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Preliminary Notes on the Behavior and Ecology of the Eastern Willet¹

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In 1936, the period from May 23rd to June 20th, and in 1937, the period from May 1st to 9th, were devoted to a study of Willets Catoptrophorus s. semipalmatus (Gmelin), in the salt marshes near Fortescue, N. J. Though much more work remains to be done, it is believed that data of sufficient interest were gathered during the 204 hours of actual field work to justify the presentation of a preliminary report at this time. It should be emphasized, however, that all conclusions advanced are tentative, and that discussion and interpretation have been limited because the data presented are admittedly only a fraction of what further study will disclose. The paper is published now to make available such facts as were noted, and in the hope other observers—especially amateur bird students—will initiate comparable studies. The writer might remark, parenthetically, that in ten years of bird study no other field work even began to offer as much in excitement and satisfaction as did the hours devoted to outwitting, and trying to understand, these birds.

Fortescue was chosen for the study because of the large number of Willets that nest conveniently near lodgings.

The habitat of the birds, extending many miles along the east side of Delaware Bay, is a broad expanse of salt marsh still, fortunately, for the most part unditched. Like other marshes of the region, it is dominated by large areas of cord grass (Spartina patens), cow grass (S. alterniflora), with interspersed patches of spike grass (Distichlis spicata), samphire (Salicornia sp.), narrow-leaved cattail (Typha angustifolia) and, in the marsh ponds, widgeon grass (Ruppia maritima). The marsh is cut, in many places, by tidal estuaries and is bounded, on the west, by the low dunes and sandy shores of Delaware Bay.

Avian associates of the Willets include Black Ducks (Anas rubripes); Black-crowned Night Herons (Nycticorax n. hoactli); Marsh Hawks (Circus hudsonius); King (Rallus e. elegans), Virginia (R. l. limicola), Clapper (R. longirostris crepitans), and Black Rails (Creciscus jamaicensis stoddardi); American and Fish Crows (Corvus brachyrhynchos and C. ossifragus); Red-wings (Agelaius p. phoeniceus); Meadowlarks (Sturnella magna); and Sharp-tailed (Ammospiza c. caudacuta) and Seaside (A. m. maritima) Sparrows. Migrating Snow Geese (Chen hyperborea atlantica) and Brant (Branta bernicla hrota) improve feeding conditions for the Willets (see Section X).

Concerning the behavior of the Willet, little is known. Recent studies of shore-birds by Huxley, Tinbergen, Pettingill, and others, and the flash-pattern of the wings (closely resembling that of *Chettusia gregaria*), interested the writer in making observations of this accessible, and strikingly marked, species. The older literature concerning the bird is summarized by Bent (1929). As this paper was being written, two more items appeared (Stone, 1937; Tomkins, 1938).

My thanks are due to the American Museum of Natural History for the loan of a mounted Willet, used in studying sexual behavior; to Dr. G. K. Noble for bibliographic assistance; to Mrs. Margaret Morse Nice, Dr. Ernst Mayr. Dr. N. Tinbergen, and Mr. D. S. Lehrman for criticism and suggestions; to Mr. Richard H. Pough and the Rev. Benjamin B. Brown, for much appreciated transportation; and

^{1.} Awarded the Linnman Prize for Ornithological Research in 1938.

to Mr. A. D. Simmons for his superb photograph of a flying bird (Fig. I). The New Jersey Game Commission kindly granted essential permission to collect a small number of Willets; only one was taken.

I. TECHNIQUE

The major part of the time used in field work was passed in blinds. Seventeen days were devoted, in 1936, primarily to one nest, within twenty feet of the blind. In 1937, studies were made from a blind the floor of which was six feet above the marsh; this elevation was most helpful and alone made possible the observations on which territorial findings are based. This year two pairs were closely, watched. Throughout the two periods the behavior of several score of birds was under superficial observation. The 1937 blind was situated between two marsh ponds where, the previous year's observations had demonstrated, Willets were likely to be present in numbers; it was erected early in April, before the return of the birds, and was so casually accepted by them that they constantly fed almost beneath its floor. The birds became so accustomed to my presence that often they would not flush as I passed to and from the blind.

Incubating birds, in 1936, were extremely shy, once they had been flushed. Although a large wooden tripod was left near a nest for three days, the addition of a small camera, before the observer entered the blind—distant about seventy feet—kept the bird from its nest during a long period, and it immediately flushed at the click of the shutter. This nest was not the one watched over a long period, though the blind had been in position about five days. It is doubtful whether a picture could have been secured without the remote control device. By contrast, Seaside Sparrows, feeding young, accepted the presence of the tripod and camera within a few moments, and permitted the taking of more than thirty pictures nearly as quickly as the threads could be pulled. In both cases there was equal disturbance of nesting cover.

Ordinarily, when the 1936 blind was entered, it was kept between the observer and the nest, and the incubating birds did not flush. The noise made by walking through the grass seemed not to disturb them.

In 1936 one attempt to mark individual birds was successful. Ordinary artists' oil colors were squeezed onto the edges of nests, after the method reported by Johnson (1935); and one bird which, subsequently collected, proved to be a female, wore a conspicuous red smear on her breast.

A mounted Willet was used, as in earlier studies (Noble and Vogt, 1935), to test the reactions of birds in the field. Bausch and Lomb 7x35 binoculars, and a Leica camera were used. Plate I shows the distribution of territories, location of blinds, etc.

II. METHODS OF SEX DETERMINATION

So much of the paper is concerned with the relations between the sexes that methods of sexing these birds, which seem to exhibt no sexual dimorphism, should be explained at the outset. As a matter of fact, discrimination between the sexes proved surprisingly easy; the marked female collected had been provisionally identified as to sex days before she was shot. Size gives the first clue; though measurements of a series of skins in the collection of the American Museum of Natural History showed an overlapping, in the field the female frequently may be known by her larger size; surmises as to sex, based on size, were repeatedly checked against behavior in three pairs, and the sexes verified. This criterion, alone, however, is not entirely trustworthy since birds appear differently in various lights, and their bulk—as determined by compressed or expanded feathers—varies with the weather and the birds' emotional states.

Attacks, in defense of territory or mate, are by the male bird only, though the female will bluff occasionally; similarly, only the male responded—with an attack reaction—to the mounted bird. This attack reaction extended into the incubation season and the male could be depended on to fight the mount. When the male was incubating, as well as before incubation had begun, the female was tested with the mount—and never attacked.

The female is more sedentary in her habits than the male; she seems not so given to making wide flights, as he, and when feeding on the territory she often confines herself to a smaller area than does the male. The female of the 'east pair'—so-called from the relation of its territory to the blind—did most of her feeding on a space (see Plate I) of S. patens not over 100 feet square.

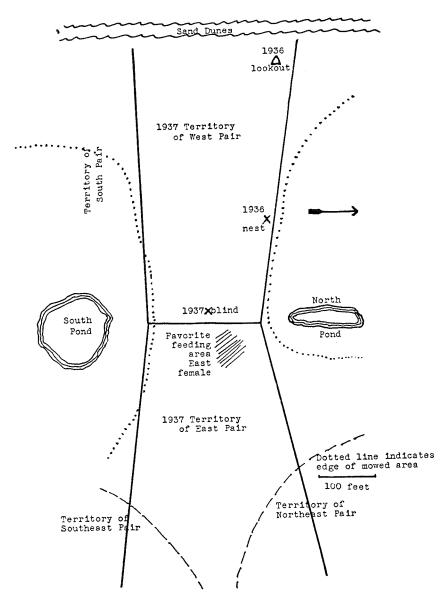


PLATE I. Schematic representation of Willet breeding areas, distances estimated.

The female is careless about territorial bounds, when feeding, and will sometimes trespass, unmolested. The male, on the other hand, is visibly uneasy when he trespasses, and, except at the beginning of the breeding cycle, he is usually driven off at once.

