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Aspects of the Breeding and Foraging Biology of American Oystercatchers at Fisherman Island National Wildlife Refuge, Virginia

Robert L. anderson
College of William & Mary - Arts & Sciences

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ASPECTS OF THE BREEDING AND FORAGING
BIOLOGY OF AMERICAN OYSTERCATCHERS AT
FISHERMAN ISLAND NATIONAL WILDLIFE REFUGE, VIRGINIA

A THESIS
Presented to
The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
Robert L. Anderson III
1988
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

[Signature]
Author

Approved, May 1988

[Signature]
Mitchell A. Byrd, Ph.D.

[Signature]
C. Richard Terman, Ph.D.

[Signature]
Stewart A. Ware, Ph.D.
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The staff of the Back Bay National Wildlife Refuge was very cooperative in granting access to Fisherman Island. The Chesapeake Bay Bridge-Tunnel Commission and its police force were very helpful, even going so far as providing water.

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ABSTRACT

This study investigated aspects of the breeding and foraging biology of the American Oystercatcher, *Haematopus palliatus*.

The population at Fisherman Island was studied to determine reproductive success and various breeding-related parameters. The impact of diurnal tidal cycles on the behavior of two breeding pairs nesting in different habitats was measured and contrasted. One pair nested in a densely-populated, heavily-vegetated area next to a sand-mud tidal flat; the other in a less densely-populated open beach with no adjacent tidal flat.

These two pairs were also contrasted in regard to the impact of the habitat differences on agonistic behavior and foraging. The latter was gauged by a determination of the caloric intake from the preferred prey item on the island, the Stout razor clam, *Tagelus plebius*, and other aspects of foraging behavior.
ASPECTS OF THE BREEDING AND FORAGING BIOLOGY OF THE AMERICAN OYSTERCATCHER AT FISHERMAN ISLAND NWR, VIRGINIA
INTRODUCTION

The Haematopodidae are a unique, monogeneric family of shorebirds which are comprised of a questionable number of species. Estimates range from four to eleven with six being the most widely accepted number among British and American ornithologists (Pettingill 1985). The group possesses a cosmopolitan distribution along much of the world's coastlines except for the Arctic and Antarctic continents. Three species are brownish-black and white, the other three are black. Baker (1975, 1977) discusses the uncertainty of species limits.

Sexes are generally alike but are distinguishable in the American Oystercatcher by the slightly shorter and redder bills of males. The eyes are bright yellow with scarlet eye rings. There are two molts per year, a complete post-breeding and a partial pre-breeding. The precocial young are nidifugous but remain dependent on the parents for food for some time. Juveniles resemble adults but have duller dark-tipped bills, paler eye colors, and require three years to achieve adult plumage.

*Haematopus palliatus* is unique in several respects among shorebirds: it is one of the few Charadriiids which breed along the mid-Atlantic coast; it nests in areas frequently subjected to human and natural disturbance (coastal barrier islands); and it belongs to the only shorebird family adapted to feed primarily on lamellibranch (bivalve) molluscs.
Kilham (1979) has pointed out the scarcity of breeding data on the species in his brief observations of five breeding pairs on two Georgia coastal islands. This scarcity became evident in 1973 when I made a cursory study of the breeding success and population size at Fisherman Island, which comprises the southern tip of Cape Charles, Virginia (Northampton County). No well documented accounts of such simple parameters as clutch size or incubation period were available. Perhaps one reason for this is the extreme wariness of the species. Bent (1929) describes the oystercatcher as "one of the shyest and wildest of our shore birds, ever on the alert to escape from danger; I have never shot one and seldom have had half a chance to do so." He goes on to describe the breeding habitat as "the same broad sandy beaches as the Wilson's Plover and Least Tern select for their breeding grounds."

Dewar (1915) was one of the first to point out that the specialized feeding habits of oystercatchers prevent any significant interspecific food competition. This does, however, restrict their breeding range since they must nest near a reliable source of bivalve molluscs (except for those which feed on chitons or limpets).

American Oystercatchers do not exhibit the inland nesting which has occurred in Great Britain with *Haematopus ostralegus* (Heppleston 1968). There this species is considered a pest of the cockle (*Cardium edule*) and mussel (*Mytilus edulis*) industries. *Haematopus palliatus* is not regarded as such in
America, although it is often seen on commercial oyster beds. The majority of oysters are in water too deep for oystercatchers.

Oystercatchers are probably more abundant now than earlier in the century. H. H. Bailey (1913) writes:

This large and showy bird fell an easy mark to the spring gunners (cf. Bent above), breeding as it did during the height of the spring migration of beach birds, from May 10 to 25. Nesting among the sand dunes or flat beaches back from the ocean, over which the spring gunners tramped daily, these birds were right in the line of travel, so to speak, and were either killed or their nests broken up.

Perhaps this accounts for the wariness Bent observed some years later. Their numbers prior to this period are not well known, although Bent (1929) felt it must have been much more common in the days of Audubon and Wilson. Bent cites Audubon's reports of the species at Portland, Maine and breeding on the Labrador Peninsula, although he felt Audubon to be mistaken about the latter.

An indication of the current population trend is not clear; however, range extension northward has been occurring during the breeding season. Birds have nested on Long Island since 1957 (Bull 1964) and Massachusetts since 1968 (Finch 1975). Peterson (1980) states that it is casual to Nova Scotia, but it appears that significant breeding is not occurring in the coastal New England area.

To the south, the species is found from Baja California to northern Chile on the west coast. On the east coast it extends southward throughout the West Indies to eastern Argentina.
The primary objectives of the study were:

1. To determine current reproductive success on Fisherman Island, Virginia in terms of numbers of eggs produced and young successfully fledged, as well as add some knowledge to the little that is known about the bird's breeding biology.

2. To compare the behavioral ecology of a breeding pair nesting on inner beach habitat having little vegetation with a breeding pair nesting on a tidal mudflat edge having much denser vegetation. In addition, the populations in both habitats were compared for certain breeding-related parameters such as internest distances and territorial areas.

3. To determine mean daily caloric intake for the pair nesting next to the tidal flat based on consumption rates of the primary prey item for oystercatchers at Fisherman Island, the stout razor clam, *Tagelus plebius*. 
METHODS AND MATERIALS

The study was conducted during the months of June through mid-August of 1981 and 1982. Some preliminary observations occurred during the winter and spring months preceding these periods. Behavioral observations were made with 9x binoculars and a 20x telescope from blinds atop 15 and 20 foot towers placed 24 and 30 meters from each observed pair. Although entering the blind caused some disturbance at first, the birds soon habituated to my presence, and observations were not begun until they were in an obviously undisturbed state, i.e., had begun to feed or preen. Additional observations and photographs were taken from a small portable blind placed closer to the nests.

In 1981, nearly all oystercatcher nesting territories on Fisherman Island (N = 51) were visited every three days to determine laying dates, predation levels, nest placement, and hatching dates. The location of nests relative to potential damage from high water was determined. Nests were also grouped according to the amounts of surrounding vegetation and molluscan shell bits lining them. The vegetation and shells were classified into four arbitrary categories (none, light, moderate, heavy) and a correlation matrix was constructed to suggest habitat preference for the area immediately surrounding the nest (Fig. 2).
Since most nests were located along the island's perimeter near the water, internest distances were determined by simply measuring the distance between adjacent nests and determining means for different parts of the island.

Egg dimensions were taken with threaded adjustable calipers and measured to the nearest 0.5 mm. Shell thicknesses were measured with a micrometer accurate to 0.001 inch and converted to mm.

Two breeding pairs nesting in each of two different habitats were compared. In 1981, a pair which nested in a heavily-vegetated and heavily-populated Spartina patens strip along the edge of a tidal sand-mud flat was observed for 77.45 hours. In 1982, a pair which nested in a less populated inner beach habitat with no adjacent tidal flat and little vegetation (generally thought of as more typical oystercatcher breeding habitat) was observed for 74.13 hours in an attempt to compare the influence different habitats and years on behavior.

The assignment of tide stage periods (High, Ebb, Low, Flood) was accomplished by recording the high and low tide times for Fisherman Island from Tide Tables (1981, 1982). The times midway between high and low tide were considered the midpoints of the ebb and flood stages (ebb following high tide and flood preceding it). In this way, the 90 minutes (approximately) both before and after maximum high tide are considered the high tide period. The next 180 minutes (again, approximately) are considered the ebb tide period, etc. By this method, the impact
of different tide stages on behavior could be quantified. In order to estimate caloric intake, I divided the razor clams (*Tagelus plebius*) into five size categories based on their lengths relative to the known length of an oystercatcher's bill (85 - 95 mm). If a clam was as long or longer than the bill, it was placed in class five, if slightly shorter, class four, etc. Caloric values were then determined for clams with shell lengths in the middle of each size category and used as a mean value for that category (Fig. 15).

What are believed to be accurate caloric values for each size class were determined by using a shell length to body weight regression (Grussendorf 1979). His research related shell length to ash-free dry weight (AFDW) in a productivity study of the stout razor clam at nearby Lynhaven Inlet Virginia:

\[
\log_{10} \text{AFDW (mg)} = a + b \log_{10} \text{shell length (mm)}
\]

I have reproduced part of Grussendorf's Table 6 showing the regression of AFDW on shell length in Table 11. For my estimates of AFDW, I averaged Grussendorf's intercept (a) and slope (b) values for June and July to yield one value for each. From the coefficients of determination, it can be seen that almost all of the variation in AFDW (mean 98.7%) is explained by variation in shell length making this parameter an accurate determinant of caloric content. Thayer, et al. (1973) gives a value of 5.471 kcal gram\(^{-1}\) AFDW for *T. plebius*, a figure which
agrees very closely with a value obtained by Holland (pers. comm.).

Kendeigh (1970) and Kendeigh, et al. (1977) derived a formula for determining existence metabolism (M) for non-passerines at 30° C. He defines existence metabolism as the number of Kcal needed to maintain constant weight in captivity. Since the major part of the diet of oystercatchers at Fisherman Island consists of *T. plebius*, I attempted to determine the approximate percentage of Kendeigh's predicted existence metabolism that is obtained from this organism. Since the clams are handled extensively during capture, a good estimate of their length relative to that of an oystercatcher's bill is possible. The clam was then placed into one of the size categories described above and assigned a caloric value.

Analysis of data was done with the Statistical Analysis System (Helwig, et al., 1979), the Statistical Package for the Social Sciences (Nie, et al., 1975) and also by reference to Sokal and Rohlf (1969).

