GEOGRAPHIC AND LOCAL VARIATION IN NESTING PHENOLOGY AND CLUTCH SIZE OF THE BLACK OYSTERCATCHER[1]

MARIE-AUDE L'HYVER

Biology Department, University of Victoria, P.O. Box 1700,
Victoria, British Columbia V8W 2Y2, Canada

EDWARD H. MILLER[2]

Biology Department, University of Victoria, P.O. Box 1700,
Victoria, British Columbia V8W 2Y2, Canada and
Research and Public Programs, Royal British Columbia Museum,
Victoria, British Columbia V8V 1X4, Canada

Abstract. The Black Oystercatcher (Haematopus bachmani) is a year-round resident with an extensive range from southern California to Alaska. Because of the size of this range (about 28° of latitude) and its simple, nearly linear shape, we hypothesized that the species would exhibit adaptive geographic variation in nesting phenology and clutch size. Museum egg collections provided information for the entire nesting range, while field observations on about 40 breeding pairs on Cleland Island, British Columbia, provided information on local variation.

Nesting in Alaska starts about 15 days later than in southern California but trends in between are irregular. Birds on the exposed outer coasts of British Columbia and Washington start to nest about a week later than those in the San Juan Islands and Strait of Juan de Fuca. On Cleland Island the onset and duration of breeding were similar in 1982 and 1983, and individual females laid similar-sized clutches at similar times in both years. There is no measurable geographic variation in duration of nesting or in clutch size. Clutch size averages 2.4 across the nesting range and was about 2.1 on Cleland Island from 1970 to 1983. Initial and replacement clutches on Cleland Island are similar in size but, in museum samples from throughout the range, three-egg clutches were collected later than two-egg clutches.

The weak geographic trends in timing of breeding and their absence in clutch size were unexpected. Our findings may reflect (1) moderate seasonal and latitudinal fluctuations in the species' year-round coastal marine environment and (2) clutch size that is limited primarily by the optimal working capacity of parents. Research topics that can explore these possibilities include: proximate influences on breeding; heritability and individuality of breeding attributes; breeding energetics; and spatiotemporal variation in trophic ecology.

Key words: Black Oystercatcher; geographic variation; local variation; nesting phenology; clutch size.

INTRODUCTION

Geographic variation in avian nesting phenology and clutch size has generally been interpreted as an adaptation to geographically varying environmental conditions (e.g., climate, food). These conditions can also have proximate effects on the onset and length of breeding (Lack 1947, 1948; Perrins 1970; Murton and Westwood 1977; Ricklefs 1980; Price et al. 1988). General interpretations such as these have rarely been tested by intraspecific studies over an extended geographic range (Koenig 1984). We carried out such

a study on the Black Oystercatcher (Haematopus bachmani), which breeds and is a year-round resident over a great latitudinal range (from Bristol Bay, Alaska, in the north [59° N, 160° W] to Abreajos Point, Baja California, in the south [27° N, 114° W], and extending west to Amchitka Island, Alaska [51° N, 179° W]; Gabrielson and Lincoln 1959, Eley 1976, Hayman et al. 1986). Using data from museum egg collections we investigated geographic variation in clutch size and the timing of breeding over this range.

Patterns of local variation can provide reference levels for assessing geographic variation, and proximate causes of local variation may help to identify those environmental factors that underlie adaptive geographic variation. We therefore

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coupled our study of museum collections with an intensive field study of a breeding population on Cleland Island (British Columbia) and a survey of nests around southern Vancouver Island.

Because of the extensive and essentially linear range of *H. bachmani* we hypothesized that its breeding phenology would exhibit clear and pronounced geographic trends, with a later start and a briefer nesting period in the north due to harsher weather and a later and briefer period of food availability there. We also predicted that clutch size would increase with latitude, in keeping with a widespread trend in north-temperate birds to have larger clutches where seasonally fluctuating food supplies permit them (Campbell and Lack 1985).

Only one of these predictions was met and it was met only weakly. *H. bachmani* begins breeding about 15 days later in Alaska than in southern California (only about 0.5 days delay per degree of latitude), but trends in between are irregular. Neither clutch size nor duration of nesting exhibits geographic variation. We suggest that these patterns reflect moderate seasonal fluctuations in food supply or optimal working capacity of parents, or both.

