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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

ASPECTS OF THE BREEDING AND FORAGING

BIOLOGY OF AMERICAN OYSTERCATCHERS AT

FISHERMAN ISLAND NATIONAL WILDLIFE REFUGE, VIRGINIA

A THESIS

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The Faculty of the Department of Biology

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by

Robert L. Anderson III

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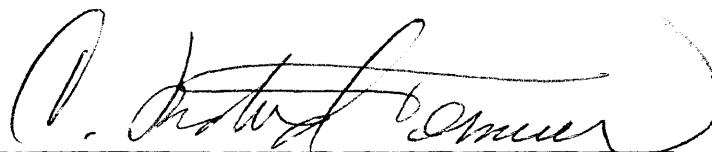
APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Robert L. Anderson

Author

Approved, May 1988

Mitchell A. Byrd

Mitchell A. Byrd, Ph.D.

C. Richard Terman

C. Richard Terman, Ph.D.

Stewart A. Ware

Stewart A. Ware, Ph.D.

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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 shore-birds 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 moults 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 Charadriids 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 H. 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.

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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.

NW FLAT

NW SPIT

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.

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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.
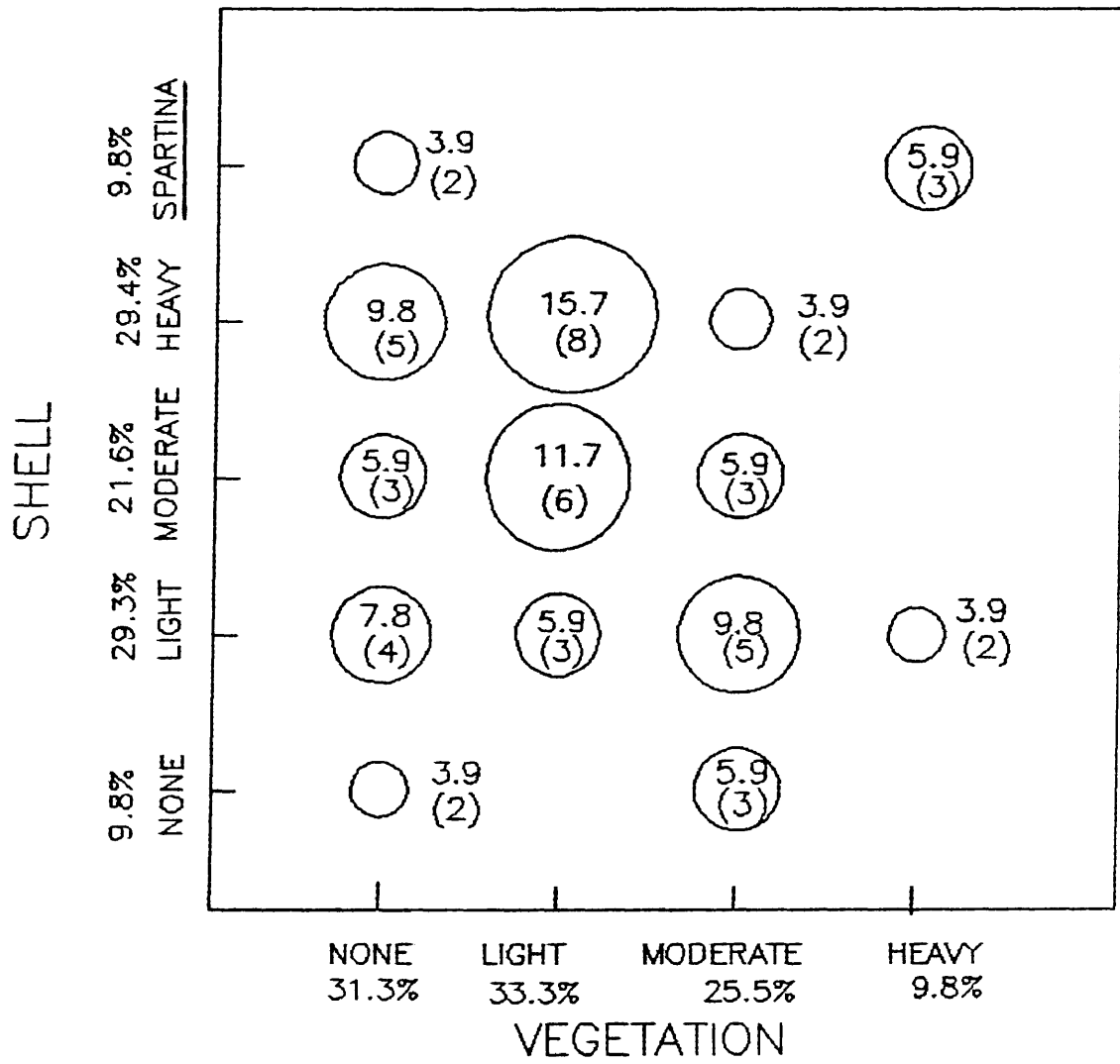
Internest Distance

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. $\pm$ 333.8 meters, N = 9). Those adjacent to tidal flats had a mean value of 76.8 meters (S.D. $\pm$ 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

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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, Dircksen 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.

| | Beach Pair | | | | Mudflat Pair | | | |
| | Male | | Female | | Male | | Female | |
	N	Time	N	Time	N	Time	N	Time
Piping	168	147	135	84.6	119	100.1	120	93.9
Flight Piping	33	50.3	19	25.8	16	19.2	9	12.9
Face Away	13	16.5	10	23.2	7	14.2	4	3.9
Strafe	34	28.2	2	0.9	26	6.0	3	2.0
Lunge	5	0.9	1	0.25	4	0.25	1	0.05
Butterfly Flight	4	3.8	1	1.25	0	----	0	----
Displacement	1	1.0	8	5.0	2	0.7	1	0.17
Intrasp. Chase	21	2.1	0	----	1	0.16	1	0.5
Total	279	259.8	176	141	175	140.6	139	113.5

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, occasion-
ally 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 rela-
tion 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.

