

THE WILLETS OF GEORGIA AND SOUTH CAROLINA

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THE New World genus *Catoptrophorus* has been placed between *Heteroscelus* and *Totanus* in the American Ornithologists' Union Check-list of North American Birds (1957). There is but a single species, divided into two subspecies, *semipalmatus* and *inornatus*. The current edition of the Check-list does not provide common names below the species level, but it is convenient, and should confuse no one, to continue to use the terms "Eastern Willet" for *C. s. semipalmatus* and "Western Willet" for *C. s. inornatus*, although the terms "coastal" and "inland" would be more appropriate.

Some confusion as to the status of the two forms on the western Gulf coast has existed in the past. Ridgway (1919) considered that the breeding form on the coast of Texas was *inornatus*, although he gave one breeding record for *semipalmatus* from Texas. Griscom and Crosby (1925:440, 531), aware of this confusion, collected breeding specimens from the vicinity of Brownsville, Texas, which Jonathan Dwight examined and identified as *semipalmatus*. However, they considered that the breeding birds from northeast Texas were probably of the western form. Subsequently, Bent (1929) concluded that all the coastal breeders were *semipalmatus* and that *inornatus* breeds only inland in the western states and the Canadian provinces. This view has been concurred in by others, and the ranges are so indicated in the 4th edition (1931) and the 5th edition (1957) of the A.O.U. Check-list. Ridgway's (1919) measurements and descriptions need to be revised to accord with this latter determination of the distribution of the two subspecies.

The ranges of these two subspecies as quoted from the current Check-list are:

C. s. semipalmatus—"Breeds in southwestern Nova Scotia (locally) and from southern New Jersey and Delaware south along the Atlantic coast to Florida; from extreme southern Texas (possibly Tamaulipas) eastward along the coast of Louisiana, the islands off southern Mississippi and Alabama, to the west coast of Florida; also locally in the West Indies (the Bahamas, Grand Cayman, Beata Island, St. Croix, Antigua).

Winters locally along the Gulf of Mexico coast (Tamaulipas, Texas, Louisiana, Florida), on the south Atlantic coast from Virginia to Florida, and in the West Indies (Bahamas, Greater Antilles); south to Central America (rarely on the Pacific side), Venezuela (Margarita Island), British Guiana, and northern Brasil (Pará).

Casual north to Newfoundland and Prince Edward Island."

C. s. inornatus—"Breeds locally from eastern Oregon, Idaho, central Alberta, southern Saskatchewan, and southern Manitoba south to northeastern California, western Nevada (Douglas County), central Utah, northern Colorado, western and northern Nebraska (rarely), and eastern South Dakota; formerly in western and southeastern Minnesota and Iowa. Recorded in summer south along the Pacific coast of México to Panamá and Ecuador.

Winters locally from northern California (Humboldt Bay) south to the Galápagos

Islands of northern Chile (Arica, Iquique); also from South Carolina to Florida, along the Gulf of México in Mississippi, Louisiana, Texas, and México, and around the Caribbean from Central America to northern Colombia.

Migrates in spring chiefly along the Pacific and Gulf coasts and through the interior; in fall, over the spring route but also spreading to the Atlantic coast."

Simply stated, typical *semipalmatus* breeds along the Gulf and temperate portions of the Atlantic coast of the United States, and *inornatus* is an inland breeder in at least eight western states, and three of the Canadian provinces. Both of these races have wide although interrupted ranges. Present knowledge gives little light on the migration orbits of the local populations, and their relationships. There has been no modern systematic study of the genus *Catoptrophorus*, as done by Pitelka (1950) for the genus *Limnodromus*.