These differences were often observed in the pair whose female was collected, and they were repeatedly checked in 1937 by watching copulations, after I had reached a decision as to which sex was which.

These sex differences render it relatively easy, in markedly territorial birds like Willets, to follow the actions of individual birds; they are first assorted and separated by their innate drive to claim a territory and much of the time the observer need solve merely a two-bird puzzle.

III. VOICE AND POSTURES

"The real difficulty in the investigation and the recording of the behavior of higher animals," writes Konrad Lorenz (1935), "consists of the fact that the observer himself, as a subject, is so similar to the object of his observation, that a true objectivity cannot be achieved." In making the observations on which this paper is based, a deliberate effort was, at all times, made to subordinate the factor of human psychology and to reach conclusions, as far as possible, on the basis of cause and effect. Meaning is attributed to observed phenomena only when certain reactions have been observed to follow certain wellmarked stimuli. The field student of bird behavior faces a problem much like that of the palaeontologist who finds a femur, humerus, and maxilla and with these attempts to approximate the whole animal. Rare, indeed, is the researcher who, like Mrs. Nice (1937), has fragments accumulated by almost daily observations over several years. Data comparable to hers are not available on any shore-bird, and the writer, with only two vacation periods on which to draw, does not suggest that he has found more than fragments-or that all of these fragments are susceptible of valid interpretation.

The fragments, in this case, are not fossils, but certain phenomena apprehended through the ear and through the eye. Since this attempt to gain an understanding of the biology and psychology of the Willet was limited by the hearing, observation, and interpretation of notes

and bodily behavior, it would seem logical to describe these calls and postures and give, so far as possible, their meaning.

While the Willets' vocabulary is large, the number of syllables is not, with the result that their language (if it deserves this name) seems to include many homonyms. It thus becomes difficult to attach definite significance to certain calls.

One note, however, leaves no doubt as to its valence. It is preceded by a slow dik-ing (see below) as a male approaches a female and seeks copulation. Its tempo is augmented until the bird is clicking faster than one can count—nearly as rapidly, indeed, as does the cicada (Tibicen sp.)—and continues until about the end of the sexual act. The call is loud and can be heard at distances estimated to exceed one-eighth mile. It was heard scores of times, when the male giving it was visible, only as a preamble or accompaniment to the sexual act. This is unquestionably the note recorded as kuk-kuk by J. T. Nichols (Bent, 1929). It might be named the male copulation note. The female was heard to give, during copulation, a grunting eh-eh note.

Another note closely associated with nesting and copulation is a throaty whistle, somewhat suggesting the whistle of the Pintail (Dafila acuta tzitzihoa), that was recorded in the field as yoick-yoick or yoicker-yoick. This was noted at the beginning of a search for a nesting site or scrape (V-2-37); by the male shortly before attempting copulation (V-3-37) and when copulation had been refused by the female (V-3-37); seemingly as an invitation to hunt a nest site (V-3-37); during scrape ceremony (VI-10-36), and by the female, who apparently used it to drive the male to his incubating duties (VI-8-36). It was frequently heard during the 1936 season but the fact that the blind was on the ground made it impossible to watch the birds at a distance; only further observations will narrow the meaning of the note.

A call that was described in my notes as a twitter or as the *Wren note* because of its resemblance to the song of a basso Long-billed Marsh Wren (*Telmatodytes palustris*) was recorded on four occasions: when defending the female from an intruding male—the twitter given by the bristling husband (V-I-37); by an undetermined member of the east pair to warn the male of the west pair not to tres-

pass, though the west female was feeding on the east territory (V-4-37); by the west male in calling the female to him from the east territory; and, on the next day, by the same male, in an apparent attempt to call the female, who failed to respond. Because this note was so successful in either driving or calling another bird, it might be called the *compulsion note*.

The justification for the interpretation of compulsion here may be shown by a quotation from my notes. On May 4, 1937, the west male had been driven from the territory of the east pair at 5:20 P.M.

5:25—Male flies to the west side of his territory and gives pill-will-willet call. Female feeding (still on east territory).

5:30—Male feeding toward blind. Diks, flies few feet south, calls pill-will-willet. Female not far from blind now.

5:40—Male flies west again, pill-will-willeting. His lady ignores him—and eats.

5:50—Male perched on jetsam to west, female eating well in east pair's territory.

5:51—Male flies to blind and lands, pill-will-willeting. His unwillingness to trespass farther is obvious.

(It should be explained that my blind, by happy accident, was on the boundary between the territories of the east and west pair. The latter, occupying the land used by the long-studied pair in 1936, received most attention in 1937.)

5:55—Male pill-will-willets. No response from female. Then he leans over (forward) and gives Wren note and she comes at once.

A simple note, given in a confusing variety of situations, is a staccato, reedy dik, often rapidly repeated, and not very loud. It was recorded as expressing emotion under the following circumstances: antecedent to copulation note; between series of Wren notes in threatening interloper; associated with Terning (see below) in mobbing; alone, when threatening interloper on territory; when excited by mounted bird on territory; when attacking Crow (Corvus sp.); when flushed from nest; when scolding the observer; and sotto voce—by incubating female—as male scales silently over the nest. Diks are also heard when, so far as I ascertained, they seem not to have any particular relation to an emotional state. The note is used by both sexes and repetitions were counted up to 188 times a minute. It is

usually associated with emotional stress and, judging by my observations, most frequently anger. On May 2, 1937, distant diks that sounded, to my ear, like all others, attracted the attention of every Willet in sight; the birds stopped feeding and stood, for a short period, with necks erect. This is the note recorded by Julian Potter as "quip, quip, quip" (Stone, 1937).

A wailing call that might be represented by the word k-a-aty (to be pronounced as is the feminine name) was frequently heard, and though its interpretation was not always clear to me, it rarely failed to call forth marked interest. Since it was given, interspersed with Terning (see below), by birds chased by dogs, and by mobbing birds, it is presumably associated with predators; however, it was also given by the west male as he flew off his territory to attack another Willet.

A note that suggested the sound made by ruffling a deck of cards was heard three times, near or at the nest, in 1936. On May 31 the male flew over the female, which I had just flushed from her nest, and uttered it; on June 6 the female gave the same note just before going to the nest; and the next day the male uttered it as he dropped near the nest; the female half rose from the eggs, then resumed incubation. What the note means to the birds is not clear to me.

On May 3, 1937, the west pair were prowling through long grass and the male uttered a chattering note—the only time I recorded it—that was apparently a means of maintaining contact with the female since, when she again came into sight, the note stopped. A similar action by Phalaropes has been reported (Tinbergen, 1935). This might be called the *contact note*.

This list of calls leaves to be described two that are, perhaps, most interesting of all because of the light they seem to cast upon the relationships and sociology of the birds.

The first of these—a strident teee-eeer—I immediately named, in the field, the Tern note because it was "very like the high pitched and thin Arctic" Tern (Sterna paradisaea) call; unlike the Avocet's (Recurvirostra avosetta) "gull-cry" (Makkink, 1936) it seems not to be specific for any predator—indeed, the most interesting thing about it is that, though it is at times evoked by predators, it is repeatedly



FIG. 2. The male attacking the mount.

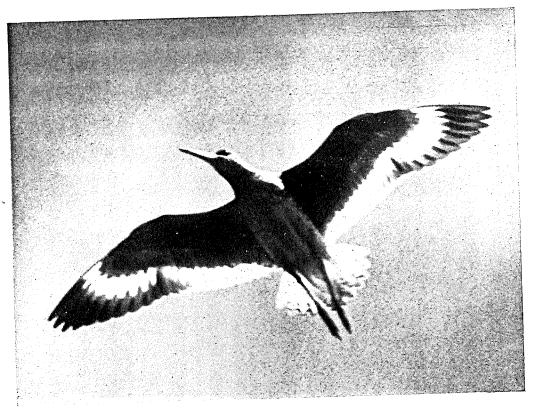


Fig. 1. Eastern Willet. Photo courtesy of Albert Dixon Simmons.

given for no ascertainable cause. It is, however, like the gull-cry of the Avocet, seldom heard early in the breeding cycle, but common when eggs have been deposited.