MEAN TIME OF PIPING DISPLAY (SECONDS)

PERCENT TOTAL OBSERVED TIME
SPENT IN AGONISTIC BEHAVIOR

JULY

JUNE

● Agonistic Behavior

○ Piping Display
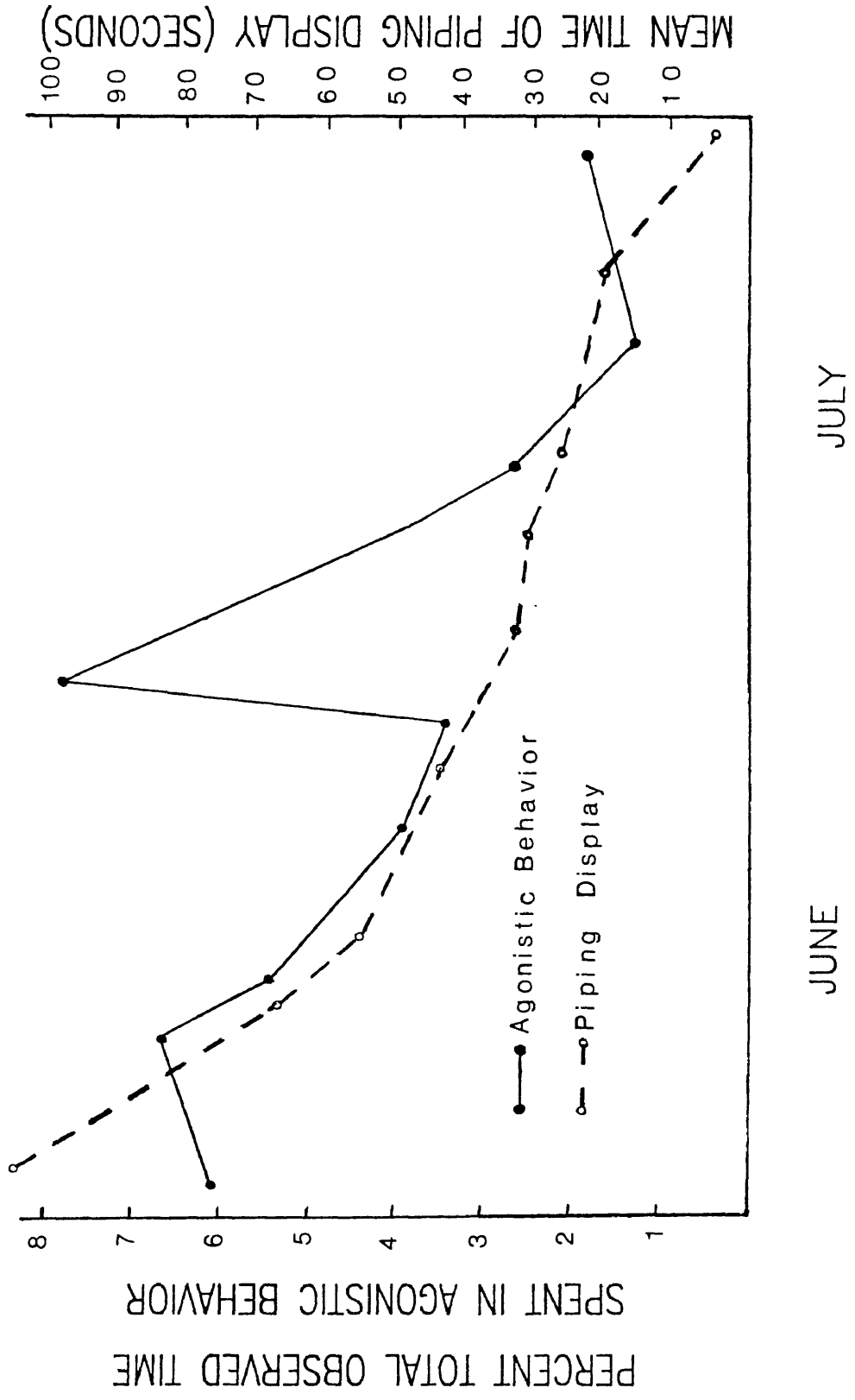
Only once in each year did I see oystercatchers engage in actual fighting involving mutual bill grasping and tumbling. These encounters lasted just under a minute in each case and involved disputes over feeding rights to areas in the middle of the northwest flat which were outside the general area of 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° 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 (<u>Larus</u> <u>argentatus</u>), and great egret (<u>Casmerodius</u> <u>albus</u>).

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 <u>H</u>. <u>ostralegus</u> (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

Percent Total Observed Time

Beach Male
Mudflat Male

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

PREDOMINANT BEHAVIORS

Percent Total Observed Time

Beach Female
Mudflat Female

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

Table 2

BEHAVIORS OF MALES AND FEMALES IMMEDIATELY PRECEDING
AND FOLLOWING COPULATION

DATE	PAIR	SEX	PRECEDING	FOLLOWING
May 15	OB	M	Tosses shell bits into nest in which female stands	Forms scrape by leaning on breast, kicking sand
		F	Half crouches then stands in new scrape	Inspects scrape by pushing bill into sand
May 16	OB	M	Chases Fish Crow, returns and briefly pipes; stretches wings and approaches female	Begins to feed along water edge
		F	Stands with bill tucked in middle of territory	Stands on one leg
May 17	OB	M	Forms scrape by leaning on breast and kicking sand	Walks slowly near female, preens
		F	Walks slowly near male who is making scrape	Stands near male, preens
May 17	OB	M	Same as preceding	Feeds briefly at water edge
		F	Stands near scrape-forming male	Follows male to water edge, does not feed

Table 2 (continued)

DATE	PAIR	SEX	PRECEDING	FOLLOWING
May 29	OB1	M	Slowly walks in dunes near female	Flies to edge of territory for brief piping
		F	Slowly walks in dunes with male	Follows male to territory edge for brief piping
May 29	OB1	M	Stands near water edge next to female	Walks to nest area and probes scrape with bill
		F	Stands near water edge next to male	Follows male to nest scrape area, begins probing
Apr 5	EB1	M	Forms scrape by leaning on breast and kicking feet	Walks slowly near female
		F	Walks slowly near scrape-forming male, probes sand	Stands while male walks nearby
Apr 5	EB1	M	Walks slowly in nest scrape area with female	Stands near female, preens
		F	Walks slowly in nest scrape area with male	Walks slowly near male, occasionally probes sand

