THE FRONTAL SHIELD OF THE AMERICAN COOT

BY GORDON W. GULLION

DURING the fall of 1949, in connection with a study of the breeding behavior of the American Coot (*Fulica americana*), several coots were trapped at Lake Merritt, in down-town Oakland, California. These birds were held captive on the University of California campus at Berkeley or, after various experiments, released on nearby lakes. The finding of swollen frontal shields on a large proportion of these coots in the fall led to a series of observations and experiments on the shield.

STRUCTURE

The frontal shield of the American Coot (and other coots of the genus *Fulica*) is a fleshy protuberance extending dorsocaudad onto the forehead from the upper mandible. Ridgway and Friedmann (1941: 41) say that "the rhinotheca or covering of the maxilla [is] continued upon the forehead, where it widens into a more or less gibbous or expanded plate or frontal shield. . . ." Speaking of breeding American Coots, these authors say (p. 213) that the "frontal shield [is] larger than in winter birds, dark reddish brown or chestnut. . . ." According to Coues (1903: 862), the shield "is said to swell in the breeding season after a shrunken winter state."

Callus.—The reddish portion of the shield (Fig. 1B) cannot truly be called the shield since it is not continuous structurally with the covering of the maxilla (see Ridgway and Friedmann, *loc. cit.*). It is not, therefore, comparable with the shields as defined for other Fulicinae (except perhaps *Fulica ardesiaca*, the Slate-colored Coot) and for the several genera of gallinules, reed-hens and water-hens. The reddish portion, or *callus*, is horny or corneous in texture and is distinctly an accessory to the shield proper, the latter being white and continuous with the rhinotheca of the maxilla in the American Coot.

Histology.—Frontal shields of eight coots were imbedded in celloidin. Transverse and longitudinal sections were made and the details that follow represent a composite picture derived from the study of these sections. The histological nomenclature follows Maximow and Bloom (1942).

The callus is a pigmented, keratinized layer, a *stratum corneum*, derived from the underlying epithelial elements. It is about 0.05 mm. thick. There is a sharp demarcation, both in color and structure, between the callus and the underlying cellular elements.

The cellular Malpighian layer underlying the callus is continuous with that covering the maxilla and comprises the true rhinotheca. It is of normal epidermal construction, resembling calloused portions of human skin (cf. Maximow

and Bloom, 1942: 337) and ranges from 0.085 to 0.141 mm. in thickness. The cells of the Malpighian layer, all of which are nucleated, are flat toward the surface but become more polyhedral towards the middle of the layer. These cells are connected to one another by distinct intercellular bridges. The innermost cells, which are densely packed, narrow, and columnar, are consistently and conspicuously vacuolated beneath the callus, but not vacuolated where the callus is not overlying. Dermal papillae containing both blood vessels and nerve fibers penetrate the germinal layer at regular intervals (about 0.05 mm. apart).

The dermis or corium is composed of very thick and dense connective tissue fibers and is, apparently, elastic in nature (hence accounting for the yellowish cast apparent in coot shields). Between these heavy fibers are masses of cells which serve to enlarge or flatten the shield. Data not presented here indicate that these may be chondrocytes. Towards the posterior end of the shield, the dermis is penetrated by bundles of smooth muscle and anteriorly the dense connective tissue is without the cellular aggregations responsible for variation in size.

Under the dermis is a layer of fine but dense connective tissue fibers, the periosteum, which is attached to and closely envelops the maxilla.

Size.—The shield (plus callus) varies in size, depending upon the physiological state of the bird. The swelling of the shield is the result of extensive vacuolation of the masses of cells between the heavy fibers of the dermis. The vacuolation commences close to the periosteum and progresses peripherally until distended cells immediately underlie the Malpighian layer.

The shield increases not only in thickness but also in length and breadth (Figs. 1C and 1D). Fresh growth of the callus is evidenced by growth posteriorly and laterally (Fig. 1B). The flat shield of non-breeding coots (Fig. 1A) is about 2.1 mm. thick, 4 to 8 mm. wide, and 4 to 10 mm. long. In breeding coots the swollen shield and callus (Fig. 1E) may be over 3.6 mm. thick, as much as 14 mm. wide, and up to 17 mm. long.

Development

Observations in the field and on the flock of captive birds have revealed certain basic facts about the development of the frontal shield in adult coots.