In 1937 when, up to the time I was forced to abandon the study. I had been able to find no evidence of eggs, it was five times recorded on May I, during a fight; once on May 3 during the first mobbing (see below—Section IX) of the year; twice on May 7, during—apparently pointless—mobbing; and once on May 8 as supposed east male attacked a Fish Crow. In 1936, when most of the birds had eggs from the time of my arrival on May 23rd, the Tern note was recorded on the 23rd, 25th, 26th, 28th, 30th, 31st, June 2nd, 3rd, 4th, 6th, 7th, 8th, 9th, 10th, 11th, 14th, 16th, 17th, 19th, and 20th—usually many times a day. During 1937, alive to the possible significance of the Terning, I carefully recorded all instances; in 1936, before its meaning and development had become significant, I unquestionably failed to record it in some instances. Therefore, it is obvious that as the nesting cycle developed this note played an increasingly important part in the behavior of the birds.

In early May, the first Terning was heard during fights, noted as especially vicious, but whether the call came from the attacker or the attacked, I could not determine. It was also heard when, later, I flushed birds from their nests, and it brought an angry group about my ears, from estimated distances of a quarter of a mile. It was frequently heard as predators—Crows and a domestic house cat—were mobbed. The gravity of its message to the birds was constantly apparent; time after time birds would jerk to attention at the note, and, usually, a number would congregate about the screaming bird and, with a semblance of hysteria, add to the racket. In early May, however, "ganging up" was exceptional. The most interesting functioning of this call will be discussed under Section IX.

The pill-will-willet call that has supposedly given this bird its name, naturally bridges the gap to a discussion of postures—well defined and often-repeated bodily movements—since it accompanies the most spectacular behavior of the Willet. The call itself is, by human standards, a rich, ringing, sweet and moving performance. It may be

heard, on calm days, at distances estimated to exceed, considerably, a half mile. While it may, for the Willets, be characterized by differentiating shades of tone, pitch, and emphasis, to my ears it was repeatedly the same pill-will-willet though given under a wide variety of circumstances. There is no question in my mind, after hearing it hundreds of times, that its most important function is territorial and that, in this usage, it is analogous with the songs of passerine species. It is given not only when attempting to secure territory (see Section VI) but as a warning when strange birds trespass on, or pass over, a territory, and in driving birds from a territory. It is also given, along with the Tern note, while mobbing; by the approaching bird in nest relief; before returning to a vacant nest with clutch; and when objecting to a human interloper. Tomkins (1938) reports it as "incessant at all hours . . . of the night." In my experience, nocturnal calls were rare; this may be true only of the portions of the breeding cycle before hatching of the eggs.

Its most striking—and probably significant—manifestation is in connection with a gesture I called, in my field notes, Spottying from its similarity to a performance I have watched in the Spotted Sandpiper (Actitis macularia). It is undoubtedly analogous to the Blacktailed Godwit's "ceremonial flight" (Huxley, 1926). In this act the male, rapidly and loudly calling pill-will-willet over and over again, would rise into the air and, with wings arched stiffly downward and moving in short, quick beats, fly in circles—occasionally out of sight over the marsh, when the performance would stimulate other birds to the same action; at times over the territory he was attempting to take from another male; frequently over the approximate bounds of his own territory. Flying in these circles, he would mount higher and higher, often until he nearly vanished. At times he would drop thirty or forty feet only to zoom upward again with a vigor and lightness it was difficult not to call ecstatic. The tips of the wings flicker like tongues of black and white flame and at extreme heights the ruptive pattern, as in the Nighthawk (Chordeiles minor), so breaks the wings that only the inner, dark areas are visible. Against an intense blue sky, or piled cumulus clouds, this display is as stirring a performance as I have ever seen in the bird world. This performance is more fully described in Vogt, 1938.

After flying about in circles of varying diameters, and for varying amounts of time, the male would begin to descend, often almost perpendicularly, often with wings barely moving as it rode the wind head-on, and with long legs drooping. The pill-will-willeting usually continued, unabated, until the male had dropped near to the ground; the final descent was noiseless.

Often—but not always—after the male had been Spottying for a time, the female would fly up and hover a few feet below him, also giving the <code>pill-will-willet</code> call; in her flight, voice and descent, I could never detect the wild vigor and abandon that seemingly possessed the male.

Comparable behavior has been noted in many shore-birds (Bent, 1927, 1929) and discussed in detail in the case of the Black-tailed Godwit (Huxley, 1926), and the Phalarope (Tinbergen, 1935). The former says, "The ceremonial flights of the Godwit and many other waders, such as the Redshank, Lapwing. Purple Sandpiper, Curlew, Snipe, etc., are similar to song in that they are prominent from afar, and stand often in some relation to territory, but (like the waders' territory itself) they appear not to be quite so specialized."

Certain differences in Willet behavior from that of species studied by Huxley and Tinbergen should, however, be noted. The Willet is a highly territorial bird and guards the boundaries of its demesne, through much of the breeding season, as vigilantly as does any passerine. In driving off interlopers the ceremonial flight is frequently used, probably at least till the end of incubation. It was also observed as an integral part of the actions of a pair that was trying to lop off a piece of the east pair's territory. These observations would seem to indicate that the ceremonial flight is definitely territorial in character.

That it in addition serves to unify the pair (Huxley, 1914) also seems very likely since the female so frequently participates in it; however, the ceremonial flight in the Willet often does not—though further observations may indicate it sometimes does—have anything to do with "desire for a sex partner" as in Phalaropes (Tinbergen,

1935). It is given over extended periods by mated pairs; on May 27th the male of an incubating pair did the ceremonial flight in chasing two birds that flew across his territory.

Hostility is displayed, in Willets as in other birds, by bristling—erection of the feathers in such a manner that the apparent size of the bird is increased. This is often accompanied by a longitudinal flattening of the body with the neck drawn in and the long bill extended as a prolongation of the body axis; this gives the bird such a striking resemblance to a huge snout-beetle (Rhynchophora) that, in my notes, I called the posture Beetling

Hostility is also shown by exaggerated strutting, similar to that I have seen in the Spotted Sandpiper (Actitis macularia). With head up, body erect, and breast thrust forward, the bird advances with exaggeratedly long steps that at once brought back old memories of the cake-walk. (At the time this was written I was not familiar with the application of the term to similar posturing of the Semipalmated Plover [Bent, 1929].)

At times, in the stress of battle, the Willet will lie down, much as does the Avocet (Makkink, 1936).

I cannot agree with this author's interpretation of such behavior as "disgust," which seems to carry a strongly anthropomorphic connotation. Rather, since such behavior suspends the fighting, it functions as a means of securing a truce. It seems possible it may derive from a temporary "inferiorism" (Allen, 1934) that, however, does not last; as is well known, a bird on its own territory commonly possesses a moral (or psychological) superiority over invaders of its own species.

Two tail-displays were noted. In the first, the sexual, the tail is narrowed and depressed. The gesture characterizes male birds that are seeking copulation and both sexes in nest-site hunting or scraping. Selous (1927) reports similar display in both sexes of courting Redshanks (*Totanus calidris*).

The intimidation tail-display differs from the sexual in that the tail is somewhat depressed, spread, and tilted sideways, with its upper surface extended before the opponent.

My experience agrees with that of Tomkins (1938) in finding no "broken wing" performance.

