THE DISPLAYS AND CALLS OF THE AMERICAN COOT¹

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DISPLAYS and calls are of paramount importance in the social behavior of birds. A call or the exposure of some bright plumage spot may serve as a social releaser to communicate one bird's attitude or intentions to other birds, whether aggressive or friendly. This being the case, it seemed desirable to investigate in some detail the displays and calls of the American Coot (Fulica americana) in order to understand properly the breeding behavior of this species. This paper presents a segment of thesis research conducted at the Museum of Vertebrate Zoology, University of California, at Berkeley, on coot breeding behavior. Some other aspects have been published or are in press (Gullion, 1950b, 1951a, 1951b, 1952).

The greater part of this study was made in the San Francisco Bay area of California, with two lakes figuring prominently—Lake Temescal, a 12.0 acre lake at the western base of the Berkeley Hills in Oakland, Alameda County, and Jewel Lake, a 2.7 acre pond in Tilden Regional Park, Contra Costa County.

DISPLAY MECHANISMS

The American Coot is highly territorial in behavior, perhaps more so than most other birds, and must constantly fend off the invasion threats of other coots. Among resident birds this is true even during the winter season. Displays and calls constitute the aggressive behavior which serves to establish and maintain territorial security.

Displays by the coot consist of five elements used in various combinations. These elements are as follows:

Body posture.—Three different postures constitute the bases for coot displays. The normal posture with head and neck erect is the basis for amiable displays. But a coot with its head depressed is in a posture characteristic of any one of the several aggressive displays. The third posture, that of a bowed head, constitutes the basic form of courtship and mating displays.

Under tail coverts.—Several of the American Coot's displays are based upon the use of the white under tail coverts as "social releasers" (cf. Tinbergen, 1948). These coverts may be expanded to present an extensive area of white or they may remain in the inconspicuous normal condition presenting only a small patch of white. The position of the tail, whether normal, depressed, or

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raised, increases the usefulness of these coverts by further increasing or decreasing the amount of white visible.

Wing arching.—This element is important in most displays. It often is the difference between a certain body posture indicating either an anti-social or a definitely sociable attitude. In the typical wing arch, the wings are held stiffly erect and apart from the body (see figs. 1D, 1E, 2C and 2D). Whether or not the white tips on the secondaries play a part in the recognition of this arch is not known.

The ruff.—In all aggressive displays the neck feathers are erected to form a ruff (see fig. 2A). The effect is one of increased neck size, forming a black background for the conspicuous red and white frontal shield. It was found that males are capable of forming a much larger ruff than their mates and when a pair is displaying together, as in nest defense, the sexes can be distinguished on this basis. With one exception, the ruff is not erected in friendly or courtship displays.

Frontal shield.—This structure, a fleshy protuberance extending dorso-posteriorly onto the forehead from the upper mandible, plays an important role in the social life of the coot. Since a paper devoted to a study of this structure is in print (Gullion, 1951b), further consideration of it will not be given here.

Although calls and displays are used to supplement one another in the field, for the sake of clarity they will be discussed separately.

DISPLAYS

American Coots combine the five elements discussed above to form fourteen distinct displays in addition to the normal position. Apparently each display has a certain social significance. Five are intra-specific aggressive displays and two are inter-specific aggressive displays concerned with territorialism; five more are involved in courtship; one is a general warning display; and one, a display given by young begging food from adults.

Normal posture.—This is the posture held by a coot when foraging undisturbed (see fig. 1A). The head is erect, the tail is held horizontally with the under tail coverts inconspicuous. The wings are held close to the body. As the coot swims in an unhurried manner, its head bobs, applying the principle of parallax to its feeding (cf. Grinnell, 1921). Head-bobbing of the coot is not necessarily in unison with the movements of the feet. When the bird is feeding on plant material this head movement is fairly slow, but it is quickened when insects are being hunted on the water's surface.

