

SOCIAL ORGANIZATION IN A NESTING POPULATION OF EASTERN WILLETS (*CATOPTROPHORUS SEMIPALMATUS*)

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ABSTRACT.—The breeding ecology of eastern Willets (*Catoptrophorus semipalmatus*) was studied over a 3-yr period in a salt marsh on the Atlantic coast of Virginia. During the study, 171 adults were color-marked. Willets are strictly monogamous and show strong site and mate fidelity from year to year. Normally a pair bond dissolves only after one member dies or fails to return in the spring. With an estimated annual adult mortality of 15%, the average life of a pair bond is 3 yr. The sexes share in most aspects of breeding, including brood-rearing, but females abandon both mate and brood about 2 weeks after the chicks hatch. Males apparently incubate at night and sometimes relieve the female at the nest during the middle of the day. In this area Willets defend separate nesting and feeding territories, though nest-site defense decreases through the incubation period. When mates are lost, males retain their original nesting and feeding territories, while females pair with available mates near their original nesting territory. Females compete for mates, and males select the most aggressive females.

Nesting was particularly synchronous in lowland marsh sites, where the onset of egg laying was slightly earlier than in upland sites. Nest density was the highest reported for any scolopacid, and the highest densities were in sites closest to the marsh. Nest spacing is achieved through agonistic behavior, but there is evidence of a counter-tendency leading to nest clumping. Several features of the Willet social system resemble characteristics typical of colonial species of birds. These are discussed along with other aspects of social organization and the selective forces operating on it. Received 26 January 1981, accepted 13 July 1981.

WILLETS (*Catoptrophorus semipalmatus*) nest in two disjunct populations in North America. A western race, *C. s. inornatus*, breeds in low densities in the great plains and intermountain regions of the northern United States and southern Canada. The nominate race, *C. s. semipalmatus*, occupies coastal salt marshes from Nova Scotia to Mexico and, very locally, in the Caribbean. Coastal Willets often achieve much higher breeding densities than inland birds, probably reflecting the combination of limited nesting habitat, predictable food supply, and stable water conditions typical of coastal systems.

Shorebirds have received much attention from biologists during the past two decades because of the diversity of mating systems within the group (Pitelka et al. 1974). Surprisingly, some of the most accessible species, such as the Willet, remain the least studied. No comprehensive studies of the nesting ecology of the western race have been published, although Sordahl (1979) presented a discussion

of its vocal repertoire and ecological correlates. Studies of the breeding behavior and biology of eastern Willets are limited to those of Vogt (1938), Tomkins (1955, 1965) and to a recent investigation of nest-site selection by Burger and Shisler (1978). None of these studies made extensive use of marked individuals. The present study describes, on the basis of observations of marked adults, (1) the spatial and temporal structure of a breeding Willet population, (2) the environmental factors influencing breeding phenology and density, and (3) the roles of the sexes during the nesting period.

STUDY AREA

The study was conducted at the southern end of Wallops Island, Virginia (37°40'N, 75°20'W), one of a series of narrow Atlantic barrier islands paralleling the mainland of southern Maryland and Virginia. Intervening between the mainland and the islands is a complex system of cordgrass (*Spartina alterniflora*) marshes, bays, intertidal creeks, and mudflats. The study site has a particularly well-developed, high

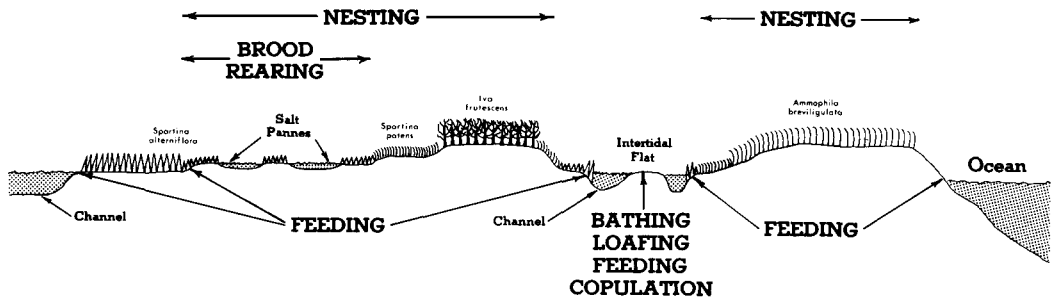


Fig. 1. Schematic cross section of the study area depicting the major habitats and their significance for breeding Willets.

marsh system, consisting of the short growth form of cordgrass, patches of highwater grass (*S. patens*), a mosaic of shallow ponds and flats, and a basically linear zone of low shrubs dominated by marsh elder (*Iva frutescens*). Various parts of the high marsh are flooded during the biweekly spring tides or following strong northeast winds. Although not often influenced by tides during the Willet nesting season, the marsh elder zone can be flooded at unpredictable intervals during severe storm tides. Seaward of the high marsh is a zone of sand dunes sparsely vegetated with dune grass (*Ammophila breviligulata*). The study site is shown in schematic cross section in Fig. 1.

Intensive work was restricted to an area of about 105 ha, which includes intertidal marsh (21 ha), high marsh (50 ha), and a sand dune system (34 ha). About 75% of the dune system has been modified for construction of a roadway, so the vegetation is denser in some areas and sparser in others than on natural dunes. Both the altered and unaltered dunes are immune to all but the most devastating storm tides and are used extensively by nesting Willets. The Willet population under study is part of nearly continuous population, which exists throughout the barrier island system wherever suitable nesting habitat exists.

METHODS

Field work was conducted from late April until late June in 1977, from mid-April to early July in 1978, and from late April to mid-June in 1979. Occasional visits were made outside the main study periods, and some additional information was collected in the spring of 1980.

Nest searches were conducted in two ways. First, two people dragged a 30-m section of rope across all open sites to flush incubating birds. Normally, Willets sat tightly until the rope passed over the nest and then flushed immediately. Second, observers walked systematically and repeatedly through shrubby areas, leaving only the most impenetrable sites unvisited. These and other techniques were

most effective during the hotter parts of the day, when birds showed the strongest attachment to the nest site. I estimate that at least 80% of the nests were located by two such intensive searches during 1978 and 1979 after the techniques had been perfected. A few additional nests were located by accident during the course of work in the study area. About one-half of the short cordgrass habitat in the high marsh was dragged in 1977, but no nests were located. Although I did not search this area in 1978 and 1979, four nests were found in 1980 while I was conducting other work. This suggests that I underestimated the use of this habitat by nesting Willets. The population in this area was small, however, compared with that in other areas less vulnerable to flood tides. Nest locations were marked precisely with a small piece of colored tape, and the general sites of the nests were identified with colored flags 5 m away.

