

6. There are favored travel routes to wintering grounds. These are indicated on a migration map, and the need for closely chained feeding and resting habitats along the principal river systems which the birds follow is emphasized.

U. S. Fish and Wildlife Service
Brigham, Utah

WILSON'S PLOVER IN ITS SUMMER HOME

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Plate 12

THIS paper is intended to give a tentative view of the life history of Wilson's Plover (*Pagolla w. wilsonia*), compiled from notes made during the past nineteen years. About two hundred visits have been made to the nesting areas during the spring and summer seasons, and many more in autumn and winter. The notes mention about one hundred and five nests, with casual references to many more. Unfortunately it has not been practicable to present more complete studies of particular family groups.

A few visits have been made to plover habitats in Duval County, Florida; Glynn County, Georgia; and Charleston County, South Carolina; but most of the time involved has been spent along the lower Savannah River, in that most interesting progression from cypress swamp through fresh, brackish, and salt marshes to the beaches bordering Callibogue Sound and the Atlantic Ocean.

MIGRATION

March 3, 1931, is my earliest spring record, but that was of only a single bird, and no noteworthy migration occurred that year until some time during the night of March 14-15, when numbers of the birds arrived. The first groups of migrants do not stay long but pass on to more northerly breeding grounds. One may find many birds, or none, at almost any time from the middle of March to the first of April, about which latter date our local birds arrive. The first large flocks of spring contain both sexes.

The peak of the nesting season is in May and June, although a few nests may be found as late as early July. The birds remain sparingly on their territories until late July. By August 1, there is a noticeable thinning of the numbers to be found on the beaches and mud flats, although they are still to be found until early September, and an occasional one may be seen until the middle of October. My

latest autumn records are of single birds seen on October 17, 1930, and on the same date in 1931.

My notes contain nothing on family relations after the nesting season—whether the adults of a pair stay together in autumn and winter, or whether young and adults migrate together or separately.

Apparently the birds of this coast do not withdraw very far in winter, for there are January records from northern Florida at the mouth of St. Johns River, about 115 miles south of the Savannah River (Howell, 1932: 219).

HABITAT

The most desirable summer habitat is in the areas with a high salinity, but it is unknown whether this is as a concomitant of open ground of a certain kind, of some particular food, or of another factor or combination of factors. Open ground that appears to have desirable physical characteristics but does not have an ample plover population extends along the river banks some distance inland beyond the present range of the plover. In this locality, the favorite nesting grounds are on the open areas of the sandy islands and on the edges of the dunes. Apparently they are also close to creek entrances with mud-sand flats. I doubt if a hard-packed beach of sand is suitable.

The nests are frequently placed close to a piece of drift-trash or similar low windbreak. Sometimes a nest is on a slight eminence but equally often it is not. One nest was in the heel of a lady's slipper that had washed ashore. On Turtle Island, South Carolina, several nests on the side of the island toward the sound, where open ground was scarce, were placed just under the edge of the overhanging grasses (*Spartina patens*) but still on the open sand. Usually nests are not near thick vegetation.

In the choice of habitat, whether feeding ground or nesting ground, shelter from view is not liked. This plover is largely a running bird, often running away from an intruder in preference to taking flight. To a great extent, it feeds by standing still until food is sighted, then running directly to it. I think it does not like mud flats where the ground is soft and running is difficult; neither does it do much wading.

In 1923, the plovers nested only on Oysterbed Island, which is near the mouth of Savannah River. In 1928, a pair took up residence near Field's Cut, five miles up from Oysterbed. In 1929, another pair settled a mile beyond that. By 1935, the species had reached the mouth of Habersham Creek, eleven miles from Oysterbed, while in 1939, three pairs nested on Hutchinson Island, opposite the city of

Savannah and fourteen miles inland from the 1923 range. In the spring of 1942, one or more pairs were engaged in establishing territory a half mile farther westward, although this habitat had been available but not used in previous years.

While the plovers were extending their range in this fashion, there were changes in the river and its banks. Dredging opened out the channel so that there was an increasing salinity beyond the plover's range; additional open areas suitable for plover nesting were formed; then vegetation rendered them unsuitable in places, and many other things happened which cannot be detailed here, even if they were all clear and measurable. The extension of the range inland is thought to be due to population pressure, as there has undoubtedly been a considerable increase in numbers since the early 1900's. It is unknown what increase in range there has been along the coast.