Patrolling.—Seemingly, whenever a coot has reason to believe some aggressive action may be necessary against other coots approaching its territory,

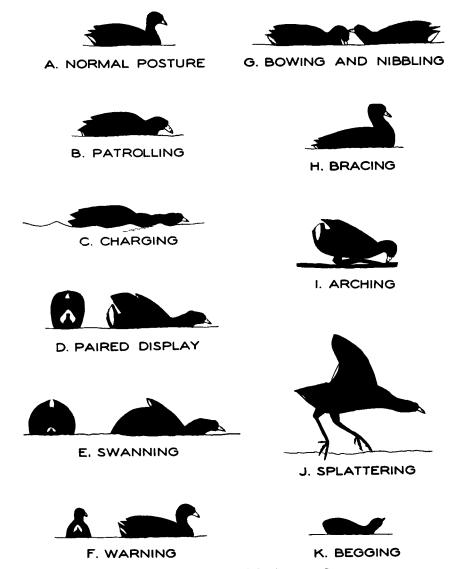


Fig. 1. Display postures of the American Coot.

it pulls its head down and slightly forward, the neck feathers are erected to form the ruff, the tail is slightly depressed and a patrol against invasion commences (see figs. 1B and 2A).

A bird may proceed to further aggressive display or retire to the normal

posture from this position. Other coots, but not other species (except the Ruddy Duck, Oxyura jamaicensis), respect this display and often no further display is necessary to defend territory intra-specifically. The patrol is seldom accompanied by call notes.

Charging.—If an intruder enters a territory before the resident bird can go into patrol the defender generally moves toward the invader in a charge (see figs. 1C and 2B). In this display the neck is extended forward on a horizontal plane, the tail and wings are held in the normal position, but the ruff is erected and the frontal shield is prominent. The bird swims rapidly leaving a noticeable wake.

All species of ducks and small geese occurring in the San Francisco Bay area react to this display and other coots often take evasive action while still 100 feet from the charging bird.

Splattering.—This display is a rapid charge. The bird retains essentially the same head posture as in the charge while it runs over the water with flapping wings (see fig. 1J). The attacked bird very often flees in like manner, but holds its head erect rather than on a nearly horizontal plane (see fig. 2F). Splattering normally begins as a charge, the bird gradually increasing its speed, but occasionally, if the circumstances require it, a splatter may commence directly from the normal posture.

This form of attack may be pressed against other species of waterfowl as well as coots and because of the intensity of the attack it generally succeeds in its purpose. Frequently a fleeing coot when closely pursued will dive to escape its attacker.

It should be pointed out that splattering is used also as a means of escaping danger when flight is not necessary. It then is not a display and the head is not held at the low angle of the display (see fig. 2F).

Paired display.—This display is used entirely in intra-specific territorial activity, and always occurs in connection with strife and usually along territorial borders. This display is normally the final action of aggression and regularly follows charging and splattering. In paired display the head is held low, the wings are arched high above the back, often with tips crossing, and the tail is held vertically, or even tilted over the back, bringing the expanded white under tail coverts into prominence (see fig. 1D). The ruff is erected and the frontal shield is prominent.

It must involve two or more coots if it is to be more than a fleeting display, with the birds presenting their tails to one another as they pivot close together (see fig. 2C). Non-territorial birds engage in this display infrequently but the border disputes between territorial birds often involve repeated displays lasting several minutes at a time. As many as seven coots have been seen in mutual display. Generally like sexes reciprocate in display, but frequently a

pair will display against a single bird. This latter incident occurs most frequently when a chase carries the pursuing bird into the pursued bird's territory.

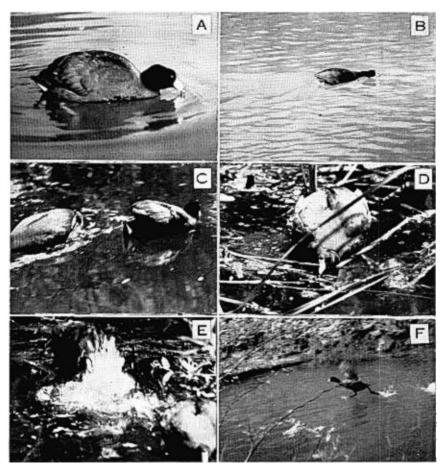


Fig. 2. A. A coot patrolling—note the ruff; B. A coot charging; C. A paired display with two coots pivoting tail to tail; D. A coot swanning; E. A male coot churning while his mate swans nearby; F. A coot splattering to escape its pursuer.

Paired display often is interspersed with fighting and nearly always follows a fight; it in turn is generally followed by "displacement feeding and preening" (Armstrong, 1947:110), the separated birds preening and diving for food which is seldom eaten but is dabbled nervously. During displacement activity the opposing birds slowly work apart, each moving into its own home area.

