CLUTCH INITIATION DATES, CLUTCH SIZE, AND EGG SIZE OF THE AMERICAN OYSTERCATCHER IN VIRGINIA

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ABSTRACT.—The timing of egg laying, clutch size, and egg size of the American Oyster-catcher (*Haematopus palliatus*) were studied over six consecutive breeding seasons in Virginia. Synchrony of laying dates occurred in each of five localities of the study area in at least one year. Mean clutch size was 2.8 eggs (mode = 3) in first clutches and 2.4 eggs (mode = 2) in replacement clutches. Individual females laid replacement clutches of the same size and laid eggs of similar average volume in all years. A change in mate had little effect on the date on which females initiated their first clutches in successive years. The average egg size in a clutch was correlated with the size of the laying female. Egg-size ordering occurred within clutches, the first-laid egg being smaller than the second egg and about equal in volume to the third. We propose that the second egg is largest because it has the highest probability of hatching, and the resulting sibling hierarchy reduces the frequency of sibling competition. *Received 19 October 1983, accepted 19 April 1984.*

SYNCHRONY of clutch-initiation dates, uniform egg size, and four-egg clutches are assumed to be adaptations of many shorebirds (Charadrii and Scolopaci) for living within the constraints of high-latitude breeding seasons. Clutch-initiation dates occur over a very brief period (Holmes 1971), and replacement clutches are uncommon (Pitelka et al. 1974), because the period of abundant food resources is brief and the season is telescoped (Holmes 1972, Nettleship 1973, Pitelka et al. 1974). A definitive clutch of four eggs of similar size and shape apparently forms the optimal configuration for minimizing the rate of heat loss when the clutch is uncovered (Norton 1970).

Uniform egg size within a clutch also implies no differential allocation of parental care to the chicks (Miller 1979). Uniform chick size may be as important a consequence of four similarly sized eggs as that provided by the energetic advantage during incubation, particularly because a definitive clutch of four is also found in many shorebirds nesting in the temperate zone (Maclean 1972).

Oystercatchers (Haematopodidae) are one of the few families of shorebirds whose young depend almost exclusively on the adults for food.

Clutch size in this group is usually less than four eggs, and this may be related to the extensive parental care (Maclean 1972). Egg-size ordering within a clutch is undocumented in oystercatchers, but it might be expected to occur in them rather than in shorebirds that do not feed their young. This is because, through preferential feeding, oystercatcher parents have a greater potential for "control" over which of their chicks survive (Alexander 1974). This potential control might be extended to the eggs, particularly if food is limiting or variable (Howe 1976), if preferential feeding is impractical, and if the probability of raising all chicks is dependent on the food supply.

The purpose of this paper is to document variations in clutch size and egg size in American Oystercatchers (*Haematopus palliatus*) and to elucidate seasonal and annual patterns in the timing of egg laying. By comparing individually known females over several breeding seasons, we have attempted to gauge repeatability measures (Falconer 1981) of these characteristics, as well as the effect of female size.

METHODS

Study area.—Study sites were located on Wallops and Assawoman islands, Virginia (37°50′N, 75°35′W) in 1978–1983 and on the salt marshes and dunes around the Chincoteague Channel, Virginia (37°55′N, 75°23′W) in 1981–1983. For purposes of comparing

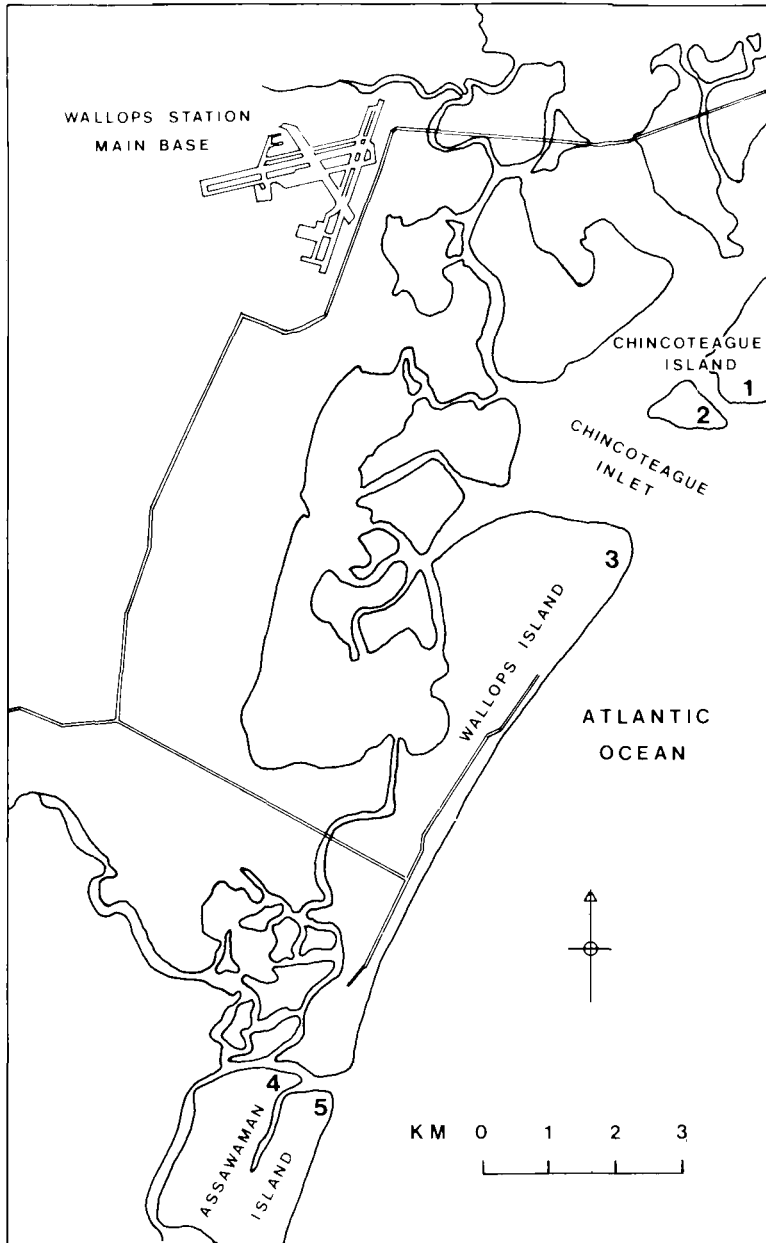[3] Present address: 364 Waterloo Avenue, Guelph, Ontario N1M 3K2, Canada.