Areas of territories were calculated by outlining the territory on a U.S. Army Corps of Engineers aerial photo of known scale and then tracing the outline with a compensating polar planimeter (Keuffel and Esser).
RESULTS

Breeding Schedule

During the winter, oystercatchers gather in dense flocks of up to 250 birds in Eastern Shore (Northampton County, Virginia) marshes. In late winter, usually during favorable weather in February, oystercatchers begin to exhibit behavior in defense of territories (Baker and Cadman 1980). However, I have seen territorial behavior as early as the last week in January during mild winters in the Virginia Capes. If severe weather intervenes, flocking behavior is resumed. Birds remain active in their territories, except for those losing all eggs or young, until early August when territories are abandoned.

Breeding Population

In 1973, during a cursory study of oystercatcher breeding success at Fisherman Island, I found 36 - 38 breeding pairs defending territories. Of these, 16 pairs were known to lay eggs. In 1981 - 82, approximately 51 pairs defended territories. Confounding the problem of determining a breeding population in the Eastern Shore barrier islands are large flocks of apparent non-breeding adults (Lind 1965, Harris 1967) in nearby marshes. Such flocks were noted during censusing of other species in June 1983. However, there is no doubt that the breeding population on Fisherman Island has increased in recent years.
Site Fidelity

In 1982, I noticed that pairs were occupying the same general territories as in 1981, and in some cases were using the same nest scrapes, especially around the food-rich Northwest Flat area. Two distinctive males, one missing its outer left toe and the other with an unusual hoarse voice, were seen in the same territories in both 1981 and 1982.

The Northwest Flat area was the scene of much agonistic dispute as birds engaged in extensive piping displays (Huxley and Montague 1925, Miller and Baker 1980) over territorial rights. The loud vocalizations involved in the display are the predominant sound of the island in early spring. Although extensive observations were not made in January through March, it was obvious that the Northwest Flat area was the location of the earliest agonistic disputes over territories. Challengers often landed in or near territories prompting frequent outbreaks of piping displays. It was obvious that this resource-rich area was being fiercely contested for territorial claims.

Nest Placement

Nearly every nest was located in a way which provided an incubating bird with a 360° view. Twenty-nine nests (56.8%) in 1981 were located out of reach of all but the highest storm tides, and in 1973 only one nest was lost to high water. Five nests were on top of a dune ridge on the Northwest Spit (Fig. 1).
Figure 1

Aerial photo (1977) of Fisherman Island NWR at high tide. Oystercatcher nest locations in 1981 are shown by dots. Scale: 6.5 Cm = 1 Km.
formed from dredge spoil which contained a large amount of shell. Nine nests were just west of Route 13 on the northern neck of the island, and were placed on sand fill from the road's construction. The distribution of nests in relation to the amount of surrounding vegetation and molluscan shell bits is given in Fig. 2. Some nests on open sand with little or no adjacent vegetation were completely lined with bits of broken shell (heavy category). These comprised 25.5% of all nests, some of which were very conspicuous due to the contrast between the bleached white shell and the darker substrata. One nest in 1981 had been formed in washed-up dead *Spartina* stem wrack which covered a large area of the beach. Another nest was located less than 15 meters from the noisy traffic of Route 13. The majority of nests (68.6%) were next to vegetation, while even more (80.3%) were lined with varying amounts of shell bits. The plant most often associated with nests was the beach goldenrod, *Solidago sempervirens*, a broad-leaved perennial unlike most of the narrow-leaved plants typical of beaches; it was found associated with 41% of all nests.

Recently, oystercatchers have been occurring regularly on the rock islands of the Chesapeake Bay Bridge-Tunnel during spring and summer. In 1984, a nest on the fourth island was photographed (D. J. Abbot, pers. comm.) indicating the selection of an unusual nest location for this species.
Figure 2

Percentage distributions of 51 nests in 1981 according to amount of molluscan shell bits added by oystercatchers and amount of vegetation in the square meter surrounding the nest. Bits of dead *Spartina* stem were sometimes used to line nests instead of shell. Numbers in parentheses represent number of nests.
Internest Distance

Fig. 1 shows a greater nest density on the northwest part of the island, especially around an area I have called the Northwest Flat. Of the 51 pairs producing eggs in 1981, 32 pairs had territories on the island's perimeter and were immediately inshore from large tidal flats which were exposed twice daily at low tide. The remaining nests were located on outer (i.e., exposed to direct ocean surf) or inner (no direct ocean exposure) beaches or on top of dunes. These were not adjacent to tidal flats. Internest distances were measured for those nests which were located along the island's periphery; this included all nests except a small number atop a dune ridge on the northwest spit. Including these would have only diminished the mean internest distance for nests in that area.

Internest distances along the outer beach of the southern and eastern sides of the island, generally thought of as typical oystercatcher habitat (Bent 1929, Kilham 1979), had a mean value of 536 meters in 1981 (S.D. ± 333.8 meters, N = 9). Those adjacent to tidal flats had a mean value of 76.8 meters (S.D. ± 43.3 meters, N = 32). These means are significantly different (p < 0.001).

Territories

The mean square area of tidal flat territories was 1.54 ha (S.D = 1.03, range = 0.72 - 4.1 ha). Although beach nesters had much greater internest distances, not all of the territory
between nests was defended. Consequently, the borders of these territories were not easily determinable, making area measurements difficult.

The dominant plant species within territories were: *Spartina alterniflora*, *S. patens*, *Ammophila breviligulata*, *Panicum amarum*, *P. amarulum*, *Solidago sempervirens*, *Myrica* sp., *Iva lumbricata*, and *I. frutescens*.

Other bird species nesting within the territories of oystercatchers include the herring gull (*Larus argentatus*), royal tern (*Sterna maxima*), sandwich tern (*S. sandvicensis*), osprey (*Pandion haliaetus*), willet (*Catoptrophorus semipalmatus*), piping plover (*Charadrius melodus*), eastern meadowlark (*Sturnella magna*), and seaside sparrow (*Ammospiza maritima*).

**Agonistic Behavior**

Beach nesters were seen to carry out piping displays in defense of territory usually close to the nest. Tidal flat nesters, whose territories are essentially contiguous and located along the shoreline edge, appeared to be aware of distinct borders. Piping displays were frequently carried out along these borders during March and April. Only one nest was found more than 25 meters inland from the mean high water line. Occasionally, an intruder would fly into a territory and land well inside the border. This invariably prompted a display of piping behavior from the residents.
The majority of territorial defense is done by males (Table 1), but often the female joins the male in driving other oystercatchers from the territory.

The following behaviors were involved in the defense of territories:

**Piping Display** - The subject of much study in *H. ostralegus* (Selous 1901, Huxley and Montague 1925, Dirksen 1932, Makkink 1942, Armstrong 1947), piping is an elaborate display involving very loud vocalizations consisting of a rapid staccato series of evenly-pitched notes which increase and then diminish in volume. During the display the bill is held pointed downward almost vertically and open about a centimeter at the tip. The neck is arched forward and is raised up and down rapidly resembling an exaggerated feeding motion. The wings are held away from the body a short distance at the carpal flexure while the breast feathers are fluffed and spread laterally on each side giving the bird a larger appearance when seen anteriorly. The tail is held horizontally or occasionally pointed upward, the angle apparently depending on the intensity of the display (see Kilham 1980, Miller and Baker 1980). All the while the birds pace rapidly about in a serpentine path, often changing direction 180°.

The mean length of time for a piping display was just under a minute (0.88 min. for the beach male, 0.84 min. for the mudflat male), and was slightly less for females (0.63 min. for the beach female, 0.78 min. for the mudflat female). Times for
Table 1

Amount of observed time devoted to specific components of agonistic behavior (minutes) during 77.45 hours of observation of the mudflat pair and 74.13 hours of the beach pair.

<table>
<thead>
<tr>
<th></th>
<th>Beach Pair</th>
<th>Mudflat Pair</th>
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<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>Time</td>
</tr>
<tr>
<td>Piping</td>
<td>168</td>
<td>147</td>
</tr>
<tr>
<td>Flight Piping</td>
<td>33</td>
<td>50.3</td>
</tr>
<tr>
<td>Face Away</td>
<td>13</td>
<td>16.5</td>
</tr>
<tr>
<td>Strafe</td>
<td>34</td>
<td>28.2</td>
</tr>
<tr>
<td>Lunge</td>
<td>5</td>
<td>0.9</td>
</tr>
<tr>
<td>Butterfly Flight</td>
<td>4</td>
<td>3.8</td>
</tr>
<tr>
<td>Displacement</td>
<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td>Intrasp. Chase</td>
<td>21</td>
<td>2.1</td>
</tr>
<tr>
<td>Total</td>
<td>279</td>
<td>259.8</td>
</tr>
</tbody>
</table>
both total agonistic behavior and duration of piping display diminished as the season progressed (Fig. 3).

Piping occasionally occurs under circumstances other than defense, such as when one member returns from an extended absence. In this case, the piping bird invariably faces 90° or more away from its mate as it lands and pipes.

Territorial defense involves piping displays lasting as long as an intruder remains in or near a territory, occasionally up to 20 minutes early in the breeding season. Lengthy encounters frequently occur when one or a small group of oystercatchers approach, fly over, or land in an occupied territory. Birds often enter a neighbor's territory by walking slowly into a defended area until a bout of piping ensues. Sometimes resident birds will allow an intruder to get as close as a meter or less without piping. At this time the resident(s) often assumes a posture which I refer to as the "facing away display" (probably the pseudo-sleeping attitude of Makkink 1942). This was most often practiced by females (Table 1). As the intruder approaches, the resident(s) points its bill away from the intruder or tucks it in the scapulars in an apparent conflict avoidance or appeasement display.

In the beach pair, the female spent 40% more time than the male in the facing away display, but in the mudflat pair the male performed it more (Table 1). Typically, both piping and facing away involve a resident pair and one or a small group of conspecifics.
Figure 3

Percent of observed time devoted to all forms of agonistic behavior and mean length of time of piping display in relation to time of breeding season for mudflat pair in 1981. The general trend of decreasing agonistic behavior with the progression of breeding season is shown.
Only once in each year did I see oystercatchers engage in actual fighting involving mutual bill grasping and tumbling. These encounters lasted just under a minute in each case and involved disputes over feeding rights to areas in the middle of the northwest flat which were outside the general area of the territories.

Occasionally, piping displays are directed at other species such as willets (Catoptrophorus semipalmatus) or laughing gulls (Larus delawarensis). Here again, the beach pair performed more often, but this is probably because other species are more likely to be encountered there.