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

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

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.
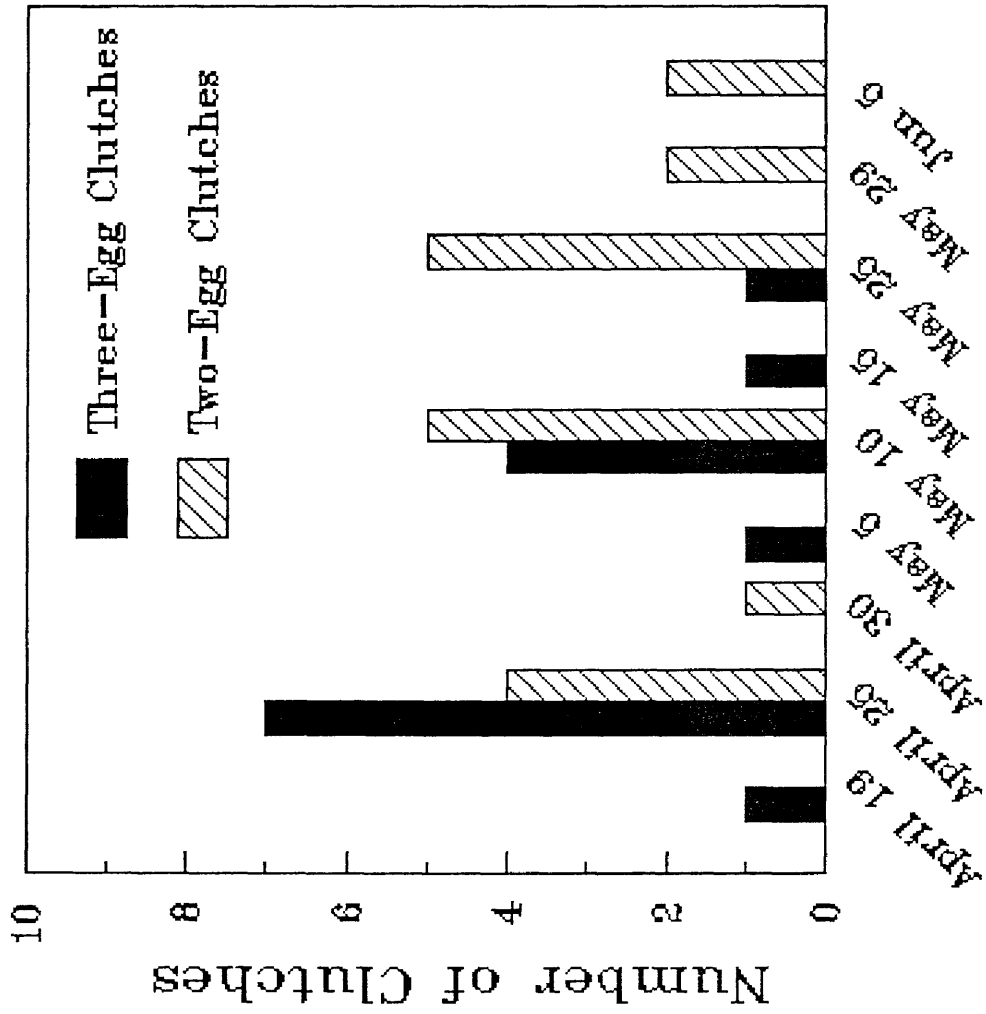
Figure 7

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 of the influence of territorial
quality on time of egg production.

Number of Clutches (y-axis, values 0 to 12)

x-axis categories: April 19, April 25, April 30, May 5, May 10, May 12, May 15, May 25, May 30, Jun 5
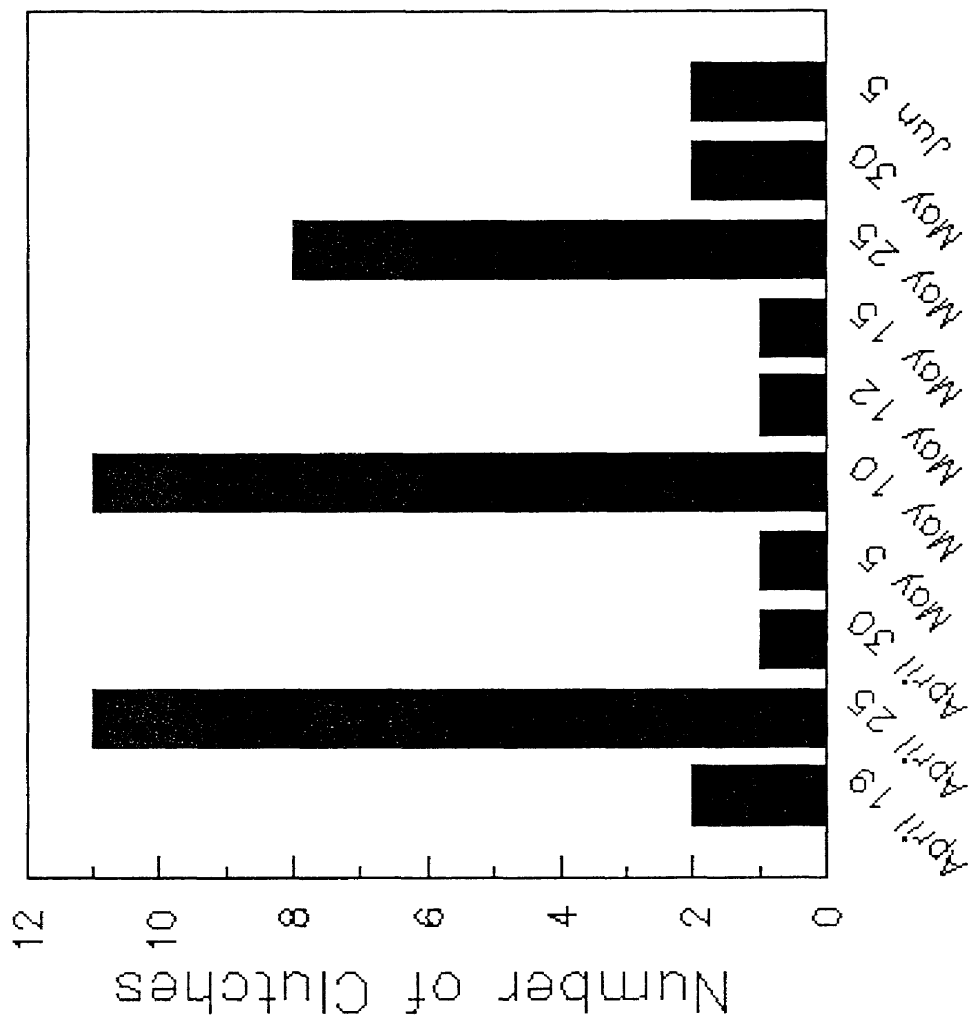
by the predation pressure on the island, but I feel they represent probable first attempts at laying. These results suggest a synchrony of clutch initiation within localized areas on the island.