Fig. 1. Map of study area including five breeding sites: (1) Chincoteague Island (mean of 5 nests per year), (2) Chincoteague Point ($\bar{x} = 13$ nests), (3) northern Wallops Island ($\bar{x} = 7$ nests), (4) the sand spit of southern Wallops Island ($\bar{x} = 8$ nests), and (5) Assawoman Island ($\bar{x} = 6$ nests).

the synchrony of clutch-initiation dates among localities, we divided the study area into five localities: (1) Chincoteague Island, (2) Chincoteague Point, (3) northern Wallops Island, (4) the sand spit of southern Wallops Island, and (5) Assawoman Island (Fig. 1). Fieldwork was conducted at the study sites within

the period 1 March to 31 July for six successive breeding seasons from 1978 to 1983. Observations in all seasons began by at least 6 April.

Data collection.—Over the study period, 60 adults (30 females, 30 males) were trapped at the nests with drop traps lined with fish net (Mills and Ryder 1979).

The adults were banded with aluminum bands and unique color-band combinations and were weighed and measured. From 1978 to 1980, all territories were searched periodically, although we were not always certain of clutch sequence (i.e. whether first or replacement clutch) or the order of egg laying. To obviate this problem, we searched territories throughout the prelaying and laying periods in the 1981–1983 breeding seasons.

Eggs were marked, weighed, and measured. All weights used in the analyses are of eggs weighed within 48 h of being laid. Weight can be difficult to determine in the field, particularly on windy days, whereas length and breadth measures are more precise. We therefore wanted a method for predicting volumes. Sixty-eight eggs from museum collections were filled with water to determine their volumes. Regression coefficients were calculated with volume as the dependent variable and the product of egg length (EL) times breadth^2 (EB^2) as the independent variable (Väisänen 1969). The resultant formula was used to calculate the volume of all eggs measured: Volume (cm^3) = $0.47736 \times EL$ (mm) $\times EB^2$ (mm^2) − 1.318(mm^3); $r^2 = 0.96$. Fresh egg weight (EW) was a good predictor of the calculated volume: Volume (cm^3) = 0.757 EW (g) + 5.96 (cm^3); $r^2 = 0.87$, $n = 170$. In the subsequent text, egg size and volume are used synonymously.

Statistical analysis.—The clearest method for detecting the effects of the female, clutch sequence, and year on egg size is to look at the effects of each factor in two two-way designs (Sokal and Rohlf 1981). We tested for the effects by using a mixed-model, two-way analysis of variance (ANOVA) with females as a random factor, and assumed no interaction between females and the fixed factor (e.g. year or clutch sequence). We then estimated the variation attributable to females and to the fixed factor and the significance levels of the two factors by using the interaction term as the error term. We used mean values to avoid the confounding effects of different cell sizes produced by differently sized clutches. When using year as the main effect, we examined only first clutches to avoid any confounding of clutch sequence in the design. In the comparison of means, we used t-tests on every pair of means, while controlling the experiment-wise error rate by lowering the value of α to α/n where n is the number of paired comparisons made.

To test for differences in egg size across years, across clutches within a year, and within differently sized clutches we used a one-way analysis of variance. We also tested for differences in egg size as a result of egg order by means of a one-way analysis of variance.

The ratio of the between-individual component of variance to the total variance measures the correlation between repeated measurements of the same individual and is known as the repeatability of a char-acter (Falconer 1981). Heritability, the resemblance between relatives, may be much less than repeatability, but it cannot be greater (Falconer 1981). The within-individual component arises from environmental fluctuations between successive measures and the systematic effects of age. The between-individual component comprises both permanent environmental effects and a genetic component (Findlay and Cooke 1982). We calculated repeatability measures by using the results of a one-way analysis of variance applied to (1) egg size among females across years, (2) egg size among females across clutches within a year, and (3) date of first clutch initiation across years.