Adults were trapped on the nest by approaching cautiously, finding the marker over the nest, and placing a long-handled landing net over the nest with a sudden horizontal thrust. More than 50% of the nesting adults were trapped in this manner (171 birds over 3 seasons). These birds were then weighed, measured, color-banded on the tibiotarsus with four bands, and marked on the white wing stripe with colored spray paints in a sequence duplicating the color-band combination. The wing markings permitted ready identification of individuals in flight. The first 29 birds trapped in 1977 were also given patagial tags, but all failed to return in 1978. This group probably suffered excessive mortality (Howe 1980) and was not included in survivorship analyses.

Size was a fairly reliable criterion of sex. In 14 pairs, sexed by observation of copulatory position or by examination after subsequent collection, males always weighed less than females. It was, therefore, assumed that the smaller members of pairs were males, despite some weight overlap in the population as a whole. Important conclusions about sex roles, however, were always based on marked birds

sexed either by dissection or copulatory position. Eggs were weighed, measured, and floated (Hays and LeCroy 1971), and the incubation period was determined for some nests. A flotation index was developed so that the approximate date of onset of incubation could be estimated from only one nest visit.

A detailed map of the study area was prepared from low altitude infrared aerial photographs. In 1978 and 1979 the precise locations of many nests were plotted on these maps in the field. The positions of nests remote from recognizable landmarks were plotted later after careful measurements in the field of the distances to other nests or remote landmarks. Observations of individually marked birds were plotted on daily maps, and composites were drawn at the end of each season.

RESULTS

Arrival on the breeding grounds.—Willetts occurring on the Virginia coast in winter probably belong to the western race *inornatus* (Tomkins 1955). Breeding birds of the eastern race rarely arrive before the first week of April. In 1978 and 1979, when I made early visits to the study area, the first Willetts were seen on 8 and 11 April, respectively. A large influx typically takes place during the third week of April. Observations of marked birds suggest that most experienced breeders arrive before the end of April (48 of 70 marked birds were found by 24 April 1979; many of those found later could easily have been overlooked). Flocks of Willetts migrating north during the first half of May may be composed of breeding adults from higher latitudes but probably include many younger birds on their first northbound migration. No direct evidence of age-related differences in migration schedules was obtained in this study.

Although there is no apparent difference in the spring migration schedules of adult males and females (18 of 30 marked birds located prior to 20 April 1979 were females, $\chi^2 = 0.6$, n.s.), paired birds from the previous year do not necessarily arrive together. This was concluded on the basis of repeated observations of marked birds without their mates over a period of days and of marked birds courting new birds but later pairing with their former mates. Because paired birds depart separately after breeding season, it seems unlikely that they would arrive together in the spring, particularly as there is no evidence of pair association or formation by Willetts on the winter-

ing grounds (Tomkins 1955, Kelly and Cogswell 1979).

Occupation of feeding territories.—Shortly after arriving, adult Willetts reoccupied feeding territories used during previous years. Although feeding territories were sometimes contiguous with subsequent nesting areas, as previously described for eastern Willetts in Delaware Bay (Vogt 1938), they were more commonly separated from the nest area by as much as 500 m. A similar situation prevailed in the Georgia population studied by Tomkins (1965). Whereas separation of feeding and nesting areas is probably necessitated by the relatively abrupt transition between suitable nesting and feeding habitats on Wallops Island, the expansive, highwater grass meadows of Delaware Bay apparently permit both nesting and feeding within one territory (Vogt 1938). The structural and vegetational heterogeneity of the area is shown in Figs. 1 and 2.

The typical feeding territory of a pair is a patch of cordgrass along a tidal creek ranging from deep water (accessible only at low tide levels) to higher ground at the transition to short cordgrass, highwater grass, or dune grass. Fiddler crabs (*Uca* spp.) are the prey most often taken by Willetts in this habitat. We could usually identify these and other prey while they were being handled. A few pairs defended linear feeding territories as long as 70 m along the outer sandy beach, where mole crabs (*Emerita talpoida*) were taken in the wave-wash zone. Both members of pairs use the full range of feeding sites within the feeding territory. When both are present simultaneously, they usually feed apart. If the female passes close to her mate while he is carrying a food item, she may threaten, causing the male to drop the item. Generally, however, hostile interactions between members of well established pairs are infrequent, and there is no indication of spatial partitioning of the feeding territory. Although both sexes defend the territory against conspecifics, using a variety of vocal and visual aggressive displays (see descriptions in Vogt 1938, Howe 1974), my observations suggest that males take a much more active role in defense when both birds are present. In one instance, however, I watched a female fly in and vigorously attack an intruder that was involved in a hostile standoff with her mate.

In addition to exclusive feeding territories

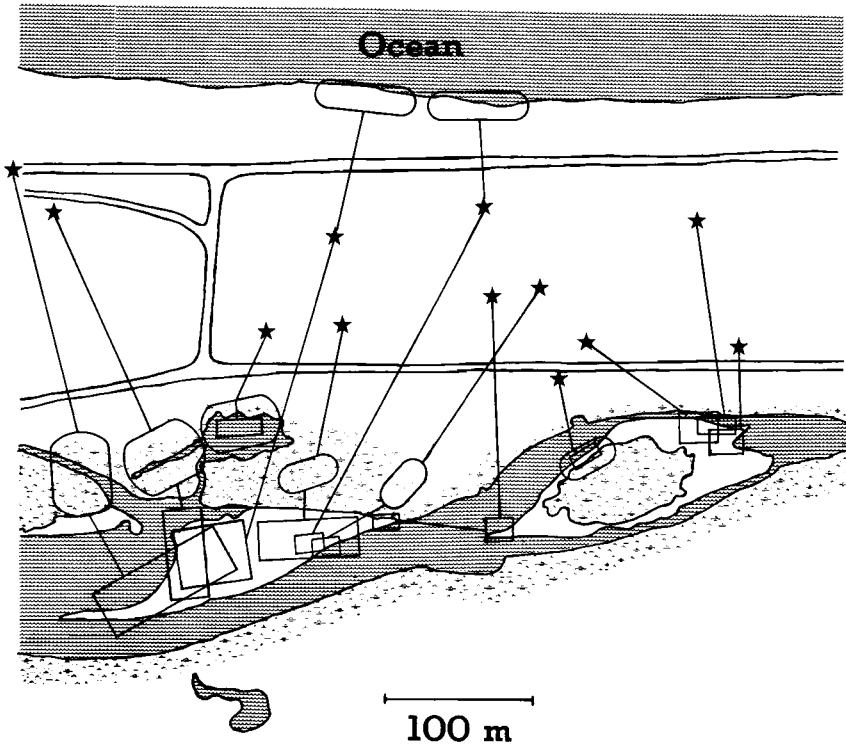


Fig. 2. Map of a portion of the study area showing the spatial relationships of nest sites (stars), feeding territories (with curved boundaries), and bathing/loafing sites (rectangles) of Willet pairs. Stippled areas represent cordgrass along a tidal creek. Clear areas within this zone represent intertidal flats. Clear areas between the creek and the ocean are dunes and disturbed upland sites. Nests are shown only for those individuals for which the locations of feeding or loafing sites could be ascertained.