The various calls and postures will be referred to further in discussing courtship, territory, etc.

IV. Monogamy and Time of Pairing

Willets had been on their breeding grounds about two weeks before my arrival in 1937; Robert Haines and Philip C. Walton reported to Julian K. Potter that they had arrived by April 18. The population density is high—nearly eighty birds were present in one mobbing aggregation—and, despite vigorous territorial defense, the birds move about a good deal. For these reasons, I was unable to secure data on pairing. On several occasions, however, I watched territorial establishment, and in each case the acquisitive male was accompanied by a female. This would indicate that pairing takes place before territory assumption unless these birds had been evicted from their territorial tenacity.

Females I was able to watch closely were repeatedly approached by males, early in May, which suggests that there is a surplus of this sex; that they had not yet found mates, but would later; or that they are polygamous.

On November I, 1937, Alexander Sprunt, Jr., of Charleston, S. C., wrote me: "I will be interested to know whether you will run across any instances of more than one female using the same nest. It occurs locally, and I have records of several instances. Sometimes the multiple number of eggs is accepted, sometimes the interloping female's eggs are rolled out of the nest.

"Highest number of eggs in one nest found here has, to date, been eight." In the thirteen nests observed by the writer, the clutches ranged from one to four eggs. No instances of double-occupancy were observed. As is noted in Section VIII, there is a notable difference between New Jersey and southern coastal Willets in their flushing reactions, possibly the result of different ecological conditions. Whether double-occupancy of nests may also be correlated with a difference in nesting-cover is not known. In any case, these large clutches of eggs

suggest the possibility of parasitism-often, apparently, a habit that is rather casually assumed, as by some of the Ducks-or of polygamy. This last possibility I cannot believe to be very common because of the repeatedly observed preoccupation of known males both with their territories and their mates.

V. SEX RECOGNITION

It is usually possible, on the territory, to recognize the sex of Willets under observation, as has been pointed out. Since the human observer can do this, it seems highly probable that the birds, themselves, are able to recognize sex without resorting to the trial-anderror method reported by Allen for Grouse (1934) and Whitman for Pigeons (1919). My conclusions on this point, as regards the Willet, tentatively agree with those of Makkink (1936) on the Avocet: "... the birds must be able to distinguish each others' sex already in the beginning of the meeting . . . by means of . . . characters which are too subtle for our discrimination." The possibility that individual birds were known, as individuals, to these unmated males, cannot be ignored in view of the reports of Whitman (1919) and Schjelderup-Ebbe (1935). This acquaintance seems less probable, however, in the case of wide-ranging, free birds that are not members of a flock nor, so far as could be determined, even possessed of a near-by territory, from which they might come to know the females subsequently approached. In early May, 1937, repeated approaches by males to a mated female were observed. As will be described below, at this period there was no perceptible territorial defense; when, early in the season, the male interloper pitched into the territory near its feeding owners, no difference in the behavior of these two birds toward the newcomer was perceptible. Yet, so far as could be seen, the approaching male was, for not even an instant, uncertain as to which was the female. Dropping from the air at a precipitous rate, he would land near the female, and begin moving toward her.

Tinbergen (1935) expressed the opinion that "the emotional state of the reacting bird had influence on its discrimination power." While, in the case of the Willets, there was no evidence of this, further observations may cast light on this interesting psychological problem.

VI. DEFENSE OF FEMALE AND TERRITORY

The two causes of strife between Willets are discussed together because protection of the female as a defense-motive seems to be replaced by protection of the territory as a defense-motive in such a way that it is impossible to determine—at least without vastly more study, and an improved technique-where the first ends and the second begins. Certain it is, however, that as the breeding season progresses, one gives way to, or is masked by, the other. For example, during the first days of May the bird I called west male, made few attempts to protect his land, though he was valiant in repulsing males that approached his mate. Later his land was sacrosanct. (See Tinbergen, 1936. "By comparative observation we find in various species a great many different objects 'defended' against competitors. We conclude that an object is 'defended' when we see the fighting restricted to its vicinity. It is well to emphasize that our knowledge of these objects is no hypothesis, but a fact.")

Something about May Day morning, 1937, seemed to exert an aphrodisiac effect upon the birds, and attempts by wandering malespresumably unattached—to make off with attached females seemed especially frequent. A description of one of these encounters, translated out of my field short-hand, may illuminate the subject.

The west pair have been having their troubles with interlopers.

8:20 A.M.—As another male approaches from the north, west male twitters (=Wren note) warningly. Newcomer-X-answers. West male pill-will-willets. West female (which has been feeding, for some time) settles down as though asleep on nest, with legs folded underneath and her bill in scapulars. X approaches her, strutting (= cake-walk). West male dik-diks and comes closer. X works around to opposite side of west female until their relative positions are thus:

west female west male and threatens (?) with strutting approach. West female gets up, jumps clean over back of west male, so positions are: X

west male

West male rushes X, who retreats a few feet, and feeds. West female again settles down, as though to sleep, and west male moves off a score of feet to slightly elevated perch on heap of grass. Twitters from time to time.

west female

Here the female was threatened—and defended—but no attempt was made to defend territory. The strange male was allowed to feed in peace—something that would not have occurred later. (The territorial bounds subsequently guarded by the west male so closely agreed with those of the bird I named the "white male" in 1936, that they suggested to me the possibility this was the same bird defending the same territory. Pettingill [1936] believes the same male Woodcock returns to the same territory.)

Another sexual defense, the same day:

1:41 P.M.—A presumptive male, vigorously pill-will-willeting, drops in near west female—which, twenty minutes before had been seen in inferior position in copulation. New male approaches her, and she and west male both go toward interloper with breasts thrust out, taking very long steps (= cake-walk). Newcomer stands ground until west male rushes in as though to attack and then flies off with the west male in pursuit.

On May 2 (5:50 A.M.) there was again defense of female but not of territory—probably by east male; the male drove an interloper from his mate but permitted him to feed near-by. In this instance the tail-tilting, noted above as a minatory gesture, was very noticeable.

The dominance of sexual defense (by which is meant defense of the female, as distinct from defense of territory) over territorial defense did not, however, exclude territorial defense to the degree that, subsequently, territorial defense seemed to make sexual defense unnecessary by preventing wandering males from approaching mated females. The response of the west male to a mounted bird, on May 2, was obviously territorial defense—since a dead mount cannot approach a female (see Fig. 2). It should be remembered that the previous day, the west male had defended its female but not territory; a half hour after the attack to be described, there was again pure sexual defense.

3:21 P.M.—The mounted bird, bent with body axis parallel to the earth, just west of blind [about fifty feet away]. The west pair come in to territory, from east. The female dropped by the blind, the male flew casually westward. Then it spied mount, rushed to within three feet, diked several times, and attacked vigorously. Pecked back of head from left side, jumped over it and hit from right, jumped on its back and hammered head more, then stood on back a few seconds as though puzzled. Jumped to earth, went around front, and pecked near eyes,

making feathers fly, until I rescued dummy. The male was loath to leave and it stayed within thirty-five feet as I picked up the mount. [At the time of this attack the mount was a considerable distance from the female. The sex of the mount is unknown.]

On May 4, the so-called southeast male exhibited what was apparently mere sexual defense—the interloper was permitted to feed near-by—; and the west male showed the same defense but this may have been because the conflict took place on the periphery of the territory where limits, and emotions aroused by them, were often vague.

From this time on, territorial defense became increasingly obvious and because strange males were not permitted within territorial bounds, clear sexual defense vanished. Interesting evidence of the strength of the territory-defense urge was experimentally shown.

An abortive attempt to trap the west male—defeated by the wind, if not by other factors—left me with a four foot square of white mosquito netting that for some days was permitted to lie in the middle of the territory. The west pair obviously eyed it with some suspicion at first, though they subsequently came to feed in its vicinity without apparently paying it attention. On May 5, at 5:00 P.M., the mount was placed in the center of the square of net. No birds were present on the west territory.