A three-way contingency table was constructed to observe the pattern of egg-size ordering in successive years. The table was analyzed using log-linear models after the example of Fienberg (1970) and Bishop et al. (1975). In addition to testing the assumption of mutual independence, which characterizes classical contingency analyses, the techniques of Fienberg can be used to calculate the frequencies of events that would be expected under all possible conditions of dependence (interaction) between two or more classifying variables. Goodness-of-fit tests are then used to determine which of a series of hierarchical models that are based upon various assumptions of dependence best explain the observed frequencies of the event (Harder 1980).

If social stimulation tends to promote synchrony in the initiation of first clutches in neighbors, then females in a locality should tend to lay at more similar dates than females in different localities. One way to test for synchronization is to compare the variance of observed clutch-initiation dates of birds in one area (s_1^2) with the variance of observed clutch-initiation dates of all other birds (s_2^2) and to compute the ratio of variances (s_2^2/s_1^2). We obtained 500 random partitions of the data into samples of size n_1 (the number of nests in the locality in question) and n_2 (the number of total clutches initiated in a year $- n_1$), computed the variance ratio for each, and then looked to see if our observed value fell in the upper 5% tail of the distribution of 500 empirically obtained ratios (Sokal and Rohlf 1981).

RESULTS

Clutch initiation.—American Oystercatchers breeding in Virginia initiated clutches over a short period. Initiation dates of first clutches ranged from as early as 6 April (1981) to as late as 13 May (1982); the mean spread of dates for 1981–1983 was only 25 days, however. The average date of initiation of first clutches for 1981–1983 was progressively later in the successive breeding seasons (Fig. 2). Frequency distributions of clutch-initiation dates before 28 April are similarly shaped in the 1981 and 1982
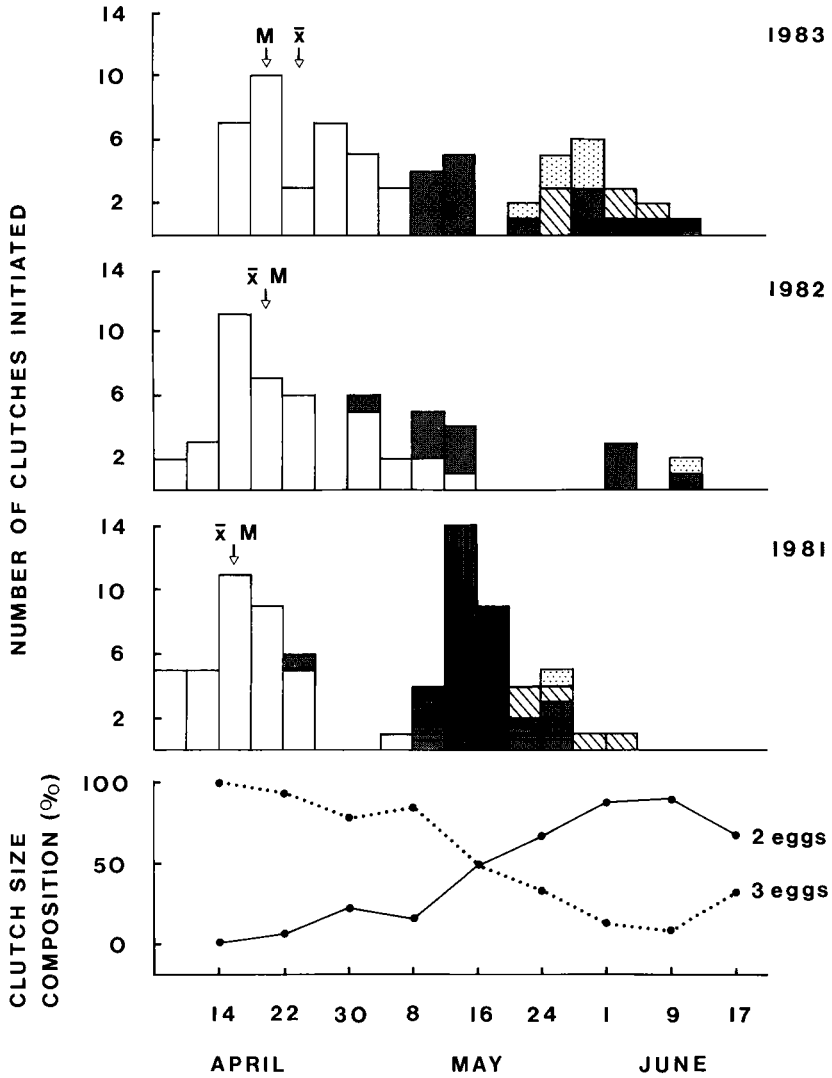
Fig. 2. Frequency histograms for 1981–1983 breeding seasons illustrating number of first clutches (open bar), second clutches (gray bar), third clutches (crosshatched bar), and clutches of unknown sequence (bold stippled bar). Location of mean ($\bar{x}$) and median (M) laying dates are indicated by arrows. The bottom panel shows the proportion of two- and three-egg clutches ($n = 156$).

breeding seasons. In 1983, the curve is flattened from an increase in the spread of clutch-initiation dates, and the mean date of first clutch initiation is slightly later. The 1983 field season was characterized by a cold, wet April, and this most likely caused the shift in clutch-initiation dates.