First, enlargement of the shield is closely associated with breeding activity. All breeding birds have a large shield, and furthermore, single, non-resident birds show a marked increase in shield-size on the wintering grounds in the one or two weeks prior to departure for their breeding grounds.

Second, birds permanently paired and defending territory throughout the year, whether resident or migrant, retain the enlarged shield as long as they remain paired and on territory. (For a more complete discussion of coot territorial behavior, see Gullion, 1950: 41–72).

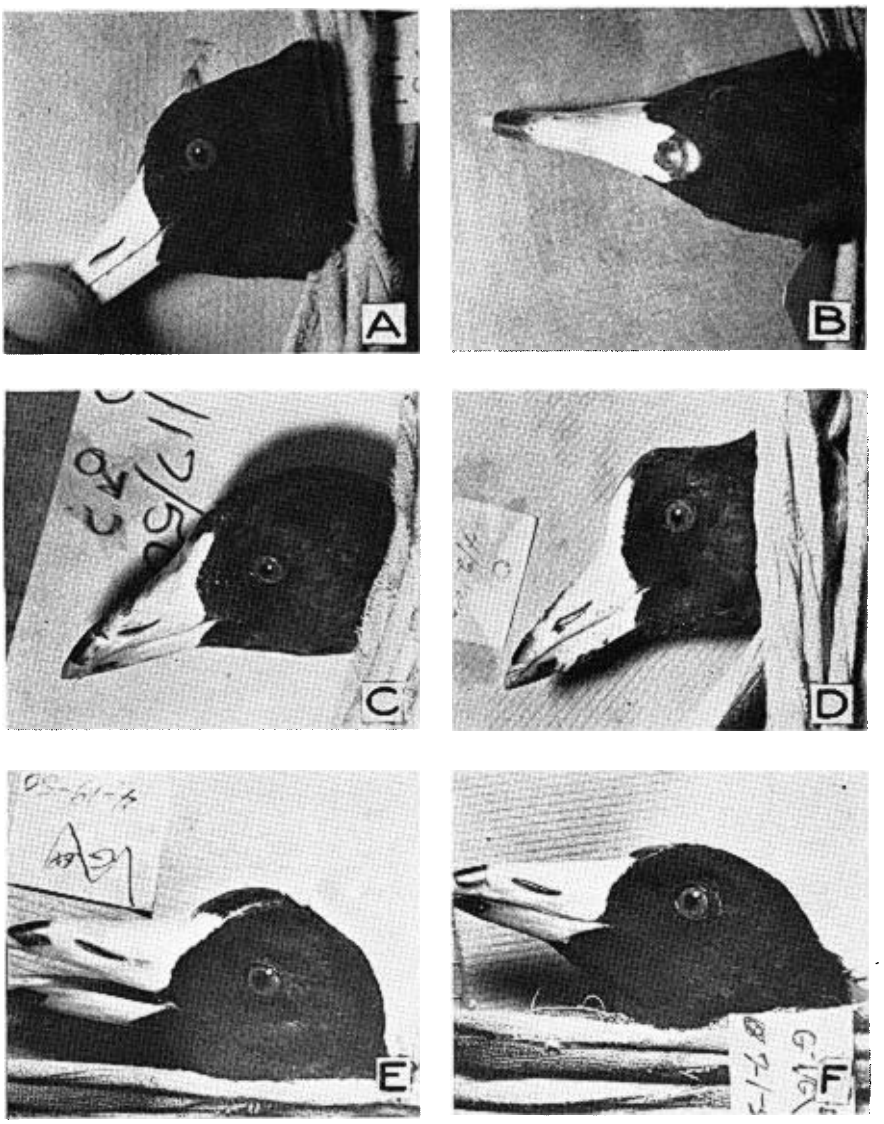

Fig. 1. Photographs of shield conditions in the American Coot. A. A flat shield, ♀ T97; B. New callus growth as it appeared 10 days after a testosterone implant, ♀ 79; the shiny portion laterally and posteriorly represents the new growth; C. ♂652 on the day of a testosterone implant, possessing a semi-swollen shield; D. ♂652 16 days after C was taken, and 7 days after attaining its full shield-growth; E. A naturally developed swollen shield on a dominant coot (♂T94) at the peak of breeding activity; F. The same bird as E showing the final subsidence of the shield about 2 months following the failure to establish territory and to breed.

Third, loss of territory and the reduction of breeding activity result in a decrease in shield-size and eventual regression to the flat shield characteristic of immatures in mid-winter.