with fixed boundaries, many pairs share open intertidal mud- or sandflats with other breeding birds during periods of low tide. These areas are used primarily for bathing, loafing, and copulation, and only casually for feeding. Pairs consistently use specific sites on mudflats, but much spatial overlap occurs, especially at high water levels when the exposed areas are small. Furthermore, there is considerable turnover of individuals during the period of mudflat availability, and birds representing different breeding pairs may occupy the same sites at different times.

Intertidal flats could be described as communal multipurpose sites were it not for the variable patterns of site defense shown by the birds using them. At times individuals defended an area up to 30 m or more in radius, while at other times "intruders" were tolerated at very close range. The dynamics of space utilization by Willets on intertidal flats are com-

plex and merit further study, using marked individuals. It should be emphasized that marked resident Willets were rarely observed feeding outside of their traditional feeding territories. A segment of the study area in which the feeding territories and bathing and loafing areas are plotted for several pairs is shown in Fig. 2. These maps were generated by combining the daily plots for these birds over a 3-yr period.

Pair formation.—Because all marked birds were breeding adults trapped on the nest, there was little opportunity to study the behavior of individuals known to be pairing for the first time. As more and more of the breeding population was marked, however, contrasts in the behavior patterns of marked and unmarked individuals could be interpreted with increasing certainty as differences between paired and unpaired birds. This interpretation of certain behaviors was later corrob-

orated by changes observed in the behavior of marked birds that lost their mates. The greatest difficulty was in distinguishing male behavior from female behavior, because positive sex identification of unmarked birds was possible only when precopulatory displays were incorporated into behavioral sequences. Many of the common displays have been described elsewhere (Vogt 1938; Tomkins 1955, 1965; Howe 1974; Sordahl 1979) and are not reported in detail here. Several behavior patterns that clarify some important elements of the social system of the species, however, are described briefly.

A major difference between paired and unpaired birds is in the performance of aerial displays (Vogt 1938). These displays reach heights of 100 m or more, cover broad areas irrespective of territorial boundaries, and occur frequently from spring arrival until well into the brood-rearing period. Despite having wing-marked more than 60 breeding birds and observing more than 100 aerial displays in 1979, I never observed a marked bird participating in this activity. Because all marked birds were paired, I tentatively concluded that aerial displays are given only by unpaired birds. The possibility remained, however, that paired birds perform aerial displays before nesting, at which time the wings are unmarked.

In late April 1980, I therefore made a special effort to locate color-banded individuals among aerial display participants before nesting was initiated. Only two marked males were found giving displays. The marked mate of one of these had apparently not returned, as she was not seen at all during the season. This male eventually paired with an unmarked female. The former mate of the other male was present on the study area but had already paired with a different male. This evidence supports the hypothesis that aerial displays function in mate-attraction and are performed only by unpaired birds. This interpretation conflicts with Vogt's (1938) contention that breeding adults continue to perform aerial displays throughout the nesting period.

Vogt's (1938) conclusions about sex roles in aerial displays are supported by my observations. Males perform the displays. A responding female flies up toward the male, hovers underneath him, engages in vocal duetting, and then follows the male back to the ground

in a slow descent, both birds holding the wings high above the body and quivering the primaries. The sexes of unmarked birds could often be determined from subsequent precopulatory behavior or judged on the basis of relative sizes and plumage richness. I never observed females initiating aerial displays.

Aerial displays often terminate in sites suitable for nesting, and hostile encounters with other birds may result. Because such encounters rarely convey clear dominance by the displaying male and because repeated flights by a single male often terminate in different areas, it seems likely that nesting territories have not yet been selected by many males during the period in which aerial displays are performed. Experienced males maintain their nesting territories after mate loss (see below) and probably convey territorial dominance to females in the process of mate selection.

The interactions among birds after an aerial display are complex, especially if more than two birds are involved. Individual identities quickly become obscured in a flurry of rapid movements, threats, agonistic posturing, inciting behavior, fragmented nest-site selection behavior, and loud, persistent vocalizations (most displays described by Vogt 1938, Sordahl 1979). These courting groups also attract other Willets that were not participants in the original aerial display.

A few fortuitous observations of known-status, marked individuals provide insight into the significance of these courting groups. The mate of female YG-YX, for example, did not return in 1979. On 22 April YG-YX was first observed associating with an unmarked bird (U1, presumably male) in a potential nesting area about 150 m from her nest of the previous year. A second unmarked bird (U2, presumably female) appeared, eliciting threats from both YG-YX and U1. Several times YG-YX chased U2 in flight, but U2 continued to return to the vicinity of U1. Similar sequences continued over a period of several hours, with YG-YX typically the aggressor against U2. Gradually U2 became more aggressive toward YG-YX, threatening her in a crouched posture and repeatedly landing near U1. Threats toward U2 by U1 gradually diminished over this period and then ceased. The interaction culminated with a fight between U2 and YG-YX, in which each bird grasped the other's leg,

neck, or wing with the bill, essentially immobilizing each other at one point for a period of 18 min. During this fight, U1 stood close by giving occasional "kip" calls and directing threats at one of the other two. Eventually U2 was successfully supplanted by YG-YX. The next day YG-YX associated amicably with U1 in the same area and repeatedly perched on a high pole, giving territorial calls ("pill-will-willet," Bent 1929) to intruders. YG-YX was later collected and the sex verified as female. The same week a similar incident occurred in which a marked female fought repeatedly with an unmarked female that had paired with her mate of the previous year. Again, the male showed little aggression as he stood nearby and kipped. The original mate succeeded in supplanting the new female and later nested with her former mate. These observations demonstrate the occurrence of competition among females in the pair-formation process and suggest the possibility that much of the aggression in groups of Willets after an aerial display represents competition between females for the displaying male.