In the region about the river entrance (the optimum habitat, because well-populated when the species was fewer in numbers than it is now) there is now such a population that the nesting ground is filled as completely as it is likely to be, while fairly suitable ground remains unpopulated farther inland. This premise is based upon the observation that the individual plover territory does not seem to contract much under population pressure. In other words, the plover territories remain about the same size in the larger colonies as where there are few resident pairs.

Two birds (a male from well inside the summer-habitat area and a female from the inland edge) had their stomachs filled with the remains of fiddler crabs of the genus *Uca*, probably *Uca minax* in both cases. Probably some species of land crab furnish a considerable portion of the food of the species, as they are numerous, available at all times during the summer season, and range over all the plover habitat in this locality. Thinking that some species of *Uca* or *Sesarma*, or some combination of two or more species, might be a major factor in habitat determination, I made an attempt to plot the plover habitat against the range of the crabs. Years of experience along the river had fairly well outlined the places where each species of crab would be found. The results, however, were not definite enough to permit any conclusions. Howell (1932: 220) lists such other food as shrimps, crawfishes, scallops, beetles, bugs, and spiders. The plovers have been seen to run along near the water's edge and gather bits of food left by the swells. Perhaps the shrimps, scallops, and such things are gathered in this manner. Much food, such as beetles, flies, crickets, and the like, is available on the territory.

BEHAVIOR

In any consideration of bird behavior during the reproductive season, it must be remembered that there are often out-of-season or out-of-sequence rehearsals of bits of behavior—rehearsals that are relatively unimportant but which tend to confuse the picture. Some of the interpretations given here may be incorrect for that reason.

Pairing.—The formation of the pair takes place prior to territory establishment. Later, when the males are engaged in determining the territories, females may or may not be present, and do not seem to be involved in the encounters between the males. The copulation ceremony often takes place away from the nesting ground.

I think that, in the main, the foregoing paragraph is true, though it is not intended to assert that pairing is invariably done before territories are marked out or that it is completely disassociated from the establishment of territory by the male. Males will chase other males from the vicinity of the female in courtship, and they use certain behavior in both situations. Later on in the incubation period, the female takes an active part in nest defense, even to the extent of driving her own mate from the vicinity of the nest.

Courtship is initiated by the male, and consists in posturing, in scrape-making, and in the pursuit of other males in the vicinity of the female. The posturing is done by puffing out the throat so that the dark neck-band, both front and back, stands out like a ruff, and in puffing the feathers of the breast so that they stand out wider than the feathers of the upper parts. The bird sometimes stands erect, but it has a sort of running crouch when, with the feathers puffed out, it chases another male away from the female it is trying to impress.

In scrape-making as it is done in courtship, the male approaches the female, picks a suitable nest site, and settles into it as though preparing a nest hollow. He picks up bits of shell or small sticks and arranges them. If the female is uninterested and moves away, he follows and again picks a spot near her for more scrape-making. After the pair is formed and territory is established, a similar performance takes place in locating the nest. At that stage the female has accepted the male and goes to him when he settles in a possible nest site and calls.

Courtship has been observed here as early as the middle of March, long before the birds were settled on territory. Bent (1929: 257) noted courtship activities in Florida in the month of March.

In the literature there are accounts of courtship flight in other species of plovers. In the present species, I have seen no flight that could be described as ceremonial, either in courtship or in territory

establishment. In the latter performance, males will chase each other until they fly and circle about for some distance, soon to return to the disputed ground. It is behavior which is common to nearly all of the shorebirds in many different situations, and I have not been able to find any deep significance in it.

No evidence of courtship feeding has been observed. Lack (1940: 176) does not list the plovers among those groups normally indulging in this behavior.

Copulation.—When ready for copulation, the female postures before the male, often moving ahead of him if he turns away. She crouches and spreads her wings slightly. The male walks up behind her and, for a little time, perhaps a minute or so, marks time with a sort of 'goose step,' lifting each foot alternately forward and back in the same place. He sometimes moves up behind her with this step, then mounts her back, tramples for a minute or so, working his feet in among the feathers, and then takes hold of her head with his bill before copulating.