Natural Control.—Perhaps the best illustration of shield-growth is that provided by the data on birds (4♂♂, 4♀♀) held in captivity (Fig. 2B). Birds in the flat condition (F, Fig. 1A) in mid-January progressed to the semi-swollen condition (SS, Fig. 1C) by early February and to the final swollen condition (S, Figs. 1D and 1E) by early March. I considered a shield flat when it was concave, semi-swollen when it was smooth, and swollen when a convexity was apparent. By March 4, a nest had been constructed and territorial behavior had begun. One captive female (♀ T00) displayed frequently and the approach of the breeding season was generally apparent. As in wild populations, courtship and territorial activity reached a frenzied peak in early April, and the shields of the captive coots were at their maximal size. Constant disturbance, plus crowding and lack of suitable habitat, however, precluded actual nesting. Breeding behavior then tapered off and was no longer evident after about May 12. Subsidence of breeding activity resulted in a decrease in shield-size (Figs. 1E and 1F).

That shield-growth precedes migration was indicated by observations in Berkeley's Aquatic Park, a salt-water impoundment on the Alameda County waterfront. No territorial or paired birds were present among the 100 to 110 coots wintering there during 1949–1950, and all shields were flat. By March 10, about one-half of the birds present were showing marked shield-enlargement and by March 24 the population had correspondingly decreased by about one-half. Most birds with swollen shields had departed, only three or four birds with swollen shields remaining behind. Of the 43 coots remaining on March 24, only four or five had flat shields, the shields of the others mostly being semi-swollen or a little further enlarged. Sixteen coots remained on March 29, all with either flat or slightly swollen shields. Seven were present on April 12, all with semi-swollen shields. All had departed by April 21.

Decrease in shield-size accompanying loss of territory was demonstrated by seven November-trapped Lake Merritt coots, selected for their swollen shields, and released on Lake Temescal, in the northeastern part of Oakland, in mid-December. By early February not one of the four surviving birds possessed a swollen shield, and not one was engaged in territorial activity. On the other hand, three pairs of territorial birds showed no regression through the winter and several captive birds were beginning to show gradual swelling in winter. Furthermore, migrant, paired coots at Lake Merritt, sporadically defending territories through the winter, also had enlarged shields throughout the non-breeding season. By March 26, the four transplanted birds were beginning to show shield-growth. By mid-April, two of the males had fully enlarged shields and were paired and on territory.

Subsidence of shield-size following cessation of breeding activity, as described above for the captive flock, has not been adequately observed in the field.

Experimental Control.—Between late January and the first of July, 1950, a series of sex hormone implants were made in seven birds (3♂♂, 4♀♀). The hormones, testosterone and estradiol, were implanted subcutaneously as pellets weighing about one milligram each. Figure 2A gives the individual records of each experimental coot.

Testosterone implants in both sexes, with one exception, resulted in a rapid growth of the frontal shield (Figs. 1C and 1D; and birds ♂T96, ♂652, ♂654, ♀653 in Fig. 2A). Maximum shield-size, once attained, remained constant so long as the hormone pellet was present, and in one case it persisted for at least one month after the pellet was removed. The one exception to this rapid growth was ♀79. A testosterone pellet implanted immediately following the removal of an estradiol pellet from this bird failed to induce shield-growth. However, another testosterone implant, made 54 days later, resulted in the usual rapid growth (Fig. 1B).

The results of the estrogen implants were not as spectacular as those of testosterone, nor were they in any way conclusive. The failure of two estrogen-implanted females to develop larger shields during the time that most of the control birds were doing so, suggests an inhibitory effect. However, one of these birds (♀77) began to show some increase in shield-size about forty days after the implant, and a female (♀81) with a naturally swollen shield, after receiving an estradiol implant, failed to show any evidence of regression for at least 49 days after the implant.

On the other hand, estradiol implants in two birds previously treated with testosterone resulted in abrupt decreases in shield-size. The shield of ♂T96 commenced immediately to recede from its maximum development at a surprising rate (Fig. 2A). The shield of ♀653 failed to respond for about twelve days, then receded at a rate comparable with that of the male.

Eight coots (4♂♂, 4♀♀) being held for other purposes under the same conditions and as part of the same flock were used as controls in these experiments. These are the same captive birds discussed earlier. Their shield-growths are shown in Figure 2B.