Occupation of nesting areas.—When pair bonds have been established, pairs spend more and more time exploring suitable nesting areas. On Wallops Island most vegetated sites above the normal intertidal zone were potential nesting sites, including, to a small degree, the areas of short cordgrass that are vulnerable to moderate flood tides. The preferred areas (Fig. 1) were the zone of highwater grass bordering groves of marsh elder, partly open areas within the elder, sand dunes vegetated with dune grass, and disturbed upland sites partly vegetated with a mixture of grasses and scattered small shrubs, e.g. marsh elder and wax myrtle (*Myrica cerifera*). The cordgrass, highwater grass, and marsh elder zones are hereafter referred to collectively as lowland sites, because they border the marsh and are vulnerable to extreme tides. Dunes and disturbed areas are termed upland sites, because they are essentially immune to tidal influence.

Before selecting a nest site, pairs often fly from the marsh or beach and land in potential nest areas. During these exploratory flights, both birds often quiver their wings below horizontal like a male in aerial display and then raise the wings and give "pill-will-willet" calls as they slowly descend to the ground. Pair

members then usually wander through the grass performing nest-scraping behavior similar to that described for other Charadrii. I have not observed nest-site selection in detail.

During this stage Willets actively defend the potential nest area with the same vocalizations and other threat behaviors used in defense of feeding territories. Males perform most of the defense, frequently giving "pill-will-willet" calls to other Willets flying over. Strongly paired birds generally supplant single intruders that land nearby but often tolerate neighboring pairs at close range. Possibly these birds are recognized individually and their presence accepted as a result of previous encounters. Nest defense subsides markedly when incubation begins. This happens in part because the nonincubating bird must leave periodically to feed, and it suggests that mate guarding may be the primary function of defense near the nest site.

Precopulatory behavior and copulation occur as soon as birds arrive and continue through the egg-laying period. Precopulatory displays are often performed by unpaired males early in courtship, though copulation rarely results. Established pairs normally copulate on the intertidal flats shared with other Willets. More rarely, birds may copulate in the feeding or nesting territory. As pointed out by Sordahl (1979), Willet copulations involve extremely conspicuous wing-flashing and loud, persistent calling audible up to 500 m. Although Willets show no apparent response to copulations of nearby pairs, the frequency of copulations on mudflats suggests a "contagiousness" similar to that found in gulls and terns (*Larus delawarensis*, Southern 1974; *L. atricilla*, Burger 1976; *Sterna hirundo*, Gochfeld 1980).

Temporal distribution of nesting.—The onset of nesting was highly synchronous, with the first eggs being laid 1.5–2 weeks after the peak arrival period. The temporal distribution of first eggs in 1978 and 1979 is shown in Fig. 3. In 1979 nesting began earlier and appeared more synchronous than in 1978, when high water delayed nesting in over one-third of the lowland habitats. This fact alone may account for the greater spread of nesting in that year. In both years about 84% of the nests were initiated within a 2-week period.

In each year there was evidence of a secondary peak of nest initiation 2.5–3 weeks after the

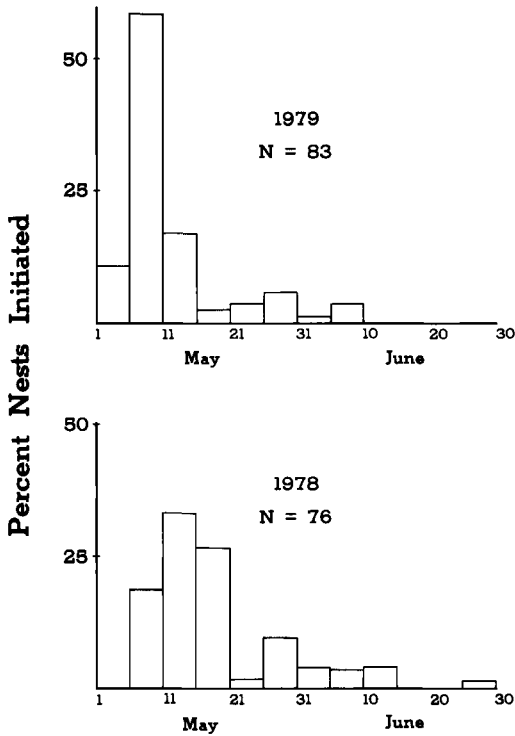


Fig. 3. Frequency distributions showing the timing of first eggs in Willet nests in 1978 and 1979.

first. A similar bimodal pattern was found in the Georgia Willet population studied by Tomkins (1955), who presented information for 91 nests over 50 yr. The correspondence between these results suggests that the second peak is real, probably representing either replacement clutches or delayed breeding by younger birds. Among other scolopacids, secondary peaks have been observed in populations of Dunlin (*Calidris alpina*, Holmes 1966, 1971a) and Western Sandpiper (*C. mauri*, Holmes 1972). Holmes showed that replacement clutches accounted for at least some of these late nests, but the possibility of first breedings by young males could not be ruled out. Data for Stilt Sandpipers (*Micropalama himantopus*, Jehl 1973) showed no secondary peaks but revealed a broader spread and later nest initiation among new pairs. I was unable to distinguish first-time breeders from experienced breeders. The possibility that the secondary peak in Willets is a result of replacement clutches is supported by three instances of renesting by marked individuals. The inter-

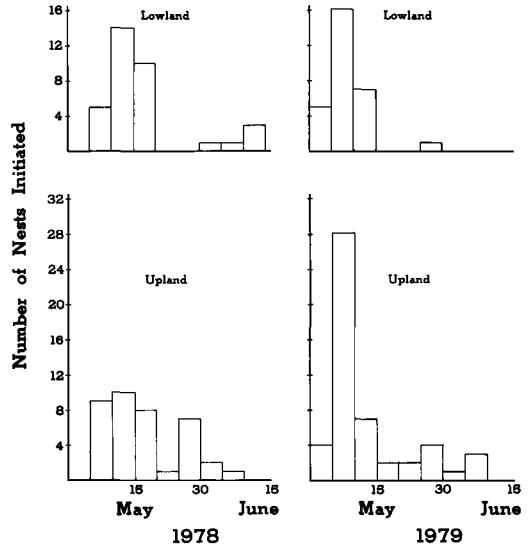


Fig. 4. Frequency distributions showing the timing of first eggs in Willet nests in 1978 and 1979, partitioned by habitat type. Upland nests include those in vegetated dunes and disturbed sites. Lowland nests include those in marshy sites and in the marsh elder zone bordering the marsh.

val between the loss of the first clutch and the laying of the first egg of the replacement clutch was a minimum of 10 and 13 days in two instances and exactly 12 days in the third.