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 (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).

Tidal Flat Nesters

109 (2 nests)
115 (11 nests)
120 (1 nest)
125 (1 nest)
130 (10 nests)
156 (2 nests)

$\overline{X}$ = 123.7 (May 2)

Beach Nesters

130 (1 nest)
132 (1 nest)
136 (1 nest)
146 (8 nests)
150 (2 nests)

$\overline{X}$ = 143.5 (May 22)

An F-test shows a highly significant difference between the two means.
F = 9.556, p 0.001

Table 5

Average Clutch Size of American Oystercatchers
at Fisherman Island N.W.R. (1981 - 1982)

	Total Clutches	1 Egg	2 Egg	3 Egg	Egg Total	$\bar{X}$	Standard Deviation
1981	50	11	24	15	104	2.06	0.72393
1982	48	5	14	29	120	2.50	0.68417

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:

$$V \ (mm^3) = 0.47736 \ x \ L \ (mm) \ x \ W^2 \ (mm^2) - 1.318 \ mm^3$$

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

CLUTCH TYPE	MEAN	S.D.	RANGE	N
One-Egg				
Length	55.32	2.66	51-60	11
Width	38.68	0.98	37-40	11
Two-Egg				
Length	56.94	2.17	51-60	34
Width	39.16	1.43	35.5-41	34
Three-Egg				
Length	56.22	2.34	52-61	36
Width	39.24	1.37	37-43	36
$\overline{X}$ Length	56.40			81
$\overline{X}$ Width	39.13			81

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

Table 7

Known hatching dates for oystercatchers at Fisherman Island NWR 1982

Date	May 5	May 11	May 13	May 15	May 17	May 21	May 23
Absolute Date	125	131	133	135	137	141	143
No. of Nests	1	2	1	2	1	1	1

Date	May 25	May 26	May 27	May 29	May 31	Jun 3
Absolute Date	145	146	147	149	151	154
No. of Nests	1	1	2	1	2	1

$N = 17$, $\bar{X} = 141.3$ (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.