Gonad Activity.—Microscopic examination of testes revealed a direct correlation between state of gonadal activity and shield-size. Males with enlarged shields, killed in mid-winter, were found to have an extensive proliferation of the testicular interstitial cells. A great deal of spermial debris was present within the tubules of several birds. No spermatogenesis was evident.

Non-breeding males killed during the breeding season all possessed more or less enlarged shields, but in none was the shield greatly enlarged. Correlated with this was a general proliferation of the interstitial cells and a certain amount of spermatogenesis, although not as much as was expected for that season. Unfortunately, no breeding birds could be obtained for examination.

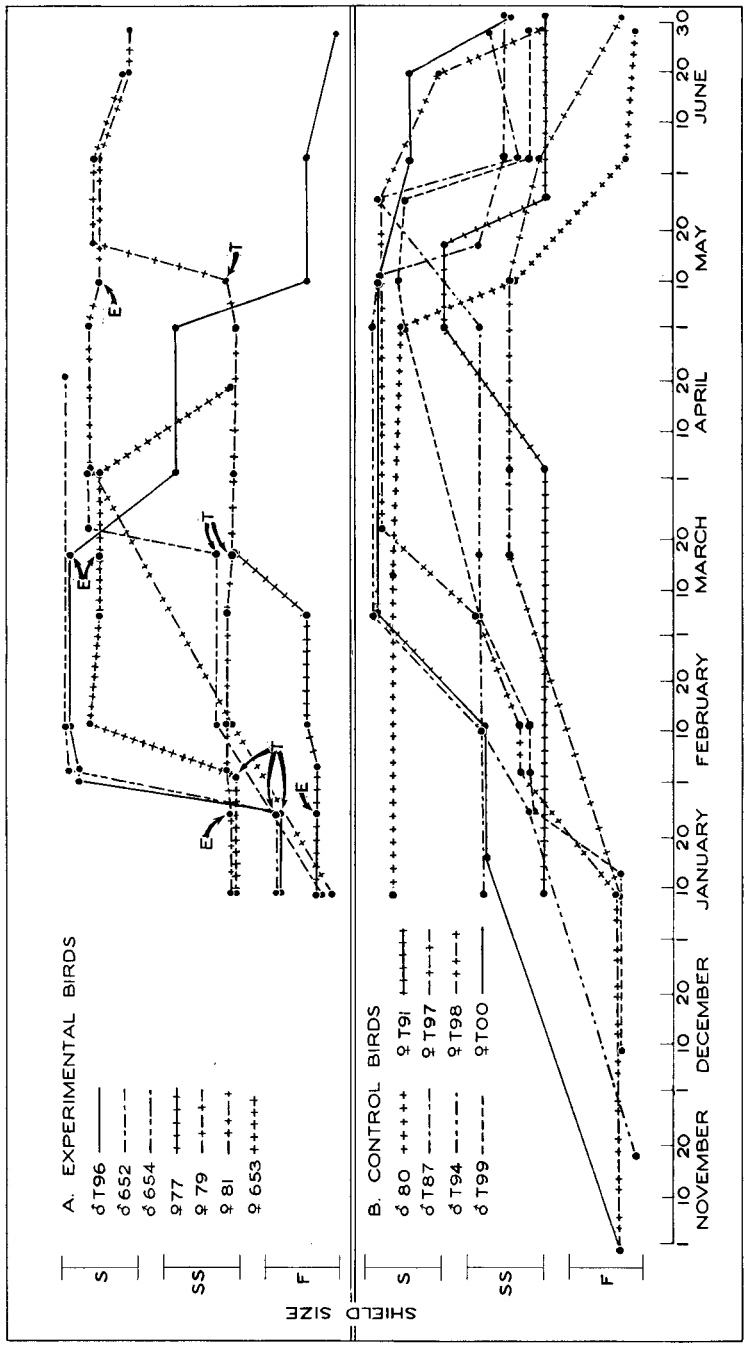

Fig. 2. Development and regression records of the shields of 15 captive American Coots. A. Records of experimental birds, showing the reactions following testosterone and estrogen implants (indicated by the letters T and E). B. Records of control birds held under the same conditions and as part of the same flock as the experimental birds.

The testes of males with flat shields showed no proliferation of interstitial cells and no evidence of spermial debris. The tubules were filled with large but inactive gonial cells.

