt the other two may have returned since they definitely did not remain on Aquatic Park.

All three of the coots released on Stow Lake in San Francisco remained there for the remainder of the winter season and presumably went north in the spring migration. One of the two coots released near Suisun City had returned over a minimum airline distance of 31 miles to Lake Merritt in a little over a month.

Once these tagged coots returned to Lake Merritt, they remained in a certain general area. On each visit to the lake it was possible to find each tagged bird within a few hundred feet of where it was seen on the previous visit. This eliminates any possibility of shuttling back and forth accounting for their apparent homing behavior. Furthermore, populations on Lake Temescal and Aquatic Park remained very stable throughout the winter, which might not have been the case had shuttling of coots from one lake to another occurred to any considerable extent.

Of the Gray Lodge birds, five were released on Lake Temescal (where one subsequently died) and two on Aquatic Park six days after being trapped. One from Lake Temescal was found in the industrial area near Aquatic Park two days after its release. After three days all had left Lake Temescal and no tagged birds could be found on Aquatic Park. No returns have been received on this lot of coots away from the Bay Area, but if they had returned to their home area they might easily have been overlooked among the many thousands of coots present at Gray Lodge. A return over the 100-mile distance between the Bay Area and the refuge would not be surprising since Rüppell and Schifferli (1939) recorded returns within two months of at least 5 out of 16 marked Black Coots (*Fulica atra*) taken from Zurich, Switzerland, and released at Berlin, Germany. One of these birds covered the intervening 415 miles in four days.

It is probable that at least some wintering American Coots have an attachment to a "home" wintering ground and a strong instinct to "home" to that area. The departures from Lake Temescal might have resulted from the condition of a saturated population there, but this could hardly explain the returns from either Aquatic Park or from the Suisun area. Birds departing from both of these latter areas were leaving areas at least as satisfactory as, and in the case of the Suisun Marshes, an area much more suitable than, their preferred wintering area at Lake Merritt.

The complete failure of the Stow Lake releases to return is probably related to their lack of familiarity with the intervening area. Griffin and Hock (1949) have demonstrated the importance of knowing a terrain in the homing of Gannets (*Morus bassanus*) and the lack of movement from Stow Lake was perhaps due to this factor.

Banding returns have shown that individual coots return to Lake Merritt year after year and they probably have no occasion for crossing to the San Francisco Peninsula. Since only first-year coots were used in this experiment, final conclusions are difficult to draw, but, on the other hand, perhaps it is equally interesting that some of these coots returned along a route they had gone over only once before. The fact that the three Stow Lake birds did not even leave Stow Lake until the northward migration started seems to support this belief.

It may be recalled from the foregoing that the birds transported by Rüppell and

Schifferli (1939) were carried north, so they supposedly were homing over familiar ground. However, these authors did believe that one of their coots was a resident on the Vierwaldstätter See at Luzern, Switzerland, but, since their observations ceased in mid-March, their evidence is not convincing.

Rüppell and Schifferli concluded that the Black Coot has a strong attachment to its chosen winter quarters. This seems to be true also of the American Coot.

#### DISCUSSION

*Territory establishment and maintenance.*—In the American Coot, as in the Canvasback (*Aythya valisineria*), the territory is sought and established after pair formation is completed (Hochbaum, 1944:58). The female selects the elements constituting the new territory and the male primarily carries out the task of establishing the limits of the territory and guarding those limits. However, if the male is not available at the moment a violation of the territory border occurs, the female has no hesitancy about protecting it. Nylund (1945:120) suggests that pair formation followed territorial establishment among Black Coots (*Fulica atra*) on a small Finnish lake.

Not only is the territory established following pair formation but the desire to defend it is lost within one or two days if one mate disappears. This fact was illustrated in 1950 by the loss of territorial behavior on the part of the JL-S♂ after the disappearance of his mate and by the temporary abandonment of territory by the LT-M♀ when her first mate vanished.

There also seems to be a tendency for birds to give up a territory and move elsewhere if they cannot secure it satisfactorily. I believe this was the cause of the abrupt change of mates in both the LT-M and LT-W pairs in mid-April, 1950. At least two pairs on Lake Temescal that were defending winter territory subsequently departed when they were unable to secure nesting areas; it is not known whether they departed as a pair or individually. Also, the LT-W♀ departed after the LT-SW pair began regaining lost territory in early May. Cramp (1947:197) attributes the same reaction to a failure to secure territory in the Black Coot in England.