In Vacuo Piping - The beach pair piped twice when no conspecifics were near. In both cases the in vacuo piping followed shortly after extended piping displays. Kilham (1980) describes a similar example of in vacuo behavior (see below) following an extended agonistic encounter.

Intraspecific Chasing - Occasionally the resident male (rarely the female) would chase another oystercatcher flying over the resident's territory. This involved following immediately behind the intruder until it was 100 - 200 meters outside the resident's territory. No vocalizations were given and the resident would soon return.
**Strafing** - Intruders would occasionally elicit a brief, low altitude (1 meter or less) flight from a resident which would aim the closed bill at the intruder while flying directly at it. This is quite effective at driving intruders out of a territory. The attacked bird quickly sidesteps or tumbles out of the way.

**Butterfly Flight** - This term has been used to describe a characteristic type of display flight in the Charadriidae (Huxley and Montague 1925, Miller and Baker 1980). The former authors use it to describe the unusual slow wingbeats sometimes used by oystercatchers. Makkink (1942) describes it as resembling the flight of an owl. The flight is similar to that of a Black Skimmer (*Rhynchops nigra*), wherein the wings are moved through a greater arc than normal and their speed is about halved. The mudflat pair did not exhibit butterfly flight, but the beach pair performed it four times. The context of each is described below.

(1) June 18 - Male flew to south territory border where neighbors piped in response while he stood facing $90^\circ$ away from them. After 30 seconds he flew back to the female using butterfly flight and uttering piping notes. Upon landing, he turned to face away from the female.

(2) June 23 - Male flew north to a group of seven oystercatchers, chased one in flight and returned to his territory center. In a few seconds, he strafed a bird to the
north after he made a brief butterfly flight over his territory. After a minute, he strafed a pair to the north and briefly chased another oystercatcher overhead. He and mate then walked to their south territory border where they were strafed by a bird there.

(3) July 9 - The pair approached birds at the south territory border, piped at them and preened briefly. After three minutes, the male flew at an overhead oystercatcher using butterfly flight, landed, and in two minutes flew south to join six birds in a piping display at his south border.

(4) July 18 - Male piped as birds flew overhead; soon he flew over neighbor's territory using butterfly flight after which he returned to the center of his territory where he stood quietly for some time.

Interspecific Aggression - Oystercatchers showed overt aggression toward the following species, especially if they were near the oystercatcher's young, by charging at them with head lowered and bill pointed forward: tricolored heron (*Egretta tricolor*), snowy egret (*Egretta thula*), Virginia rail (*Rallus limicola*), willet (*Catoptrophorus semipalmatus*), laughing gull (*Larus atricilla*), and common tern (*Sterna hirundo*).

Invariably, oystercatchers avoided aggression toward the following species: glossy ibis (*Plegadis falcinellus*), black scoter (*Melanitta nigra*), royal tern (*Sterna maxima*), herring
gull *(Larus argentatus)*, and great egret *(Casmerodius albus).* Although the mudflat pair were observed for 4.3% more total time than the beach pair, the latter performed more acts of agonistic behavior and spent more total time in agonistic encounters (Table 1). However, t-tests do not indicate significant differences between the pairs for these parameters. Comparisons between sexes for total observed time spent in agonistic behavior relative to other predominant behaviors are shown in Figures 4 and 5.

Nest Building

Most territories contain three to five nest scrapes but only one is used for eggs. Depending on substratum condition, these scrapes may persist for several years. In the three pairs I observed making scrapes, all were formed by the male who leaned forward onto its breast and alternately kicked each leg slowly backward. As does *H. ostralegus* (Makkink 1942), the male will often stand, rotate 90° or more and continue this behavior until the nest is complete. Copulation generally occurs during this time period (Table 2). While the male is nest building, the female often walks slowly nearby probing the substratum with her bill held vertically as though sensing for moisture or consistency. Oystercatchers are known to have sensory corpuscles of the Herbst type in the tips of their mandibles (Burton 1974).
Figures 4 and 5

Comparison between sexes of the percentages of total observed time spent in predominant behaviors. Loafing refers to birds which were standing or sitting quietly, perhaps with the bill tucked in the scapulars. The hidden category refers to birds which were not visible to the observer because of obscuring vegetation in the territory. During this time birds were probably sitting or standing as described for loafing.
Predominant Behaviors

- Intrasp. Agonistic
- Intersp. Agonistic
- Loafing
- Foraging on Mud
- Foraging in Water
- Foraging in MHW Zone
- Preening
- Out of Territory
- Offer Food to Chick
- Hidden

Bars represent the percent total observed time for Beach Male (solid) and Mudflat Male (hatched).
PREDOMINANT BEHAVIORS

- Intrasp. Agonistic
- Intersp. Agonistic
- Loafing
- Foraging on Mud
- Foraging in Water
- Foraging in MHW Zone
- Preening
- Out of Territory
- Offer Food to Chick
- Hidden

Percent Total Observed Time

- Beach Female
- Mudflat Female
<table>
<thead>
<tr>
<th>DATE</th>
<th>PAIR</th>
<th>SEX</th>
<th>PRECEDING</th>
<th>FOLLOWING</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 15</td>
<td>OB</td>
<td>M</td>
<td>Tosses shell bits into nest in which female stands</td>
<td>Forms scrape by leaning on breast, kicking sand</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Half crouches then stands in new scrape</td>
<td>Inspects scrape by pushing bill into sand</td>
</tr>
<tr>
<td>May 16</td>
<td>OB</td>
<td>M</td>
<td>Chases Fish Crow, returns and briefly pipes; stretches wings and approaches female</td>
<td>Begins to feed along water edge</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Stands with bill tucked in middle of territory</td>
<td>Stands on one leg</td>
</tr>
<tr>
<td>May 17</td>
<td>OB</td>
<td>M</td>
<td>Forms scrape by leaning on breast and kicking sand</td>
<td>Walks slowly near female, preens</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Walks slowly near male who is making scrape</td>
<td>Stands near male, preens</td>
</tr>
<tr>
<td>May 17</td>
<td>OB</td>
<td>M</td>
<td>Same as preceding</td>
<td>Feeds briefly at water edge</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Stands near scrape-forming male</td>
<td>Follows male to water edge, does not feed</td>
</tr>
<tr>
<td>DATE</td>
<td>PAIR</td>
<td>SEX</td>
<td>PRECEDING</td>
<td>FOLLOWING</td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
<td>-----</td>
<td>-----------------------------------------------</td>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td>May 29</td>
<td>OBl</td>
<td>M</td>
<td>Slowly walks in dunes near female</td>
<td>Flies to edge of territory for brief piping</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Slowly walks in dunes with male</td>
<td>Follows male to territory edge for brief piping</td>
</tr>
<tr>
<td>May 29</td>
<td>OBl</td>
<td>M</td>
<td>Stands near water edge next to female</td>
<td>Walks to nest area and probes scrape with bill</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Stands near water edge next to male</td>
<td>Follows male to nest scrape area, begins probing</td>
</tr>
<tr>
<td>Apr 5</td>
<td>EBl</td>
<td>M</td>
<td>Forms scrape by leaning on breast and kicking feet</td>
<td>Walks slowly near female</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Walks slowly near scrape-forming male, probes sand</td>
<td>Stands while male walks nearby</td>
</tr>
<tr>
<td>Apr 5</td>
<td>EBl</td>
<td>M</td>
<td>Walks slowly in nest scrape area with female</td>
<td>Stands near female, preens</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>Walks slowly in nest scrape area with male</td>
<td>Walks slowly near male, occasionally probes sand</td>
</tr>
</tbody>
</table>
In 1981, most nests (41 or 80.2%) were lined with small bits of broken shell, while almost 10% each were not lined or lined with bits of dead *Spartina* (Fig. 2). On May 15, 1981, a pair approached a scrape the male had made earlier. The male then tossed two small shell bits into it with sideways flicks of the bill while facing 90° away from the nest. During this time, the female was seen to adopt the copulatory solicitation posture (see below). Two minutes later, after preening briefly, the pair again began to probe the sand with their bills and toss bits of shell or dead plant matter to their sides but not into scrapes. After another two minutes, the male sat and rotated 90° in place; it then stood and rotated again before resuming scrape formation behavior.

Soon, the female inspected the scrape by probing with her bill, and both began to toss shell bits in the area immediately around the scrape. The female then walked some distance away while the male continued to toss shell bits. Within two minutes, she returned and crouched in the scrape while the male continued the sideways tossing of shell bits. Within a minute, the female assumed the copulatory solicitation posture and the male mounted. In less than two minutes, the male formed another scrape and the female immediately probed it with her bill while the male tossed shell bits into and around it.

After a minute, the female began to toss shell bits into the nest while the male stood in it and slowly rotated. The two then traded places and the female slowly probed the scrape
with her bill. She then stepped out of the scrape and continued to probe the nearby sand. Within five minutes, the pair, which always stayed close together, flew to a nearby mud flat to feed. Two days later, the pair was observed for six hours before similar scrape-forming behavior resumed in mid-afternoon during flood tide. It appeared that considerable overwash had occurred the previous day destroying some of the scrapes.

Similar behavior was seen in a neighboring pair nearly two weeks later (May 29). Insufficient observations during April and May did not allow for determining the dates inclusive of this behavior. The earliest copulation noted was April 5, and it is safe to assume that this behavior continues into early June dependent upon a variety of proximate factors such as predation, weather, and tidal overwash.

Clutch Initiation

The mean laying date for 1981 was May 10 (N = 40, S.D. 14.07 days, see Table 3). Figs. 6 and 7 show three peaks of laying centered around April 25, May 10, and May 26; all are accurate to within ±48 hours. These peaks all occurred in different parts of the island: that of April 25 along the northwest spit; that of May 10 primarily along the area just west of Route 13; and that of May 26 along the inner beach just east of Route 13 on the north side of the island. Whether these dates represent first or subsequent clutches is obscured
Table 3

Dates of egg laying for oystercatchers at Fisherman Island NWR 1981

<table>
<thead>
<tr>
<th>Absolute Date:</th>
<th>109</th>
<th>115</th>
<th>120</th>
<th>125</th>
<th>130</th>
<th>132</th>
<th>136</th>
<th>146</th>
<th>150</th>
<th>156</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date:</td>
<td>Apr19</td>
<td>Apr25</td>
<td>Apr30</td>
<td>May5</td>
<td>May10</td>
<td>May12</td>
<td>May16</td>
<td>May26</td>
<td>May30</td>
<td>Jun5</td>
<td></td>
</tr>
<tr>
<td>Nests</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 egg:</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 eggs:</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 eggs:</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Nests:</td>
<td>2</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>40</td>
</tr>
</tbody>
</table>

N = 40, X = 130.15 (May 10), S.D. = 14.07
Figure 6

Number of two- and three-egg clutches in relation to laying dates in 1981. Distinct periods of concurrent laying occurred in different regions of the island as shown by the peaks of Apr 25, May 10, and May 25.
Figure 7

Total number of clutches in relation to laying date in 1981. Peaks of laying occurred in different locations on the island and may be indicative of the influence of territorial quality on time of egg production.
by the predation pressure on the island, but I feel they represent probable first attempts at laying. These results suggest a synchrony of clutch initiation within localized areas on the island.