Paired display is not sexual behavior as believed by many authors (cf. Wetmore, 1920:395; Dawson, 1923:1559; Townsend, 1925:6; Walker, 1932:322 and Breckenridge in Roberts, 1932:457).

Fighting.—The climax of aggressive action is actual combat. In coots this is vicious and has been known to result in the death of the vanquished bird (Henshaw, 1918). In most disputes between neighboring pairs the fighting is interspersed with paired display, the latter act consuming much the greater part of the effort. Previous display does not always occur before fighting starts, especially if the issue is territory and the intruding bird is determined to secure it.

When birds are about evenly matched in determination, the fight starts with both birds sitting on their tails, propped against their wings on the water. Their adversary is grasped by the breast with the long claws of one foot, leaving the other foot free to slap the opponent. Frequent quick jabs with the bill are made to knock the opposing bird off balance but usually result only in a bill full of feathers. As the fight progresses the weaker bird is slowly forced onto its back. If possible, the stronger bird will hold the loser under water, leisurely plucking out feathers. The vanquished coot often escapes by swimming long distances under water.

Strange coots caught in territorial waters without a disposition to fight are frequently subjected to sub-surface mauling. Defending birds will hit other coots directly from flight without landing first and have been seen diving after an intruder directly from full flight. Underwater fighting certainly occurs but what form it takes is not known.

Infrequently as many as four birds may be engaged in one fight. The typical fighting posture has been observed in coots only four days old.

Swanning.—This is distinctly an inter-specific display given against such diverse objects as thrown stones, fishing plugs, turtles, snakes, ducks, Black Phoebes (Sayornis nigricans), dogs, and man. It seems to be employed almost exclusively in defense of nests or young.

Unlike paired display, the wings play a dominant role in swanning, being not only arched over the back, but also expanded laterally with the primaries touching the water. The tail is not lifted to expose the under tail coverts but the head is extended as in paired display, the ruff is erected and the frontal shield is prominent (see fig. 1E). The whole effect makes a coot appear at least twice its normal size (see fig. 2D). Occasionally during times of extreme anxiety a bird defending a nest will lapse into a momentary paired display.

Churning.—This display is intimately related to the four combative displays just described. Bent (1926:364) gives the best description of this activity when he says, "it often 'backs water' vigorously with both feet, raising

the body backwards out of the water" (see fig. 2E). The feet are used alternately in this action.

Churning is primarily a displacement activity arising from two different circumstances. Most frequently it occurs when swanning or some other effort fails in the defense of the nest or young. Churning occurs also when success in aggressive action is attained so rapidly that the bird seems to be left with a surplus of aroused energy and 'lets off steam' by this action.

Warning.—Whereas the preceding displays are anti-social, the warning display is sociable, warning other coots of danger. An alarmed bird lifts its tail exhibiting the white under tail coverts but not expanding them (see fig. 1F). This seems to be the only general alarm signal given by coots. It is seen when a low-flying hawk, vulture, or airplane is overhead, when a dog, cat, or man suddenly appears close by on the shore, or when the coot is some distance away from, but in the general line of attack of, a charging coot. It probably is given as a result of any general alarm and it may be momentary, or repeated at frequent intervals if conditions change rapidly, or it may be maintained continuously if the cause for alarm persists. There is no indication that other species respond to this display.

Billing, bowing and nibbling.—These displays, though separate entities, are so closely related that it seems best to treat them together.

Billing, as the name implies, consists of two birds touching bills upon meeting. It apparently is used between potential mates during pair formation and for recognition of young by parents.

Bowing follows billing, the submissive bird going into a bow (see fig. 1G, left bird) and presenting its head and neck to the nibbling activities of the dominant bird. The nibbling bird works its bill through the feathers of the other bird, often burying its entire bill among the breast and back feathers.

Since these actions are important in pair formation and courtship they will be discussed in detail in a later paper (see also Gullion, 1950a:74-75).

Bracing.—The brace is not completely understood. It was observed on relatively few occasions and each time it immediately followed a meeting after a period of separation. It has been observed only among paired coots; both sexes participating in it. Bracing consists of a swimming bird raising the forepart of its body high in the water with the ruff erected and the head stiffly erect (see fig. 1H).