An overwhelming pressure exerted by an excessive number of coots may also prevent or reduce the effectiveness of territorial establishment. The numbers of coots present in a confined flock held on the University of California campus in Berkeley prevented a successful nesting there. One pair that attempted to establish a territory was kept so busy chasing intruders that it found little time for the other activities necessary for successful nesting. Cramp (*op. cit.*: 196) notes that a pair of Black Coots, overwhelmed by an invasion of migrant coots, gave up all attempts to defend territory.

Various other factors may also cause coots to abandon territory. It was noted that the lowering of the water level at Lake Temescal caused abandonment of two areas and the shifting of a third, while ice at Honey Lake caused coots to abandon territory for as long as the ice persisted. Huxley (1934), studying the Black Coot in England, noted the same thing in regard to physical forces. He points out (p. 272) that "*mechanically enforced abandonment of territory*" resulted in a loss of "their 'territorial' instinct of combativeness." Huxley then concluded: "Territorial activity in Coots must thus be determined partly by internal state, and partly by the external fact of being actually in a staked-out territory."

The intervention of other species may be just as important in determining the success of territorial maintenance. In July, 1949, a pair of coots with one two-week-old young was seen on Stow Lake. This pair had to tolerate interference by such species as Mute Swans (*Cygnus olor*) and Black Swans (*Chenopsis atrata*), both of which were pointedly avoided, and despite repeated attacks against Mallards and Brewer Black-

birds (*Euphagus cyanocephalus*), this pair seemed to be ineffective in its attempts to protect its territory.

In other areas the maintenance of territorial areas was least effective during the time that resident coots were incubating. The LT-M pair was able to seize and maintain its largest territorial area while both the LT-E and LT-SE pairs were incubating. As the LT-E eggs hatched, the LT-M pair was driven from its holdings, and later, when the LT-SE eggs hatched, the LT-M pair was forced from all of its territorial holdings. Similarly, the LT-W pair held LT-SW territory and made frequent excursions into the LT-E area. Simultaneous hatching of the clutches of these two pairs permitted the respective adults to increase defense activity sufficiently to rout the LT-W pair from all its holdings with the result that this routed pair was wholly without territory within 48 hours of the hatching of the last egg in the LT-SW nest.

*Interspecific conflicts.*—The aggressiveness of the American Coot toward the more heavily hunted species of aquatic game birds has received more attention from students of game management than any other characteristic of this species. Various claims have been made as to its effect upon the breeding success of other species. Sooter (1945:99) after studying the nesting of coots and waterfowl at Malheur Lake in southeastern Oregon, concluded: "Coot pugnacity reduces, to an unknown extent, the number of nesting sites available to other species." He points out further that the increased territorial behavior during the breeding season may drive other species of water birds from desirable feeding areas. Munro (1937:172), after studying waterfowl in British Columbia, concluded: "The size of duck broods is not conspicuously influenced by the presence of coots." Earlier he (1919:64) noted that coots regularly nested close to nests of the Red-necked Grebe (*Colymbus grisegena*) in British Columbia. Hochbaum (*op. cit.*) does not report any coot interference in the nesting of Canvasbacks at Delta, Manitoba, nor does Bennett (1938) record any interference in the nesting of Blue-winged Teal (*Anas discors*) in Iowa. Low (1940:161) records coots nesting within a yard of Redhead (*Aythya americana*) nests in Iowa without causing a single nest failure and the same author later (1941) made no mention of coot interference in the nesting of Ruddy Ducks. In fact, both Bennett and Low note that Blue-winged Teal and Ruddy Ducks appropriated coot structures for their own use. At Lake Temescal unused coot structures (usually brood nests) were taken over by Mallard hens to brood ducklings.

My observations have been essentially the same as Sooter's. Through the nonbreeding season, from September to March, coots show little antagonism toward other species, although they frequently engage in disputes with other coots. Other species occasionally get trampled in the rush of these affairs, but normally coots retire before the advances of ducks. Even during the period when coot territorial behavior is in the violent expansive stage, ducks and other species usually are ignored. During the period of incubation ducks will be tolerated within the territorial areas but not in the immediate vicinity of the nest.

With the hatching of the brood the status changes abruptly and ducks as well as most species of small vertebrates, including garter snakes (*Thamnophis elegans*), mud turtles (*Clemmys marmorata*) and all species of small birds venturing within a coot's reach become subject to attack (fig. 3).