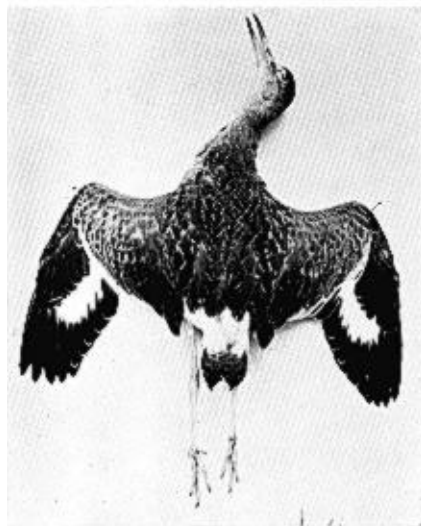
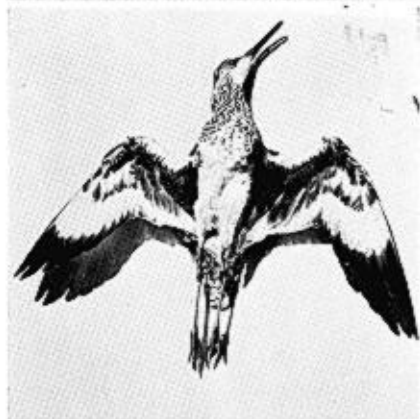
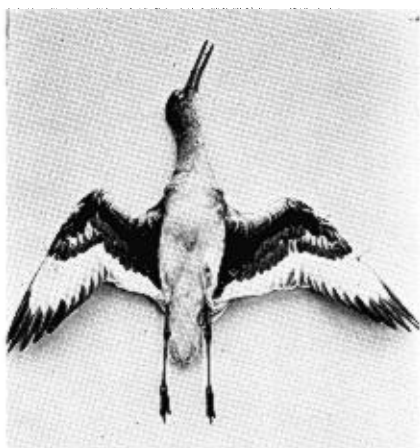
The present work deals mostly with the breeding habits and habitats of Eastern Willets of the coast of South Carolina and Georgia, but both subspecies must be considered, because both regularly occur in this region. The ranges as given in the Check-list are incorrect for this region, and need revision. The Eastern Willet arrives in late March, breeds and leaves in June and July. I have been unable to find any specimen from August to mid-March. Sprunt and Chamberlain (1949) state, as regards South Carolina "No winter specimens have actually been taken but this Eastern subspecies undoubtedly winters occasionally."—a rather ambiguous statement. Migration in any species of bird is seldom total, including all members of the population, and if an occasional Eastern Willet does remain in South Carolina over winter, the fact is of little moment to the population at large.

It may be that a critical study of the specimens from the Gulf coast will show that *semipalmatus* is not a common winter resident there since Burleigh (1944 and in litt., 1961) stated that he did not find a single individual during his eight winters on the coast of Mississippi. There are few such definitive accounts for most observers lump the subspecies together, even though they can be readily distinguished in the field.

The range of *inornatus*, as given in the Check-list, also needs to be revised, for this subspecies is present locally in Georgia and South Carolina in fair numbers all year long. I have collected about 40 specimens of both subspecies and in each case *inornatus* was in the gray plumage shown on Fig. 1, top, and not at all like the speckled *semipalmatus* (Fig. 1, center) or the juvenile of that form (Fig. 1, lower). The juvenile *semipalmatus* (Fig. 1, lower) was taken on 30 July. Its juvenile plumage, while not entirely grown, is sufficiently distinct to be obvious in the field. It would not have molted again before

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FIG. 1. (TOP) *C. s. inornatus*, adult male, 21 March 1962 ("smoky-gray" plumage). (CENTER) *C. s. semipalmatus*, April 1962 (breeding plumage). (LOWER) *C. s. semipalmatus*, female, 30 July 1962 (incomplete juvenal plumage).



leaving in the fall migration. I do not know what the plumage of the Eastern Willet after the postnuptial molt is like.

There are a few data suggesting that there are differences in timing of the breeding Willets of the south Atlantic coast. In the Savannah area the peak of the spring migration is in late March, and the nesting season from late April to June.

Stewart and Robbins (1958) give the peak of spring migration in Maryland as 25 April to 15 May, and the nesting season from mid-May to late July—a lag of about a month in 6 degrees of latitude, or about 360 miles.

The late D. J. Nicholson, the veteran oologist of Orlando, Fla., once asked me why he could find Willet nests at Matanzas Inlet (St. Augustine) in late March, while on Amelia Island (Fernandina) about 50 miles to the north, he could not find nests until late April.

These data are scant, but the inference is that there is some difference in the breeding schedule. Considering the relatively short season of gonadal sufficiency, I think of the possibility that these birds comprise different populations, in which free gene flow may be as effectively interrupted as by a mountain range, or any other natural barrier.

My acquaintance with the Willets began in the 1920's and has continued whenever possible ever since. The area most thoroughly covered is about the entrance to the Savannah River, with some time spent from the mouth of the St. Johns River in Florida, to Charleston, South Carolina. From 1959 through 1962 special attention was given to the breeding birds in the Savannah area. In 1959, the Willet nesting region was visited 50 times between mid-March and the end of June; in 1960, 30 visits were made; in 1961, 58 visits; and in 1962, 81 visits.

A previous paper (Tomkins, 1955) gave a résumé of the nesting schedule, and contained a graph showing the egg dates according to the experience of the late Gilbert R. Rossignol from 1907 to 1937, and my own data from 1923 on, a continuous record in the same locality for nearly 50 years. Later records show no significant changes.

Bent (1919) probably summarized most of the important information published before that date. One valuable paper has been published since on the Eastern Willet, but nothing extensive seems to have been published about the nesting behavior of the Western Willet. Vogt (1938) spent a few weeks with several pairs of breeding Willets at Fortesque, New Jersey, in 1936 and 1937. He was much interested in their behavior, particularly territoriality, according to the viewpoints then current in ornithological literature. He spent much time in a blind watching a few pairs, and he seems to have known little of the prenesting behavior. He did not stay until the young hatched. His birds ap-

parently fed and nested on the same territory. The birds I have known have a feeding range separate from the nesting location.