Territorial defense.—One typical territorial combat between males is worth describing in detail. It was quite apparent that the fighting was definitely over territory and not over a female or in defense of a nest, for there was no female near and no nest in the territory. On this day, June 9 (later in the season than the usual courtship and territory-establishment period), three males, one of which took no part in the fight, were on a slight, sandy eminence topped off by a knoll a few inches higher. Two weeks before, this ground had been included in the territory of another pair, and a brood of young ones had been hatched nearby. None of the three males was concerned with that territory and nest, for the pair was then escorting the brood of young ones some little distance away.

At the commencement of the fight, one male spread its tail and crouched as though in a nest. Each time it did so, another male would run at it, but after several such parries the displaying bird stood its ground and showed fight. Both birds then circled around over the sand. One of them would fly and run the five or six intervening feet directly at the other which would try to avoid it. One or more times a bird was knocked down in that way. The action was extremely rapid and hard to follow. After perhaps five minutes of this combat, one bird moved away about fifty feet and stopped while the victor stood on the knoll and uttered some loud *peets*. The third male stood for a time, then squatted a little and moved closer, only to be driven away. Each time the victor stood erect and used the

peet note from the highest point on the knoll. The bird that had been defeated in the fight stood quietly about fifty feet away and was not bothered by either of the others.

It seemed that it was the squatting of another male that released the pugnacity of the territory-holding male. One might question if this is exactly the same as scrape-making. It seems to me that it probably is the same, though possibly an abbreviated or conventionalized form of it.

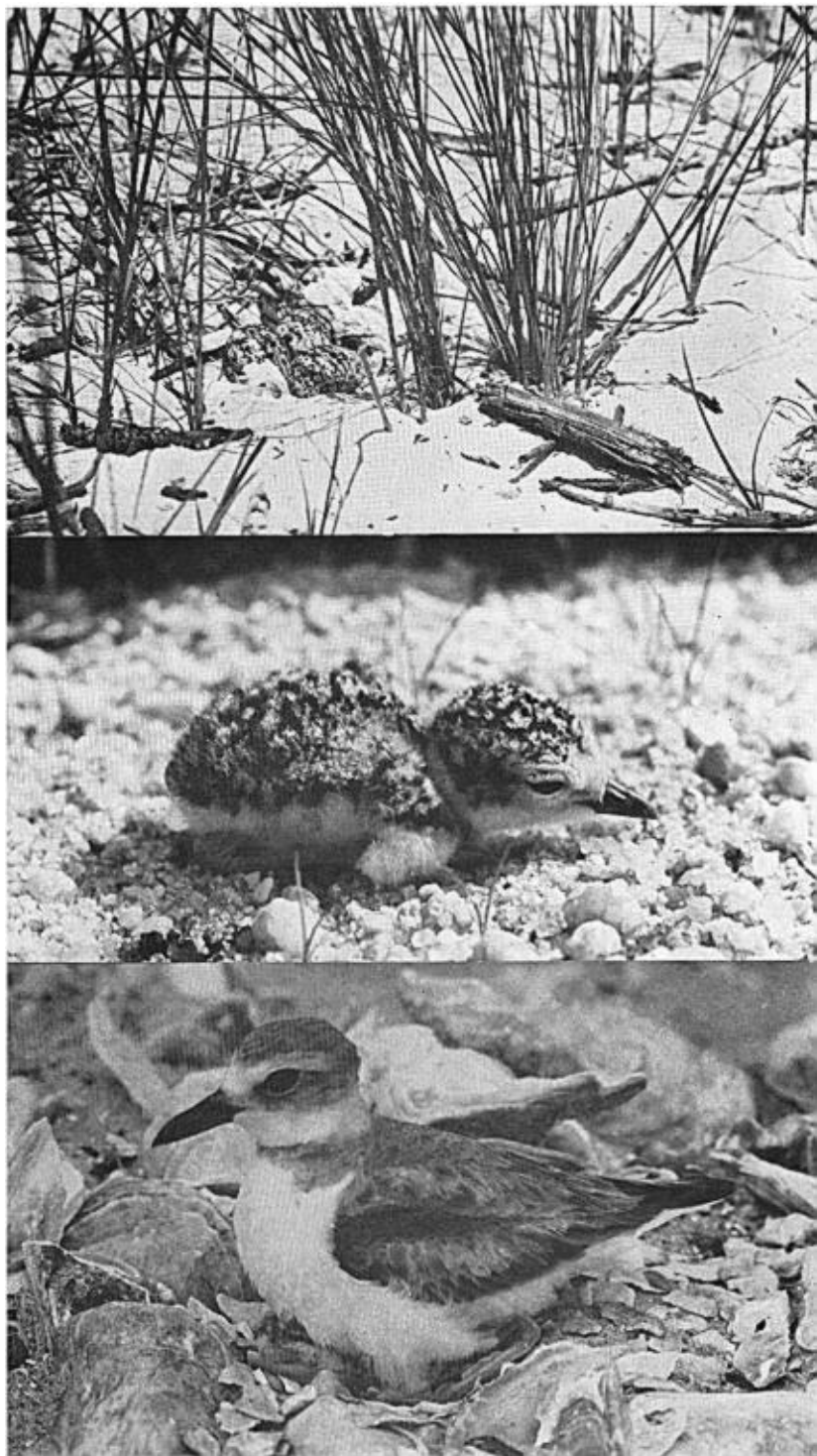
When a female exhibiting the injury-feigning behavior comes near a male, he is quite likely to run at her and drive her away. Her display is similar in some respects to the scrape-making of the male, and possibly it brings from him the same reaction that such behavior would if done by another male in courtship competition or territory establishment.