The time of initiation of replacement clutches was related to the date on which the first clutch was lost. High spring tides during 24–26 April 1981 caused most nests to be lost, and a peak of renesting occurred from 12 to 18 May. In 1982, the spring tides occurred before the majority of females had laid and after eggs in the first clutch had hatched. In 1983, nests were lost to both spring tides and predation at about the same time. This pattern of nest loss resulted in a small second peak of laying from 5 to 12 May. The pairs represented by this peak lost their nests a second time to predation, all with-

TABLE 1. Clutch size of *Haematopus palliatus* on Chincoteague, Wallops, and Assawoman islands, Virginia in six breeding seasons, 1978–1983.

Year	n	Number of eggs in first clutch					Number of eggs in second clutch				Number of eggs in third clutch				Number of eggs in clutches of unknown number			
		1	2	3	4	u[a]	1	2	3	u[a]	1	2	3	u[a]	1	2	3	u[a]
1978	33	0	1	2	1	0	0	0	0		0	0	0		2	9	18	
1979	43	1	14	18		0	1	3	4		0	1	1		0	0	0	
1980	18	0	0	0		0	0	0	0		0	0	0		2	6	10	
1981	83	1	2	31		6	1	17	11	5	0	4	1	3	0	1	0	
1982	54	0	4	31		6	0	9	1	2	0	1	0		0	0	0	
1983	63	0	4	19		13	1	8	6	1	0	6	1		1	2	0	1
Total	294	2	25	101	1	25	3	37	22	8	0	12	3	3	5	18	28	1

[a] u = clutches with unknown number of eggs.

in 4 days, resulting in a third peak of laying in late May and early June (Fig. 2).

Approximately three quarters of the total variance in clutch-initiation dates was explained by the effects of female and year. About 59% of the variation in clutch-initiation dates was explained by variation between females ($P < 0.001$) and about 16% by variation between years ($P < 0.001$). The repeatability (r_a) measure for date of clutch initiation for those females that laid in three consecutive years was high (total phenotypic variance = 97.8, r_a = 0.73, $n = 22$) and indicates that females tend to lay at about the same time each year. An examination of the year-to-year correlations between clutch-initiation dates, however, makes clear the facts that in 1983 females were less likely to lay at the same dates as in 1981 and 1982 (1981–1982, $r = 0.740$, $P < 0.0001$, $n = 22$; 1982–1983, $r = 0.485$, $P < 0.02$, $n = 23$) and were also less likely to lay on the same dates relative to their neighbors (Spearman rank correlation coefficients: 1981–1982, $r = 0.816$, $P < 0.0001$; 1982–1983, $r = 0.463$, $P < 0.02$). Again, a cold wet April and persistent high tides in some nesting areas caused some females to lay at a later date in 1983 than in previous years, and this fact alone would lower the year-to-year correlation.

When known females on a territory attained new mates ($n = 4$) in successive breeding seasons, they still tended to lay at about the same date as in the previous year. In the two instances when males retained their territories but acquired different mates in the subsequent breeding season, however, these new females laid 16 and 26 days later than the original residents.

Synchrony of clutch-initiation dates of first clutches (as defined by a significant $s_2{}^2/s_1{}^2$ ratio, see methods) occurred in all five localities in at least one of the three years of intensive study (1981–1983). Females nesting on the sand spit of southern Wallops Island in 1982 were more synchronous than the general population (six nests, $P < 0.05$). There was evidence of synchrony in all three years among the females on Chincoteague Point (nine nests: 1981, $0.05 < P < 0.1$; 1982, $P < 0.01$; 1983, $P < 0.01$). At the north end of Wallops Island, there was significant synchrony in 1983 (four nests, $P < 0.01$) but not in either 1981 or 1982. Synchrony was also detected in 1983 on Chincoteague Island (5 nests, $P < 0.01$) and in 1981 on Assawoman Island (5 nests, $P < 0.01$).

Clutch size.—The average clutch size declined as the season progressed. Most first clutches in 1981–1983 contained three eggs (Table 1). About two-thirds of first replacement clutches (second clutch) contained two eggs. Second replacement clutches (third clutch) contained two eggs in all but three nests. In 1979, 42.4% of first clutches contained two eggs, and in 1978 one clutch (3.0% of all clutches) contained four eggs.

The proportion of three-egg clutches declined through the breeding season (Fig. 3), but females laid three-egg clutches as late as 1 June in 1981 and 2 and 13 June in 1983 (Fig. 2). Females normally lay a maximum of two replacement clutches when preceding clutches are lost, but one female laid three replacement clutches in 1979, although one and possibly two of these were incomplete. Females that laid replacement clutches in 1981 and 1983 tended to lay

TABLE 2. Egg dimensions (mean ± SE) of first, second, and third laid eggs of *H. palliatus* in Virginia.