Nests were checked only every three days, and it is quite likely that some first clutches were not noted due to loss from predators in 1981. The fact that pairs establish territories earlier around tidal flats than beaches is reflected by differences in laying dates between the two areas. An F-test was performed on the absolute dates of laying for the two areas and shows a highly significant difference with tidal flat pairs laying earlier than beach pairs ($F = 9.56$, $p < 0.001$; see Table 4).

Clutch Size

Table 5 shows mean clutch sizes for 1981 and 1982; however, the mean for 1981 is undoubtedly too small due to heavy egg loss from predation by fish crows ($\textit{Corvus ossifragus}$) and possibly other predators (see Predation). Because of predation loss, the sample size of undisturbed nests was too small to determine if clutch size remained the same or decreased for subsequent clutches. However, Fig. 6 shows a tendency for three-egg clutches to predominate in April followed by mainly two-egg clutches in May.
Table 4

Absolute laying dates (1981) for birds nesting next to tidal flats (N = 25 nests) compared to those nesting on a beach with no adjacent tidal flat (N = 15 nests).

<table>
<thead>
<tr>
<th>Tidal Flat Nesters</th>
<th>Beach Nesters</th>
</tr>
</thead>
<tbody>
<tr>
<td>109 (2 nests)</td>
<td>130 (1 nest)</td>
</tr>
<tr>
<td>115 (11 nests)</td>
<td>132 (1 nest)</td>
</tr>
<tr>
<td>120 (1 nest)</td>
<td>136 (1 nest)</td>
</tr>
<tr>
<td>125 (1 nest)</td>
<td>146 (8 nests)</td>
</tr>
<tr>
<td>130 (10 nests)</td>
<td>150 (2 nests)</td>
</tr>
<tr>
<td>156 (2 nests)</td>
<td></td>
</tr>
</tbody>
</table>

\[ \bar{X} = 123.7 \text{ (May 2)} \]

\[ \bar{X} = 143.5 \text{ (May 22)} \]

An F-test shows a highly significant difference between the two means.  
\[ F = 9.556, \ p = 0.001 \]
Table 5


<table>
<thead>
<tr>
<th>Year</th>
<th>Total Clutches</th>
<th>1 Egg</th>
<th>2 Egg</th>
<th>3 Egg</th>
<th>Egg Total</th>
<th>X</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981</td>
<td>50</td>
<td>11</td>
<td>24</td>
<td>15</td>
<td>104</td>
<td>2.06</td>
<td>0.72393</td>
</tr>
<tr>
<td>1982</td>
<td>48</td>
<td>5</td>
<td>14</td>
<td>29</td>
<td>120</td>
<td>2.50</td>
<td>0.68417</td>
</tr>
</tbody>
</table>
Egg Size

Width and length means obtained from 81 eggs in 1981 are shown in Table 6. Analysis of variance showed no significant size differences among the length and width means from one, two, and three egg clutches. A one-way ANOVA revealed significant variation among females for both egg length ($F = 2.51, p < 0.01$) and width ($F = 5.23, p < 0.001$). I was able to determine laying sequences for only three nests but found the second egg to be the largest in all cases. I also found a slight positive correlation between length and width of eggs ($r = 0.0526, p = 0.324$) which, however, is not statistically significant despite a sample size of 81 eggs. Shell thickness was measured for six eggs and yielded a range of 0.43 - 0.48 mm. Egg volume can be determined from the formula:

$$V (\text{mm}^3) = 0.47736 \times L (\text{mm}) \times W^2 (\text{mm}^2) - 1.318 \text{ mm}^3$$

where $L$ and $W$ are length and width; $r^2 = 0.96$ (Vaisanen 1969, Nol, et al. 1984). Using this formula, the volumes of eggs from pairs nesting around the more densely populated tidal flats were compared with those of beach nesters and no significant differences were noted (t-test, $p < 0.4$). Neither was there any significant differences in mean clutch size between the areas, although I feel predation levels obscured these findings.
Table 6
EGG LENGTH AND WIDTH MEANS FOR 1981

<table>
<thead>
<tr>
<th>CLUTCH TYPE</th>
<th>MEAN</th>
<th>S.D.</th>
<th>RANGE</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-Egg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>55.32</td>
<td>2.66</td>
<td>51-60</td>
<td>11</td>
</tr>
<tr>
<td>Width</td>
<td>38.68</td>
<td>0.98</td>
<td>37-40</td>
<td>11</td>
</tr>
<tr>
<td>Two-Egg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>56.94</td>
<td>2.17</td>
<td>51-60</td>
<td>34</td>
</tr>
<tr>
<td>Width</td>
<td>39.16</td>
<td>1.43</td>
<td>35.5-41</td>
<td>34</td>
</tr>
<tr>
<td>Three-Egg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>56.22</td>
<td>2.34</td>
<td>52-61</td>
<td>36</td>
</tr>
<tr>
<td>Width</td>
<td>39.24</td>
<td>1.37</td>
<td>37-43</td>
<td>36</td>
</tr>
</tbody>
</table>

\[ \bar{X} \text{ Length} = 56.40 \quad 81 \\
\bar{X} \text{ Width} = 39.13 \quad 81 \]

No significant differences exist among means for each of the three clutch types.
Incubation

Insufficient observations were made to determine the roles of the sexes in incubation. Females, though they take extended breaks for feeding, incubated much more than males. I never witnessed a male delivering food to an incubating female.

In 1973, I found the incubation period for three nests to be 25 - 27 days. Only two of 17 nests examined during hatching in 1981 and 1982 contained eggs which were hatching simultaneously. This suggests that incubation begins prior to the laying of the last egg. The intervals between the laying of two successive eggs were noted for two nests and were 30 and 36 hours.

Hatching

The mean hatching date for 17 nests in 1982 was May 21 (S.D. 8.45 days, see Table 7) making the mean laying date for that year approximately April 23 - 24 (which followed a very mild winter). Although few eggs hatched in 1981, the mean laying date for that year would have produced a mean hatching date of approximately June 5.

Brooding

Brooding was infrequently seen due to the large predatory losses of eggs and young. Only females were seen brooding young. A chick would be called from hiding in vegetation by a series of soft notes from the female, after which it would
Table 7

Known hatching dates for oystercatchers at Fisherman Island NWR 1982

<table>
<thead>
<tr>
<th>Date</th>
<th>May 5</th>
<th>May 11</th>
<th>May 13</th>
<th>May 15</th>
<th>May 17</th>
<th>May 21</th>
<th>May 23</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absolute Date</td>
<td>125</td>
<td>131</td>
<td>133</td>
<td>135</td>
<td>137</td>
<td>141</td>
<td>143</td>
</tr>
<tr>
<td>No. of Nests</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Date</th>
<th>May 25</th>
<th>May 26</th>
<th>May 27</th>
<th>May 29</th>
<th>May 31</th>
<th>Jun 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absolute Date</td>
<td>145</td>
<td>146</td>
<td>147</td>
<td>149</td>
<td>151</td>
<td>154</td>
</tr>
<tr>
<td>No. of Nests</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

N = 17, \( \bar{X} = 141.3 \) (May 21), S.D. = 8.52
These 17 nests represent a sample of 35.4% of all known nests for 1982 and suggest a mean laying date of Apr 23 - 24.
crawl under her breast facing behind her. The female would then slowly lower herself over the chick until only its feet were visible beneath her while she crouched on her tarsi.

Predation

I estimated over 300 fish crows (Corvus ossifragus) were present on the island in 1981. These were probably initially attracted by the large heron colonies on the island. Oystercatchers show particular wariness toward fish crows and invariably attack or chase any which fly over a territory. Crows frequently flew over oystercatcher territories apparently looking for unguarded eggs or young. However, only two instances of direct predation were seen, one of an egg and one of a chick. During nest inspection trips, I often found that only one egg would be missing; this would be unlikely if mammalian predators were responsible. Once, a pair of crows attacked a brooding female which, while chasing one crow, lost her chick to another. This was followed by frantic searching by the female accompanied by alarm notes which gradually subsided. The female then uttered two drawn out, curlew-like notes of rising and falling inflection which I had never heard before. After 20 minutes, the pair flew out of the territory.

Egg loss in 1981 was very high, certainly in excess of 50%, and only one young was known to fledge from 51 nests. In 1982, ten chicks fledged from at least 50 nests. Unfortunately the eastern third of the island is inaccessible and could not be
checked for nests and young lost to predation. In 1981, a stray dog on the island eluded capture and the remains of a red fox were found.

**Tidal Influence on Behavior**

The semidiurnal tides of the region will obviously influence the daily behavioral patterns of shorebirds. How some of the behaviors discussed seem to be influenced by tides is displayed in Figs. 8 - 14.

**Out of Territory**

Time spent out of the territory, during which birds are foraging for mussels in neighboring salt marshes, peaked for both pairs at ebb tide (Fig. 8). This period follows high tide, the time of greatest food inaccessibility. The beach pair spent far less time outside their territory than the mudflat pair (Fig. 8). Mussels exist at a higher stratum level than razor clams and become exposed first as the tide drops. This probably accounts for the greater territorial absenteeism during this tide stage.

**Foraging**

The mudflat pair fed the least within their territory during the ebb tide stage due to their high level of territorial absence at this time. They fed most often during the low and flood tide stages; most feeding during the latter
stage occurred before the flat was completely covered. Fig. 9 shows the possibility of a temporal isolation of the sexes for shallow water foraging during low and flood tides for the mudflat pair. This pair also fed their young more during these stages.

After their chick fledged, the beach pair fed more during low and flood tides. However, the majority of their foraging and feeding of the chick prior to its fledging was spent during high and ebb tides in contrast to the mudflat pair (Fig. 13).