It occurs when one bird meets its mate returning to the nesting area, both birds approaching in a charge, dipping their bills as they pass and then bracing. Bracing also occurs, and more frequently, during change in incubation. Then the female braces and cackles as the male, often giving a high "kuk-kuk-kuk-kuk-kuk," closely pursues her. I am not sure, however, that the

brace executed on this occasion is exactly comparable with that display performed when two charging birds of the same pair meet. The brace may be given also by the female as she precedes the male to a platform when copulation is imminent.

Arching.—This display consists of three parts. After the pair is formed and territory secured, the female commences displaying her under tail coverts when swimming immediately ahead of her mate. This display, the swimming arch, is much like paired display but the wings are not arched nor is the ruff erected. It is only given by the female and she often leads the male towards the display platform while giving it. At first this is an infrequent and momentary display but later in the season it becomes more frequent and persistent.

The display given on a platform when copulation is not imminent is the standing arch. It is performed by the female standing with her head lowered, her tail elevated and the white under tail coverts expanded. She gives a low "tuk" or "punt" at about two-second intervals and often slaps the platform with one foot.

The final and climactic display in the long series of courtship displays is the *squat arch* (see fig. 11). This is given by the female on the platform when the male is nearby and copulation appears imminent. The female squats, with her tail erect (as in the standing arch), her head lowered (even under water), and she may call as in the standing arch.

Although arching seems to be primarily a female display one captive male was observed in a squat arch. On several occasions males were seen standing on display platforms in an upright position and giving a steadily-repeated "puhk." Generally they preened and often slapped the platform with one foot while their mates swam nearby.

Begging.—This display is first given by young coots when they are a few hours old and they continue to give it as long as their parents react favorably to it. It is a simple display, the hind quarters being elevated, the neck depressed and the head turned up at a sharp angle (see fig. 1K). The wings are outspread and generally quiver. Begging does not seem to be a forerunner of any adult display.

The role of the sexes.—Males take the lead in aggressive displays; normally they attack intruding males first and then return to drive out any invading females. Curiously, this is true even when the attack is pressed against a pair of Mallards (Anas platyrhynchos) or Ruddy Ducks. However, if the male coot is not available when the territory of a pair is invaded, the female will assume aggressive displays, attacking females first and males second. The courtship displays are often unisexual as described, while the alarm display may be given by either sex.

CALL NOTES

The calls of coots are not of musical quality, the calls being variously described as growls, cackles, and squawks. Calls are important in the life of coots in warning other birds of territorial rights or mutual dangers, in locating and recognizing mates and young, and in defending nests or brooding sites. Attempts to transcribe bird calls into phonetic symbols are never entirely successful, since various persons may interpret the same sounds differently. Nevertheless, an attempt was made to record and interpret the principal calls of coots in my study areas. The several types of calls fall into several categories as described in the following paragraphs.

Recognition notes.—The notes exchanged between birds of a pair or between parents and young are simple and rather uniform throughout the population. Between adults, the male gives a high, clear "puhk" and the female replies with a low, nasal "punk." When calling or dealing with young the male gives a clear "puht" while the female gives a nasal "punt."

Courtship notes.—In courtship the vocal efforts of the male are limited to a cough, given while chasing the female in precopulatory activity. In some males this cough becomes a sharp "perk" or "kerk" repeated at very close intervals. If, during a chase, the female is not amenable to mating activity, she faces the male and gives a saucy, cackling "tack-tack, tack-tack" which halts the affair. When the female is displaying on a platform, calling for the male to join her, she gives a note that varies from a low, nasal "punt, punt" or "put, put" to a sharp, clear "tuk, tuk."

Alarm notes.—The normal alarm note for a disturbed male is a "puhlk," while the female gives a "poonk." Whereas the recognition notes involve no vigorous movement, alarm notes are given with a vigorous forward thrust of the head. In time of stress the young are sent to shelter by an explosive "chuck" or "chook" note of the male or the quick nasal "punt-unt" of the female.

When the nest is approached by an intruder or young cannot be moved away rapidly enough, both parents may "growl" at the intruder, sounding much like a dog growling over a bone. This is normally accompanied by swanning and churning.

Perturbation notes.—During times of high nervous tension, as when territory-seeking pairs are trying to seize existing defended areas, calls are given which are not heard at other times. These calls are given by the defending birds as they retire from repulsing one onslaught and nervously await the next. The call given by the male is a plaintive, crowing "puhk-cowah" or "pow-ur" while the female gives a simpler "cooah."