Palmer (1941: 48) has described the behavior of the Common Tern (*Sterna h. hirundo*). He thought it probable that sex recognition was dependent on the reaction of a bird when attacked by a male on territory. A male so attacked would either fight or depart, while a female would neither fight nor leave the territory. The male Wilson's Plover does attack a displaying male that either fights or leaves, but the sexually mature female spreads her wings before him and does not leave. We humans recognize the sexes of this species by the morphological character of the colored neck-band, but it is by no means certain that the male bird uses the same character. Nevertheless, I am unable to say what system of sex recognition is used by the species.

Two days after the fight described above, a male (probably the same one) defended the same knoll, even driving away a neighboring female and a male that merely came too close. I saw no sign of his mate.

One nest, at about the middle of the incubation period, was visited five consecutive times when only the female was present. On the sixth day the male also was present. The reactions of the female to my approach were the same every day. She came to meet me, circled over or ran nearby as long as I was within about 125 yards of the nest, but did not follow me beyond that distance. At the time there were no other plovers nesting in the vicinity, but after a few days another pair established themselves nearby and both were usually to be found in a territory which adjoined that of the first pair, about 150 feet from the nest. They joined the first female in nest-defense and ran through her territory with no protest from her or her mate, possibly because of my intrusion.

Where there are a number of plover nests in the vicinity, concern



WILSON'S PLOVER: (Upper), NEST IN *Spartina patens*. (Middle), YOUNG A DAY OR SO OLD. (Lower), ADULT COVERING TWO NEWLY HATCHED YOUNG AND ONE UNHATCHED EGG.

about an intruder tends to hold in abeyance the territorial jealousy of the birds, and a group will follow the intruder through the colony for some distance. In such a group, there are usually more males than females, which appears to indicate that the female is more likely to remain in the immediate vicinity of the nest, at least during the time of incubation. Although a plover territory is seldom much smaller than a circle roughly one hundred feet in radius, in one case eighteen birds collected nearby as I moved through a colony.

Some interesting information furnished by Mr. S. A. Grimes seems to bear out my belief that the female has a measure of dominance at the nest. He has watched the birds many times as they returned to the nest after being flushed, and has found their behavior always the same. After an intruder has passed near the nest and caused the birds to leave it, they soon move back into the territory and run here and there, while the female often feigns interest in a likely nest situation, much as though she were settling on the eggs again. After some time there, she runs at the male, putting him to flight, then turns and goes directly to the nest and settles upon it. Naturally the male is fully acquainted with the position of the nest. What other meanings this behavior may have, I do not know.

Selection of the nesting site.—After the pair is formed and the birds have settled on their territory, there is a 'nest-location' ceremony, if one may call it that, quite of the general plover pattern. It serves the purpose of getting acquainted with every ground feature of the territory, aside from any possible social value it may have.

On April 15, 1942, I watched a pair of plovers for nearly an hour. This pair had a territory about 150 feet in radius, and was without territorial pressure from the boundaries. There was no competition from any other plovers and the courtship (pair-formation) time was past for them. They stayed in the territory the whole time I watched them and were present the next day. Suitable habitat existed much farther out, but it was evident that the male had no intention of going beyond the set boundaries.