In several females examined, no correlation could be detected between follicle size or general ovarian activity and the size of the shield.

Function of the Shield

Displays.—Observations have shown that the frontal shield functions in aggressive territorial displays of the American Coot, as discussed in detail elsewhere (Gullion, 1950: 13–27). The enlarged shield is normally prominent and birds engaging in anti-social displays erect the neck feathers behind the shield, forming a black background which further emphasizes the shield-size.

Recognition.—It is believed that paired birds are able to recognize their mates by the shape of the callus. I have recognized fifteen distinct callus patterns among the 130 coots handled in the course of this breeding behavior study (*cf.* Gullion, 1950: 33, Fig. 12) and there is so much individual variation among the general types that no two birds have identically the same callus-shape. In small populations an observer can identify reliably any bird at close range, on the basis of its callus-shape.

I have several times observed that, during pitched battles, a bird coming to the aid of its mate mistakenly attacks its mate. The attack continues until the mate turns about, thus revealing its callus. I also have observed that paired birds, defending the same territory, after being out of one another's sight for a little while, will often converge in a typically aggressive display until close enough to recognize one another, apparently by callus-shape, whereupon the aggressive display is replaced by a social courtship display.

Dominance.—Birds with enlarged shields maintain a dominance over coots without them, even though direct aggressive activity may be negligible. Since enlarged shields indicate either active or impending territorialism, birds lacking the swollen shields usually give wide berth to those with swollen shields, even though the latter may not be engaged in any display.

In connection with the hormone experiments discussed above, it was found that both males and females climbed from a low rank in the peck-order to dominance over their respective sexes at the same rate as their shields increased following a testosterone implant, thus agreeing with Allee's (1942: 160) conclusions on the effect of testosterone on dominance in birds. Furthermore, it was found that birds with artificially enlarged shields, when released in a wild population, obtained a distinct but momentary dominance over flat-shielded resident coots. However, these birds were unable to hold their dominant position. This is illustrated by the following experiment.

Two dominant males with testosterone implants and enlarged shields (♂652, ♂654) were released in territorial areas at Lake Temescal. Despite their ag-

gressiveness and dominance in the captive flock, they were at the mercy of the resident territorial birds. Even after fleeing from territorial areas, they were subjected to relentless attack and pursuit by non-territorial birds, something that was not experienced by a bird (♀ 653) released with a red painted bill.

It seems probable that shield-size serves initially to indicate a bird's social attitude to nearby coots, the swollen shield being indicative of an aggressive attitude. But shield-size alone is not sufficient: it must be supplemented by a pugnacious disposition and probably by a familiarity with home grounds. Although resident coots shied away momentarily, allowing the big-shielded newcomers an initial dominance, once it was realized that shield-size was not supported by an aggressive attitude, the residents turned upon the newcomers and drove them from the more heavily used parts of the lake.

Discussion

The exact substance leading to shield development is not known, but experiments with testosterone show that in both sexes the shield can be changed from the flat to the swollen condition, and behavior from the mild gregariousness of mid-winter to a highly pugnacious attitude in less than 10 days. It seems probable that a pituitary hormone, perhaps a gonadotropin, maintains an overall control upon shield-size, territorial behavior, gonad activity and migration, since all these functions may operate simultaneously.

It is of interest in this regard that the shields of breeding females are as large as those of males. Also, it was found that certain very old (to eleven years) banded migrant birds develop and retain through the winter knobbed, much enlarged shields although the birds may not be engaged in any territorial activity.

The ease with which the callus is altered in the North American Coot (*F. a. americana*) suggests that its development on this continent may represent an intermediate evolutionary stage between the non-callused shield of *F. caribea* and the callused shield of *F. ardesiaca*. At least four American Coots have been handled that had very rudimentary calli. One, in fact, had only a reddish spot on an otherwise white frontal shield.

Taxonomic Usefulness.—Ridgway and Friedmann (1941: 207) use callus-size in separating the race *F. a. americana* from *F. a. grenadensis* (Grenada American Coot) and *F. a. columbiana* (Colombian American Coot). For *F. a. americana* a maximum callus-length of 13 mm. is given while the second and third races are both stated to have calli 14 mm. or longer.

In contradiction, two experimental birds have exceeded this maximum (♂T96—12 x 15 mm.; ♂654—14 x 17 mm.) as has one of the control birds (♂T94—12 x 15 mm.). Bird ♂654, with the largest callus, still maintained its callus-size one month after the pellet was removed (68 days after reaching its extreme size), and coots have been seen at Lake Merritt with naturally

developed calli fully as large as that of ♂654.