	Egg sequence[1]			Eggs of unknown number ($n = 241$)
	1 ($n = 116$)	2 ($n = 95$)	3 ($n = 69$)	
Volume (cc)	41.68 ± 0.27[a]	43.22 ± 0.27[b]	42.28 ± 0.32[a]	42.34 ± 0.18
Length (mm)	56.05 ± 0.21[a]	57.09 ± 0.19[b]	56.95 ± 0.20[b]	56.31 ± 0.13
Breadth (mm)	39.46 ± 0.11[a]	39.82 ± 0.11[a]	39.43 ± 0.14[a]	39.68 ± 0.07
Weight (g)	47.69 ± 0.42[a]	49.65 ± 0.40[b]	47.72 ± 0.53[a]	49.30 ± 0.50

[1] Homogeneous groups indicated with superscripts. Differences tested using Multiple *t*-tests ($P < 0.015$) following one-way ANOVA (Sokal and Rohlf 1981).

the same sized clutches ($\chi^2 = 3.19$, df = 1, $n = 13$, $0.05 < P < 0.10$).

Egg size.—Egg size in the combined data set (including data for all eggs of known laying sequence, regardless of clutch number or clutch size) varied systematically with laying order (Table 2). On average, the second egg laid was the largest (most voluminous) and the heaviest. The first and third eggs were about equal in volume. When we categorized the data according to clutch sequence, we obtained a similar result. In first clutches (a sample of mostly three-egg clutches), the second egg was larger and heavier than the first ($P < 0.015$) and heavier than the third ($P < 0.015$). The first and third eggs were of equal size, but the third egg was longer ($P < 0.015$). In second clutches (a sample of two-egg and three-egg clutches), the second egg was also the largest ($P < 0.015$).

We then categorized the data by the size of the clutch. In three-egg clutches, the second egg was largest and heaviest and the first and third eggs were equal in size and weight ($P < 0.015$). The second egg was longer than the first ($P < 0.004$) and wider than the third ($P < 0.011$). In two-egg clutches, the second egg was largest ($P < 0.02$) and tended to be longer than the first ($P < 0.07$).

The pattern of egg-size ordering varied by year (Table 3). In 1982, the second egg was the same size as the first about half the time, and there was no significant difference in their volumes. The log-linear model (Fienberg 1970) that best fits the overall pattern of egg-size ordering by year indicates an interactive effect between year (Y) and egg-size order (E) and an independent effect of clutch size (C) (Table 4). The standardized deviates, which indicate the deviation from the value expected based on the

TABLE 3. Frequencies and standardized deviates[a] of clutches with first eggs greater than and equal to or less than second eggs in two- and three-egg clutches from 1978 to 1983.

Year	Clutch size	Egg order		Total
		1 ≥ 2	1 < 2	
1978– 1979	Two-egg	1 (−0.1)	3 (−0.2)	4
	Three-egg	3 (0.8)	5 (−0.3)	8
1981	Two-egg	2 (−1.1)	18 (1.3)	20
	Three-egg	3 (−1.7)	25 (0.5)	28
1982	Two-egg	4 (0.4)	4 (−1.9)	8
	Three-egg	12 (2.6)	16 (−0.3)	28
1983	Two-egg	2 (−0.1)	10 (1.3)	12
	Three-egg	3 (−0.4)	9 (−0.7)	12
Total		30	90	120

[a] Standardized deviates = $(\text{Obs} \cdot \text{Exp})/\sqrt{\text{Exp}}$ for model of complete independence (Bishop et al. 1975).

TABLE 4. Values of the log-likelihood ratios (G^2) for selected models of interaction between clutch size (C), presence of egg-size ordering (E), and year (Y) in the data from Table 3. For a given model, variables that appear together within commas were assumed to be jointly dependent, but the effect of that interaction is independent of the other specified interactions or single factor effects.[a]

Model	G^2	df	P
E, C, Y	19.99	10	0.05
EY	15.05	8	$0.05 < P < 0.1$
C, EY	6.41	7	n.s.
E, CY	14.16	7	0.05
Y, EC	19.21	9	0.05
EC, EY	5.63	6	n.s.
EC, EY, CY	0.53	3	n.s.

[a] Probabilities less than 0.05 that are associated with models of equal or less complexity indicate their inability to provide adequate explanations of the data (Sokal and Rohlf 1981).

TABLE 5. Effect of clutch size on variation in egg-size parameters (mean ± SE).

| | Clutch size | | |
	2-egg (n = 68)	3-egg (n = 286)	P[a]
Egg			
Volume (cc)	42.4 ± 0.29	42.8 ± 0.15	n.s.
Length (mm)	56.9 ± 0.25	56.6 ± 0.12	n.s.
Breadth (mm)	39.5 ± 0.14	39.8 ± 0.05	0.1 < P < 0.05
Weight (g)	48.7 ± 0.44[b]	48.7 ± 0.27	n.s.