MATERIALS AND METHODS

MUSEUM COLLECTIONS

A total of 135 clutches from 14 different museums was used in this study (Appendix). Specific collecting locations (latitude and longitude) were determined for 123 of these clutches; the other 12 were assigned to general geographic regions. The geographic range was divided into five regions with similar latitudinal ranges and similar numbers of clutches (Fig. 1). These regions correspond roughly to political states so were referred to as: Alaska, north of 54° N (AK; 29 clutches); British Columbia, 48–54° N (BC; 37 clutches); Washington plus Oregon, 42–48° N (WO; 20 clutches); California North, 34–42° N (CN; 23 clutches); and California South, south of 34° N, including northern Baja California (CS; 26 clutches). Comparisons among the five regions were made and the possibility of local geographic trends within each region was also investigated. The samples covered a longitudinal range of 57° (117–174° W), with 41° of this range in Alaska.

Important features of the nesting period include its duration, the date when laying starts, and the period of peak laying activity. Date of
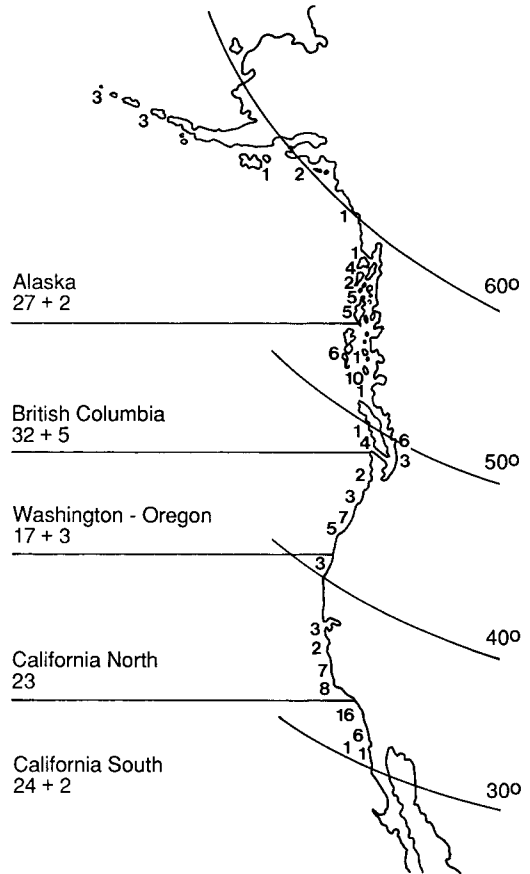

FIGURE 1.   Locations and numbers of clutches from museum collections, and their pooling into five regions. For each region, the sample sizes are the number of clutches of known precise latitude and longitude of origin, followed by the number of clutches of unknown precise collecting locality.

clutch initiation is the best kind of information for analyzing these features; unfortunately such dates can rarely be assigned confidently to museum specimens (McNair 1987). However, eggshell specimens are easiest to prepare when they are collected from freshly completed clutches and when it is most ethical for egg collectors to select them, so we assume that dates of clutch collection are predominantly in early incubation for each clutch (Väisänen 1977).

Another problem with data from museum egg collections is that a clutch may have been incomplete or already reduced in size through predation when collected. Furthermore eggshell collections are biased towards large clutches (McNair 1987). We assume that all five geographic regions

were similarly affected by these sources of error and bias.

Many data on clutch size are in the British Columbia Nest Records Scheme at the Royal British Columbia Museum. We examined but did not use this file because of the large biases inherent in such samples, especially for nidifugous species with long nesting seasons; oological collections in museums provide far more reliable data (Pienkowski 1984; McNair 1985, 1987).

LOCAL INFORMATION

Southern Vancouver Island. In the spring of 1981 (30 May–24 June) information was collected by Dr. Alan E. Burger on clutch size of *H. bachmani* nesting on small islands and coastal areas around southern Vancouver Island (20 localities in the region 48–50° N, 123–124° W).

Cleland Island, British Columbia. Cleland Island is a small island off the west coast of Vancouver Island (49°10′N, 126°05′W). It has the highest density of nesting *H. bachmani* in British Columbia or Washington (30–50 or more pairs each year; Hartwick 1974, Groves 1984, L'Hyver 1985, Purdy 1985, Purdy and Miller 1988). The laying activity of 39 pairs in 1982 and 35 in 1983 was followed daily from the first week of May to the end of July. Each nest location was mapped and each egg individually marked. Few breeding oystercatchers on Cleland Island are banded but each pair is believed to be faithful to the same territory in successive years (Hartwick 1974, Groves 1984, M.-A. L'Hyver and M. A. Purdy, unpubl. data). Each clutch could thus be associated with a particular pair and re-laying attempts could be identified. *H. bachmani* sometimes re-lays (once or even twice) but only if the entire clutch is destroyed.