As the young become older and more independent, the parents show less antagonism toward other species. Finally by the time the immatures are being treated as territory invaders, at about 70 to 80 days of age, aggression against other species wanes and the adults make an effort to avoid contact with ducks.

However, the larger species of waterfowl are respected even during the height of interspecific strife. Coots have been seen giving wide berth to Mute Swans, Black Swans

and a white Muscovy Duck (*Cairina moschata*), although these birds were violating territorial areas. Mallards are most subject to successful attack and although coots frequently attack Pied-billed Grebes and Ruddy Ducks, these species generally escape by diving, and after three or four dives their antagonist becomes discouraged and leaves them alone.

The reason for the extreme pugnacity of adult coots following the hatching of the eggs is not well understood. Attacks against marsh-inhabiting passerines can hardly be in defense of young or of a food supply. It may possibly be an attempt to defend a general area against intrusion by all potential competitors for the brood nests needed in caring for the young. During incubation a general areal defense is not necessary since the egg nest has a bird constantly in attendance. But the adults are not constantly in the vicinity of the brood nests and perhaps interspecific defense of the whole territory during this period is the most expedient means of protecting brooding sites. The gradual decrease in interspecific strife as the young require less brooding seems to support this belief.

In regard to Armstrong's statement (1947:277) "that the defence of territory seldom becomes more vehement when the eggs hatch and there are more mouths to feed," it should be stressed that this increase in the vigor of defense is probably not due to "more mouths to feed" but rather, as indicated above, due to the necessity of defending brooding sites.

*Food advantage.*—Though maintenance of territory through the winter may have a food advantage, adequate food does not seem to be the primary reason for territorial activity among coots. At Jewel Lake food was so abundant that any suggestion of a food factor governing the establishment of core areas is ruled out. Through most of the winter the core areas at Lake Temescal had no more food to offer than neutral areas, especially during the water draw-down. However, in late winter the severity of the food situation became apparent with the development of browse lines on all the weeping willows over neutral waters. Although the lack of similar browse lines over territorial waters illustrated a food advantage, it is still believed that the food situation is incidental in coot territorialism. The major factor seems to be the maintenance of the pair bond, since territorial behavior is so rapidly lost when the pair bond is broken.

A possible disadvantage of territorial behavior is exemplified by the situation in 1950 on Jewel Lake. After all nonterritorial coots were driven off the pond and the territorial limits set for the breeding season, one bird vanished, leaving the S territory without an effective pair. The spring migration was over so there was no chance for a new mate to arrive. Hence, after several weeks of solitary roaming, the odd bird left the pond, leaving the one pair to occupy an area capable of supporting two pairs.

*The function of territory.*—According to Armstrong's scheme (*op. cit.*: 274) of classification, the territory of the American Coot serves the multiple functions of reproduction (part of "B. . . . maintenance of the pair bond, C. Coition, D. Nesting and rearing young") and self-preservation ("E. Feeding. a.1. As part of the breeding territory and food furnishing for the young" and "c. Winter feeding territory consisting of whole or part of the breeding territory." and "F. Roosting."). However, as pointed out earlier, and agreeing with Lack and Lack (1933), Nice (1941) and Armstrong (*op. cit.*), the primary function is probably reproduction, with self-preservation being of very much less importance.

*Territorial areas.*—In table 2, some of the ecological requisites of suitable coot territory are suggested. A primary need is a sufficient amount of emergent vegetation with some interspersions of open water. The SW territory on Lake Temescal, with its 0.06 of an acre of emergent vegetation and about 470 linear feet of edge is probably about

a minimum usable area. In this regard it is interesting to note that among the Lake Temescal coots, the LT-SE pair had the smallest total territory, yet interspersed in this area proved adequate for successful breeding in both 1949 and 1950. On the other hand, the LT-E pair had to defend a total area more than twice as large as the LT-SE pair in order to control an area of emergent vegetation one-half that of the SE area and very little above the probable minimum area.