[a] Differences tested by one-way ANOVA.
[b] n = 39 for weights.

pattern observed in other years, are greater in three-egg clutches of the year 1982 (Table 3) than those expected by chance (Bishop et al. 1975). When the 1982 data for three-egg clutches with second eggs equal to or less than the volume of first eggs are removed and replaced with structural zeros (Bishop et al. 1975), the simple three-factor model of no interaction (Y,C,E) becomes sufficient $(P > 0.05)$ to explain the data. The proportion of clutches with no apparent egg-size ordering was considerably higher in 1982 than in any other year.

Average egg volume did not differ between clutches of two and three eggs (Table 5). In a comparison of egg size in first and second clutches laid by the same female, volume, breadth, and weight were significantly lower in second clutches than in first, and most of the total variation was attributable to differences among females (Table 6). In a similar comparison among all clutches of known sequence, however, no differences in egg size between first and second clutches emerged, but length and volume were significantly lower in third clutches than in first or second clutches (first clutch: length = 56.8 ± 1.61 mm, volume = 42.7 ± 2.19 cc; second clutch: length = 56.4 ± 1.86 mm, volume = 42.2 ± 2.37 cc; third clutch: length = 55.1 ± 1.43 mm, volume = 40.6 ± 2.14 cc, one-way ANOVA, $P < 0.015$ for differences as above).

Mean egg volume for each female was plot-

TABLE 6. Effect of female, clutch sequence, and year on variation in egg size parameters.

A. Clutch size (n = 39 females)

| | First clutch ($\bar{x}$) | Second clutch ($\bar{x}$) | Variation attributable to | | | |
| | | | Female[a] | | Clutch sequence[a] | |
Egg			R² (%)	F	R² (%)	F
Volume (cc)	43.8	42.5	71.6	3.69***	9.0	17.67***
Length (mm)	56.7	56.3	76.1	3.38***	0.1	2.40
Breadth (mm)	40.2	39.8	74.5	4.05***	7.1	14.74***
Weight (g)	50.0	48.2	78.5	4.39***	2.8	4.79*

B. Year (n = 24 females)

| | | | | Variation attributable to | | | |
| | | | | Female[a] | | Year[a] | |
Egg	1981	1982	1983	R²	F	R²	F
Volume (cc)	43.0	42.7	42.8	55.2	2.48**	0.38	0.20
Length (mm)	56.7	56.6	56.7	84.6	11.04***	0.07	0.09
Breadth (mm)	39.8	39.7	39.7	60.8	3.13**	0.35	0.21
Weight (g)	48.4	48.6	50.3	55.1	2.18*	8.80	4.00

[a] Significance levels designated as follows: *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$. Differences among means tested by two-way ANOVA of females with clutch sequence and year.

TABLE 7. Analysis of phenotypic variation in average egg size over several breeding seasons and over successive clutches in each breeding season.

	Volume	Length	Breadth
A. Egg size over several breeding seasons (n = 24 females, 72 observations)			
Between-individual variance (added variance component due to differences among ♀♀'s)	1,560.77	2.28	0.326
Within-individual variance	2,942.32	0.59	0.427
Total phenotypic variance	4,503.09	2.87	0.753
Repeatability (r_a)	0.35	0.80	0.43
B. Egg size over successive clutches 1981 (n = 23 females, 48 observations)			
Between-individual variance	3,410.46	1.89	0.43
Within-individual variance	3,132.05	0.95	0.54
Total phenotypic variance	6,542.51	2.84	0.97
r_a	0.52	0.66	0.44
1983 (n = 15 females, 37 observations)			
Between-individual variance	1,116.23	1.64	0.47
Within-individual variance	2,788.20	1.70	0.28
Total phenotypic variance	3,904.43	3.34	0.75
r_a	0.29	0.49	0.63

ted with the date of clutch initiation, and no apparent relationship was found (1981, $r = 0.13$, $n = 25$, $P > 0.05$; 1982, $r = -0.16$, $n = 23$, $P > 0.05$) except in 1983, when volume was negatively correlated with date ($r = -0.39$, $n = 29$, $P < 0.006$). This result probably reflects the larger number of second replacement clutches of lower average volume in 1983.

About 55% of the variation in egg size over the three years, 1981–1983, was attributable to differences among females rather than differences among years (Table 6). There was no indication of a difference in egg size in any of the six years of the study ($P > 0.05$, one-way ANOVA with full data set). Females for which we have data for 3–6 years appear to lay eggs of about the same average volume; there is no apparent change as a result of increasing age.

Repeatability estimates of egg characteristics over several years were available for 24 females (Table 7A). About 35% of the total phenotypic variance in egg volume in first clutches arises from differences between individuals. The remainder reflects intraindividual variation in response to fluctuating environmental conditions. Within a single season, between 29 and 66% of the total phenotypic variance arises from differences between females (Table 7B), depending on the year and the egg character.