There is some evidence that birds with lowland territories nest more synchronously than upland birds (Fig. 4). In 1979, median laying dates in the two habitats were significantly different (Mann-Whitney *U*-test, $Z = 2.18$, $P < 0.02$). This difference was primarily a function of a proportionately greater number of late nesters in the upland, rather than an indication of a temporal difference in the onset of nesting. Because of the late burst of lowland nesting due to early flooding in 1978, the difference between lowland and upland was not significant in that year. I suspect that the late upland nesters were composed largely of inexperienced birds, although I found no mensural or plumage differences between those and earlier nesters. The presence of inexperienced birds in upland sites was also suggested by data presented below on nest-distribution patterns.

Spatial distribution of nests.—I have indicated that pairs defend a nesting area, but the level of hostility toward conspecifics varies and ap-

TABLE 1. Nearest nest distances (m) as a measure of nesting density in three habitat types used by Willets in 1979.

Habitat	Num- ber of nests	\bar{x} inter- nest distance (m)	SD
Lowland (marsh sites)	18	21.1	10.7
Upland (natural dunes)	10	45.1	28.8
Upland (disturbed sites)	41	29.9	19.1

pears to decrease during the period of incubation. This is a common pattern among scolopacid sandpipers that nest in open habitats, e.g. Greenshank (*Tringa nebularia*, Nethersole-Thompson 1951), Redshank (*T. totanus*, Grosskopf 1958), Black-tailed Godwit (*Limosa limosa*, Lind 1961), Western Sandpiper (Holmes 1971b), and Least Sandpiper (*C. minutilla*, Miller 1979). The absence of persistent territorial defense results in a pattern of nest distribution that is not clearly overdispersed, as might be expected in highly territorial nesters. For example, one nest was established only 3.6 m from another in which incubation was 2 weeks advanced. The smallest inter-nest distance among nests established about the same time was 12 m.

Over the entire study area, nest density (including all nests except re-nests, regardless of initiation time) was extremely high (Table 1). If inter-nest distances are converted to areal densities, densities ranged from 4.8 nests/ha to 24.8 nests/ha. The highest density previously reported in the literature for a scolopacid sandpiper appears to be 7.5 nests/ha in an Alaskan Western Sandpiper population (Holmes 1971b). Densities were greatest where vegetation structure was most complex (patches of marsh elder and highwater grass) and lowest where vegetation was sparse and relatively homogeneous (sand dunes). Zones of intermediate complexity had intermediate nest densities (Table 1). While these differences may reflect degrees of habitat preference, they may result naturally from variation in site defense capability as a function of horizontal visibility.

There was some evidence that social attraction may lead to high local nest densities under certain conditions. In 1977 only one nest was found in a 12.5-ha area of disturbed upland habitat. The next year 19 nests were found here, 11 of which were packed into a 1.2-ha portion of the area. Because at least 60% of this

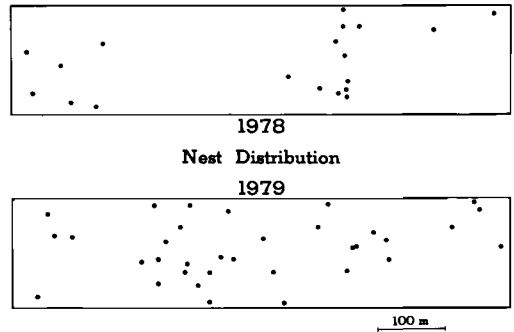


Fig. 5. Dispersion pattern of nests in 1978 and 1979 in one of the disturbed upland sites.

disturbed area appeared similar to nearby sites where Willets nested, the cluster of 11 nests could not be explained solely on the basis of microhabitat variation. Included among these 11 pairs was a marked bird that had abandoned its lowland territory of the previous year because of flooding. In 1979 a new group of 15 unmarked pairs nested in an adjacent site that had not previously been used (Fig. 5). Because these birds were unmarked, it is likely that many were first-time breeders. These patterns of settlement in 1978 and 1979 suggest that birds nesting in an unfamiliar area (whether translocated adults or first-time breeders) tend to aggregate rather than space out uniformly or randomly through the available habitat.

Sex roles during incubation.—Both sexes were found to share incubation throughout the incubation period. As one bird incubates, the nest area is often left undefended as the other occupies the feeding territory or loafing area. Multiple observations of each member of a pair in the feeding territory during the same day suggested that nest exchanges may take place during daylight hours. During 1978, when most nests were visited several times, we therefore noted the identities of marked birds flushed from the nest. The results of these samplings (Fig. 6) show a pattern of high nest attendance by females early in the morning followed by an increased likelihood of male attendance between 1000 and 1600. Birds incubating late in the day were always males. This suggests that males generally incubate at night, are relieved by the female early in the morning, and sometimes relieve the female during the middle of the day. There was no

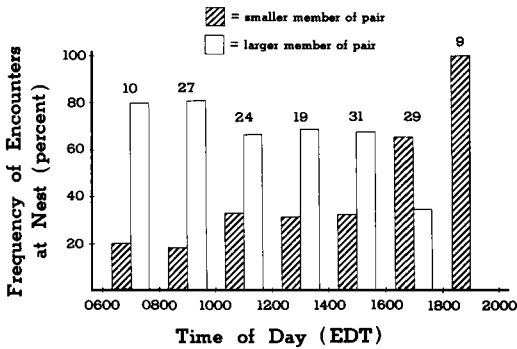


Fig. 6. Diurnal pattern of nest attendance during incubation. The smaller members of pairs have a high probability of being males. Data are based on identities of marked birds flushed from nests throughout the study area at different times of the day (EDT). Sample sizes are indicated for each 2-h block.

evidence of a changing pattern of sex roles during the course of incubation.

The incubation period was determined to be 25.2 ± 1.2 days from the laying of the last egg to the hatching of the last egg ($n = 8$).

Brood-rearing.—The normal pattern of hatching in 4-egg Willet clutches is for three eggs to hatch within a period of several hours and the fourth to hatch about a half day later. On the day of hatching, or the following day if hatching takes place late in the day, broods are led by both parents to the rearing site. This site is often separate from the parental feeding territory. On Wallops Island, many broods were taken to any of several large shallow ponds in the high marsh zone. Like tundra pools, where broods of many other shorebirds species are raised (e.g. Holmes and Pitelka 1968, Baker and Baker 1973), these ponds are often teeming with adult and larval dipterans during the principal hatching period. One such pond was used by at least six pairs with broods.