51

Out of Territory

52
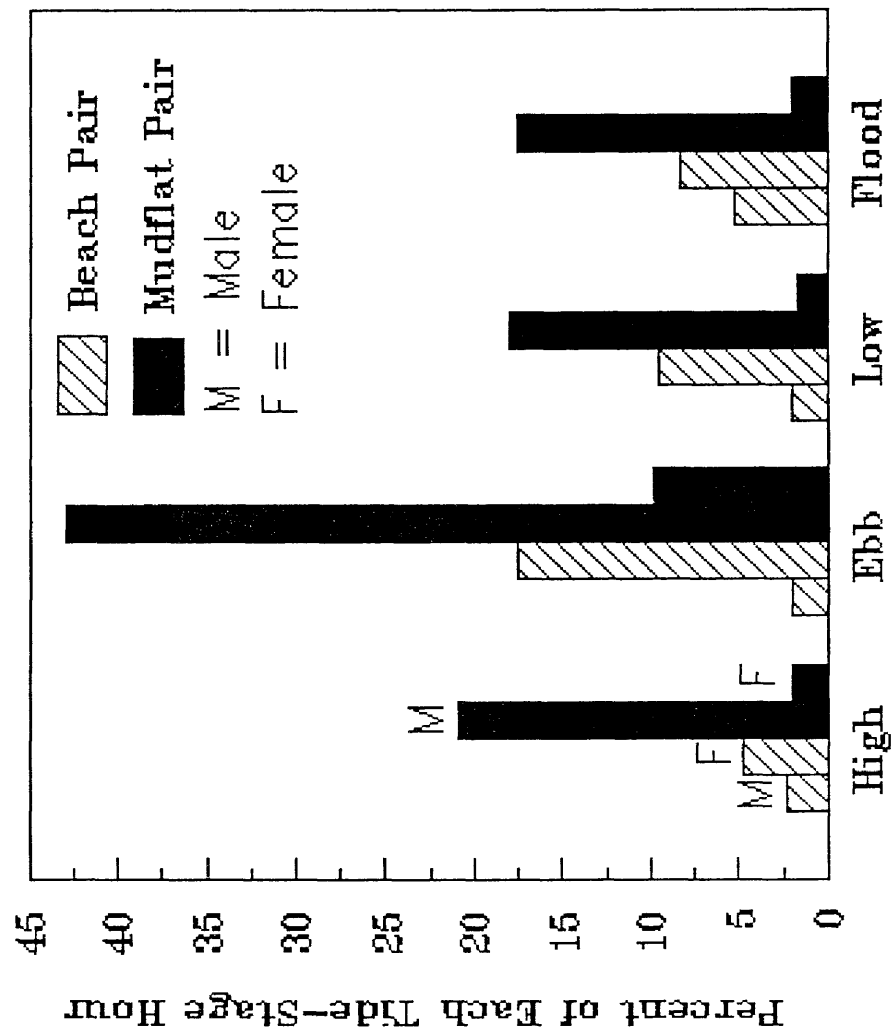
Foraging in Shallow Water
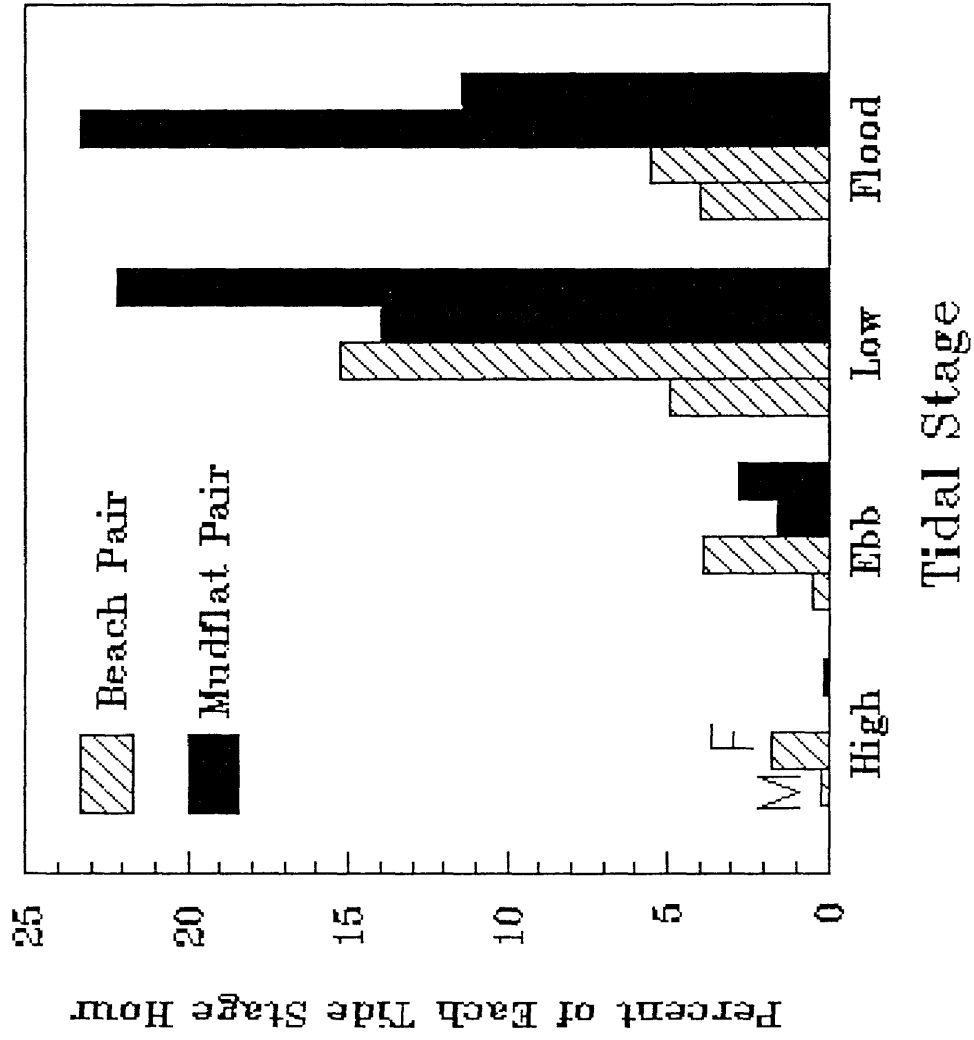
Foraging on Exposed Mud
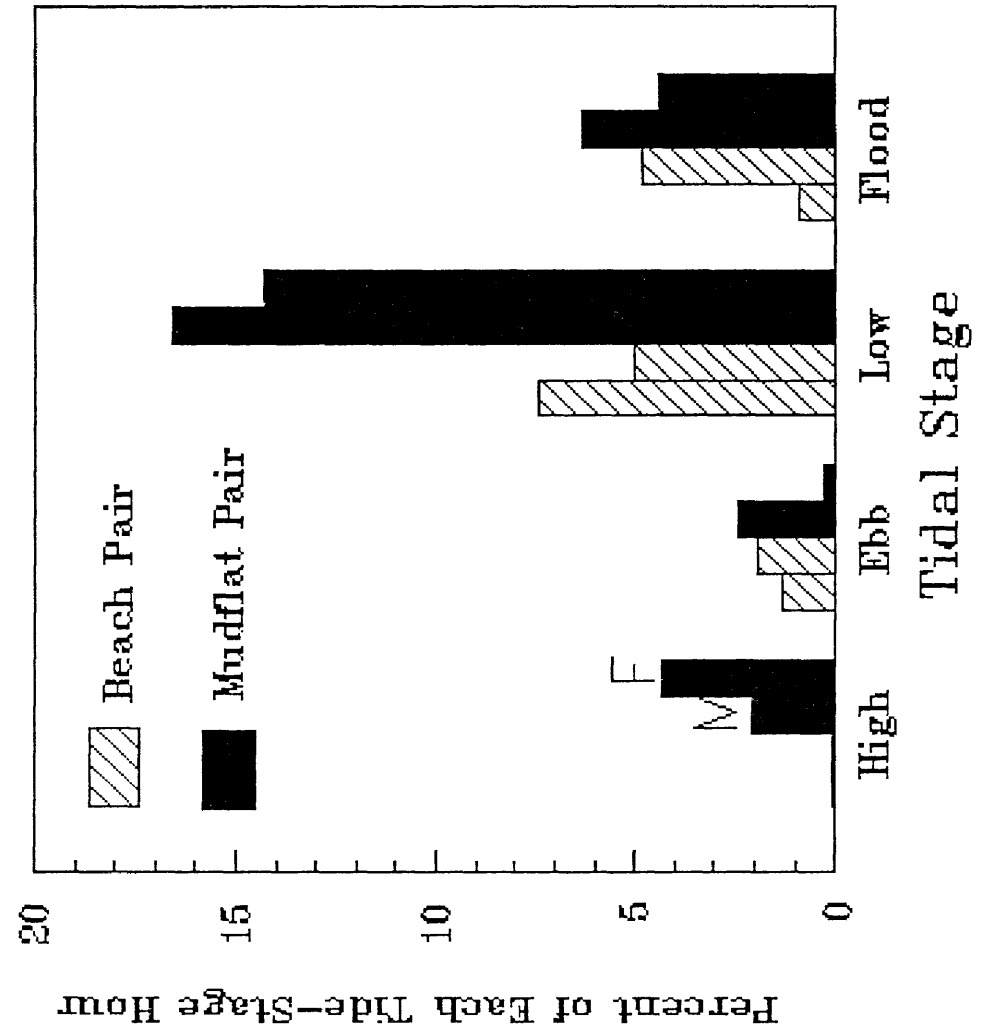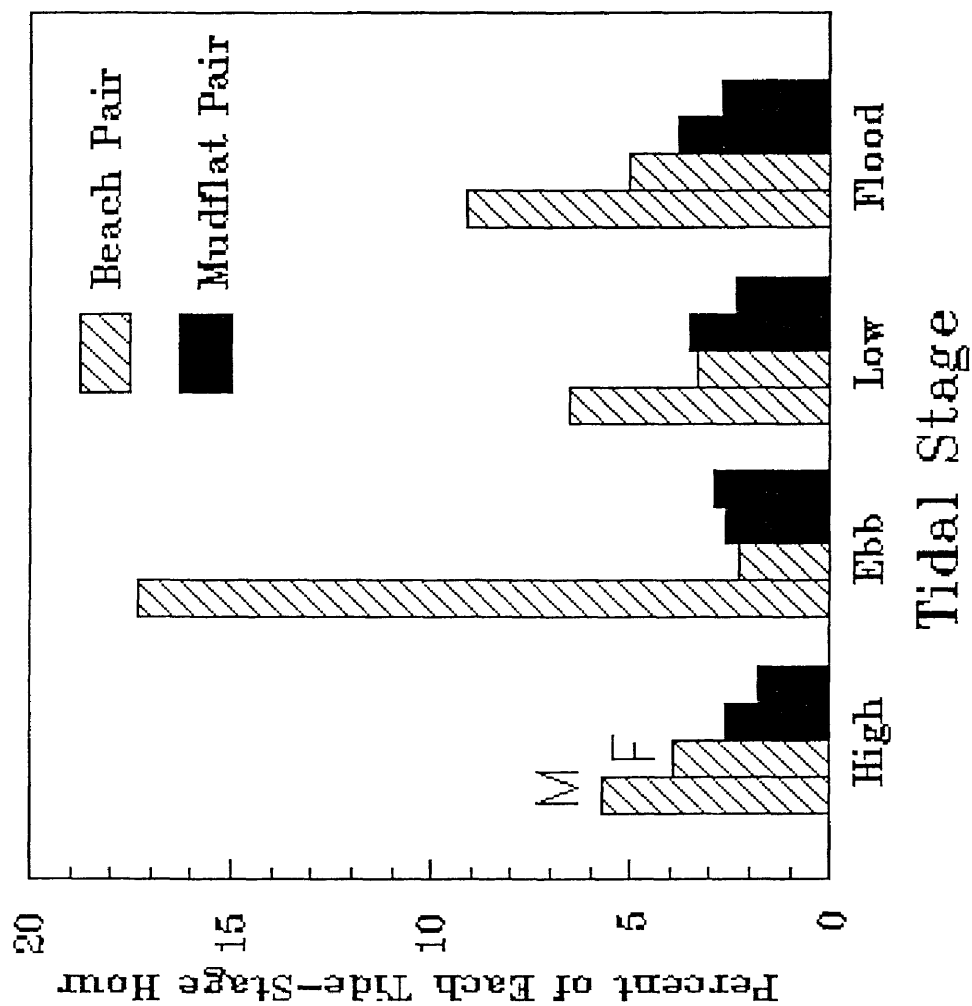