Loafing

This behavior peaked at high tide for the mudflat pair (over 70% of the female's observed time during this stage), but remained fairly evenly divided among all tide stages for the beach pair with a slight decrease during low and flood stages (Fig. 12).

Offering Food to Chick

Due to the beach pair's tendency to feed its chick large numbers of what were probably worms of the genus Nemertea from the mean high water zone, this behavior peaked for this pair during high tide when the worms are presumably more accessible. The mudflat pair spent more time feeding their chick at low tide (Fig. 13).
Figures 8 - 14

Total observed time can be divided into four equivalent tide stages (High, Ebb, Low, and Flood). How each tide stage influences various behaviors is shown by the percentages of the total observed time for particular behaviors during the tide stage.
Out of Territory

Percent of Each Tide Stage Hour

- Beach Pair
- Mudflat Pair
- M = Male
- F = Female
Foraging in Shallow Water

- Beach Pair
- Mudflat Pair

Tidal Stage

Percent of Each Tide Stage Hour

High | Ebb | Low | Flood
Foraging on Exposed Mud

![Graph showing Foraging on Exposed Mud]

- **Percent of Each Tide-Stage Hour**
- **Tidal Stage**: High, Ebb, Low, Flood
- **Beach Pair**
- **Mudflat Pair**

The graph illustrates the percent of each tide-stage hour for beach and mudflat pairs, showing higher activity at low tide for mudflat pairs compared to beach pairs.
Intraspecific Agonistic Behavior

![Graph showing Intraspecific Agonistic Behavior]

- **Beach Pair**
- **Mudflat Pair**

**Percent of Each Tide-Stage Hour**

**Tidal Stage**

- High
- Ebb
- Low
- Flood
Loafing Behavior

![Bar chart showing the percent of each tide-stage hour for different tidal stages and species.]
Foraging in Mean High Water Zone
(Beach Pair Only)

![Bar graph showing percent of each tide-stage hour for males and females across different tidal stages.]
Intraspecific Agonistic Behavior

Among tide stages, no significant differences existed between the sexes of the mudflat pair for agonistic behaviors, but the beach male's aggressive behavior peaked dramatically during ebb tide (Fig. 11). Piping behavior among most oystercatchers peaked during ebb tide. The only violent encounters I witnessed occurred at this time. On two occasions, two individuals grasped bills and fought violently. These birds were apparently contesting feeding rights in the middle of the Northwest Flat, an area outside the boundaries of the territories. Both of these events occurred as the flats were becoming exposed during ebb tide.

FORAGING

The two males spent very different amounts of time foraging within their territories (Table 8). However, since birds usually returned to their territories with mussels, it is assumed that the majority of observed time spent outside the territory (22.8% for the mudflat male; 0.75% for the beach male) involved foraging. This assumption then increases the total of the mudflat male's foraging time to 42.9% of the total observed time. The beach male spent 32.1% of its total observed time feeding. In contrast to the mudflat pair, the beach pair female exceeded the male in time out of territory (8.6% vs. 0.75% of observed time).
Table 8

Percent of total observed time spent foraging within the territory

<table>
<thead>
<tr>
<th>Tide</th>
<th>Beach Pair</th>
<th>Mudflat Pair</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>F</td>
</tr>
<tr>
<td>High</td>
<td>33.8</td>
<td>34.2</td>
</tr>
<tr>
<td>Ebb</td>
<td>32.1</td>
<td>22.8</td>
</tr>
<tr>
<td>Low</td>
<td>32.7</td>
<td>20.2</td>
</tr>
<tr>
<td>Flood</td>
<td>28.8</td>
<td>24.2</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>31.9</td>
<td>25.3</td>
</tr>
</tbody>
</table>
In each pair, one member fed the chick more than the other, and in both cases it was the adult which spent the most time outside the territory. The mudflat male made 30 extra-territorial feeding trips; in 22 of these (73%) food was brought back and invariably offered to the chick. The total observed time spent offering food to the young is almost twice as high for the mudflat male compared to the beach male (Fig. 4). This is probably due to the beach male feeding its young only one-fifth the amount of time his mate did during high tide. She undertook only 11 extra-territorial feeding trips to her mate's three with each of their trips averaging about 30 minutes, about the same as the mudflat male. About 2.7% of the mudflat male's observed time (0.6% for the female) was spent offering food to the chick compared to 1.4% for the beach male (2.3% for the beach female).

As expected, birds fed more during low water; however, oystercatchers showed a preference for feeding more during flood tide than ebb tide. This is true even though the flats are exposed for equal amounts of time during each of these stages. There are significant differences in feeding times among tide stages between the sexes in the mud pair. This is true for both shallow water and exposed flat feeding (Chi square, \( p < 0.005 \) for each case; Figs. 9 and 10).

When offering food to the young, adults hold it in a characteristic position with the bill pointed straight down. This acts as a releaser causing the chick to run toward the
adult to be fed. A parent would frequently hold food in this position for several minutes after a well-fed chick refused to eat. Only after considerable hesitation would the parent consume food it had offered to the chick.

The beach pair offered their chick large numbers of very small food items, probably worms of the genus *Nemertea* based on invertebrate sampling of the intertidal zone. These were invariably obtained in a very narrow zone at the mean high water line, a behavior which did enable them to feed at all tide stages (Fig. 14). Even with 20x magnification at fairly close range, I could not see the small food items which were being passed repeatedly to the chick. Other identifiable food items used by oystercatchers at Fisherman Island are listed in Table 9. E. von Montfrans of the Virginia Institute of Marine Science sampled the intertidal zone for invertebrates. The dominant forms in addition to *Nemertea* were *Paracerceia caudata* and *Ecoloplos* sp.

At six to seven weeks of age, oystercatchers exhibit some success at foraging for invertebrates, including small razor clams from mud. However, they are not skillful at removing the body of the animal from the shell. I have seen a group of three apparently healthy birds-of-the-year in late October unaccompanied by adults, so the length of time they are fed by parents is unknown.

The stout razor clam, *T. plebius*, is the preferred food item of oystercatchers in the densely populated northwest part
Table 9

Food Items of American Oystercatchers at Fisherman Island

1. Stout Razor Clam (*Tagelus plebius* Solander)
2. Jackknife Clam (*Ensis directus*)
3. Atlantic Ribbed Mussel (*Modiolus demissus*)
4. Common Blue Mussel (*Mytilus edulis*)
5. Oyster (*Crassostrea virginica*)
6. Florida Coquina (*Donax variabilis*)
7. Knobbed Whelk (*Busycon carica*)
8. Channeled Whelk (*Busycon canaliculata*)
9. Atlantic Moon Snail (*Polinices duplicatus*)
10. Marsh Periwinkle (*Littorina irrorata*)
11. Mole Crab (*Emerita talpoida*)
12. Hermit Crab (*Eupagurus sp.*)
13. Tube Polychaete (*Diopatra sp.*)
14. Proboscis Worm (*Nemertea sp.*)
15. *Paracerceia caudata* ?
16. *Scoloplos* sp. ?
of the island. The clams inhabit only sediments composed of greater than 2% silt and clay, and in most cases are found only where a surface film of microalgae covers the sediment. However, unlike most mud habitat species, it is a suspension feeder and not a deposit feeder. In South Carolina, samples of a similar sand-mud lagoon showed the stout razor clam, *T. plebius*, comprised 93% of the biomass. In sandy fringe areas, diversity indices for invertebrates were considerably lower than for those of the lagoon areas (Holland and Dean 1977a).

When an oystercatcher detects a razor clam, it immediately begins a very rapid series of stabbing motions, often pivoting at the pelvis instead of just with the neck. During this time the bird often rotates around the point of insertion. A characteristic narrow wedge is removed from the posterior shell margin providing easy identification of clams eaten by oystercatchers. If extracted in shallow water, the clam is carried to exposed sand or mud and placed hinge side down with its long axis parallel to that of the bird's. The oystercatcher then begins a scissoring motion with its mandibles slightly apart along the mantle margin of the shell. The body of even a large clam is almost invariably eaten whole. The mean capture time, from detection to removal from the substratum, for large clams (sizes 4 and 5 in Fig. 15) was 67.3 seconds and does not include handling time prior to consumption (S.D. ± 33.6 seconds, n = 12, range = 35 – 160 seconds).
Fig. 15

Razor clams were divided into five size classes, shown here actual size, and caloric values were assigned for the mean size in each class according to Grussendorf (1979) and Holland (pers. comm.).
On the exposed mudflat, there is a considerable variety of terrain ranging from channels and pools with a few centimeters of water at low tide, to exposed sandy bars which nearly dry out during this time. Foraging birds were noted to prefer the shallow depressions of the flat.

Most oystercatchers rely to a significant degree on mollusks (Johnsgard 1981). For the estimation of caloric consumption, I recorded only kilocalories obtained from the stout razor clam, Tagelus plebius, the primary food item of oystercatchers at Fisherman Island. I divided the clams into five size classes (see Methods) based on their lengths relative to the known mean length of an oystercatcher's bill. Due to the absence of any significant number of razor clams within the beach pair's territory, the results in Table 10 are exclusively those of the mudflat pair. However, in a period of 3.12 hours of feeding on an offshore flat (3.12 hrs by the female, 1.97 by the male) July 19, the beach pair fed its recently fledged young 25 kcal from T. plebius for a mean of 7.98 kcal hr⁻¹, which is at the lower end of the range for the mudflat pair (Table 10). On some days the chick would refuse food for nearly the entire day, which suggests a wide variation in daily caloric intake for the chick.