6:00—Male flies low over mount, pill-will-willeting and drops near-by. Feeds. 6:07—Female drops in, pill-will-willeting. Both feed toward mount; male outdistances female. He reaches square of mosquito net on which mount is placed and begins to walk around it. He does this several times, skirting net, then finally jumps at mount and strikes it with bill. Flutters back to ground. Does this four more times, carefully avoiding net, until he knocks mount over. Female, meanwhile, has come up and is standing close by. Now both birds walk slowly away, feeding.

Under more accessible conditions, the mounted bird was, several times, attacked by males—though never by females. Territorial defense was seen, many times a day, over many days. So alert were the birds to trespass that a bird merely flying across a territory usually evoked a warning <code>pill-vill-willet</code> call, this given by either the male or the female. As was pointed out above, no evidence was seen of territorial defense by females though, on a few occasions, they were seen to bluff interlopers, both in the presence of their fighting mates,

and in their mates' absence. The fighting often seemed to satisfy Selous's definition of formalization (1933) but at times it was a serious affair.

8:13 A.M., May 7, 1937—A strange pair (at least I do not know where they came from) drop near the west pair, south of the blind. Pill-will-willets are exchanged, then a stranger rushes the west male. The latter spars, exchanging wing blows (the clashing of the primaries could sometimes be heard) and then lies down. Beetles forward, attacks stranger, who grabs west male by base of bill and shakes him as they flop around. West male finally pulls loose, and does not continue fight. Newcomer, however—I suspect south male—walks slowly off. Females, during this, had not participated. West male shakes head from side to side as though bill hurt.

It has been pointed out, above, that the so-called spotty performance seems to be used in securing territory. When, in 1937, I took up my observations, the entire mowed strip of Spartina patens. east and west of the blind, seemed to be occupied by two pairs of birds whose territorial boundary lay just about at the blind. By the time I left, nine days later, the so-called northeast pair—utilizing the spotty performance—had carved a piece off the territory of the east pair. The pair seeking territory systematically utilized the ceremonial flight over the area they were trying to appropriate. Time and again, giving the pill-willet call, they dropped onto the desired land; and time and again they would be driven away—sometimes after an exchange of threatening postures—by the owner. As nearly as I could tell, they secured title to the land by the process of wearing down the owner's resistance over a period of several days. It is probable that had they sought the center of the territory, their efforts would have been vain; in the cases I observed, it was peripheral sections of territory that were lost to interlopers. Outlying portions of territory are apparently less vigorously defended: there seems to be a sort of territorial center of gravity, the distance from which proportionately reduces vigor of defense.

The east pair lost a sizable area, and the west pair a small piece—never very vigorously defended—to the south pair, whose holding included South Pond (Plate I) and but little mowed area. Then the northeast pair lopped another piece from the east pair, leaving them as little of the mowed strip as the southeast and northeast birds had.

As late as June 19, 1936, the spotty performance was noted, though the history of the calling birds was not known.

Another probable territorial act is the habitual use, by Willets, of the same position on the territory as what I called a "look-out"; this was more obvious during incubation than before it. It is very like the "Standplatz" of Herring Gulls (Larus a. argentatus) (Goethe, 1937). In 1936 both the male and the female under extended observation constantly—though not invariably—stood on a bare patch, where cattails formerly had grown, while the mate was on the nest. From here they would watch the territory, protest against passing birds, and, in the case of the male, initiate defense. This look-out was used so consistently, and from it there so often rang out the warning pill-willet, that I could not help regarding it as the catoptrophorine equivalent of the passerine song-perch. It was situated approximately half the length of the territory away from the nest.

It is apparent to the writer that fighting, in Willets, is: (1) in defense of the female, at a period when the territory is not invariably defended, and (2) in defense of the territory. This fighting was never observed when the birds were known to be away from their territories, as on the feeding grounds at the bay edge, but observations there were casual and, probably, inconclusive.

Unfortunately it was not possible to stay in the field, in 1936, long enough to study the relationship of young birds to the territory. No young were seen, none of the eggs under observation had hatched, and there was no perceptible change in behavior to suggest the presence of young in the tangled grasses. Willets, like other members of their family, are precocial; Tomkins (1938) reports that soon after hatching the birds apparently desert the nest by "at least a half mile"; furthermore, Arthur Wayne (Bent, 1929) is authority for the statement that the adults carry their young away from the nest. What, then, is the value of territory to the Willet?

Certain possible fallacies occur in discussions of territoriality (Makkink, 1936, expressing agreement with Huxley, 1925a) in shore-birds, namely the assumption that the bird "has plenty of suitable nest-sites at its disposition and needs therefore no territorial instinct. No

more does there exist any necessity for reservation of a territory for reasons of food; soon after the newly hatched are dried, the family leaves the nest-area and makes for the water, where the food is abundant." While these statements would probably be true in the case of the Northern Phalarope, it seems dubious whether they would be in the case of such species as the Avocet and Willet. The latter, certainly, is much less numerous than it was in its aboriginal circumstances, and it seems entirely possible that when its numbers were at their peak, nest-sites and food may have been at a premium. This assumption is given support, it would seem, by the reports of Dircksen (1932) who found that on Norderoog Island the European Oystercatcher (Haematopus ostralegus) by its territoriality tended to keep its numbers low through the high mortality rate suffered by immature birds whose territorial boundaries did not permit access to mud-flats for feeding purposes. Information on territory, after hatching, and on care of the young, in Willets, is casual and inconclusive; it is possible that, like the Oyster-catchers, young Willets have a better chance of survival on ecologically superior areas. (Their concentration on mowed areas-see Section X-would, at least in southern New Jersey, suggest such a possibility). If young are not confined to the territory, of what value is it to the birds? Since the male defends the female before he defends the territory, it would scarcely seem necessary to develop the territorial urge as a means of sexual defense. Without more data than are now available, I find myself as much at a loss to interpret the territoriality of this shore-bird as have been observers of other species.

VII. COURTSHIP AND COPULATION

Courtship in a limited sense—that is, as a series of acts directly connected with, and stimulating, copulation—is a simple affair in the Willet, and corresponds remarkably to that of the Redshank (*Totanus totanus*) (Huxley, 1912). The writer is not inclined to include with courtship such phenomena of behavior as sexual defense, territorial defense, and spottying or the ceremonial flight. While these are closely associated with the reproductive cycle, they seem not to be limited to preparation for the sexual act; they apparently bear as close a relationship to nesting and care of the young as to copulation itself. Con-

cerning such courtship as may precede formation of pairs, there are no data.

Courtship, then, appears to consist of calling and posturing for a brief period. In only one instance, out of many observed, did there seem to be any possibility that the female initiated courtship; in this case, she walked rapidly toward the male as he flew into the territory. In all other observations the male initiated the courtship, usually by walking slowly toward the female. He would then begin to utter the deliberate dik-dik, which became more rapid and reedy until it developed into the clicking, described above. As the male walked toward the female he depressed the closed tail (without tilting it) and as the speed of the diks increased he raised his wings over his back and began to wave them through a narrow arc. The rate of waving increased until it could be accurately called only a vibration; of course the female could plainly see the flickering, flame-like wing-tips. Selous (1927) reports the fluttering of wings above the male Redshank's back, antecedent to copulation. The Northern Phalaropes indulge in similar behavior (Tinbergen, 1935) as, Dr. Francis Harper tells me, does the Lesser Yellow-legs (Totanus flavipes).

In the majority of cases, the response of the female Willet to the clicking and wing-waving was simply to walk away a short distance. In all such cases observed, this gave the quietus to the male's invitation. He immediately closed his wings, and usually continued to feed—the principal occupation of the Willets.