Although Jewel Lake had nearly enough usable area for three pairs, the spatial arrangement of this pond precluded the presence of a third pair of coots. Here the impor-

Table 2  
Territorial Areas in Acres

Areas and pairs	Total defended area	Total defended vegetation	Used vegetation	Defended area not used	Total edge available (in feet)
Winter core areas, 1949-50					
JL-N	0.09	.....	.....	.....	.....
JL-S	0.11	.....	.....	.....	.....
LT-E	0.54	.....	.....	.....	.....
LT-SE	0.32	.....	.....	.....	.....
LT-SW	0.17	.....	.....	.....	.....
Spring, 1950					
LT-NE <sup>t</sup>	1.27	0	0	0	0
LT-N <sup>t</sup>	0.81	0	0	0	0
LT-E	1.06	0.06	0.06	0	420
LT-M <sup>t</sup>	0.49	0.03	0.02	0.01	185
LT-SE	0.40	0.12	0.12	0	335
LT-SW	0.39	0.05	0.05	0	305
LT-W <sup>t</sup>	0.61	0.005	0	0.005	165
Summer, 1949 and 1950					
JL-N	1.39	0.35	0.33	0.05	845
JL-S*	1.38	0.64	0.24	0.40	971
LT-E	1.20	0.07	0.07	0	535
LT-SE	0.54	0.12	0.12	0	405
LT-SW	0.80	0.06	0.06	0	470
Summer averages	1.06	.....	0.16	.....	645

<sup>t</sup> Temporary territories.

\* Functional only during the 1949 season.

tance of edge and interspersed becomes evident. The map of Jewel Lake (fig. 1), shows that the vegetation occurs in solid blocks, especially at the south end. Accordingly only a little over one-half of the vegetation was used.

The average total defended area in 1949 for five pairs on Jewel Lake and Lake Temescal was about one acre, whereas the same average for vegetative areas regularly utilized (used vegetation) was 0.16 of an acre. There are few additional data from other lakes in the Bay area, but Middle Chain Lake, with an area of 2.2 acres, supported two pairs of breeding American Coots in 1949 and 1950. The emergent vegetation in this pond covers about 0.80 of an acre and is favorably interspersed with open water. The other nine ponds and small lakes in Golden Gate Park fail to support breeding coot populations either because of insufficient size or an absence of emergent vegetation.

I have found little satisfactory information from other authors with which to compare these data. Hendrickson (1936:217) in Iowa recorded ten nests from 2.5 acres of bullrushes and cattails. However, only two contained eggs and the rest may have been display and roosting platforms. Friley, *et al.* (1938:82) gave a figure of 189 nests on one-quarter of a 350-acre lake in Iowa. This is about one nest per 0.54 of an acre. How-

ever, again only 22 of the 189 nests contained eggs and since they give no further usable data, figures on territorial areas cannot be derived. It will be shown elsewhere that a single pair of coots may build as many as nine nestlike structures within its territory and maintain at least four of them in good repair at one time. Sooter (1942:127), in summarizing a further study in Iowa, gave a figure equivalent to one nest per 0.70 of an acre for a slough of 224 acres, or one nest per 0.30 of an acre for the 109 acres of emergent vegetation. These figures agree fairly closely with my data as given in table 2. Beecher (1942:29) in a nesting study in Illinois, found seven coot nests, six in 16 acres of *Typha* marsh and one in 1.38 acres of pond-growing *Carex*; this yields a figure of 2.48 acres per nest. He also gives an "edge" figure of 1718 feet per acre of *Typha* plant type similar to that at Lake Temescal and Jewel Lake, which is within the range I figured for the lakes considered in my study.

Provost (1947:495) in yet another study in Iowa reported a "highest" nest density of 1.2 nests per acre in "kettleholes." However, Provost does not specify the type of nest so his figures cannot be used for comparison. Counting all nests in good repair, there were times when the three pairs of coots on Lake Temescal attained a nest density of 4.3 nests per acre.

In considering the territorial behavior of this species it should be pointed out that the defended area does not include the adjacent dry land. Birds subject to pursuit will seldom be chased if they go onto land, or if they are, it will be for a distance of only three or four feet. Huxley (1934:270) has recorded the same behavior when pursued Black Coots "mounted the ice, even within the territorial area."

It was also noticed that defending coots drawn into other territories during a chase quickly lost their pugnacious attitude and beat a hasty retreat before the onslaught of the coots whose territory was inadvertently violated. This agrees with Howard's discussion (1948:81) of the importance of "position" in relation to territorial pugnacity.

No neutral areas existed on Jewel Lake, but such an area was present on Lake Temescal during the height of the breeding season. In 1950 this was occupied by a flock of nonbreeding coots, mostly placed there by me during or following experimental use. Birds in this neutral area were seldom molested by territorial coots. Occasionally, however, a border violation resulted in a chase extending far into neutral waters. This neutral area did not serve as an amicable meeting ground for territorial coots, as described by Howard (1948:58), since a penetration into it by an aggressive coot was usually cause for birds on adjacent territories to move to their respective border zones in typical patrol displays.