On days when all daylight behavior was observed (June 18, 22, and 24, mean observed time of 12.67 hrs day⁻¹), the mudflat male consumed a mean of 27.4 kcal day⁻¹ (S.D. = 5.1, range 22.1 - 32.3 kcal) from T. plebius. Night foraging was
Table 10
Kcal obtained from *T. plebius* by mudflat pair

<table>
<thead>
<tr>
<th></th>
<th>18 Jun</th>
<th>22 Jun</th>
<th>24 Jun</th>
<th>1 Jul</th>
<th>3 July</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>F</td>
<td>M</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>Total Kcal Captured</td>
<td>74</td>
<td>5.9</td>
<td>54.6</td>
<td>36.9</td>
<td>30.1</td>
</tr>
<tr>
<td>Kcal Foraging Hour⁻¹</td>
<td>66</td>
<td>5.4</td>
<td>30.3</td>
<td>40.5</td>
<td>18.9</td>
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<tr>
<td>Kcal Consumed</td>
<td>32.3</td>
<td>2.9</td>
<td>27.8</td>
<td>22.3</td>
<td>22.1</td>
</tr>
<tr>
<td>Total Kcal Offered Young</td>
<td>42.8</td>
<td>3.5</td>
<td>27.8</td>
<td>14.6</td>
<td>19.8</td>
</tr>
<tr>
<td>Total Eaten by Young</td>
<td>41.7</td>
<td>3.0</td>
<td>26.8</td>
<td>7.8</td>
<td>8</td>
</tr>
<tr>
<td>Kcal Hour⁻¹ Fed Young</td>
<td>37.2</td>
<td>2.8</td>
<td>14.9</td>
<td>8.6</td>
<td>5</td>
</tr>
<tr>
<td>Hrs Foraged</td>
<td>1.12</td>
<td>1.09</td>
<td>1.8</td>
<td>0.91</td>
<td>1.59</td>
</tr>
<tr>
<td>Hrs Observed</td>
<td>11.92</td>
<td>12.5</td>
<td>13.58</td>
<td>7.25</td>
<td>4.5</td>
</tr>
</tbody>
</table>
Table 10 (contd.)

Kcal obtained from *T. plebius* by mudflat pair

<table>
<thead>
<tr>
<th></th>
<th>7 Jul</th>
<th>9 July</th>
<th>14 July</th>
<th>22 July</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>F</td>
<td>M</td>
<td>F</td>
</tr>
<tr>
<td>Total Kcal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Captured</td>
<td>50.4</td>
<td>26.1</td>
<td>24.5</td>
<td>48.2</td>
</tr>
<tr>
<td>Kcal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foraging Hour^-1</td>
<td>15.9</td>
<td>17.3</td>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td>Kcal Consumed</td>
<td>33.8</td>
<td>26.1</td>
<td>22</td>
<td>48.2</td>
</tr>
<tr>
<td>Total Kcal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Offered Young</td>
<td>37.3</td>
<td>14.1</td>
<td>19.1</td>
<td>17</td>
</tr>
<tr>
<td>Total Eaten</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>by Young</td>
<td>16.6</td>
<td>0</td>
<td>2.5</td>
<td>0</td>
</tr>
<tr>
<td>Kcal Hour^-1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fed Young</td>
<td>5.3</td>
<td>0</td>
<td>0.8</td>
<td>0</td>
</tr>
<tr>
<td>Hrs Foraged</td>
<td>3.16</td>
<td>1.51</td>
<td>3.05</td>
<td>3.9</td>
</tr>
<tr>
<td>Hrs Observed</td>
<td>7.08</td>
<td>9.92</td>
<td>4.5</td>
<td>6.2</td>
</tr>
</tbody>
</table>
Table 11

The values of the terms in the linear regression: \( \log_{10} (\text{AFDW in mg}) = a + b \log_{10} (\text{shell length in mm}) \) for *Tagelus plebius* (after Grussendorf 1979). The \( r^2 \) values show the close dependence of caloric content (from AFDW) on the independent variable shell length, making the size of shells an accurate determinant of caloric value.

<p>| | | | | | | |</p>
<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>Site</td>
<td>No. of clams</td>
<td>a (intercept)</td>
<td>b (slope)</td>
<td>( r^2 )*</td>
<td></td>
</tr>
<tr>
<td>June 3-5</td>
<td>1</td>
<td>30</td>
<td>-2.2953</td>
<td>2.9453</td>
<td>0.98</td>
<td></td>
</tr>
<tr>
<td>June 3-5</td>
<td>2</td>
<td>64</td>
<td>-2.5553</td>
<td>3.0860</td>
<td>0.99</td>
<td></td>
</tr>
<tr>
<td>June 3-5</td>
<td>3</td>
<td>54</td>
<td>-2.4709</td>
<td>3.0371</td>
<td>0.99</td>
<td></td>
</tr>
<tr>
<td>July 18-21</td>
<td>1</td>
<td>54</td>
<td>-2.7026</td>
<td>3.1447</td>
<td>0.98</td>
<td></td>
</tr>
<tr>
<td>July 18-21</td>
<td>2</td>
<td>58</td>
<td>-2.8893</td>
<td>3.2314</td>
<td>0.99</td>
<td></td>
</tr>
<tr>
<td>July 18-21</td>
<td>3</td>
<td>51</td>
<td>-2.7559</td>
<td>3.1608</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>

Mean \( a = -2.61155 \)  \( \) Mean \( b = 3.1009 \)  \( * = \) coefficient of determination
not observed by Cadman (1980) or myself.

Kendeigh (1970) and Kendeigh, et al. (1977) has derived a formula for determining existence metabolism (M), the kcal required by a bird for one day to maintain body weight in captivity. For non-passerines at 30°C the equation is:

\[ M = 1.079 W^{0.67} \]

where \( W \) = body weight in grams. Body weights were not obtained at Fisherman Island; however, Cadman (1980) gives a mean body weight of 592 grams for 29 adult \( H. palliatus \) of both sexes from South Carolina in March 1977. Inserting this value into the formula gives a value for \( M \) of 77.7 kcal. If we rely on Kendeigh's caloric requirement, the mudflat male's mean daily caloric consumption within his territory represents about 35% of the \( M \) value for one day. The mean number of kilocalories consumed while foraging outside the territory is unknown.

Young oystercatchers increase in weight from about 50 to 400 grams in their first six weeks (Hockey 1984). Based on the results for June 18 (Table 10), M for a 200 gram chick can be exceeded in just one foraging hour by the parents. The value of M for a 200 gram chick is 37.5 kcal; the amount fed in one hour June 18 was ca. 40 kcal with a total for the day of ca. 43.7 kcal, all derived from \( T. plebius \). The caloric requirement for a growing chick may differ considerably from Kendeigh's existence metabolism requirement for non-passerines.
Before their chick fledged, the beach male and female, respectively, spent 84.7% and 65.8% of their foraging time obtaining invertebrates along the narrow region of the high tide line of their territory.

From Table 10, it is apparent that the chick of the mudflat pair often refused food which was offered to it. By dividing the number of consumed kilocalories by the number offered, it is evident that the chick eats about half of the razor clams offered to it. This lessens the foraging requirement of adults, since they eat what is refused by the chick. The data suggest that the mudflat pair could have easily fed two young, but the additional time a second chick would require can only be estimated.
DISCUSSION

Breeding Schedule

Hypotheses concerning the onset of breeding in birds focus on three areas: (1) general environmental cues (e.g., photoperiod or rainfall, reviewed by Wingfield 1983); (2) specific extrinsic factors, such as weather or the abundance of food, which explain differences in timing among populations or among years (Perrins 1970, Greenlaw 1978); and (3) intrinsic factors such as age and experience of both sexes, or on general factors that explain differences in timing among individuals within populations (Perrins and Moss 1974, Finney and Cooke 1978). Perrins (1970) argues that the date of laying in some species may depend on the date the female is able to find enough food to form eggs. Age and experience have long been held to be important in determining both the timing of breeding and reproductive output (Crawford 1977, Blus and Keahay 1978). The question which arises for oystercatchers is why does a species which does not lay eggs until mid-April to May begin establishing territories in February or even late January.

Attempts to establish territories in late winter suggest strong selective pressures for the early establishment of a territory. Perrins (1970) states that in some species there is a strong tendency for young hatched earliest in the season to have a higher survivability. However, these selection pressures are believed to be greater for small birds with large clutches.
Selection for early breeding would place a premium on the early establishment of territories in the most favorable habitat. This habitat appears to be the fringe marsh areas on the edge of tidal flats for birds nesting at Fisherman Island.

Perrins (1970) expects species selected for early breeding to show behavioral adaptations for doing so. He argues that the date a female lays is a result of the evolutionary advantages of early breeding -- in that more surviving young are raised -- and the physiological state of the female which will be improved by feeding in a food-rich area as long as possible prior to laying. Holland and Dean (1977b) working in South Carolina found the greatest density of stout razor clams, the primary prey item for oystercatchers on the island, to occur in the early spring. Harris (1969) reported that early-nesting European oystercatchers (H. ostralegus) raised eight times as many young as late nesters. However, once fledged the young showed no survival differential.

Loman (1982) tested the hypothesis that timing of egg laying and size of clutch are determined by (1) a tendency to delay reproduction so the female can store enough internal resources for laying a large clutch, and (2) a tendency to breed early because the survival of young hatched later might be lower. He predicts a correlation between early-breeding females and those producing large clutches. The establishment of a food-rich territory early in the season would allow a pair to both accumulate food reserves and breed earlier than other pairs. I
observed birds attempting to claim territories as early as late January in areas of high razor clam density. Baker and Cadman (1980) noted that females were the first to return to territories at nearby Wallops Island. Both of these observations are consistent with Loman's hypothesis.

Winkler (1985) found the pre-egg food limitation hypothesis to best explain clutch size differences in California gulls (Larus californicus) nesting in two different, widely-separated habitats. This resource limitation is relative, however, and not absolute. Nol, et al. (1984) feels that consistency of clutch size among female oystercatchers is due to consistent differences in territory quality among philopatric females. These results as well as those of Klomp (1970) dispute Lack's (1968) hypothesis of clutch size as an inherent trait. Klomp found that in many passerines the most productive clutch size is larger than the modal one.

Charnov and Krebs (1974) claim adult pairs laying larger clutches suffer a higher mortality rate than those laying smaller clutches. By suppressing breeding effort (i.e., by decreasing clutch size), these adults would stand a greater chance of future reproduction. Such a strategy is purported to be profitable for birds of high adult survival rate. The hypothesis implies that clutch size and survival are inversely correlated. Oystercatchers are relatively long-lived birds; Harris (1967) reported a mean life span of 11.8 years for H. ostralegus (see also Predation and Survival below). The modal
clutch size for oystercatchers is three eggs compared to four for most shorebirds.

In contrast to this, Hogstedt (1981b) feels the ability to acquire a high-quality territory is crucial to a high reproductive output and adult survival. He predicts a positive correlation between clutch size and quality of territory, and supports this with data from a population of magpies (*Pica pica*). He shows a positive linear relationship between adult survival and number of fledglings (i.e., reproductive rate) for the first four years, after which the rate remains constant.

Fig. 1 leaves little doubt about the preference of oystercatchers for areas on the island where razor clams are abundant. If more reliable data on reproductive success were available, a comparison could be made between territories of different quality, presumably the better quality, more crowded territories versus the less dense ones.