When, however, the female was sexually responsive, she would stand rigid as the male approached, then slowly incline her body forward. When her tail had been tilted above the horizontal, the male would flutter lightly to her back and to the sound of his clicking the act would be completed.

As he approached, in at least one instance where the female was receptive, she *diked* with him, and during the act uttered a grunting *eh-eh* note. At other times the female's bill was seen to move though it was impossible to determine whether or not she was calling.

The copulation was usually terminated by the female tossing the male lightly over her head—apparently, at times, much to his disgust.

On one such occasion the male rushed her with a threatening bill; on another he attempted to avoid the tossing by grabbing her neck in his bill; and the third time he was observed to give expression to his unreadiness to cease copulation he held her neck, just behind the head, and when she tossed him over her head he tumbled her with him.

In most instances, copulation was followed by quiet feeding, the birds side by side on the territory.

Copulation was observed—though it was extremely rare—as late as June II, 1936. This year Mr. Richard H. Pough reported that he witnessed one copulation that took place in the water of one of the salt marsh ponds; the female extended her neck and body along the water, apparently after the manner of the European Avocet (Makkink, 1936). At no time was an incomplete copulation, such as is reported for other shore-birds, observed; it seemed that when the impulse in the female was too low in intensity (Howard, 1929) she terminated the attempt by merely walking away.

The 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 (Fig. 1). Here, it seemed, was a clear-cut problem. It is likely that a solution can be found only by experimental methods, in the field and in the laboratory; eventually it would seem desirable to isolate the factor of wing-pattern in relation to behavior, by staining or otherwise destroying it; and possibly to eliminate calls by destruction of membranes of the syrinx. But to do this requires more effective trapping methods than now exist. One can, however, surmise what the results of such experimentation would be.

The vibrating of the Willet's wing seems clearly to satisfy Lorenz' (1935) requirement of "improbability" as a criterion of a releaser impinging upon innate perceptory patterns; through long familiarity with the bird on migration, and through more than 200 hours' observation in the courtship, nest-hunting, and incubation phases of the breeding cycle, the vibration was noted by the writer only in association with spottying and copulation. In the former case, of course, the wings are held horizontal, and in the latter they approach the

vertical. While the physical equipment—and frequently, in spottying, the behavior—are shared by both sexes, in courtship the supposed "releasing action" of vibrating wings seems as purely masculine as is the penis in the Rhea (*Rhea americana*), and is probably comparable with copulatory organs (Huxley, 1921).

Willets fall more nearly in Lorenz' Chromide type than in the lizard or labyrinthine fish types in their sexual relations. Yet, except for male displeasure at the termination of copulation, never, in my experience, did "the threatening behavior and the display of these animals reveal themselves" (Lorenz, 1935). They certainly indulge in mutual display, but in this I could see nothing of antagonism, and I cannot help seriously questioning the validity of applying such Keyserling-like concepts of sexual antagonism to birds. In some species they may be justified; in the Willets, in which an equilibrium between the sexes appears to obtain, there seems no reason for establishing a "ranking order of the individual mates," and I could see no evidence such an order existed.

The possibility that the "sudden transformation of a grayish-brown bird into one predominantly black and white at the moment of taking to wing" (the words of Lorenz, 1937, but a perfect description of the Willet) "most probably is essential for the following or flocking together reaction of the fellow-member of the species," must not be overlooked. The visual cue here, however, is probably that of pattern, whereas in the ceremonial flight and courtship the visual cue is pattern plus wing-vibration.

VIII. NESTING AND NEST RELIEF

It was impossible (vacations being limited) for the writer to remain in the field long enough in 1937 to witness actual nest construction, and determine incubation periods, or in 1936 to witness the emergence of young. The incubation period is given by Tomkins (1938) as twenty-one or twenty-two days. Obvious scraping or nest-site hunting (differentiation was impossible) was observed in 1937, however; thirteen nests were discovered in 1936, with eggs in all seen, from May 23 on; and the striking nest-relief ceremony was several times observed at close range.

Nest-site hunting (or scraping?) was observed on the first day of observations in 1937 (May 1).

9:25 A.M.—With loud pill-will-willeting, two birds come from the east and drop west of blind. There is some dik-ing, and the yoicker-yoick note . . . Both tend to depress tail, displaying to one another. One pokes around clumps and even pokes in under them as though nest hunting. Then they fly up—or, rather, one does, and gives Spotty performance—and other bird flies up below it They come down together west of blind and are joined by a third bird that seems to drive them up. All fly to the bay's edge and disappear.

On the following day, these observations were made on the west pair.

9:36 A.M.—Number 2 (presumably the male) begins to sidle toward number I (presumably the female)—tail somewhat depressed. Goes into patens clump and bends over—feeding or nidification preparation—and suddenly backs away as though scared. Walks around clump, watching it, past number I. Walking rapidly and apparently aimlessly about marsh

9:43 A.M.—Number 2 settles down in clump with movements that suggest nidification. No. I flies near. Slowly walks toward No. 2, who is sitting down and saying *yoicker-yoick*. No. I walks into clump and *appears* to walk over No. 2—as in nest relief. Walks out to east. No. 2 soon follows, and flies east, out of sight, followed at some distance by No. I.

May 3, 1937, 12:55 P.M.—The male, judging by size, led hunt for nest and after passing through several patens clumps stopped at one until the female came up to him, whereupon he bounced out as though he had been stuck with a pin. Female stayed a little while, seemed to settle down, then came out. Male went on, skirting edge of several clumps, as though continuing to hunt. Then both perched on flotsam.

Two days later I noted, of the west male, that it seemed he could "scarcely go near a tuft of grass without exploring its possibilities. I'd guess he is much more concerned with a nest site than she." Whether or not this resulted from unequal development of the sexual cycle in these two birds, or is usual behavior, as Lorenz (1935) implies in the case of *Anatidae*, I did not determine.

Seven minutes later (9:45 A.M.) I wrote: Seems to be a good hunch. Male starts back toward female, walking rather rapidly, comes to *patens* tuft that has not been cut, sticks in his head, settles down, turns around with tail high, as though shaping nest, tries several positions, comes out on south side, shakes himself, and begins to feed nearby Meanwhile, female is feeding again.



Fig. 3. An incubating Willet.

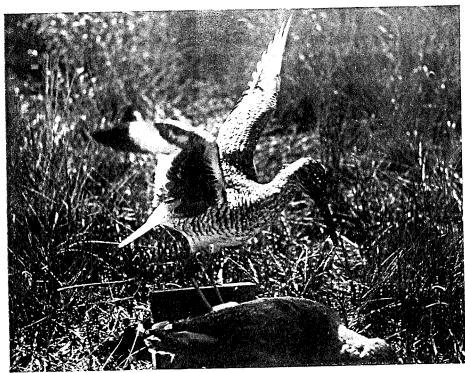


Fig. 4. The "white male" topples the mounted Willet. The wings are spread merely because the bird has just fluttered from the back of the falling mount; they were not displayed during the attack.

Since, four days later, there is no sign of nesting at this site, and since the birds have meanwhile been investigating other clumps of grass, the above performance would seem to be nothing more conclusive than the scrape ceremony that is so generally indulged in by Laro-Limicolines. In 1936 the nest was built, and scraping-site hunting had been concluded, before my arrival. In 1937 I was forced to leave before the actual nest site had been determined. Therefore, the interpretation of this behavior must await further investigation. It seems noteworthy, however, that the sexual tail-display (Section III) is common both to scraping and pre-copulatory behavior; that this scraping took place on the same days as copulation; and that I regarded an exchange of places in the scrape as closely resembling nest-relief. That is, the female appeared to walk onto the back of the male, which darted out from beneath her. I regarded the observation as tentative, however, because of the distance of the birds from me.