The male would puff the neck-ring and the breast feathers and run on ahead, much as in the courtship ceremony. He would choose a nest site and settle in it, lift his wings slightly, tip his bill and tail upward 30 degrees from horizontal, and utter a throaty note. The female would run to him at once, whereupon he would step out of the nest site, lift his wings slightly, tip his bill downward, and give a soft note that, at fifty feet, sounded like a distant dove or frog. If the female did not step into the place he had selected, he would soon

run on elsewhere and repeat the performance. The female always ran to him when he chose a spot and called. Once, when she stood facing away from him, about two feet from the site he had picked, he stepped up behind her, trampling as in the pre-copulation ceremony. When she did not crouch, as does a female ready for copulation, he stopped trampling and went on to another place. Once she stepped into the site he had selected, and partly crouched. He spread his wings and started to tread, but they did not copulate at this time. The next day both were quietly resting on the territory, and when they flew off to the adjacent marsh to feed, I found a well-prepared nest hollow.

One possible significance of scrape-making in courtship is that it may be a substitute for the offering of food as practiced by those species given to courtship feeding. The origin and meaning of the practice of courtship feeding is still obscure, but in many species it is an integral part of the pairing ceremony and continues well into the incubation period. The Black Skimmer (*Rynchops nigra*) male brings food to his mate on the nest, and often mounts her back for a moment of wing-waving before he leaves. The Least Tern (*Sterna antillarum*) offers food to his mate before copulation, and giving it appears to be an indispensable part of the pre-copulation behavior. Similar behavior has been reported in many other species.

Pettingill (1937: 238) has written of the male Black Skimmer offering a stick to his mate, apparently in lieu of food not at hand. The male Wilson's Plover does not, to my knowledge, ever bring food to his mate, but he does offer a nest site in the scrape-making performance. Obviously he cannot bring to her the nest he likes, so must go near her and pick the best one available there. After the pair is formed and the female follows her mate, he can then offer her, in turn, the various suitable nesting places in his domain, and if she accepts them it is an indication that she is ready for the actual mating. On the other hand, the squatting of a male in another's territory causes the owner to defend it, because he will not tolerate any offer of seduction there.

Incubation and care of the young.—The female appears to take a large share of the incubation duty, but the male is sometimes found on the nest. One male hovered eggs that were hatching, but was shier of my camera than was his mate. How the female obtains food while incubating is not certain, but there is no evidence thus far of the male bringing food either to his mate or to the young, so probably she leaves the eggs long enough to hunt her own food. If fiddler

crabs are a staple article of diet, she need not go far nor stay long at a time. Prior to the laying of the eggs, the pair leaves the territory together for near-by feeding grounds where crabs, crickets, and similar food are plentiful.

Forbush (1929: 472) thought that the young of the Piping Plover (*Charadrius melodus*) were never fed by the parents, but were able to obtain their own food within twenty-four hours after hatching. The young birds have an egg-tooth that disappears very quickly, perhaps in less than a day after hatching. They leave the nest very soon, and probably do not return to it after it is once abandoned.

Mr. S. A. Grimes has written me that he observed a young plover run out of the nest to hide in the pickleweed whenever the brooding bird left it and an unhatched egg, but when the parent bird returned to brood, the chick crept out of the weeds and returned to her. I once watched a nest with two newly-hatched young and a pipped egg, nearly an entire Saturday afternoon, but the young ones made no attempt to leave the nest. Sometimes the male returned to brood them, but oftener the female came. On Sunday morning, the third bird was still struggling to get out of the egg. About noon we left the nest for an hour and, on returning, found that the three young birds had left the nest. Even the egg shells were gone. It appears that the act of leaving the nest is at the insistence of the parents.

The sturdiness of a day-old plover is remarkable. It stands up on its long legs, looking very like its parents, and runs rapidly to get away from an enemy. Like most precocial birds, the young plovers have a 'crouch-concealment' that is quite effective.

One litter was hatched on an island of habitat, that was surrounded by high marshes and that was several times as large as the two territories it then contained. The family stayed there for at least twenty-one days after hatching. By that time the young birds could fly very well and, when followed, would fly off to the shelter of the marsh-grass edge, while the parents moved on in the open before me. Open ground on which to run and to learn to feed and fly is of much value—perhaps a necessity—to the young birds, particularly so if it is true that they must find all their own food.