I made few observations of chicks, because they are extremely difficult to find and observe without long-term commitment to a blind. I did, however, make regular visits in 1978 to brood-rearing sites to document the presence of marked adults showing brood-defense behavior. From these observations, composite maps were drawn to show the temporal and spatial distribution of parent birds. Most adults exhibiting brood defense could be re-located at the same site through the period of

chick growth, which was about 4 weeks (based on the difference between the time of the first nest hatch and the first observation of flying young). A few pairs moved their broods after 1 or 2 weeks to a different area. Brood rearing sites for several pairs are shown in Fig. 7. Although the maps indicate some overlap of broods, chick locations could not be determined precisely from the behavior of the adults. Considerable overlap is probable, however. At one high marsh pond (the most permanent shallow pond over the 3 yr), at least 10 pairs showed simultaneous brood defense. Mendenhall (1970) found that western Willets defend exclusive (though somewhat mobile) territories around chick feeding areas throughout the period of chick growth. More detailed observations on Wallops Island might reveal a similar pattern.

The distance that broods must travel from nest to rearing area may be an important factor in chick survival. Birds nesting in the disturbed upland sites needed to cross a tidal channel to reach the high marsh. I once observed a Willet chick taken by a Laughing Gull (*Larus atricilla*) as it swam across the channel. On another occasion a chick was attacked by an adult Willet as it traveled through the adult's territory. Young chicks are clearly vulnerable to predation as they cross open areas. This fact should result in selection favoring placement of nests as close as possible to the chick-rearing area, but such selection must be balanced against the risk of tidal flooding and raccoon predation (see below) in lowland sites. Lowland nests of marked birds were significantly closer to rearing sites ($\bar{x} = 176$ m, $n = 6$) than upland nests ($\bar{x} = 404$ m, $n = 18$, Mann-Whitney $U = 28.0$, $P < 0.001$).

Both parents attend the young during the first 2 weeks of life. Usually the male is the more vocal and aerially defensive member of the pair, but the female also performs these displays. Observations of aerial defense by one parent while the other gives "kip" calls up to 100 m away suggest that broods are sometimes divided between the parents. Frequently, however, one parent flies to the feeding territory while the other attends the chicks. Brood attendance by females declines gradually until females completely desert broods between 2 and 3 weeks after hatching ($\bar{x} = 16.2 \pm 5.9$ days, $n = 12$). At the same time (as early as the third week of June) small flocks of Willets ap-

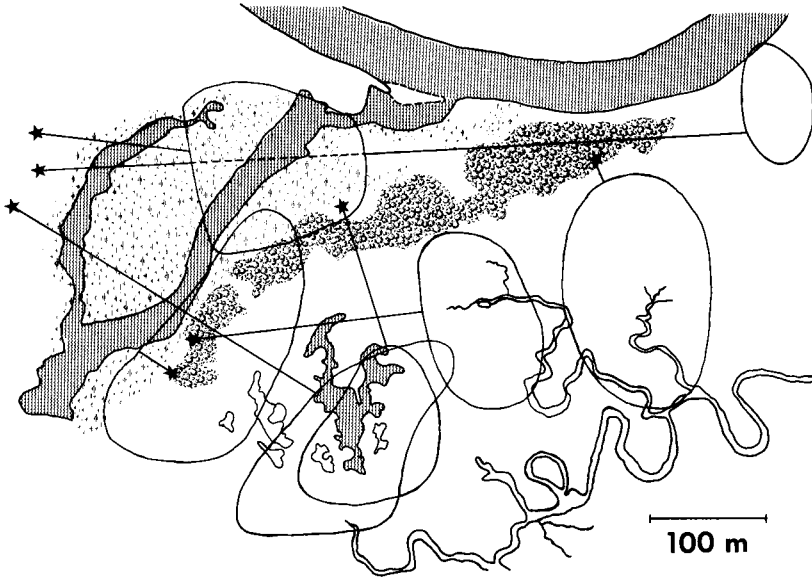


Fig. 7. Map depicting brood-rearing sites of marked pairs in relation to the nest site (stars). Most sites are in the high marsh zone, some including intertidal creeks. Shrubby symbols indicate marsh elder.

pear along the outer beaches, suggesting an early staging for southward migration by adult females. In 10 marked pairs followed in 1978, the male attended the brood for at least 2 weeks after the female departed.

Reproductive success.—In 1977 raccoons (*Procyon lotor*) were abundant on the study area, and some evidently followed my trails to nests. One nest, which I discovered while the eggs were hatching, was taken by a raccoon within $\frac{1}{2}$ h of my initial visit. I suspect that raccoons were responding both to my scent trail and to the alarm calls given by adults after flushing from the nest. Evidence of raccoon predation was found only in lowland sites and in dunes adjacent to tidal channels. All lowland nests were taken by either raccoons or Fish Crows (*Corvus ossifragus*) ($n = 45$). Most of the 21 upland nests found in 1977 were taken by a resident red fox (*Vulpes vulpes*) and only one hatched. Thus, only one of 66 nests (1.5%) was successful in 1977. The presence of several adults and broods from undiscovered nests further suggested that nest predation was enhanced by my nest visits.

In 1978, following an extremely cold winter, there were no red foxes and very few raccoons on the study area. Of 77 located nests, 36 (47%) hatched successfully. Thirty-three (43%) were

taken by predators, principally Fish Crows. In 1979, 11 of 83 nests (13%) hatched. Twenty-five (86%) of the lowland nests were lost to a pack of feral dogs, and a torrential rainstorm at the end of May caused desertion of 16 (31%) of the upland nests, all in the disturbed habitat on a relatively impermeable clay substrate.

In view of my own influence on nest predation and the presence in one year of introduced predators (feral dogs), no quantitative conclusions about normal environmental effects on nest loss can be drawn. It is clear that Fish Crows actively search for Willet nests and are important predators. Moreover, raccoons and foxes are capable of inflicting serious losses in some years. Tidal flooding is a potential threat to lowland nests but was not a crucial factor in the 3 yr of this study. Chick survival could not be determined because of the extreme difficulty of locating broods in the marsh vegetation.

Variability across years: survivorship and mate/site fidelity.—The most thorough searches for returning marked adults were made in 1978 and 1979. The results of these surveys (Table 2) show that adult survivorship is high, despite an annual migration of several thousand miles to and from northern South America. Four (18.2%) of the 22 birds marked in 1977 were

TABLE 2. Return rates of marked adult Willets in successive years.