The wide variety of nest sites utilized by the Willet is described in Bent (1929). Most of the nests seen by the writer were in dense Spartina patens near the ecotone at which this grass met Spartina alterniflora or Typha angustifolia. Though the observer stood directly over the nest, it was usually invisible because of the thick canopy of grass. The birds lay close—sometimes striking the observer's leg as they flushed—but never permitting the close approach said, by Alexander Sprunt, Jr., and Roger Tory Peterson, and by Tomkins (1938), to be characteristic of southern coastal birds nesting in exposed situations. It may be that the greater readiness of the New Jersey birds to flush is correlated with the efficient cover that so thoroughly conceals their eggs.

Incubation is by both sexes, and I was unable to determine that there is any regular on-and-off periodicity. This is also true of the Oyster-catcher (Direksen, 1932). Some nights the male incubated, during others the female; birds flushed, at night, from the territory were probably the non-incubating owners. Identification was, of course, impossible in the darkness.

The nest-relief ceremony is an interesting performance that is far more beautiful, watched within a few yards, than my field notes indicate. The role of the sexes seemed to be identical.

June 9, 1936, 9:14 A.M.—Female flies over the nest from the east and drops at usual post (= lookout) at bay. Preens vigorously.

9:27 A.M.—Female comes sneaking along through grass, looking very small. I believe she has walked all the way (at least 100 yards). She nervously walks past north side of nest, pushes through grass on east, then comes into open between blind and nest. She walks up to it and seems to bend her body slightly forward, also bending legs so as to drop body lower. Male gives soft yoicker-yoick notes. Female answers with soft, then loud, pill-will-willet and male flies off. Female pushes onto nest with back to blind.

June 10, 1936, 12:56 P.M.—Female flies to west lookout. Walks from there, feeding at first, as she goes to nest, which she does not reach until 1:41. She is extremely cautious and after walking just east of nest, climbed out of furrow through which she had sneaked, and watched for a long time. Finally pushed through grass and walked along another furrow to south side of nest—that toward blind. When within four feet, one of the birds—I think the female—gave throaty dik. As she approached, both obviously made this sound. Male did not offer to leave nest. Female bent body forward, diked two or three times, then gave pill-will-willet twice. Walked onto nest, on top of male, who suddenly pushed out from beneath her and flew south. When couple of hundred feet away, gave pill-will-willet call.

When the blind was first put near this nest, it obviously made the birds extremely nervous and it seems likely that the method of leaving the nest, at relief, described for June 9, was abnormal in that the incubating bird departed so readily. Subsequent observations indicate that the second description given is more nearly normal and that the incubating bird leaves at the touch of the reliever's breastnot merely at the call. Lorenz (1935) states, without giving examples, that "all birds avoid dorsal contact as much as possible."

The birds were frequently away from the nest at the same time. Indeed, they usually abandoned the territory in the early morning, to resort to the edge of Delaware Bay, where they fed and bathed.

Behavior on the nest was not, so far as I could tell, noteworthy. Sometimes the incubating bird faced one way, sometimes another. While on the nest, the incubating birds at times gave the impression of being bored. They would poke their bills about in the grass, sometimes catching insects, and sometimes apparently getting nothing. Occasionally they would tug at grass-blades, as though to initiate play. They would also fidget with their eggs. Boredom is an admittedly questionable interpretation to place upon such behavior, but it resembled closely

similar behavior on the part of an incubating Marsh Hawk that not only seemed to the writer to be clearly bored, but that played with bits of dried grass by tossing them about. If this was not boredom, and play-relief, what was it?

IX. Social Behavior

One of the most interesting aspects of Willet behavior is its marked socialized character. Many species of Gulls and Terns—in the manner of passerines heckling an Owl—will mob an enemy, diving at it, spraying it with excrement, and even attacking. Some of the shore-birds (Bent and others), will repel invaders in much the same way.

The Willet, whose territorial intolerance has already been described, disregards all territorial boundaries when repulse of an enemy is involved. Dogs running through the nesting grounds, a common sight at Fortescue, are followed by a motley mob of screaming, darting Willets that join the group from long distances. This, then, would seem to be normal behavior for many species of this interesting family. One needs to see nothing more than the hasty retreat beat by Crows to surmise its effectiveness, for Willets.

But Willets go one step beyond most other members of their order. They form screaming mobs, repeat the frantic Tern note, gather in knots, and vaingloriously rise and fall (exactly as above a predator)—when no enemy exists to draw their fire. This is the more remarkable since, as Mr. J. J. Hickey reminds me, the birds are often solitary, on migration, or nearly so. Although one cannot be certain, when the Willets are at a distance, that there is no enemy, I have repeatedy witnessed this apparently pointless mobbing within a few yards of the blind—when I was sure no enemy was present. What set off this hysterical behavior, I could not even surmise.

This type of mobbing cannot, so far as I can tell, be differentiated from anti-predator mobbing, except that the predator draws the flock along with him, and the pointless mobbing ends with the birds casually dispersing, or dropping briefly to the ground in a loose flock. This up-flying seems to express none of the fear ascribed to Black-headed Gulls (*Larus ridibundus*) by Kirkman (1937) in his

discussion of their flocking. In the case of the Willets, the governing emotion is clearly excitement, with, perhaps, an infusion of anger.

The power of Willets, mobbing and Terning, to attract other Willets is very great. The mob excitement is pervasive and one observation indicated that a bird was drawn from its nest to join the mob—though usually incubating birds showed a complete disregard of the uproar. Non-incubating birds seem rarely, if ever, to ignore it.

Tinbergen (1931) has pointed out that, in the case of Common Terns (Sterna h. hirundo), there is no such sharp difference between social and individual life as Eliot Howard claims. Their social life does not suddenly develop into sexual life, as in the case of Howard's Buntings (1920), but during a certain length of time now one and now the other predominates. In the Willet, so far as my observations are concerned, the difference is even more marked. Here the sexual phase is characterized by much more obviously social behavior than are the pre- and post-breeding phases, and the social behavior-evoked in many territorial birds by the presence of enemies—seems not to depend on any extra-specific animal as an agent. Makkink (1936), recording "collective rising" in Avocets, throughout the breeding season, reaches the conclusion that, "The Avocet is a true social bird in which the inclination to gather never fully dies away." The Willet seems not to be a particularly social bird, but its gregariousness certainly increases during the breeding season.

Whether or not this apparently pointless behavior is a formalized version of opposition to predators, as Selous might have suggested, its utility is obvious; it unquestionably tends to unite the birds into the semblance of a colony, despite their fierce territoriality. Whether or not their united front is actually needed for defense, the unfailing effectiveness of the mobbing and Terning tends to keep the birds from scattering, and makes them constantly available for action.

It is significant—though scarcely unexpected—that the mobbing increased in frequency and intensity as the breeding season progressed. From a rare occurrence in early May, when the birds apparently did not yet have eggs, it became, after eggs had been laid, so commonplace I neglected to note instances, and thus lost an opportunity to study accurately its growth

The power of mobbing birds assemble cooperators, gives striking support to Lorenz' (1935) generalization that: "Certain social-attack reactions of various birds are as compelling as the release of the reaction inducing the animal to join in the take-off" (a reaction, by the way, whose force this distinguished biologist seems to exaggerate). While I have never watched the mob emotion with sufficient care, as has Lorenz, to observe that its strength was proportional to the size of the mob, there seems no doubt that the social-attack reactions are among the strongest felt by Willets. Lorenz further postulates, concerning these reactions, "Perhaps they represent instinctive acts which are least depudent upon the physiological condition of the bird at the moment." How he discriminates, in wild birds, between physiological and psychological conditions, he does not say; without attempting to do this in the Willet, the writer should emphasize the increase in frequency of mobbing as the breeding season progressed.