Nearly every account of this species, no matter how brief, mentions that it is a nondescript sandpiper-like bird until it lifts its wings and displays its white spaces. Vogt says, "this writer was first impelled to study the Willet through curiosity as to the biological significance of the Willet's striking wing pattern, which is invisible when the bird is at rest, and most striking when it is in flight. . . . Here, it seemed was a clear cut problem." His final conclusions only offer some suggestions as to its function as a Lorenzian "releaser," furnishing nothing new except that he did try to interpret the meaning of the white wing pattern, but reached no definite conclusion.

I, too, am unable to assign any unqualified purpose to the white in the wings, but will suggest some possible uses:

- a. species recognition in mixed flocks of shorebirds,
- b. the pattern may be stimulatory in courtship. The wings are extended and vibrated in precopulatory behavior, on the ground and in the air. This is also done during copulation.
- c. distraction value when flushing from the nest.

But is it necessary for all such bright patterns—there are many among the shorebirds—to have absolute function and meaning? May not certain genetic changes, neither grossly favorable nor unfavorable, ride along, a package deal so to speak, with those of a more definitive effect?

MIGRATION

Our breeding Willets arrive quite regularly between 14 and 20 March. Both sexes arrive together. They seem to arrive in small groups, and the entire local population does not appear simultaneously. They seem to arrive at night. In the earlier years when my home was in Willet territory, I always heard them first in the middle of the night. In 1961 Dr. George W. Sciple saw the first groups of the season on the morning of 16 March, as he drove to work.

Eastern Willets passing to and from more northern breeding grounds, do not generally migrate through here either in spring or fall. An occasional flock has been seen to pass high overhead in spring, but these are rare. The flight ceiling of the local birds is 500 feet or less. If night migration is the general rule, it is possible that birds passing through would not be seen, but some flocks of birds resting on the beaches should have been found. I am inclined to postulate a migration route at sea.

Some of the early spring migrants are already separated from the main group into pairs, while others are actively seeking mates. Some pairs have been first found on the precise nesting territory of a previous year. Other small groups may be found on beaches which will not contain nesting territories.

The spring migration and the postbreeding migration (I dislike to call it "autumnal" migration because it takes place in late June and July) are in synchrony with the waxing and waning of the gonads. Specimens collected soon after arrival (with one exception) had no supply of fresh subcutaneous fat, merely a small supply of tough yellowish fat such as is found the year around. On the other hand, the birds of late June, while still behaving as though young were concealed nearby, had considerable accumulations of recent fat.

It is interesting to speculate on this matter of energy-producing fat. It is hard to believe that the precise amount of fat would be produced to bring the migrants to one locality with none left over. Does this mean, then, that the spring birds have a short migration, or one that is accomplished in short stages? Or does the postbreeding migration cover a much longer distance? And what determines that the egg-laying time is from late April to early June? The Eastern Willet, breeding from Nova Scotia to Tamaulipas and the West Indies, must encounter much greater extremes of temperature than are found in the Savannah area. Food is not a limiting factor, for the small crustaceans preferred by the Willets, are available here for at least 10 months of the year. It explains nothing to call it a "biological clock."

When our Eastern Willets arrive in spring, their slim testes are from 7.5 to 9 mm long. In late April and May they are 16 to 18 mm in length and about 13 mm in width. By late June, or soon after the hatching of the young, they have shrunk to 4 to 6 mm long, about the size in the winter season. They will then soon depart on the postbreeding migration. This short season of gonadal activity precludes the production of more than one brood of young—a common thing among scolopacine birds.

HABITAT

The salt marshes of the coast and the terrain around them furnish the chosen habitat of the Eastern Willet during its brief stay in spring and early summer. Now and then a pair will nest a little farther upriver where the marshes might be called brackish, but not frequently. For nearly 20 years I lived along the river, much of the time on floating dredges, etc. that covered the area well. I walked the beaches, waded in the marshes, and explored every creek, great and small, and never saw more than a half dozen pairs of Willets away from the saline region in that time. There were none in the extensive freshwater marshes.

It is not the lack of food that limits the range, for the species feeds largely upon the fiddler crabs of the genera *Uca* and *Sesarma*, and probably other crustaceans. *Uca minax* is abundant along all of the muddy riverbanks up to the edge of the river swamp at the inland edges of the freshwater marshes,

far beyond the range of the Willets. Nor does adequate nesting cover seem to be a limiting factor.