Intraspecific Agonistic Behavior
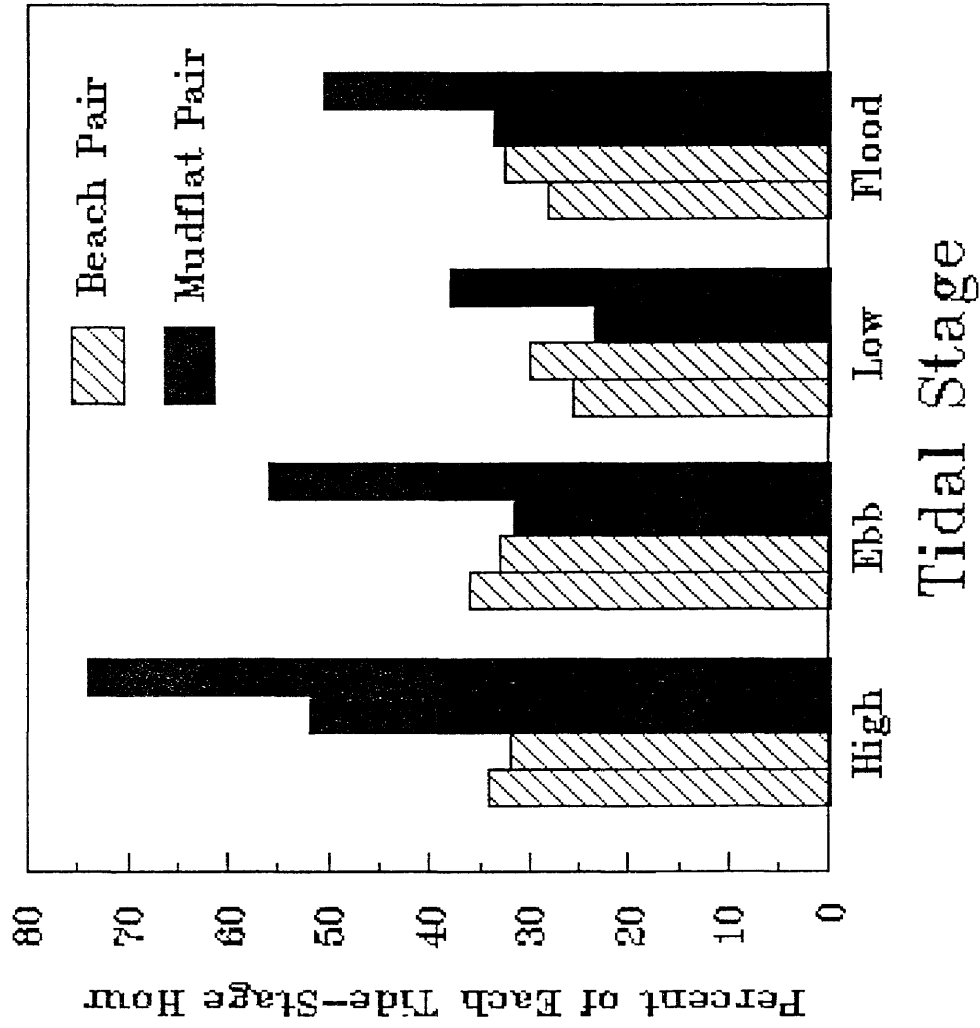
Offering Food to Chick
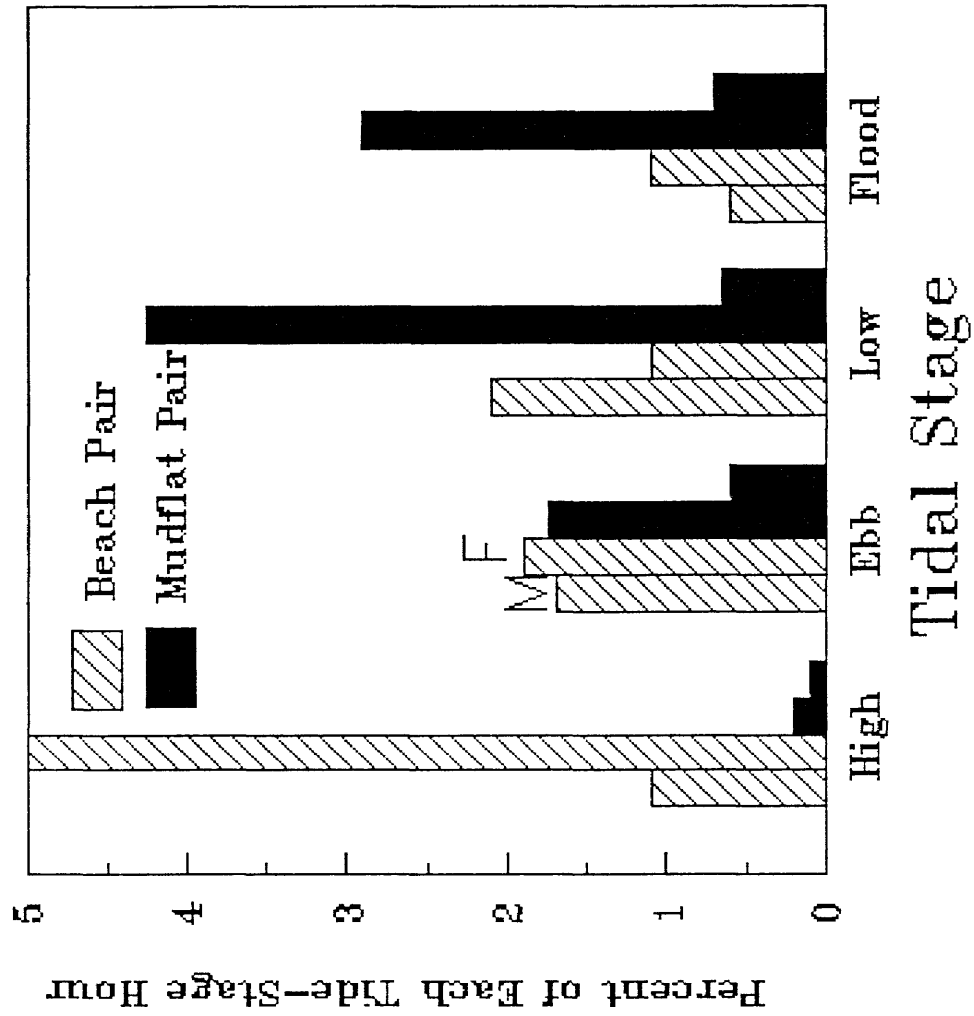
Foraging in Mean High Water Zone
(Beach Pair Only)