**Breeding Population**

There is no doubt that the breeding population on Fisherman Island has increased in recent years. J. W. Williams (unpublished data) has surveyed the Virginia barrier islands since 1975. While I feel he has underestimated the actual breeding population on Fisherman Island, his overall numbers for oystercatchers have averaged just over 1100 individuals since 1979. This shows an increase from the period prior to 1979. The largest populations are on Metomkin, Cobb, and Hog Islands.
European oystercatchers do not begin breeding until their fourth or occasionally third year (Cramp and Simmons 1983). This delayed onset of breeding is probably also true of H. palliatus. Although second-year birds are distinguishable from adults in the field, third-year birds are not. Consequently, large numbers of non-breeding third or fourth-year birds can confound attempts to determine the true size of a breeding population in an area. I would suggest that attempts to census oystercatchers take place during low and flood (incoming) tides during late March or early April when pairs are likely to be either feeding in or defending territories.

Nest Placement

In 1973, only four nests were located in the area around the now heavily used northwest part of the island. Even if I missed a few nests then, there is no doubt that this area is being used more than it was ten to fifteen years ago. When I first visited the island in 1966, the area was primarily unvegetated fresh sand spoil. As typical beach vegetation became established, including fringe growth of Spartina alterniflora and S. patens, greater numbers of oystercatchers began to nest there. Once sufficient silt was deposited, Tagelus plebius populations became established. This further increased the appropriateness of the habitat for oystercatchers.

The majority of nests in 1981 (68.5%) were placed next to low, sparse vegetation such as beach goldenrod (Solidago
*sempervirens* indicating a definite preference for this habitat feature (Fig. 2). Most researchers (Bent 1929, Tomkins 1954, Kilham 1979, Terres 1982) stress that *H. palliatus* prefers unvegetated sand beaches for nesting. Kilham (1979) hypothesizes that this nesting strategy is due to the bold plumage of the bird which offers no camouflage as do the plumages of most other shorebirds, such as willets, which nest in dense vegetation on Fisherman Island. Consequently, instead of cryptically blending with the habitat and avoiding flight at the approach of predators, oystercatchers leave the nest when a predator is hundreds of meters away; hence the need for an unobstructed view from the nest. A predator on the ground is therefore unlikely to see a bird actually leave the nest. Instead, it sees the pair walking slowly somewhere in the vicinity of the nest as they have been for weeks prior to laying. Often they rest by crouching on the ground, a position in which the bird appears to be incubating. This deceptive behavior has come to be known as false brooding (Miller and Baker 1980), and can easily confuse humans searching for nests (Kilham 1979 and this study).

The placement of the majority of nests next to vegetation may be a consequence of preferentially nesting near the tidal flats, or it could be in response to heavy avian predation (Tinbergen, et al. 1967) from fish crows or perhaps both.

At Wallops Island, Virginia, Cadman (1979) found 16 pairs of oystercatchers in an area of about 10 hectares, yielding a mean territory size of well under 1 hectare per pair. These pairs
nested along inner beaches and marsh channels. Four pairs fed entirely within their territories, while three pairs had large areas of salt marsh within their territories. Those feeding entirely outside their territories had no salt marsh in them. The lack of reports of similar salt marsh territories for oystercatchers in Georgia may be a result of the tidal range there, which is the greatest along the southeast coast -- almost seven feet compared to Virginia's 2.5 - 3 foot mean. By noting the location of the tidal debris line following spring tides and measuring how close it came to nests, the number of nests susceptible to loss by these tides or simultaneous storms is determinable. Most Virginia nests are at elevations safe from all but unusually high storm or spring tides.

Since the spoil deposition and road building in 1964, a number of shrubs (Myrica and Iva) and perennials have invaded the northwest region of the island. This will probably soon make the area unsuitable for nesting since it will obscure the unobstructed views the birds apparently require around their nests.

Approximately 20 years ago, the northwest part of the island supported nesting royal terns (Sterna maxima), least terns (S. albifrons), common terns (S. hirundo), piping plovers (Charadrius melodus), and black skimmers (Rhynchos nigra). Since these species are known to prefer open habitat for nesting, some control of vegetational succession in this area would probably benefit them as well as oystercatchers. The
present rate of succession (occurring since ca. 1962) will soon cause the area to become too densely vegetated for many of the species which have nested there in the recent past. The attractive value of fresh dredge spoil islands for such species is well documented (Parnell and Soots 1975).

Nest Building

Both sexes are involved in nest building in some other species of the Haematopodidae (H. bachmani, Hartwick 1974; H. ostralegus, Makkink 1942, Cramp and Simmons 1983). This may also be true of H. palliatus, but in this study only males were seen forming scrapes. The method of forming the scrape is nearly universal in the Charadriidae (Cramp and Simmons 1983): the bird leans forward onto the breast and kicks or scratches backward with its feet. Unlike other shorebirds but in a way similar to H. ostralegus (Makkink 1942), H. palliatus does not rotate while pressing the scrape but stands to rotate 90° or more before leaning forward to resume again. Like H. ostralegus, several scrapes are made in the territory before eggs are laid.

During nest building, the female walks slowly near the male with her bill held straight down, sometimes probing a short distance into the sand. Makkink (1942) felt this behavior to be the initial step in settling on eggs. It may serve to detect moisture below the surface which might indicate an improper nest location.
Bits of shell one to two cm$^2$ in size and short stems of dead *Spartina* are often added to a scrape by a characteristic backward tossing of the bill along the bird's side, a movement typical of many Charadriids (Hall 1959). The amount varies from none to a total lining of the scrape. This may aid the oystercatcher in locating the nest in dim light, but it may also make scrapes more visible to avian predators. Fig. 2 shows that about 25% of all nests had a heavy shell concentration with little or no surrounding vegetation. Had predation pressure been lower, it would have been possible to compare predation between the high contrast shell nests and those more cryptic.

Copulation and Clutch Initiation

Nest building and copulation occur in close association with the former apparently influencing the timing of copulation. All copulations I witnessed were initiated by females while their mates were engaged in nest building. The copulatory solicitation posture of the female serves as a strong releaser for the male which immediately stops any other activity upon noticing the female and rushes toward her. Cramp and Simmons (1983) state that in *H. ostralegus*, either sex may initiate copulation by a display. Their description of the copulatory solicitation posture differs from that which I observed in *H. palliatus*. During copulation in *H. ostralegus*, the female is reported to "usually" turn its head back toward the male who may hold her bill. I never observed this in *H. palliatus*. 
According to Cramp and Simmons, copulations only last one to two seconds with the male usually dismounting over the female's head. Average copulations in *H. palliatus*, while brief, usually last three times as long, and I never noticed a male dismounting over the female's head. Just prior to mounting, males of *H. ostralegus* begin to utter a call which differs from that of *H. palliatus* and which the female may answer.

Photoperiodism is well known for initiating reproductive behavior in birds, but as Farner and Lewis (1971) claim, photoperiodic mechanisms are probably never solely responsible for setting the precise time of reproduction. The Darling effect (Darling 1952) has been redefined by Lewis and Orcutt (1971) to state that birds are exteroceptive (i.e., environmental) factors to which other birds respond. One expression of the total response pattern is the facilitation of events of the reproductive cycle. Nol, et al. (1984) feels that the piping displays of neighbors within localized areas provide the timing mechanisms for near simultaneous clutch initiation. Figs. 6 - 7 exhibit several waves of clutch initiation, all of which occurred on Fisherman Island in different parts of the island where birds were within sight of each other along shorelines.

Egg Size

The slight positive, though insignificant, correlation between egg length and width I found at Fisherman Island stands
in contrast to the significant negative correlation found by Nol, et al. (1984) at Wallops Island, Virginia. Their results showed that, over three years, 55% of egg size (= volume) variation was due to differences among females. This indicates that females tend to lay eggs of consistent volume in successive years with little effect of year on size. Also detected by Nol, et al. (1984) was a positive correlation between female body weight and egg volume \((r = 0.47, p < 0.05, N = 19)\).

Nol's et al. (1984) study revealed a tendency for second eggs to be larger than first or third eggs. Although I was able to determine exact laying sequences for only three nests, I found the second egg to be the largest in each case. The reason for egg size ordering may lie in a different level of risk to which each egg is exposed. Since incubation in oystercatchers begins after the second egg is laid (Nol, et al. 1984), the first is exposed to greater risks from predation and environmental factors. Thus, possibly more resources are being allocated to the egg with the greatest chance of survival. A number of studies suggest the survival chances of nestlings are positively correlated with the size of eggs (Parsons 1970, Schifferli 1973, Lundberg and Vaisanen 1979, Birkhead and Nettleship 1982).

The refuge staff informed me of fairly heavy concentrations of DDT found in soil samples on the island, some as high as 400 ppm. This may be the result of the use of the island as a coastal artillery battery and antisubmarine warfare base during
World War II when DDT may have been used carelessly. Because of this, I examined shell thicknesses from several post-hatching egg fragments from different parts of the island. I found no evidence of thinning when compared with values for oystercatcher eggs laid prior to 1947 from South Carolina (Blus and Lamont 1979). In fact, the measurements I obtained were in the range of 0.12 - 0.15 mm thicker than pre-1947 egg shell thicknesses given for the South Carolina birds.

Predation and Survival

Many researchers point to low productivity as being typical of oystercatchers: for *H. moquini*, Summers and Cooper 1977, Hockey 1983; for *H. bachmani*, Hartwick 1974, Groves 1984; for *H. ostralegus*, Heppleston 1972. All researchers state that gull predation, crow predation, and human disturbance, which leads to predation, are prime causes for loss of eggs and young. However, few studies report losses of eggs and young as high as those I observed in 1981.

High egg and juvenile mortality is to be expected for an open-area, ground-nesting species. Since the modal clutch size for *H. palliatus* is only three eggs (a mean of 2.8 reported by Nol et al. 1984), it could be expected that such low productivity might be offset by an adult longevity sufficient to produce enough young to maintain a stable population. Stearns (1976) suggests that where juvenile mortality is high, there will be selection for spreading the risk of breeding among many
broods, i.e., the parents should be long-lived in order to breed more in a lifetime to compensate for high juvenile mortality. He found a high positive correlation between the mean number of seasons an individual breeds and the ratio of mean juvenile mortality for a variety of organisms.

Using the formulas $e = \frac{1}{m} - \frac{1}{2}$ and $n = \frac{1}{m} + x$, where $m$ is the mortality of breeding adults, $e$ the expectation of life, $n$ the average age, and $x$ the age of onset of maturity (3 for a bird which first breeds in its fourth year), Harris (1967) found the mean expectation of further life after sexual maturity for European Oystercatchers to be 8.3 years and the mean age to be 11.8 years. Several birds over 25 years have been found with two at 34 and 36 years noted (Nice 1962, 1966; Glutz von Blotzheim, et al. 1975).