The salt marsh is a unique zone in many ways. Its vegetation is distinct, there are no amphibians, many of the birds are committed to life there, and there are many endemic invertebrates—crabs, shrimps, marine worms, etc. It is rich in species, some of them present in great numbers. Largely unspoiled by man, it is nearly a primitive wilderness. In the Savannah region the salt marsh covers a wider band than anywhere else on the southeastern coast of the United States, perhaps because of the tidal range, which averages 7.5 feet in the Savannah area, and is often much higher during the spring tides.

According to Oney (1954) the coastal region of Georgia contains about 308,177 acres of salt marsh, roughly 0.9 per cent of the area of the state. It is a guess, and only a guess, that the breeding Willet population is not greater than two or three pairs to the square mile of this area. Nothing offers a clue why geophysically similar freshwater areas of the East contain no breeding Willets (or any wintering ones) at all.

The dominant higher plant of the wet salt marsh is a cord grass, *Spartina alterniflora* which forms dense bands of vegetation from about mid-tide range up to the flatter "marsh table" where it blends into other vegetation. Below the *Spartina* belt the receding tides bare extensive mudflats, live oysterbeds, and sandbars. Much of this area is punctured thickly with the holes of fiddler crabs, burrowing shrimps, etc., greatly increasing the total exposed area and the retention of water, with a corresponding increase in animal life.

The feeding habitat of the Eastern Willet is here in the salt marshes, not in the dense vegetation but on the oysterbeds and mudflats, the sparsely vegetated marsh table above mid-tide, and around the edges of the marshes. Sometimes they feed on the beaches.

The nesting habitat is on slightly higher ground near the marsh or the beach, usually above the reach of the tides but vulnerable in times of extremely high tides.

The eastern end of U.S. Highway 80 is on Tybee Island, Chatham County, Ga., close to the Atlantic Ocean. The area I have worked most thoroughly in recent years, is along this highway from Tybee Island across Lazretto Creek and the salt marshes about 6½ miles to Bull River. I estimate about 100 pairs of Willets nest there. The population has been quite stable for many years. The main part of the Willet population is concentrated in the eastern 2½ miles with the rest thinly scattered over the remainder. They nest along the sides of the road (even with much automobile traffic passing within a few feet), on parts of an old railway bed, and on some sand and shell banks from road construction. The nesting grounds and the feeding grounds are in general separate. Some food is picked up near the nest sites, but not the major part.

VOICE

The voices of our breeding Willets are loud and strident, and may be heard long before the bird comes in sight. They are full of small nuances, seemingly dependent on the nervous excitement of the bird at the time. Most of the calls fall into three categories to which some semblance of use can be assigned. The best known is the *Pill-will-willet* call which gives the bird its name. It is sometimes given in two syllables, usually in three, sometimes in four. It seems to be connected with territory, *i.e.*, the presence of the mate, whether on nesting territory or elsewhere. Often it is a challenge to another male. It is usually used by the male, although Vogt (1938) reports it as sometimes given by the female. This call is heard commonly day and night during pair formation, somewhat less so during incubation, and occasionally while escorting young in the marsh. I have never heard the Western Willet give this call in this locality. Dawson (1923) writes of the migrating Western Willets in California, "I have besought these passing birds a hundred times to say *willet*, but they have refused." However, Bent (1907) describes the nesting of the western subspecies in southwestern Saskatchewan, and clearly tells that their notes sounded "like *pill-will-willet*," and Taverner (*in* Roberts, 1932) recognized the call on the breeding grounds in the west.

The second call, a sharp *Kleep* or *Klip* is an alarm call that both sexes repeat incessantly when any intruder nears their territory. It varies in intensity and rapidity. Sometimes when an incubating bird flushes, this call approaches a scream.

The third recognizable call, a plaintive *Phwee-hoo*, rising on the first part, falling on the second, appears to be a summons from one of a pair to the other. One bird may alight on a pole or wire, call quietly or loudly, and the mate soon appears.

When the newly hatched young are separated in the grass, they have a thin wiry call which cannot be heard very far. It presumably serves to keep the family together and to inform the adults of the location of the young. It is only heard at that time, and if the young birds when a little older have any other call, it has not been recognized. More fieldwork could profitably be done on this matter.

PRENESTING BEHAVIOR

For about three weeks or more after arrival, and before egg-laying the Willets gather in flocks in open places in the marsh and engage in courtship behavior. I have been unable to determine just what sets off these gatherings or ends them. A flock will be noisy and active in one place and then begin to leave, only to settle down in an equivalent place somewhere else. Even though many are paired upon arrival, and though some pairs go at once to a location where there has been a nest in other years, still at times they join

the courting flock. Although this species comes under the influence of the tidal rhythm—as much of the feeding is done on the low tides, and the birds must withdraw from the marshes when they are covered with water—these gatherings are not entirely correlated with the tides, and the groups gather at various times, even after some eggs are laid. At such times the nesting territories are vacant. These social gatherings may be desirable to stimulate physical and psychological conditioning for successful nesting. There is some similarity to the “leks” used in communal courtship by the Ruff (*Philomachus pugnax*), the American Woodcock (*Philohela minor*), and certain grouse, among others.