A male at Jewel Lake in 1950, following the unexplained disappearance of

his mate, wandered around the pond several days giving a wailing "cow-wah" before disappearing himself.

Warning notes.—Vocal efforts are used extensively in the protection of nesting areas and to warn birds when they are violating or about to violate another coot's territory. These calls are highly variable, but in the male they may be described as a quick "puhk-ut," "puhk-uhk," "puhk-uk," "puhk-kuk" or "pit-tuck." The female variations are "punk-unk," "punk-uh," "punk-unk-uh" and "punk-tunk-tunk." all nasal in tone.

Intimidation notes.—A paired coot often moves to the limits of his territory and crows. This is seemingly a challenge to other males to violate his territory. The crow is basically three-parted, loud, and not often repeated. It may be transcribed as a "puhk-kuh-kuk," "puh-koo-oot," "kuh-kuh-kuk" or "cook-uh-ook." Frequently a male from an adjoining territory will accept the challenge and move quietly but quickly to engage the crowing male in battle.

Females give a comparable call, which is a hollow crowing sound that varies from "kaw-pow" and "kah-kow" to "kra-kow." This is seldom a challenge; at least, a fight has never been seen to ensue and usually the call is given following crowing by a male elsewhere on the lake.

Sexual dimorphism in vocal apparatus.—Since the morphological basis of sexual differences in voice indicated above is the subject of a previous paper (Gullion, 1950b), it will not be discussed further here.

DISCUSSION

Perhaps the displays of the American Coot have been less understood than any other part of the behavior of this species. The patrol activity seems to have been entirely overlooked by earlier authors. Wetmore (1920:395) describes bracing, Bent (1926:364) describes swanning, and Dawson (1923:1557 and 1560) describes the alarm signal and churning. Nearly everyone who has written about the coot describes splattering. The same may be said for the paired display, but invariably it has been wrongly associated with courtship. Wetmore (1920:395) discusses billing, while Breckenridge (in Roberts, 1932: 457) and Sooter (1941:38) both correctly describe arching as a precopulatory display on a platform. Sooter also accurately describes the swimming arch in Iowa coots.

Displays and calls of other Rallidae.—Nylund (1945:108) shows four displays of the Black Coot (Fulica atra), illustrating (1) paired display, (2) the male following his mate in precopulatory display, (3) a young coot begging, and (4) a begging young too old to stimulate parental feeding being attacked by a parent. These illustrations appear to be identical with the cor-

responding displays of the American Coot. Later, in his English summary (p. 121), Nylund states: "The coots show no marked display behavior," a statement which hardly agrees with his earlier discussion or the findings of others studying the Black Coot.

Witherby et al. (1947:205) describe paired display, bowing, and nibbling in the Black Coot while Cramp (1947) describes splattering in addition to these other three displays. A swimming arch immediately preceding copulation in the Black Coot was reported by Höhn (1949:209). Tinbergen and Moynham (1952:21), discussing some displays by birds, state: "A male Coot, for instance, threatens other Coots by facing them with the head pointing forward and downward. This movement displays the white frontal plate" They also describe a "friendly gesture," which may correspond to the patrol, in which the conspicuous white bill and frontal shield are hidden.

Wetmore (1926:121) describes fighting in the White-winged Coot (Fulica leucoptera) in Argentina which is like fighting of the American Coot, while Sclater and Hudson (1889:158) describe a similar alarm display in the White-winged Coot. The display of the Red-gartered Coot (Fulica armillata) attributed by Wetmore (1926:118) to mating, sounds much like paired display since it involved wing arching and the display of the white under tail coverts. He may, however, be describing the swimming arch.

This general use of conspicuous under tail coverts by the members of the genus Fulica, and perhaps also in the several genera of gallinules, is of interest. The question arises as to the value derived by the exhibition of under tail coverts in the Black Coot and Red-knobbed Coot (Fulica cristata) when those coverts are as dark as the rest of the bird (Dresser, 1903). Still, the Black Coot, at least, gives many of the same displays as the white-coverted American Coot. The South American species of Fulica all possess the white coverts with the black median area as in the American Coot (cf. Sharpe, 1894:209–225).