■ Male

▧ Female

Percent of Each Tide-Stage Hour

35 30 25 20 15 10 5 0

High   Ebb   Low   Flood

Tidal Stage
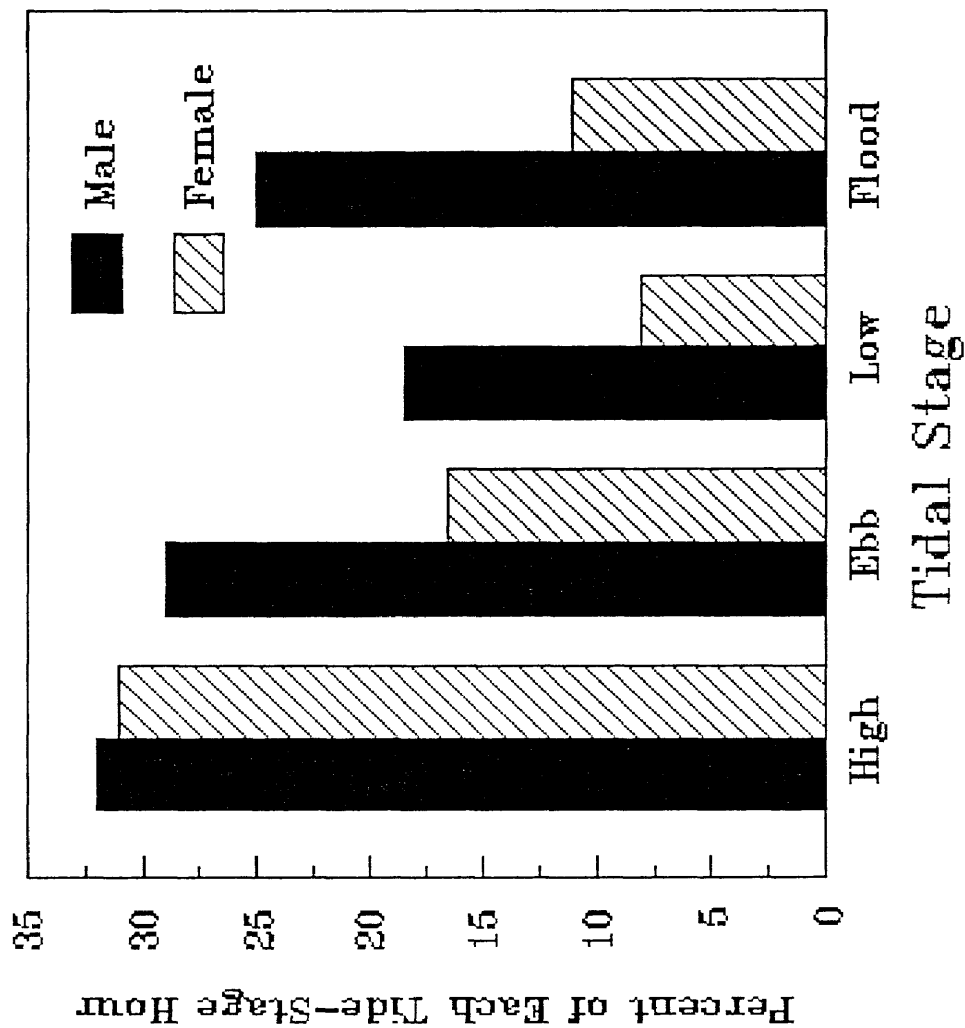
Intraspecific Agonistic Behavior

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

Tide	Beach Pair		Mudflat Pair	
	M	F	M	F
High	33.8	34.2	2.0	4.8
Ebb	32.1	22.8	5.7	4.4
Low	32.7	20.2	31.6	37.4
Flood	28.8	24.2	30.6	15.9
$\overline{X}$	31.9	25.3	17.5	15.6