*Territory borders.*—It should be emphasized that the territory limits shown in figures 1 and 2 are definite narrow border zones which were seen to be defended time after time. As pointed out elsewhere (Gullion, 1952b:84-86), the patrol action is taken only before a territory border is violated and the displaying bird invariably moves to the border zone to carry out this display. If the intruding coot already has crossed the border, the resident bird makes a charge, progressing only as far as the border zone if the intruder promptly retreats. However, if the resident has to take more violent actions, as splattering, it very often progresses far beyond the territory boundary. The climax of the charge is a paired display if the invader offers resistance, or a short patrol if there is no opposition. Whichever the climax, it occurs in the border zone, the zones indicated in figures 1 and 2.

The question arises as to how these border areas are recognized by the resident coots. On Jewel Lake in 1949, breaks in the cattail edge on each side of the pond seemed to constitute the boundary reference points. On Lake Temescal willow trees along the shore-line seemed to be the boundary markers for the east end of the zone between the

E and SE areas and for the south end of the zone between the SE and SW areas. Similarly, willow trees served to mark the northern limits of the SW and E areas. However, the junction of the three border zones northwest of the island was without apparent reference points. Numerous observations of patrol activities by the SE pair in the acute angle of this junction indicated the existence of a recognized border zone there. Perhaps the presence of a stretch of shallow water at that point, providing easier feeding, afforded a reference point for the coots.

#### TERRITORIAL BEHAVIOR OF OTHER MEMBERS OF THE RALLIDAE

Although alike in many ways, the American Coot and Black Coot differ markedly in the extent of the winter territory they defend. The coots on Lake Temescal maintained core areas of about one-fifth to one-half their breeding territory whereas the Black Coots defend a winter area somewhat larger than that required for breeding. This permits a certain amount of compression during the spring adjustment of the Black Coot (Huxley, 1934:274) and also permits new pairs to become established with a possibility of breeding success. In the American species the effect is the opposite, that is, more pairs can establish and defend areas in late winter than will be able to maintain secure breeding territory.

Cramp (1947:194) gives areas for the secure territories of seven pairs of Black Coots in England. These averaged about 0.86 of an acre, with a range from 0.5 to 1.1 acre. A pair with only 0.3 of an acre was not able to maintain its area long enough to raise its two chicks. Nylund (1945:120) studied two pairs of Black Coots in Finland whose territories included about 40 to 50 meters of shore-line. Gibson (1920:43) found two pairs of White-winged Coots (*Fulica leucoptera*), one pair of Red-gartered Coots (*Fulica armillata*) and one pair of Black Gallinules (*Gallinula chloropus*) nesting simultaneously in an Argentine marsh of about 12 acres.

Cramp (1947:197), speaking further of territories of some Black Coots in England in 1944, remarks: "It will be seen that the territories were remarkably similar to those in 1943." This use of identical areas in succeeding seasons seems to have been the case on both bodies of water under study in the San Francisco Bay area. He also records a disappearance of interspecific strife in mid-September, about the same time the immatures had left their home areas.

The aggressiveness of the American Coot toward other species of vertebrates is not unique among the Rallidae. Cramp (1947:197-198), summarizing his study of territorialism in the Black Coot, remarks: "Generally, the Coots reserved their aggressive behavior for adults (and sometimes young) of their own species, but were from time to time seen to attack other species," but he does not note increased aggressiveness following hatching of the brood. Stuart Baker (1929:35) says of the Black Coot in India: "Coots are very gregarious and do not fight among themselves but are great bullies to other birds." Alley and Boyd (1947) did not report an increase in interspecific strife following the hatching of a clutch. Nylund (1945:121), summarizing a study of the Black Coot in Finland, states that "the coots, both male and female, regularly drive intruding ducks away from the territory. The Common Pochard is especially violently attacked. The Great Crested Grebe again is left quite unmolested and is permitted to breed in immediate vicinity of the coots nest." He also says that "the male coots fight their neighbours at the borders of the territories . . ."

Howard (1948:161), discussing the interspecific territorial behavior of the Moor-Hen or Black Gallinule, remarks that "the intolerance it displays towards other species is . . . remarkable, and its pugnacious instinct seems to be peculiarly susceptible to stimulation by different individuals belonging to widely divergent forms. At one moment a Lapwing may be attacked, at another a Thrush or Starling, harmless strangers that

have approached the pool to drink; even a Water-Rail, as it threads its way through the rushes, may fail to escape detection; and, which is still more curious, a covey of Partridges will evoke response if they approach the pool too closely."