Female size.—Females were heavier than males (females, $\bar{x} = 638 \pm 42$ g, $n = 30$; males, $\bar{x} = 567 \pm 113$ g, $n = 30$; $t = 2.75$, $P < 0.01$). Average egg volume (EV) ranged from 35.85 cc to 45.18 cc ($\bar{x} = 41.94 \pm 0.504$ SE). To test for a relationship between female size and egg volume (EV), we first used body weight as an index of size. Body weight and EV were correlated significantly ($r = 0.47$, $P < 0.05$, $n = 19$). Body weights of oystercatchers are known to fluctuate markedly in the breeding season, however, especially around the egg-laying period (Mercer 1968). We therefore also tested for a correlation between EV and the geometric mean (GM) of eight external body measurements, (Mosimann 1970, Mosimann and James 1979), this geometric mean being free of short-term seasonal bias. Female size as represented by GM is correlated significantly with EV ($r = 0.508$, $P < 0.025$) but accounts for only 4% more of the variation in egg volume than does weight. Whether one uses body weight or the GM of body measurements, it is apparent that larger females tend to lay more voluminous eggs than do smaller ones, although clearly female size was not the only factor affecting egg size in our study. Similar analyses of male measurements and weights revealed no influences of male size on egg size.

TABLE 8. Comparison of nest-initiation dates in 11 species of shorebirds.

Species	Mean number of observations	Range (number of days)	Location	Comments	Reference
American Oystercatcher (*Haematopus palliatus*)	28	25	37°50'N, 75°30'W	Mean of 3 yr	This study
Black Oystercatcher (*H. bachmani*)	8	21	48°38'N, 123°17'W	Total of 5 yr	Drent et al. (1964)
	17	24	48°18'N, 123°32'W		
African Black Oystercatcher (*H. moquini*)	55	84	33°05'S, 17°57'E	1 yr	Hockey (1983)
European Oystercatcher (*H. ostralegus*)	45	42	51°42'N, 5°16'W	Mean of 3 yr	Keighley and Buxton (1948)
Black-bellied Plover (*Pluvialis squatarola*)	3	5.5	75°40'N, 84°35'W	Mean of 4 yr	Hussell and Page (1976)
Willet (*Catoptrophorus semipalmatus*)	80	21	37°40'N, 75°20'W	Est. (by Nol), 2 yr[a]	Howe (1982)
Ruddy Turnstone (*Arenaria interpres*)	13	13	81°49'N, 71°18'W	1 yr	Nettleship (1973)
Western Sandpiper (*Calidris mauri*)	58	26	61°30'N, 64°50'W	Mean of 3 yr[a]	Holmes (1972)
White-rumped Sandpiper (*C. fuscicollis*)	6	12.5	68°40'N, 101°59'W	Mean of 2 yr	Parmelee et al. (1968)
Dunlin (*C. alpina*)	12	9	61°31'N, 64°50'W	Mean of 3 yr	Holmes (1971)
	18	22	61°30'N, 21°40'E	Mean of 5 yr	Soikkeli (1967)
Stilt Sandpiper (*C. himantopus*)	14	14	58°45'N, 93°00'W	Mean of 3 yr[b]	Jehl (1973)

[a] Replacement clutches not identified.
[b] Range estimated from hatching dates.

DISCUSSION

Most first clutches in our study area were initiated within a 20-day period in all intensively studied breeding seasons (1981–1983). The oystercatchers we studied were slightly less synchronous in the spread of initiation dates for first clutches than a population of breeding Willets (*Catoptrophorus semipalmatus*) found nearby (Howe 1982, Table 8) but more synchronous than *H. moquini* in South Africa and *H. ostralegus* in Scotland (Table 8). As expected, shorebirds nesting at higher latitudes are more synchronous in clutch-initiation dates than are American Oystercatchers (Table 8), although interspecific differences in nesting synchrony cannot be accounted for solely on the basis of latitude differences (e.g. *H. ostralegus* vs. *H. palliatus*).

Social stimulation probably affects laying dates in oystercatchers. Birds within localities had lower variances in the dates of initiation of their first clutches than did the general population in the study area. Synchrony within localities was most consistent where the largest numbers of oystercatchers nested (Chincoteague Point). Oystercatchers are very vocal and aggressive toward neighboring pairs, frequently participating in long piping displays in the prelaying period. This extensive piping may stimulate egg laying in some females. Consistent differences in environmental factors affecting females in different localities probably do not explain this synchrony, as neighboring

pairs of oystercatchers used widely differing foraging sites, and these differences were as great as the differences between sites (Nol in prep.). The high repeatability estimate obtained here is confounded by the effect of social stimulation, and no inference about a heritable component can be made.

Most replacement clutches contained two eggs. With some exceptions, most clutches initiated after 3 June contained two eggs. The average volume of eggs in later clutches was smaller, and this is probably a result of food limitations later in the season. Similarly, in Red-billed Gulls (*Larus novaehollandiae*) in New Zealand, egg volume and clutch size declined as the season progressed, and, in that case, the decline appeared to be closely related to the decline in the amount of food (swarms of planktonic euphausiids) over the breeding season (Mills 1979). The food of American Oystercatchers does not fluctuate as rapidly as do zooplanktonic populations, but possibly it is reduced enough through oystercatcher predation (O'Connor and Brown 1977) to affect both the size and number of eggs in replacement clutches.