Assuming that the ten young fledged in 1982 is more typical of production at Fisherman Island, this represents an addition of 10% to the population. Granting each adult an average of 8 breeding seasons and allowing for mean annual mortality for juveniles and adults, it would seem -- without sophisticated mathematical analysis -- that the island's population may be in a state of slight decline. Whether the production of young on other islands is greater or similar is not known. Productivity on other barrier islands without large crow populations should be investigated.
TERRITORIES

Oystercatchers employ different kinds of territories (Cadman 1980 and this study). In some only nesting occurs, in others only feeding, while the most commonly occurring type encompasses nesting and feeding. Fig. 1 shows several nesting-only territories on top of a dune ridge on the northwest spit which were surrounded by birds with nesting-feeding territories. These dune top nesters were apparently trying to get as close as possible to the prey-rich tidal flats, but were prevented from feeding on them by neighbors whose territories intervened. Although Leopold, et al. (1985) points out the efficiency of long distance (1 - 6 km) transport of prey in H. ostralegus, the birds nesting on top of dunes were the first to abandon their territories in 1981. None successfully hatched eggs.

Tagelus plebius, the stout razor clam, which comprises the primary prey item for oystercatchers on Fisherman Island, meets the general criteria for economic defendability for monogamous, non-colonially nesting birds (Krebs and Davies 1978, p. 4). The prey is relatively scattered, in this case over a number of hectares. It is predictable in that the density should be fairly constant from year to year, and it is not greatly abundant (i.e., it takes time and effort to secure it).

The presence of a dense razor clam prey base may tend to offset the spacing out of oystercatcher territories which normally occurs as a result of predation pressure from avian predators (Tinbergen et al. 1967). The presence of dense
vegetation in nesting areas may serve to reduce predation risk by the protective cover it provides, especially for young prior to fledging. The combination of these two habitat features seems capable of allowing a very high territorial density. I would suggest that this has considerable significance for the management of this species.

Vines (1979) studied breeding *H. ostralegus* in areas of high (15 - 15.8 nests/km$^2$) and low (3.5 - 4 nests/km$^2$) density. She considered the duration of aggressive encounters to be a poor measure of aggressiveness, since it is influenced by the persistence of the intruder. To compensate for this in measuring the level of agonistic behavior of the two pairs, I included the number of occurrences of individual agonistic behaviors as well as their duration (Table 1). Vines (1979) uses the number of intrusions into a territory as a useful relative index of the amount of pressure put on a territory owner. Intrusions, which usually involve a bird walking slowly or flying into a territory, are probably less likely in a densely-vegetated territory along a marsh edge, especially at high tide when the flat is inaccessible. Vines feels it is possible that intruders judge the suitability of an area by the intensity of defense. Her results showed a frequency of intrusion 5.6 times higher in the high density (yet open) habitat.

Although the density in the tidal flat area was four times higher (32 pairs/ 0.5 km$^2$) than Vines' high density area, I
observed less agonistic behavior in the mudflat pair than in the less crowded beach pair. Decreases in both the intensity and duration of agonistic encounters with time (Fig. 3) are probably the result of increasing familiarity with neighbors' territories.

Vines (1979) agrees that food distribution plays a major role in determining the distribution of nesting density. However, she states that this does not clarify the mechanisms through which birds achieve adaptive spatial organization. Proximate mechanisms not linked to food may be equally responsible for spatial patterns correlated with food distribution. The abundance of vegetation in the area of highest nest density at Fisherman Island affects visibility, which in turn has been shown to negatively correlate with levels of aggression in other species (Jenkins 1961). Vines, however, found no qualitative difference in territorial behavior within 30 meters of nests; the quantitative results were greater near the peripheries of territories in the high density area. Because there was no difference in territorial behavior within 30 meters of nests in both populations, she rejects the possibility that differences in territorial behavior are due to physiological and genetic differences in aggressiveness.

Davies (1980) and Patterson (1980) hypothesize that (a) territorial behavior, especially territory size, varies in relation to the environment so as to maximize the fitness of the individual, and (b) a result of this is the adjustment of territory density to variations in the habitat. Brown (1969)
proposed three levels of limitation of populations with three levels of suitability of habitat—
(1) A mosaic pattern exists: the population is not sufficiently dense enough to prevent any individual from breeding in its preferred habitat by the territorial behavior of others.
(2) Some individuals become dissuaded from breeding in the preferred habitat by the territorial behavior of birds already established, but they breed in other less favorable habitats.
(3) All habitats where breeding could possibly occur are occupied by territorial individuals, and a surplus of potential breeders exists as non-breeding floaters, the population reserve.

These levels need not be mutually exclusive. Some populations stay at one level for many generations, but others may contain, in various parts of their range, populations at all levels.

Fretwell (1972) also suggests that fitness should decrease with increasing density of settlement. Whereas Brown (1969) asserts that individuals will be excluded from higher quality territories, Fretwell feels potential settlers assess habitat quality and move according to their own best interests. If Brown's third level of limitation is reached, individuals will be entirely excluded and remain non-territorial. Birds which attempt to nest on top of dunes along the northwest spit were obviously in less favorable habitat since all tidal flat edge available for feeding nearby was occupied by other territorial birds. Had these "inland" nesters raised young, they apparently
would have had to feed themselves and their young entirely by making extra-territorial feeding trips. Such trips are well documented for *H. ostralegus* (Tinbergen and Kruuk 1962, Hulscher 1964, Norton-Griffiths 1969, Leopold, et al. 1985). This may be a long-established strategy of visiting an extra-territorial feeding area with the outgoing tide (see ebb tide Fig. 8). In a study of long-distance (1 – 6 km) prey transport in *H. ostralegus*, Leopold, et al. (1985) found the energy content of lamellibranch prey items exceeded the transportation costs by factors of ten to fifty. It is conceivable that dune top nesters could have fed themselves and young with such trips, but the absence of a parent, especially the more aggressive male, would place eggs or young in jeopardy.

It may have been coincidental, but the question remains as to why the male with the presumably better quality territory spent such a large amount of time apparently feeding outside of it. One net result is that more food becomes available inside the territory for the female and young with this strategy.

The higher visibility of the beach pair may have been the cause of the relatively higher amount of agonistic behavior for this pair. This in turn may have prevented the adults from leaving for extra-territorial feeding. Table 8 shows a much greater total foraging time for the beach pair, no doubt due to their smaller, less nutritious prey. But as pointed out, if the time spent outside the territory of the mudflat pair (presumably foraging) is included in foraging time, the total foraging time
exceeds that of the beach pair. This may point to another advantage of tidal flat territories in that they afford protection for the young allowing for lengthier stays outside the territory.

Brown and Orians (1970) in an elaboration of Brown's (1969) three levels of population density, state that in the third level, densities are so high that some individuals are prevented from breeding entirely. In 1982, a pair attempted to nest on the border between two beach pairs and just inland of both, but was so viciously and incessantly harassed by both neighboring pairs that the pair abandoned without laying. Nothing similar to this was noted along the denser mudflat edge. This suggests that Brown's level two may have been reached on at least part of the island.

Cadman (1980) describes a similar crowded assemblage of oystercatchers in an area of marsh channels at Wallops Island, Virginia where the channels are exposed for foraging at low tide. It is puzzling why early researchers did not describe such an apparent preference for nesting around such habitat, unless it is possible that this represents a recent shift in habitat use.

Management Recommendation

I have already made two recommendations (see Nest Placement and preceding section) regarding the control of plant succession in the area around the northwest flat. This would not only benefit oystercatchers but other species as well.
Fisherman Island and several other barrier islands have a history of being used as isolated retreats by boaters, especially during the three major summer holidays. On these weekends, well over a dozen boats and five times as many people may visit the island. This has undoubtedly resulted in the disturbance of beach nesters, and it may be a primary reason for the current absence of nesting terns and black skimmers from areas where they bred in the past. It would seem imperative for the Fish and Wildlife Service to eliminate as much disturbance as possible during the breeding season, which for oystercatchers begins quite early in the year. This should be more feasible now that the jurisdiction for the island has changed from Back Bay NWR in Virginia Beach to the Eastern Shore of Virginia NWR, a very short distance to the north of Fisherman Island.

Foraging

By examining Table 10, it is apparent that the chick of the mudflat pair often refused food offered to it. This suggests that food limitation is not presently a factor in feeding young for mudflat pairs. I found that the mudflat chick accepted only about half of the food offered to it. Since adults eat what chicks refuse, raising only one chick considerably lessens the foraging burden of an adult. This also indicates that the mudflat pair could probably have easily fed a second chick.

Although Kendeigh's et al. (1977) existence metabolism is purported as being the requirement for maintaining weight in
captivity, one would expect a free-living bird to consume more
and not less than Kendeigh's predicted caloric requirement. Of
course his formula is calculated for 30°C (86°F), and
frequently in June and July the temperatures were well above
this. A large number of kilocalories may have been obtained by
adults while outside the territory. This may well be a strategy
which insures that the prey base in the territory is not over-
exploited so that sufficient resources remain for feeding young.
Parents, however, may obtain a major share of their caloric
requirement outside the territory. If the sole purpose of
extra-territorial feeding trips was simply to secure a mussel
for the chick, the mean length of time for such trips would
likely have been less than the 33 and 47 minutes, respectively,
for the male and female of the mudflat pair. The female's mean
time is derived from only two trips, however.

Since the beach pair possessed a poorer quality territory in
terms of razor clams, logic would suggest that they should have
spent more time foraging outside the territory than the mudflat
pair. The role of primary extra-territorial forager can
apparently be assumed by either sex, and may be determined by
familiarity with mussel beds in the area or a tendency for the
more aggressive male to remain in territories where little
shelter is available for young.

The mudflat pair's chick fledged in early July, about 18
days before the beach pair's chick. This suggests the advantage
to the mudflat pairs may lie in allowing breeding to occur
earlier than for beach birds. The nature of the food consumed by the beach pair made a comparison of caloric uptake too difficult, and there is the question of quality of food also. The advantage of the mudflat territory probably lies in allowing females to secure sufficient resources early enough in the season to begin breeding earlier than other pairs. Such habitat may not be abundant for oystercatchers, but it seems to offer distinct advantages when available.
REFERENCES


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Robert Lee Anderson III