Two opposing tendencies seem to be in dynamic balance: (1) the flocking or gregarious tendency, effective all year long is centripetal; (2) there is the territorial spacing, which is in general centrifugal. Similar tendencies, in apposition, may be found in many species, particularly the water birds.

It follows naturally that the Eastern Willets select nesting sites around the periphery of the courtship area, which is itself unsatisfactory for nesting. This logically brings up the hypothesis that the breeding population of Willets is not evenly spread over the available nesting habitat, but consists of a series of flock groupings, centered on particular courtship areas, leaving vacant or thinly populated habitat. My field experience indicates that this does occur. It would be more readily noticed with a scant population, and less so where the population more nearly filled the available habitat.

The earliest arrivals in spring often appear to be paired, staying together or flying off together. There are also triangles, two males competing for the attention of one female. On one occasion, 3 days after the first spring arrivals were seen, two birds made a number of circuitous flights, coming back each time to land on one spot of suitable nesting terrain. Each time they landed the male attempted copulation. This male which was collected had testes slim and about two-thirds maximum length. During the prenesting period many courtship flights take place. Some of these are bisexual, others clearly competition between males. The frequency of these male bouts and their continuation for several weeks, suggests a slight excess of males in this local population. In no case, however, have three birds been found in amicable association on the nesting grounds. On the communal courtship-feeding grounds the scene is too confused for interpretation. It may be that an excess of males furnishes a social stimulus which leads to satisfactory nesting.

Competition between males may come to actual combat on the ground. Two birds will spar at each other much as young roosters do, and one may grab the other by the mandibles close to the head and throw it down. The female takes no part, but will often squat on the ground, perhaps a sign of readiness to mate. A pair may be standing quietly near the nesting territory. A male *pill-*

willets not far away, and the resident male immediately answers in kind and takes flight to give chase, while the female may or may not squat for a moment. The two males circle around, *pill-willeting* incessantly until the intruder leaves. Later in the season, when several pairs with nests nearby have been protesting my presence, if one male *pill-willets* it gets a quick response from another with perhaps a short chase on foot, but combats are rare then. The birds are monogamous and usually stay together. If either one flushes from the nest, the mate soon appears and both *kleep* loud and long.

Vogt tried to distinguish the sexes by size, but finally had to depend on behavior. He only collected one bird. From the weights and measurements of about a dozen breeding birds I have collected here, it is clear that the female is slightly larger on the average, but the sizes overlap so much that the only criterion in the field is the behavior.

In precopulatory display on the ground, the male standing behind the female lifts and extends his wings and vibrates them through a very short arc, conspicuously displaying the white in them. He also does this during copulation. A similar display is seen when two competing males in flight shorten the wing arc and vibrate the wings rapidly. This is probably the behavior called "Spottying" by Vogt, because he saw a resemblance to the flight of the Spotted Sandpiper (*Actitis macularia*). The designation does not seem particularly apt to me, because the scaling flight of the Spotted Sandpiper is intermittent, while that of the Willet is continuous. I prefer to use the term "Wing-waving." On the ground the arc of wing movement is so short that there is no lifting effect. In the air, either in forward motion or hovering the arc is somewhat greater. In the air the performance blends into and out of the normal flight. On the ground the Wing-waving is not easily confused with any other performance.

TERRITORIALITY AND NEST SITE DEFENSE

To the male, territory has three aspects:

- a. In the prenesting time and perhaps later, territory is where the female is, whether on the nesting site, or out in the wetter marsh area. He defends it physically against other males, and by clamor against other intruders.
- b. During incubation, it is also where the female is—on the nesting grounds.
- c. In postnesting time, it is with the young that are hiding in the marsh, although this is somewhat of a flock reaction.

The female appears to share in the latter two situations and perhaps also in the first.

If one goes into an area with numerous Willet nests, he is attended by protesting birds all through it. By marking some of the birds, it was found that each pair would follow an intruder only a hundred yards or so, and was then replaced by another pair. There is no actual defense of the nest, as far

as I could see, just a lot of clamor. The old Negro saying is applicable, "He fight wit he mout." Toward other species of birds there seems to be no animosity. Gull, tern, Dunlin, plover, all are simply ignored. Wilson's Plovers and Least Terns, as well as some passerines, nest only a little way off, but they are not pursued or troubled. In this particular area there are no hawks during the nesting season, and behavior toward raccoon, feral dogs, and cats, was not observed. When a Willet stalks through the tern territory it is dive-bombed by these pugnacious sprites, but the Willet simply bobs its head and goes on. Rarely, a Willet in the vicinity of nest or young, will walk around with drooping wings, perhaps coming back toward the intruder. This has some vague resemblance to a distraction-display ("Injury-feigning," "Cripple-display") but it would be a rash observer who would so name it.