Females tend to lay the same sized replacement clutch from year to year. This consistency in clutch size over several years probably results from consistent differences in territory quality among females rather than from a genetic component. Birds in poor territories may be contributing a greater proportion of their total energy reserves to a 3-egg first clutch and then can lay only a 2-egg replacement clutch, whereas birds occupying richer feeding territories can lay a second 3-egg clutch. This is currently under study.

Over a third of the yearly and annual variation in egg size arose from the between-individual component of the total phenotypic variation. At least part of this component is attributable to the effect of female size. A high repeatability in egg size from year to year has been found in at least six species of shorebirds (Väisänen 1969, Väisänen et al. 1972, Miller 1979), in Darwin's finches (Grant 1982), and in Great Tits (*Parus major*; Ojanen et al. 1979, Van Noordwijk et al. 1981). In at least some species, egg size has also been found to be heritable [Great Tit, Van Noodwijk et al. 1981; Red Grouse (*Lagopus lagopus scoticus*), Moss and Watson 1982].

Within-clutch ordering of egg size in shorebirds has received considerable attention, primarily because eggs laid last in other Charadriiformes (notably larids) are usually smaller, and this pattern may have considerable adaptive significance (Coulson 1963, Parsons 1970, Gochfeld 1977, Lundberg and Väisänen 1979). The literature on shorebird egg size is confused, however, because of the apparent equation of increased size with increased length or breadth. In American Oystercatchers, an increase in length does not necessarily influence volume and, therefore, the size of an egg. In those studies in which researchers found an increase in only one of the components of volume with laying sequence (e.g. Miller 1979, Nol and Lambert 1984), egg size as measured by volume has usually remained constant (e.g. Cairns 1977). Thus, a special explanation for the adaptiveness of egg-size ordering in most shorebirds with four-egg clutches need not be sought.

In American Oystercatchers, the first egg is smaller than the second egg but about equal to the third egg in three-egg clutches and smaller than the second egg in two-egg clutches. Eggs hatch in the order that they are laid. There are at least three hypotheses to explain the adaptive significance of egg-size ordering, but most explain only consistent increases or decreases in egg size over the laying sequence (e.g. larger later eggs being laid because of increased predation of incomplete clutches, Warham 1974, Miller 1979, Clark and Wilson 1981; higher provisioning in later laid eggs enhancing the competitive position of chicks hatched from those eggs in the case of hatching asynchrony, Howe 1976; smaller, later eggs being laid as a form of brood reduction, Parsons 1975, Gochfeld 1977, Braun and Hunt 1983).

The explanation for the larger second egg in clutches of the American Oystercatcher may reside with the different *risks* to each of the eggs. Incubation is commenced after the second egg is laid (pers. obs.), and thus for the initial 2 days the first-laid egg is exposed to increased risk of loss from predators and environmental fluctuations. The probability of loss of the first egg is likely to be higher than that of the eggs in an incubated clutch (Miller 1979). Although eggs hatch in the order they are laid, the first two eggs hatch relatively synchronously, and the resultant young may leave the nest before

the third egg has hatched. Disturbance from predators or other sources can cause the parents to abandon the third egg to attend the hatched young. The second egg, therefore, may have the highest probability of survival, and this could account for the pattern of egg-size ordering within clutches.

The magnitude of egg-size differences (4% by volume) in American Oystercatchers is small compared with those in most larids (10–30% of volume, see Parsons 1970, Davis 1975, Nisbet 1978, Lundberg and Väisänen 1979) but similar to that recorded in Roseate Terns (*Sterna dougallii*) late in the breeding season (Nisbet and Cohen 1975). In American Oystercatchers, fresh egg weight and the weight of the young at hatching are correlated ($r = 0.82$, $n = 8$, $P < 0.025$), the heaviest chick coming from the second egg. Within broods, the differences in chick weights parallel those among egg weights, unlike the situation with Black-legged Kittiwakes (*Rissa tridactyla*), in which asynchronous hatching markedly enhances weight differences within the brood once all chicks have hatched (Braun and Hunt 1983).

Even relatively small differences in egg size can result in a sibling social hierarchy. The sibling social hierarchy in *H. palliatus* is similar to that described previously for *H. ostralegus* and *H. bachmani* (Groves 1978, Safriel 1981). When a parent arrives with food, one chick rushes toward that parent while the others remain crouched or standing with the second parent. If the other chicks run to be fed, the dominant chick turns and chases its siblings. Only when the dominant chick seems to be satiated does the next in rank emerge to be fed. In *H. ostralegus*, the social hierarchy among chicks in a brood follows the weight hierarchy at hatching (Safriel 1981), and it is probable that this is true of *H. palliatus* too.

The social hierarchy facilitates brood reduction during periods of low food availability, because subordinate chicks either starve or are eliminated by predators (Safriel 1981). In periods of food abundance, all chicks in the brood can be fed. The sibling hierarchy also might promote a more efficient distribution of food if less of the parents' and chicks' energy is wasted during sibling competition (Hamilton 1964, Hahn 1981). This advantage alone might provide an impetus for parental manipulation of egg size independent of the predictability of resources.

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