	Num- ber	Returns in 1978	Returns in 1979
Birds marked in 1977	22	14 (63.6%)	11 (78.6%) ^a
Birds marked in 1978	71	—	54 (76.1%)

^a Excludes four of the original 22 that were undetected in 1978 but present in 1979.

not found in 1978 but returned in 1979. This suggests that (1) individuals occasionally fail to migrate north in some years; (2) these birds were present but undetected in 1978; or (3) experienced breeders sometimes emigrate to other breeding areas. Emigration seems unlikely in view of the strong site fidelity of experienced breeders (see below). Because some marked birds go undetected for one reason or another, actual adult survivorship may be higher than indicated in Table 2.

Mate fidelity from one year to the next was high over the entire study period, indicating that Willets typically pair for life. Both of the pairs marked in 1977 remained together in 1978, and 17 of 18 pairs marked in 1978 were observed together in 1979. Only one case of divorce was detected during the study. In all other cases of re-pairing, the mate of the previous year had apparently failed to return. In one instance described above, a marked bird obtained a new mate, which was later replaced by the original mate. This probably occurred because of disparate spring arrival times of the pair members. A similar situation probably led to the one substantiated divorce. With such a stable pair bond, the life of a pair is essentially a function of survivorship. If an age- and sex-independent survivorship rate of 85% among breeding adults is assumed, the average life of a Willet pair bond is 3 yr.

Fidelity to feeding territories and nesting areas was similarly high. All marked pairs reoccupied precisely the same feeding territories used in previous years. Nest sites were moved short distances each year but were almost always in the same limited area and in similar spatial orientation to the nest sites of neighboring marked pairs. The single exception to this involved a marked male that moved to an upland site when his nest area of the previous year was flooded.

The distances that nest sites were moved

TABLE 3. Distances (m) between successive nests of marked Willets in 1978 and 1979.

Status of individual	n	\bar{x} distance (m)	SD
Mated to same bird	9	62.4	38.2
Mate status unknown	10	34.4	29.7
♀ mated with new ♂	2	281.0	100.7
♂ mated with new ♀	2	25.8	33.6
♂ returned after 1-yr absence	1	507.7	—

varied more among the few marked birds known to have changed mates. One male that failed to return in 1978 was found in 1979 nesting with a new mate some 500 m from his original nest. Other males that changed mates in successive years were repeatedly observed in their former nesting area, and two nests were located 2 m and 70 m from the previous year's site. The evidence, therefore, suggests that nest-site tenacity persists among males, regardless of mate changes. In contrast, females apparently abandon their former nesting areas after mate loss and re-pair with neighboring territorial males. The choice of nest site in these instances is probably limited to the area defended by the new male. The average distances between nests in successive years is shown in Table 3 for birds with various pairing histories.

DISCUSSION

The key elements of social organization.—Observations of marked individuals during three breeding seasons show the Willet breeding system on Wallops Island to be characterized by four general patterns:

1. Strong pair bond. Willets are strictly monogamous, pair for life, and both sexes share in all nesting and brood-rearing activities, including territory defense. Barring the death of one pair member, pair bonds normally remain intact irrespective of reproductive success.

2. Strong site fidelity. The most strongly defended area is an intertidal feeding territory, which is maintained from year to year. Nest areas are also traditional, but their defense is more variable. Males apparently determine the location of feeding and nesting areas. Broods are led to traditional brood-rearing sites, usually different from the adult feeding territory. Spatial and temporal stability is probably enhanced by high adult survivorship.

3. High nest density. The nest density on Wallops Island is the highest reported for any scolopacid. This probably results in part from the physical separation of a large area of suitable feeding habitat from a relatively small area of safe nesting habitat. The higher nest density in lowland sites may indicate a preference for these areas, which are usually closer to feeding and brood-rearing areas than upland nests. There is evidence for aggregation of nests in newly occupied areas, independent of habitat variation.

4. Nesting synchrony. In both upland and lowland nesting sites, most nests were initiated over a period of 1.5–2 weeks in early May. There were more late nestings in upland habitats, suggesting the possibility that the proportion of first-time breeders is higher in the upland population.

Data available on other species in the scolopacid subfamily Tringinae (e.g. Nethersole-Thompson 1951, Grosskopf 1958, Lind 1961, Kirchner 1963) indicate a strong conservative trend (*sensu* Pitelka et al. 1974) throughout the group. Monogamy, biparental care, and territoriality prevail in most species, the Spotted Sandpiper (*Actitis macularia*) being a significant exception in exhibiting multiple clutch production and polyandry when food is abundant (Hays 1972, Oring and Knudson 1972). The Willets examined in this study conform to the basic tringine pattern in the roles of the sexes, but they achieve nest densities more typical of colonial species of birds. In most respects, the Willet breeding system closely resembles that of American Avocets (*Recurvirostra americana*), although paired Avocets occasionally copulate with other birds and their nesting is not particularly synchronous (Gibson 1971).

Pair and site fidelity.—Because so many departures from monogamy occur among scolopacids, the strong monogamous pattern in Willets suggests selection against a multiple mate strategy. This hypothesis is strengthened by the observation that pairs remain together over several seasons regardless of reproductive success in the previous year. In some gulls and shearwaters the likelihood of divorce is an inverse function of reproductive success (Coulson 1972, Mills 1973, Brooke 1978). The only divorce in the present study occurred in a pair that had successfully hatched young in the two previous nesting seasons. From an evolution-

ary perspective, it thus becomes necessary to explain why Willets are limited to monogamous matings.

Several aspects of the Willet breeding system point to factors that might select for monogamy. Segregation of chick and adult feeding areas should constitute an overwhelming selective force for biparental care (and, secondarily, monogamy), because chicks would otherwise be abandoned each time the parent left to feed. The majority of the Willets in the present study had separate feeding and brood-rearing areas, although the degree to which adults were dependent upon their feeding territories after the chicks hatched could not be ascertained. Selective collecting of parent birds shortly after hatching would probably be necessary to evaluate the impact of uniparental care on chick survival. A reasonable likelihood that one parent can raise at least some of the chicks could be a sufficient condition for the evolution of a multiple nesting strategy. Other possible post-hatching constraints, such as unusual brooding requirements or a need to protect chicks from intraspecific predation in crowded rearing sites, would seem to be inadequate to drive a system of obligate monogamy.

Constraints operating earlier in the nesting period are perhaps more powerful. Year-to-year fidelity to feeding territories indicates that Willet prey populations are defensible but limited (Carpenter and MacMillen 1976). Willets feed on large prey, which occur at lower densities than, for example, the dipteran larvae constituting the bulk of the diets of arctic sandpipers (Holmes and Pitelka 1968, Baker 1977). Willets may therefore require prolonged feeding bouts to maintain a positive energy budget. The daylength at the latitudes at which Willets nest places further limits on the flexibility of the feeding schedule. The patterns of nest attendance (Fig. 6) indicate that females are often replaced at the nest by males during the middle of the day. If feeding constraints are such that an incubating bird must leave the nest during the day for extended periods, the eggs are at risk from exposure to the sun (as well as predation), and selection should strongly favor biparental incubation.