The parental pair-bond appears to dissolve about the time the young birds are developing in the marsh, and the "mobbing" of an intruder takes on the character of a group activity. It is not unusual to find 20 or 30 birds over one marsh area, loudly protesting, then to return an hour later and find a similar group very noisy elsewhere.

NESTING SITE

Because the male follows the female, often with spread tail showing much white, in the prenesting days, it is logical to assume that the female chooses the nest site. There is no scrape-making as in the Wilson's Plover (*Charadrius wilsonia*) (Tomkins, 1944), where the male selects possible nest sites and makes scrapes, to be followed by the female who finally selects one. This is unlike some of the passerines, the Mockingbird (*Mimus polyglottos*), some of the icterids, etc., wherein the male arrives first, establishes territory, and accepts whichever female comes along.

The nests are made on the ground. Many are well concealed in short thick grass, others are partly concealed, while now and then a nest is placed out on the open sand or the dead oystershells with as little concealment as that of a Least Tern. A nest on oystershells is concealed by the "disruptive pattern." Those on open sand are not so protected. There is no indication that one is chosen over the other. Generally all of the sites are within commuting distance of the salt marsh where most of the food is obtained.

The nests are simply constructed, mostly of grass stems bent down to make a thin floor (Fig. 2). One nest on open shells had a well-built rim of dead grasses that must have been brought at least 100 yards, but another not far away had no foreign material at all. At old Fort Pulaski, on Cockspur Island, one nest was placed in the grassy lawn, an area of about 4 acres, completely surrounded by the high brick walls of the fort. The only egress on foot is through the arched sallyport, with gates that are closed at night, and with

numerous human beings passing through at all hours the fort is open. One nest on Turtle Island, South Carolina, was on a dense floor of drift sedge, with a few inches of water underneath.

Many nests are so near the high water mark that an abnormally high tide will flood them out. Fortunately, storm tides are rather rare during the nesting season. It is not uncommon to find the bottom of the nest wet, either from rainwater or tidal water. One bird was flushed from a full clutch of eggs in one of the normal heavy showers of summer, and the eggs were found to be in water an inch deep. The birds continued to incubate these eggs for a few days after the rain, but the nest was later abandoned.

Normally Willet nests are at least 200 feet apart, although I once found two nests with a paced interval of 42 feet. One of these nests was an early one and the other much later, which may explain the tolerance of the owners. Intervening shrubbery 3 or 4 feet high may reduce the horizontal spacing to some degree. Nests are not usually placed in thick shrubbery or in any location where the birds cannot fly in and out.

EGG LAYING AND INCUBATION

The Willet is a determinate layer (as are most of the Charadriiformes as far as is known). It lays a certain number of eggs and no more, even if some of the earlier ones are removed. It follows that some mechanism probably limits egg production, but what or how is unknown. The infrequent sets of three may be caused by the loss of one of the normal clutch, perhaps to a predator, or by one of the eggs being laid adventitiously elsewhere than in the nest. I once found such an egg, still moist, and laid without vestige of a nest, and seemingly never returned to.

Alexander Sprunt, Jr., in a letter to Vogt told of more than one female using a nest, and of finding as many as eight eggs in one nest. He did not elaborate on his reasons for the belief that this was the work of more than one female. This must be a rare occurrence. I have been finding Willet nests since 1923, and have never found more than four eggs in any nest. The late Gilbert R. Rossignol, an active oologist from 1907 to 1937 found only two sets of five in that time. Rossignol wrote Arthur T. Wayne of finding a set of five, and received the following answer, dated 31 May 1916, "I have no doubt at all that the set of n/5 Willet you took were *all* laid by the *same* bird. But *five* eggs are very rare and I have taken five only twice."

The eggs are laid at intervals of 1, 2, 3, or even 4 days. Eggs may be laid in the forenoon or in the afternoon, perhaps even at night. A set of fresh eggs weighed 157.2 grams, and the average weight of three summer females was 242 grams. So the female produces about 65% of her own weight in eggs in a relatively short time. The eggs are large and four are about all that a