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 oyster-catchers. 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. $\pm$ 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.).
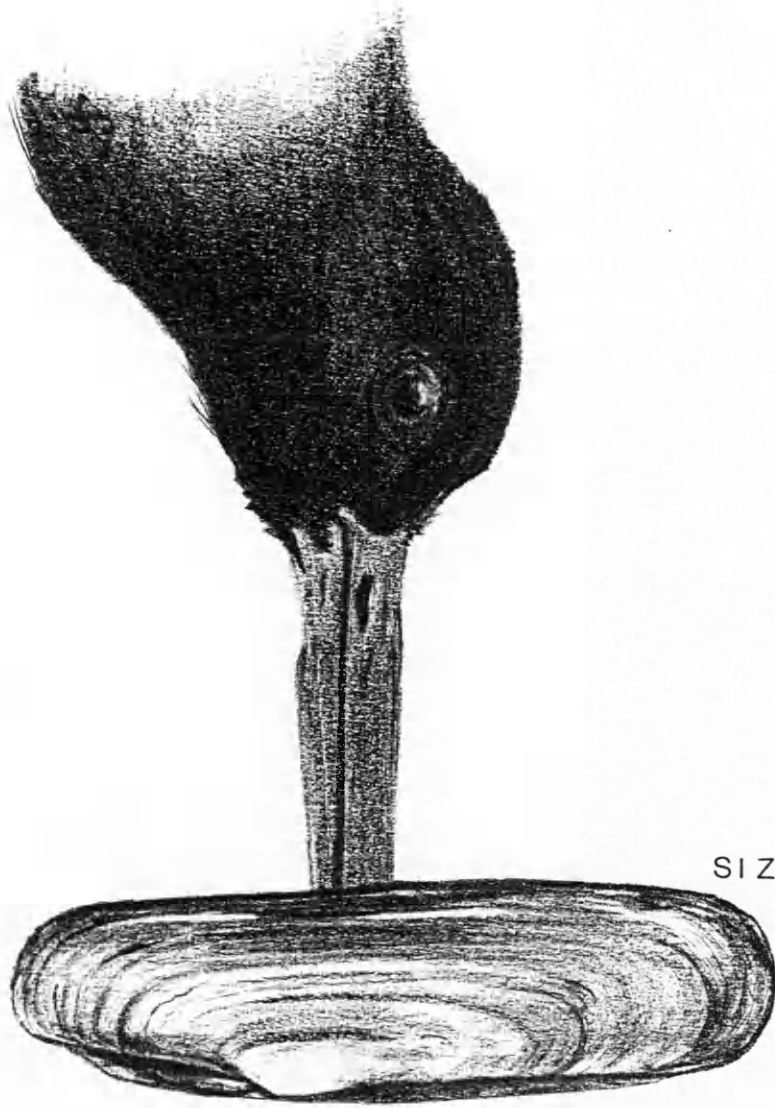
SIZE CATEGORY

5
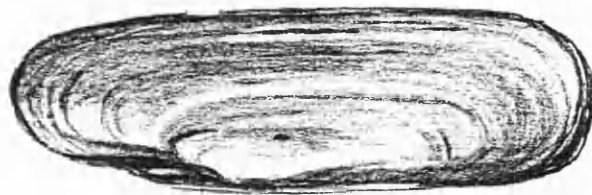
4

3

2

1

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

	18 Jun		22 Jun		24 Jun		1 Jul		3 July	
	M	F	M	F	M	F	M	F	M	F
Total Kcal Captured	74	5.9	54.6	36.9	30.1	18.9	37.9	26.1	9	19.8
Kcal Foraging Hour^{-1}	66	5.4	30.3	40.5	18.9	9.9	21.2	22.3	14.8	11.5
Kcal Consumed	32.3	2.9	27.8	22.3	22.1	10.1	30.3	26.1	8.5	12.7
Total Kcal Offered Young	42.8	3.5	27.8	14.6	19.8	8.8	23.1	26.1	3.0	12
Total Eaten by Young	41.7	3.0	26.8	7.8	8	8.8	7.6	0	0.5	7.1
Kcal Hour^{-1} Fed Young	37.2	2.8	14.9	8.6	5	4.6	4.2	0	0.8	4.1
Hrs Foraged	1.12	1.09	1.8	0.91	1.59	1.91	1.79	1.17	0.61	1.72
Hrs Observed	11.92		12.5		13.58		7.25		4.5	

68

Table 10 (contd.)

Kcal obtained from T. plebius by mudflat pair

	7 Jul		9 July		14 July		22 July	
	M	F	M	F	M	F	M	F
Total Kcal Captured	50.4	26.1	24.5	48.2	7.1	0	0	0.97
Kcal Foraging Hour^{-1}	15.9	17.3	8	12	4.9	0	0	0.7
Kcal Consumed	33.8	26.1	22	48.2	0	0	0	0.97
Total Kcal Offered Young	37.3	14.1	19.1	17	7.1	0	0	0
Total Eaten by Young	16.6	0	2.5	0	7.1	0	0	0
Kcal Hour^{-1} Fed Young	5.3	0	0.8	0	4.9	0	0	0
Hrs Foraged	3.16	1.51	3.05	3.9	1.44	0.77	0	1.39
Hrs Observed	7.08		9.92		4.5		6.2	

Table 11

The values of the terms in the linear regression: $\log_{10}$ (AFDW in mg) = a + b $\log_{10}$ (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.

Date	Site	No. of clams	a (intercept)	b (slope)	r2*
June 3-5	1	30	-2.2953	2.9453	0.98
June 3-5	2	64	-2.5553	3.0860	0.99
June 3-5	3	54	-2.4709	3.0371	0.99
July 18-21	1	54	-2.7026	3.1447	0.98
July 18-21	2	58	-2.8893	3.2314	0.99
July 18-21	3	51	-2.7559	3.1608	0.99

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 (Rhynchops 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., environ-mental) 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 $e = 1/m - 1/2$ and $n = 1/m + x$, 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 mortalitiy 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 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 $\underline{H}$. $\underline{ostralegus}$, the birds nesting on top of dunes were the first to abandon their territories in 1981. None successfully hatched eggs.

$\underline{Tagelus}$ $\underline{plebius}$, 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.

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VITA

Robert Lee Anderson III

   Born in Norfolk, Virginia, October 4, 1946. Graduated from
Granby High School in June 1964. Attended Old Dominion College
from 1964 to 1968 receiving Bachelor of Science in Biology in
August, 1968. Served in the U.S. Air Force Medical Service from
1969 to 1973. Began teaching high school biology and chemistry
at Norfolk Catholic High School from 1974 to 1979. Candidate
for Master of Arts Degree, College of William and Mary, 1980 -
1988. Environmental Inspector, City of Chesapeake, 1984 - 1985.
Biology teacher, Norfolk Catholic High, 1985 - 1986. Presently
Environmental and Natural Resources Specialist for the U.S. Army
Training and Doctrine Command, Fort Monroe, Hampton, Virginia.