Selection for monogamy notwithstanding, pair bonds are eventually terminated by the death of one pair member and rematings become necessary. One study of another long-

lived monogamous species, the Manx Shearwater (*Puffinus puffinus*), has shown that, among new pairs, the matching of experienced breeders with other experienced breeders occurs more frequently than chance would predict (Brooke 1978). Evidence from the present study indicates that males that have lost their mates retain their original feeding and nesting territories and permit (or solicit) potential new mates into the nesting territory. If two females enter a single male's territory, the male stands by passively, occasionally threatening the subordinate female, while the females compete for dominance. Ultimately, the male accepts the more dominant female as his mate. A formerly paired female, being experienced in territory defense, should have a competitive advantage over females attempting to pair for the first time in these situations. Simple dominance relationships among females, therefore, provide a mechanism by which a male can assess the breeding experience of a potential mate. Likewise, by seeking out males established in territories, females maximize their chances of obtaining experienced males. Because mateless females apparently move only short distances to obtain new mates (Table 3), it is also likely that many rematings involve birds already known to each other. This should further increase the probability of experienced birds pairing with experienced mates and augment breeding potential (Davis 1976).

Use of space.—On Wallops Island feeding and nesting areas were usually separate. While defense of the nest area subsided considerably after incubation began, feeding territories were defended persistently throughout the nesting season. This suggests that an exclusive feeding area is the most critical resource for breeding Willets and that persistent defense of multipurpose territories, as found elsewhere in the breeding range (Vogt 1938), is related primarily to food resources. Nest-area defense by males early in the season on Wallops Island is probably in large part an anti-cuckoldry mechanism.

Territorial behavior around the nest does, however, persist at low levels through the incubation period and is performed by females as well as by males. This implies that functions other than mate guarding may also be important. The most obvious of these is reducing the probability of nest predation by increasing in-

ter-nest distance. Because my visits to nests increased predation rates in 2 of the 3 yr, I cannot directly examine the relationship between predation and nest density. Nonetheless, indirect evidence for adaptive, antipredator nest spacing was obtained on a small nearby island that I visited briefly in 1978. Although the nesting habitats on this island were similar to those on Wallops Island, nest density (not measured precisely) was nearly double that of the most densely populated lowland sites on Wallops. In marked contrast to Wallops, here I failed to find evidence of nest predation, terrestrial predators (tracks, scats, broken eggshells), or antipredator behavior by Willets, and concluded the area was essentially predator-free. This observation suggests that Willet nest densities, territorial behavior, and local predator abundance are functionally interrelated. The waning of defense during incubation may reflect a lowered incidence of predators when the conspicuous activity of the nest-initiation period has subsided.

Attenuated territorial behavior during incubation may enable late-nesting birds to settle in optimal habitat from which they would have been excluded earlier. Such a mechanism may partly account for the high nest densities reached in many areas. The apparent clustering of upland nests in 1978 (Fig. 5), however, suggests that an active social attraction may also produce high nest densities, at least among birds occupying an unfamiliar area. This possibility prompts the question of whether or not Willets might derive benefits from nest packing. The most likely benefit would be enhancement of predator-mobbing effectiveness. Willets commonly hover over terrestrial predators, giving loud antipredator calls (Sordahl 1979). They also mob and dive at Fish Crows flying over the nesting or brood-rearing areas. Although mobbing is doubtfully an effective deterrent to terrestrial predators, the hunting efficiency of Fish Crows is certainly reduced when they attempt to avoid harassing Willets. Final nest-dispersion patterns may, therefore, reflect varying degrees of compromise between tendencies to space out against terrestrial predators and to aggregate to facilitate mobbing of aerial predators.

Many attributes of the Willet breeding system are more commonly associated with colonial species of birds. Mobbing, for example, is

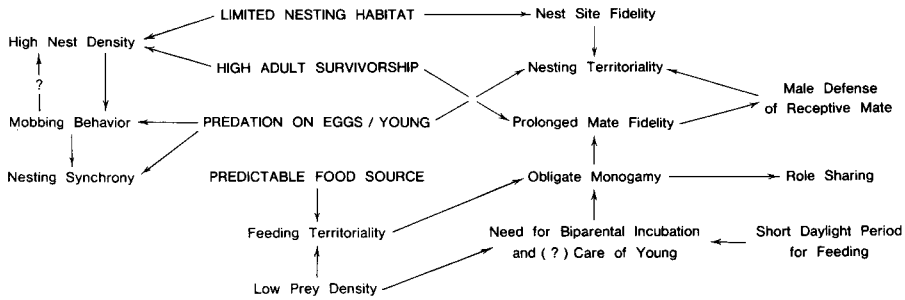


Fig. 8. Flow diagram showing hypothesized relationships between key selective forces (boldface) and significant features of the Willet social system.

a typical antipredator response of colonial nesters. Mobbing should be most effective when large numbers of birds participate. In colonial species this is ensured by synchronous nesting, which carries the additional benefit of reducing risk to individual nests through predator satiation (Darling 1938, Gochfeld 1980). The Willets studied here not only nested synchronously (Figs. 3, 4) but also nested in such dense concentrations that predator satiation arguments could conceivably apply. Furthermore, Willets have extremely conspicuous copulatory behavior (Sordahl 1979). This is a feature shared by many colonial gulls and terns in which copulations are socially facilitated (Southern 1974, Burger 1976) and believed to promote synchronous nesting (Southern 1974, Gochfeld 1980).

Considering these characteristics collectively, eastern Willets may be the most "colonial" of all scolopacids. There is, however, no evidence of unique selection for synchronous nesting or other behavior patterns in Willets as a result of nesting in high densities. It is important to note that many solitary species exhibit some of the same attributes. For example, mobbing occurs in many of the larger species of Charadrii (Sordahl 1981), and very conspicuous copulations are typical of most tringine sandpipers (L. Oring, pers. comm.). It is perhaps unfortunate that the somewhat arbitrary classification of species as either colonial or solitary may have stifled insight into the adaptiveness of many individual and population traits. A more enlightening approach may be to examine the distribution of these traits along continua of related species (or populations) with different characteristic nesting densities.

Figure 8 presents a flow diagram of hypothesized relationships between key selective forces and the Willet social system.

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