X. ECOLOGY AND CONSERVATION

Though no attempt was made, in the limited time available, to make an ecological study, certain interesting observations concerning distribution of the birds, feeding, and predation, were made.

Nowhere, on southern New Jersey's vast marshes, were the Willets found in greater abundance than about the village of Fortescue, with its swarming populations of dogs and cats. How effective these predators may be in restricting Willet numbers can only be surmised, but it was obvious that their presence makes life hectic for the birds, which are constantly being sent into an uproar by the mammals. The concentration of the birds within range of these beasts would seem inexplicable were it not for the fact that in the area where cats and dogs are most numerous, salt hay (Spartina patens) is annually cut. The birds, probing in the earth for much of their food, concentrate on the mowed areas and jealously guard such places against territorial invaders. That baymen burn over the marshes, thus destroying the matted grass cover, as a means of improving shore-bird shooting is well known. The birds concentrate on the stubble. The only place where I observed a Willet population comparable to that on mowed areas was at Egg Island, N. J., where wintering Brant, in the absence of eel-grass (Zostera marina), and Greater Snow Geese, function as effectively, from the viewpoint of Willet ecology, in cropping the grasses, as does the modern mowing machine. It seems certain that the easier feeding provided by mowed areas creates a favorable environment for the birds; it may well be a factor of major importance in maintaining their numbers at a sufficiently high point to offset destruction of favorable environment elsewhere.

During my observations, by far the greater part of the birds' food was taken on the territory. Although they resorted frequently to the bay-shore, or to inland areas, much of their time was spent probing among the grass roots. When the water in the marsh ponds was at a favorable height, these areas were frequently visited. Some food was picked off the grass blades. Surface water on the marsh was much sought for feeding and drinking. The food resources in such areas have been studied by Cottam and Bourn (Vogt, 1937) and Nicol (1935).

Off-territory feeding, like other activities, was noticeably affected by the wind. May gales piled a real surf against the bay shore, and on such days the birds flew far inland, on the marsh, presumably to bathe, eat and drink along the marsh creeks. On windless days the birds rarely flew back on the marsh, except to join in mobbing; their extra-territorial activities were concentrated along the beach. High winds were obviously distasteful to the birds and put an end to most activities. No correlation of extra-territoriality with rise and fall of tides was observed, though something similar to this has been noted by others (Bent, 1927, 1929, Makkink, 1936, etc.).

No evidence was secured that any other species was a serious competitor of the Willets though a male Meadowlark that had just defended its territory against another Meadowlark rushed the west female and drove her a few yards by sheer bluff.

Though little direct evidence on the problem of predation was secured, the following predatory species were observed on the Willets' nesting grounds: domestic dog and cat; American and Fish Crow; Marsh Hawk; Black Snake (Zamenis constrictor L.) and Snapping Turtle (Chelydra serpentina L.). Of these, the domestic animals and

the two Crows drew most attacks from the Willets; the other three animals, so far as my observations went, were ignored. Of cours, it is entirely likely that after the hatching of the young the reactions toward predators changed.

Whatever the role of Red-wings and Sparrows may have been as competitors, it is clear that they served the Willets well as buffer-species. Their eggs and young were frequently observed in the possession of Crows, and the Red-wings, especially, were valiant allies in driving off the Corvids.

One Willet nest was known to have been destroyed by a farmer's plough, but there was no evidence of deliberate molestation of the birds by man. While the residents of Fortescue saw no sense in spending so much time with the birds (and therefore concluded it must be a governmental activity!) they apparently enjoyed seeing them about the village and probably would discourage deliberate molestation.

Whatever the role of the respective predators in the areas under observation, they are not disproportionately lethal. Willets abound on the marshes and, for a number of years at least, are said to be increasing. Mowing of salt hay undoubtedly creates more favorable conditions for the birds, and it would undoubtedly be good "management" practice to remove the stakes and poles that sparsely stud the marsh. Only once was one of these observed in use by a Willet, and Crows used them daily as they watched for nests.

One dire threat hangs over the birds—the New Jersey Mosquito Extermination Commission and the C.C.C., in this region wild-life enemy number one. The extent to which the birds depend on marshes for nesting cover and food has been indicated. Ditching of the marsh for mosquito control profoundly changes the vegetation, as can now be seen just north of Fortescue, and wipes out a high percentage of animal food (Vogt, 1937). It seems, therefore, probable that if the so-called "mosquito controllers" slash the surface of the marsh with their ditches, the high density of Willets, built up under favorable conditions, will be sharply reduced. It is even conceivable that this beautiful and interesting species may be exterminated in the area.

XI. SUMMARY

- 1. Observations on the breeding-season behavior and ecology of the Willet, acknowledged not to be exhaustive, are given.
- 2. Most of the observations were made from blinds; one female was marked and subsequently collected; a mounted bird was used to test reactions.
- 3. Methods by which the observer sexed the birds—size and behavior, checked against the marked bird and against copulatory positions—are described.
- 4. Ten distinct notes—male copulation, female copulation, compulsion, contact, Tern, and territorial, plus four whose meaning has not yet been delimited—are described.
- 5. The ceremonial flight, fight postures, and tail displays are described.
- 6. The belief is expressed that the birds are monogamous, and that they are usually paired before claiming territory.
- 7. The conclusion is advanced that Willets are able to recognize the sex of other Willets without resorting to trial-and-error methods.
- 8. The female appears to be defended by the male before he defends territory. At a later date the territory is vigorously defended, by the male, both against other males and the mounted bird. Photograph is shown (Fig. 2).
- 9. Courtship and copulation are described and the possible role of the flickering wings as a releaser (Lorenz, 1935) discussed.
- 10. Both sexes participate in nest-site hunting and incubation; no on-and-off incubation rhythm was perceptible. The nest-relief ceremony is described.
- II. Typical Charadriiforme mobbing of predators is extended, in the Willet, to mobbing flights that are virtually identical—except that they are indulged in in the absence of predators.
- 12. Willet populations are noted as denser on marshes that have been cropped by man or Geese, and observations are given on feeding

and predators. Dangers to the birds, inherent in the mosquito-control work, are pointed out.

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Black-Crowned Night Heron Colonies On Long Island

By ROBERT P. ALLEN

INTRODUCTORY

There is obvious value and interest in accurate information on the breeding distribution of the birds of any given locality. Data of this nature on colonial nesting species are more readily obtainable than for solitary nesters and may be assembled in advance of more complicated distributional material. Information on the breeding localities of the Black-crowned Night Heron (Nycticorax n. hoactli) in the New York City region has never been brought together and analyzed. The present paper treats localities occupied during recent years on Long Island. In New Jersey the mapping of heronries is in progress; data for the Hudson River valley are still incomplete.

At the present time there are three species of herons breeding on Long Island, the Black-crowned Night Heron, the Yellow-crowned Night Heron (Nyctanassa violacea) and the Eastern Green Heron (Butorides v. virescens). The last named may occupy nest sites within the breeding areas of the Black-crown and, in addition, may nest in isolated locations. No attempt has been made to map the breeding distribution of the Green Heron, although its occurrence in Black-crown heronries is indicated. The Yellow-crown is known as a nester in but one location on Long Island, and as it appears to have first nested on the Island in 1937, no study has been made as yet of the local habits of these particular pairs. Therefore, this paper will confine its discussion to the breeding distribution of the Black-crowned Night Heron in this area.

Griscom (1923) wrote as follows of the Black-crowned Night Heron:

Long Island. Common summer resident, rare in winter. No large rookeries now known. In fact the nesting of the Night Heron is something of a mystery. The few small nesting colonies located do not account for the multitudes in every marsh on the Island.

This lack of information on the breeding of a common summer resident on such well-worked ground as Long Island creates an additional incentive for a census in this region.