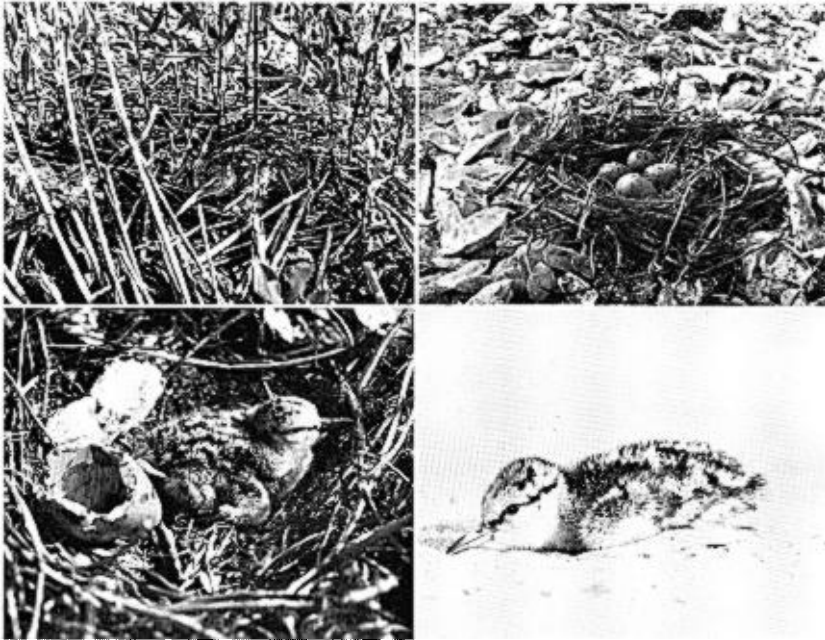


FIG. 2. (UPPER LEFT) Typical concealed nest. (UPPER RIGHT) Atypical nest, not concealed. (LOWER LEFT) Newly hatched young, with eggshell, showing the characteristic breakage of normal hatching. (LOWER RIGHT) Young Willet, about 2 days old. The plover-like bill and the down pattern, characters which may not be evident in dried specimens may be seen clearly.

bird can cover. Both birds are known to share in the incubation duties and neither has a vascular brood patch. One nest contained two eggs of Wilson's Plover in addition to a full clutch of Willet eggs. After some of the Willet eggs hatched, and the birds abandoned the nest, I opened the plover eggs and found that they contained nearly full-term embryos.

In only one case have I known of eggs being laid in the same nest, following destruction of the first set. This nest had a full clutch of four which were destroyed by a mower after the clutch had been completed at least 11 days. Eight days later there was one egg in the nest, and 3 days after that (or 11 days after the first set was destroyed) there were four eggs. The nest was not followed through to hatching. In another case, three eggs disappeared one night, and the fourth on the following night. About 3 days after the eggs disappeared the male of this nest (who had been marked by putting paint pigment on the grasses that hung over the nest) was seen copulating with another bird nearby, and it was seen in the locality for several days afterward, but did not stay long enough for a new set of eggs to be hatched. The

place was searched carefully, but no second nest was found, and the old one was not used.

According to general understanding, the incubation period is "the elapsed time between the laying of the last egg in a clutch and the hatching of that egg when all hatch" (Nice, 1945). In an earlier account (Tomkins, 1932) I reported the incubation period as 24–25 days, based on only one clutch. Subsequent observations have shown from 22 (possibly 21) to 29 days. The reason for this variation is not at all clear. It is generally thought to be a matter of varying parental attentiveness, but there is some evidence of another reason. In several instances I have found that the adults have left the nest after one or two chicks hatched, and upon opening the remaining unhatched eggs, I found that the embryos were in different stages of development, indicating the possibility that incubation was started before the clutch was complete.

One clutch of Willet eggs was weighed in the field, 13 times, from completion of the clutch until they hatched 29 days later. The accuracy of the weights was not particularly good, due to the constant breeze in the field, but at the start the average weight per egg was 39.2 grams, and when near hatching 34.7 (a loss of 4.5 grams). A single newly hatched chick from another nest weighed 22.5 grams. This chick had been hatched long enough to dry off.

THE YOUNG

The eggs may hatch in the morning, afternoon, or perhaps at night. It takes about 2 days for the chicks to break through the shell, and the opening is consistently on one side toward the larger end (Fig. 2 lower left). The parents remove the eggshells from the nest, sometimes only a few feet, often to some distance. As soon as a fairly large hole is made, the chick begins to breathe atmospheric air, and its breathing can readily be seen. It has a shell-breaker ("egg-tooth") on *both the upper and lower mandibles*, but these are shed very soon. One chick although still wet had struggled out into the vegetation on my coming. As I put it back in the nest with the rest of the brood for photographing, the shell-breaker came off and was lost in the oystershells, but the scar was still visible. At hatching the chicks seem to have considerable vision, and are homoiothermal to quite a degree. The mild climate may be of assistance in this matter. They are well covered with down, which is buffy in some, but plain gray in others. They are quadrupedal at first but soon develop strength in the legs and can stand up and run. At hatching, two young birds had tarsi 30 mm long, about 50 per cent that of the adults. The legs are quite necessary to their sojourn in the marsh, and develop faster than the wings. Another young bird, perhaps a week old, had tarsi 47 mm long. Within a couple of hours (in the daytime at least) after drying off, they leave the nest and it has no meaning to either young or old after that. There is no evidence

that they are ever fed or brooded by the parents. It has been impossible to determine much about the possibility that the young birds are brooded at night, or in cold weather. I wonder how the young birds are cared for in the colder climate of Nova Scotia.