The displays of the Black Gallinule (Gallinula chloropus) seem to be remarkably similar to those of the American Coot. The platform activity of the Black Gallinule or Water-Hen as described and figured by Howard (1940:40) is identical with the arching of the American Coot. In fact, figures 1 and 2 of the plate facing page 40 (Howard, op. cit.) could as well refer to the American Coot as the Water-Hen, at least insofar as the posture is concerned. Howard (op. cit.) further describes bowing and nibbling in the gallinule similar to that occurring in the American Coot. Miller (1946:14) describes churning and swanning in the Black Gallinule which closely resembles the corresponding display of the coot (he calls it injury-feigning, but is probably incorrect in doing so). Fighting in the Black Gallinule, as described by Witherby et al. (1947:199), is like that of the coot. Pennock (in Bent, 1926: 347) describes wing arching and the exposing of conspicuous white tail

coverts in this gallinule, believing it to be courtship activity, and Morley (1936:121) describes Black Gallinules charging in a manner similar to that of an American Coot.

Other rallids possess coot-like displays to varying degrees. The Corn-Crake (Crex crex) erects its tail feathers in a fan-shaped manner in both courting and territorial displays (Witherby et al., 1947:176) while the Water-Cock (Gallicrex cinerea) raises its tail when alarmed (Deignan, 1945:107), much as the coot does. In fact, the practice of raising the tail when alarmed seems to be general among the Rallidae. Deignan (op. cit.:110) also describes the use of white under tail coverts in the courtship display of the Blue Reed-Hen (Porphyrio poliocephalus). The Virginia Rail (Rallus limicola) runs around the vicinity of its disturbed nest "with drooping wings" (Walkinshaw, 1937: 473), thus resembling the swanning of the coot. Nibbling occurs in the Water-Rail, Rallus aquaticus (Witherby et al., 1947:194).

Little comparison can be made between the calls of the various rails, especially as transcribed by a number of different persons. However, it is worth noting that the sexual dimorphism found in the voice of the American Coot is also known in both the Black Coot and Black Gallinule, and perhaps occurs in other species. Rüppell (1933) found a sexual difference in the voice and the syrinx in the Black Coot and noted a difference in the voices of the sexes in the Black Gallinule, but did not examine the syrinx of the latter species. Later, Grimeyer (1943) stated that the only reliable field differentiation between sexes in the Black Coot is based upon voice characters.

Injury-feigning.—The instinct that is so common among waterfowl and shore-birds to feign injury does not seem to exist in the coot. Not once in the several hundred times I have chased coots off nests or away from young have I seen any indication of injury-feigning. Nor have any references to this behavior in the genus Fulica been found in the literature. Perhaps this behavior is rare in the family Rallidae since the only unquestionable instances recorded are for the genus Rallus. Grinnell et al. (1918:287) and Kozicky and Schmidt (1949:359) report injury-feigning in the Clapper Rail (Rallus longirostris) and Witherby et al. (1947:194) report the same behavior in the closely related Water-Rail.

SUMMARY AND CONCLUSIONS

The strict territorialism exhibited by the American Coot is associated with an array of displays and calls. All anti-social displays have certain features in common, *i.e.*, the neck ruff and the prominent shield. These two features are supplemented by wing arching and the exposure of conspicuous white under tail coverts when more aggressive displays are required.

The response of other coots varies with their own internal state. If the

shield of an intruder is flat and its pugnacity at a low ebb, a call or at most a moderate display by the defending bird causes the intruder to retreat; if, however, the shield is swollen and the intruder is seeking territory, the defender uses the gamut of anti-social displays, even including actual combat, in its attempts to repulse the invader.

While each sex has a definite tonal quality to its calls, there seems to be a great deal of individual variation among birds of each sex. Certain of the notes seem fairly uniform throughout the population, *i.e.*, the alarm and growling notes, but the notes associated with normal activities vary from bird to bird, being similar only in sequence and mode of delivery.

The sexual difference that exists in the calls of adult coots makes it relatively easy to ascertain the sex of birds in the field. It is surprising that this difference in call notes of the American Coot has not been pointed out by earlier authors.

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Figure 2F is by Stephen A. Fenton and Al Jonez, of the Nevada Fish and Game Commission; all other figures are by the author (figs. 2A and 2B are reproduced from Kodachrome transparencies).

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