If callus-size is to be used as a taxonomic tool for separating races, age of the individual as well as correlation between date of capture and the breeding season obviously must be taken into account in view of the amount of seasonal variation occurring in the callus. The shield and callus figured by Ridgway and Friedmann (1941: 206, Fig. 14) is only semi-swollen, equivalent in size and shape to that possessed by ♀ T00 while in non-breeding condition during late January and early February (Fig. 2B). By early March this female possessed a shield and callus much larger than that shown in the figure in question.

Other Rallidae.—Frontal shields are characteristic of a number of rallid genera. They are well developed in *Tribonyx*, *Gallicrex*, *Gallinula*, *Porphyriornis*, *Pareudiastes*, *Porphyrula*, *Porphyrio*, *Notornis* and *Fulica* (*cf.* Sharpe, 1894: 5–6). In addition at least the genera *Porphyriops* and *Amaurornis* have the posterior portion of the culmen distinctly expanded although not sufficiently to form a frontal shield.

Seasonal variation comparable to that recorded for the shield of the American Coot is known to occur in some other rallids. Witherby *et al.* (1947: 208) report a seasonal variation in the Black Coot (*Fulica atra*) in England. During the breeding season the male Water-Cock (*Gallicrex cinerea*) of the Orient "acquires a fleshy horn at the end of the frontal shield" which is absent in winter (Robinson and Chasen, 1936: 71). The Red-knobbed Coot (*Fulica cristata*) of Africa has an enlargement of the red knobs during the breeding season (*cf.* Priest, 1934: 31). Sclater and Salvin (1868: 467), in discussing the South American "*Fulica frontata*," allegedly a distinct species whose principal diagnostic character was a much expanded shield, concluded that the bird was in reality a Red-gartered Coot (*Fulica armillata*) "with the frontal shield very much developed," a statement suggesting that this species may also have a seasonal variation in shield-size.

Summary

The frontal shield plays an important role in the life of the American Coot. Paired birds recognize one another at least in part by means of shield-shape and -size, and the social behavior of birds can be predicted from the size of the shield.

Since territory defense and enlargement of the frontal shield are synchronous phenomena, it seems probable that both result from the same stimulus. Furthermore, the secretions governing shield-growth and territorial behavior are apparently also involved in migratory and sexual behavior.

Acknowledgements

The hormonal work was made possible by the generosity of the Schering Corporation of Bloomfield, New Jersey, which supplied a sufficient amount

of their "Progynon" (estradiol) and "Oreton-F" (testosterone) to one of my colleagues to make these experiments possible. Further thanks are due A. Starker Leopold, Alden H. Miller, Frank A. Pitelka, Oliver P. Pearson and Robert E. Bailey, all of the Museum of Vertebrate Zoology, for assistance, encouragement and criticisms in this study.

Literature Cited

Allee, W. C.
1942 Social dominance and subordination among vertebrates. *Biol. Symposia*, 8: 139–162.

Coues, Elliott
1903 Key to North American birds. Dana Estes and Co., Boston.

Gullion, Gordon W.
1950 The breeding behavior of the American Coot (*Fulica americana*) in the San Francisco Bay area, California. Univ. Calif., M. A. thesis (unpubl.).

Maximow, A. A., and W. Bloom
1942 A textbook of histology. Saunders, Philadelphia.

Priest, Cecil D.
1934 The birds of Southern Rhodesia. William Clowes and Sons, London, vol. 2.

Ridgway, Robert, and Herbert Friedmann
1941 The birds of North and Middle America. *U. S. Natl. Mus. Bull.* 50, Pt. 9.

Robinson, Herbert C., and Frederick N. Chasen
1936 The birds of the Malay Peninsula. H. F. and G. Witherby, London, vol. 3.

Sclater, P. L., and Osbert Salvin
1868 Synopsis of the American Rails (Rallidae). *Proc. Zool. Soc. London*, 31: 442–470.

Sharpe, R. Bowdler
1894 Catalogue of the birds in the British Museum. London, vol. 23.

Witherby, H. F., *et al.*
1947 The handbook of British birds. H. F. and G. Witherby, London, vol. 5.

Museum of Vertebrate Zoology, University of California, Berkeley