There is little information on territorial areas of most other members of the Rallidae. Howard's (1940) study of the Black Gallinule or Water-Hen in England is a classic. He worked with a pair occupying an area of about 0.33 of an acre. Miller (1946) studying the same species in southeastern Pennsylvania reported concentrations varying from about 16 pairs (with eggs in all nests) in a four-acre cattail marsh to 12 pairs in a ten-acre tule marsh.

Beecher (1942:29) gave nest density figures for several rails in Illinois. He located four King Rail (*Rallus elegans*) nests at a density of 1.69 acres per nest; 54 nests of Soras (*Porzana carolina*) averaged 1.78 acres per nest and 19 Black Gallinule nests averaged 1.19 acres per nest. Kozicky and Schmidt (1949), studying the Clapper Rail (*Rallus longirostris*) in New Jersey, found 56 egg nests in 430 acres of saltmarsh, a density of one nest per 7.70 acres. Stuart Baker (1929:26) records "nearly a dozen" Elwe Crakes (*Porzana bicolor*) breeding in an Indian area of about 1.25 acres and says (p. 35) that where the Blue Reed-Hen (*Porphyrio poliocephalus*) "is very common, half a dozen nests may be found quite close together."

Stuart Baker also noted disputes among Gray-breasted Rails (*Rallus striatus*), White-breasted Water-Hens (*Amaurornis phoenicurus*) and the Water-Cock (*Gallinula cinerea*).

Oliver (1930:334) says of the Black Woodhen or Weka (*Gallirallus trolodytes*) of New Zealand: "Each pair has its own territory, the boundaries of which are respected by other wekas. The male is the chief defender and . . . if the female gets killed, he soon finds another mate, but if the male is killed, another pair occupies the territory." Smith (1952:400), writing about the recently rediscovered Takahē (*Notornis hockstetteri*), comments: "An interesting characteristic of the bird is its sense of property. Each mated pair ranges freely within what appears to be fairly well-defined feeding territory."

Schwartz and Schwartz (1952), in their recent paper on the Hawaiian Coot (*Fulica americana alai*) make no mention of territorial behavior in this race. However, they do suggest it when they say (p. 448) that nests "were often within 10 or 15 yards of each other."

It seems probable that the territorialism exhibited in the American Coot is a more or less universal trait of the family Rallidae. The statement by Grinnell, Bryant, and Storer (1918:316) that coots are gregarious and colonial nesters does not wholly agree with my findings in the Bay area, nor does the statement by Provost (1947:495) that "their gregariousness, so prevalent at other times of the year, was hardly forsaken in the breeding season." This apparent difference in the gregariousness may be the difference between resident and wholly migrant coots. All those studied by Provost were migrant coots whereas all those I have watched have been permanently resident coots.

The size of territories definitely varies with the density and distribution of suitable nesting cover. Among the rallid species, the size of optimum territory may vary directly with the size of the species involved. Thus the Black Gallinule requires about 0.25 to 0.33 of an acre for its minimum territory whereas the larger American and Black coots take from 0.6 to about 0.8 of an acre for minimum territory.

#### SUMMARY

Winter core areas are protected by resident coots in California. These areas have the apparent function of maintaining the pair bond and providing the permanent pairs with



a secure area in which to begin nesting activity early in the season. Core areas vary from 0.09 to 0.54 of an acre in extent and comprise from 6.5 to 59 per cent of the fully expanded summer territories.

With the onset of the spring reproductive season the resident pairs go about securing their territories as nearly as possible along the previous year's lines. These territories range from 0.54 to 1.39 acres in extent, depending on cover types, and they average about 1.06 acres. Nonresident and yearling birds attempt to establish territories, even by forcing a wedge between established territories. If this fails they abandon further efforts and move elsewhere.

During the actual period of incubation, attendance to the eggs necessitates a reduction in territorial behavior. Immediately following the hatching period, however, pugnacity flares to a higher pitch than attained previously and for a short time most vertebrates, coot-sized or smaller, become exposed to vicious and relentless attack when invading coot territorial waters. Second broods result in a repetition of this peak later in the season, when even immatures from the first brood will be driven from their home areas.

As the young develop into immatures, interspecific strife wanes. As the immatures attain their first winter plumage they become indistinguishable from adults and are eventually driven from their home by persistently attacking parents.

Following the departure of the young, the resident adults gradually defend less and less area, allowing their breeding territory to shrink to the winter core area by October.

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