Injury-feigning and other behavior.—The injury-feigning behavior is very commonly seen in the colony at any time after there are eggs in the nest. The display is very like that of the Killdeer (*Oxyechus v. vociferus*) pictured in Nature Magazine (1940: 153–154). The female Wilson's Plover utters a guttural note, spreads her tail, and beats one or both wings on the ground as she creeps or runs along. She

abandons the pose in one place to run or fly to another and repeat. For some time it seemed that this was done only by the female, but more careful observation proved that the male also does it, though in lesser degree. This behavior, which probably follows an inherited pattern, appears to be followed whenever and to whatever degree the bird desires. There is a vague resemblance to the scrape-making of the courting male, to the display of a male in territory establishment that sets off a fighting reaction in another male, and to the posture of the female ready for copulation, yet I have no reason to think the resemblance more than fortuitous.

Certain acts are associated with definite procedures and with fairly definite reactions in other individuals, and may be described rather recognizably. Some of these acts have appeared to be used in more than one situation, although there is a chance that slightly different displays have been confused. Four such acts are listed here. More ample descriptions will be found elsewhere in this paper.

1. The courtship posture.—This is used by the male in the pair-formation and in territory establishment.

2. Scrape-making.—Three uses of this by the male have been noted. First, it is used in pair-formation; second, in nest-location on the territory; and third, it appears to incite territorial fighting when done by a male in territory claimed by another male. In this latter use, an abbreviated or conventionalized form may be used.

3. Trampling—Used by the male before copulation.

4. Injury-feigning.—Performed mostly by the female, sometimes by the male, at any time after eggs are laid and until the young are fairly well developed.

Only three notes can be listed in like manner, with some certainty of the situations in which they are used:

1. The clear *peet* of the male appears to be the plover song, the declaration of territory established, though it is also given by a male solicitous over the safety of young, both on the ground and awing.

2. The low 'dove' note used in the nest-location behavior, evidently a call of the male to the female.

3. A harsh guttural note used in injury-feigning.

I regret the lack of exact information of the uses of these and other notes.

After reading the accounts of the behavior of other species of the family Charadriidae, it appears that much of the courtship behavior is quite similar throughout the group. Several accounts are quoted here from different observers, as compiled by Bent (1929).

Jourdain (*in Bent*, p. 145) recounts that the Lapwing (*Vanellus vanellus*) is a social bird, several pairs of which nest close to each other. They have a scrape-making act in the ritual of courtship. The males have encounters much like the territory fights of the present species.

Townsend (*in Bent*, p. 218) describes a posture used by the Semipalmated Plover (*Charadrius semipalmatus*) in its courtship, which might well have been written of Wilson's Plover.

The action of the Ringed Plover (*Charadrius hiaticula*) advancing toward a male as described by Selous (Jourdain, *in Bent*, p. 230), seems comparable to the treading described in this paper. Stanford (*in Bent*, p. 230) writing of the same species, tells of posturing by the male that is very similar to that of the present species, and also cites scrape-making.

In the case of the Piping Plover (*Charadrius melodus*), Tyler (*in Bent*, p. 237) tells of similar posturing as well as scrape-making.

No one could give much time to this species without realizing that it is an excellent subject for study. Its life from earliest spring until the young leave the nest, is spent out in the open. The sexes are easily distinguished, and it may be found nesting in colonies where its reaction to others of its kind may be observed, as well as in isolated pairs where complications caused by too close neighbors do not exist. One needs only a good pair of eyes, perhaps aided by binoculars, plus a high resistance to the sun, to see much that goes on in plover life. Elaborate blinds or equipment usually are not required.

LITERATURE CITED

- BENT, ARTHUR C.
1929. Life Histories of North American Shore Birds. Order Limicolae (Part 2). U. S. Nat. Mus., Bull. 146.
- FORBUSH, EDWARD H.
1929. Birds of Massachusetts and other New England States (2nd ed.), vol. 1. (Boston, Mass.)
- HOWELL, ARTHUR H.
1932. Florida Bird Life. (New York, N. Y.)
- LACK, DAVID.
1940. Courtship Feeding in Birds. *Auk*, 57: 169-178.
- PALMER, RALPH S.
1941. A Behavior Study of the Common Tern. *Proc. Boston Soc. Nat. Hist.*, 42: 1-119.
- PETTINGILL, OLIN S., JR.
1937. Behavior of the Black Skimmer at Cardwell Island, Virginia. *Auk*, 54: 237-244.
- 1231 East 50th St.
Savannah, Georgia