An important bit of Willet behavior that may have been overlooked for some time was first noticed in 1959, and later observations indicate that it is of regular occurrence. If all the eggs do not hatch at the same time, the first young birds leave the nest, and the parents go with them abandoning the rest of the eggs, which would hatch within a day or so. In 1960, I ran an experiment with four nests, using two for each test. Nest A was a few days earlier than nest B. The eggs had been numbered as soon as they were found. Two eggs from nest A were traded with two eggs from nest B. In each case the adults left with the first young to hatch. I opened the other eggs and found well-developed embryos in each.

There is no question that this trait may seriously affect the nesting success, and the replacement rate. I can see no way that interference of any kind has caused this to happen. In an altricial species, where the young are cared for in the nest, the effect may be negligible.

The adult Willets attempt to get the young into a nearby marsh as soon as possible. Mrs. Alva Hines of Hiltonhead Island near the outer beach has a shop near a tongue of *Spartina* marsh that reaches into the island. In 1961 she saw adult Willets escorting young birds straight down the hard road past her shop and into the marsh. Whenever a car came down the road, the young Willets would hide, resuming their trek when all was clear. In 1963, I saw much the same thing, with one young bird moving across a four-lane road from the nesting area on an old railway bed, to the marsh across the road. The adults shrieked and flew back and forth, but the young bird apparently moved under its own volition, for there was no sense of guidance in the frantic calls and flights of the parents.

The young birds may be seen now and then, but they are furtive and rail-like in behavior until they reach the flight stage. The adults leave the region before the young are able to go with them, and I do not know much about the autumnal migration. Two young birds, able to fly but without fully grown primaries could usually be found in a particular isolated marsh. If disturbed they would fly away a quarter mile into the larger marsh. If I came back an hour later, they would be found again in the home marsh.

POPULATION AND NESTING SUCCESS

In the region I have described the Willet population has been stable for many years. There has been some shifting of populations, following the disturbance of road building, or the growth of vegetation, but it has taken place slowly and has not hampered the species to any noticeable degree.

In the 1961 season, 19 nests were found, marked, and visited as often as possible. The nesting success was of a low order but exact data cannot be furnished, because it was not certain just what had happened to some of the nests. In 1962 a smaller area was worked more carefully. Sixteen nests were located and definite data obtained concerning them. The 16 nests contained 56 eggs—they would have contained 64 eggs with full clutches. Two nests were abandoned with eggs in them; seven eggs were left unhatched in the nests; in some cases the eggs simply disappeared; and it is believed that 11 young birds hatched and left the nests. To maintain its numbers the local Willets would need to have a long reproductive life if this success is typical.

Some of the egg loss may have been from predators. Several eggshells in early to middle incubation stages were found on the mudflats, punctured by some avian predator. One nest was probably broken up by a raccoon. Another nest was hatching one afternoon but the next morning it contained only the legs of two young Willets. A few feet away on the mud were the fresh tracks of a raccoon and an otter. One cloudy morning a gray rat snake (*Elaphe obsoleta quadrivittata*) was caught in the act of trying to swallow a Willet egg. This and other species of snakes, as well as raccoon, otter, and mink are all common in the area.

FOOD

The food of the Eastern Willet consists largely of the small crabs that are so abundant in the salt marsh. About a dozen stomachs have been examined, without attempting to make a detailed analysis, and all contained many chitinous fragments, mostly of the genera *Uca* and *Sesarma*. Three species of *Uca* (*minax*, *pugnax*, and *pugilator*), and two species of *Sesarma* (*cinerea* and *reticulatum*) abound in the area, as well as many other small crabs. One bird killed on the road contained the torso of *Sesarma reticulatum*. In the field the birds have been seen to eat some species of *Uca* frequently, sometimes not far from the nest. One bird regurgitated a pellet, about 8 mm in diameter which was round, firm, and was composed of chitinous fragments. No sand has been found in any stomach. Some Willets will feed along an outer beach, where no marsh crabs occur. None of these has been collected and what they feed on there is unknown. A young Willet, perhaps a week old, had a small gastropod, probably *Littorina irrorata*, in its stomach. This snail is abundant in the salt marsh, as are many other species.

SUMMARY

The ecology and some of the ethological traits of the breeding Eastern Willets in the vicinity of Savannah, Georgia, has been under observation for some years, and are recorded in some detail.

Minor mention is made of the occurrence of the nonbreeding Western Willets in the same locality.

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