In most cases exact clutch size was known although partial clutch predation by Northwestern Crows (*Corvus caurinus*) and Glaucous-winged Gulls (*Larus glaucescens*) may have introduced some error. Clutch size was assumed to be known only when no additional eggs were laid after a three-day interval. This assumption was based on the observation that the laying interval between successive eggs in a clutch had a strong mode at two days ($n = 57$). We knew dates of clutch initiation more often than dates of clutch completion so we used the former as estimates for the timing of nesting.

Statistical analyses. We analyzed data with SAS (SAS Institute 1985a, 1985b) and BIOM (Rohlf

1988; see Sokal and Rohlf 1981). We used standard parametric and nonparametric tests, as appropriate, and accepted $P = 0.05$ for them. Details on statistical tests are in the text and tables.

RESULTS

TIMING OF NESTING

Geographic variation in the timing of nesting. We found only weak evidence of earlier or longer nesting seasons at low latitudes (Table 1). In AK the date of clutch collection averaged 15 days later than in CS but intermediate regions did not exhibit a regular trend (Fig. 2). Total length of the season also varied irregularly across regions. Mean and median dates of clutch collection varied significantly among regions. Two homogeneous groups with similar means (by Duncan multiple range test) and medians (by median test) were distinguished: AK plus WO; and BC, CN plus CS. WO and CN were grouped only by the Duncan test. On other statistical tests, AK differed significantly from BC and CS, while the latter differed significantly from WO (Table 1). The presence of latitudinal trends was examined further through nonparametric correlations between date of collection and latitude (Fig. 3). There was a moderate significant trend towards later dates at higher latitudes overall (Spearman's rank correlation coefficient, $r_s = 0.30, P < 0.001$) and, within CN, a significant positive correlation between collection date and latitude ($r_s = 0.51$, $P = 0.02$). Nesting in BC was not significantly early in relation to latitude (for nesting date and latitude, $r_s = -0.28, P = 0.16$).

Local variation in the timing of nesting. Egg-laying activity on Cleland Island showed a slightly more conspicuous peak in 1983 than 1982 but otherwise was similar in both years (Fig. 4). Hartwick (1974) also noted slight differences between years in the timing of nesting on Cleland Island. We were confident of the identity of 18 pairs that nested in both years; the dates of initiation of their first clutches were similar in both years ($r = 0.71, P < 0.01$). Nol et al. (1984) reported a similar finding for the American Oystercatcher (*H. palliatus*), and Harris (1969) found that one pair of Eurasian Oystercatchers (*H. ostralegus*) was the first to lay eggs in six successive breeding seasons. On Cleland Island, laying dates in 1983 averaged three days earlier than in 1982 for these pairs ($\bar{x} = 2.9$, SD $= 10.9$), but one female laid 27 days later and another laid 16 days earlier in

TABLE 1. Summary of collection dates for clutches in museum collections.

| | Collection dates | | | | | |
Region	Earliest	Latest	Range (days)	Median[a]	$\bar{x} \pm SD$[b]	n
Alaska	25 May	2 July	38	11 June	13 June ± 10.6	22
British Columbia	5 May	25 June	51	1 June	2 June ± 9.4	34
Washington–Oregon	17 May	30 June	44	11 June	11 June ± 11.0	20
California North	17 May	20 July	64	1 June	5 June ± 16.1	22
California South	9 May	20 June	42	26 May	29 May ± 11.8	24

[a] Median dates of clutch collection varied significantly across regions (Brown Mood test: $\chi^2 = 25.7$, df = 4, $P < 0.01$).
[b] Mean dates of clutch collection varied across regions, with significant differences ($P < 0.05$) between AK-BC, AK-CS, and WO-CS (multiple comparisons among pairs of means, using Hochberg's GT-2 method: GT-2 = 3.41, 4.32 and 3.65 respectively, with df = 117).

1983. Dates of clutch initiation on Cleland Island did not differ from collection dates for the BC museum sample, and also agreed broadly with estimates from nearby field studies (Table 2). However, clutch initiation began about a week later on Cleland Island than on Mandarte Island and Race Rocks (Table 2).

Laying of replacement clutches on Cleland Island began in the first few days of June in both years, but peaks of laying for first and replacement clutches were not distinguishable. For 13 females, the interval between loss of the first clutch to laying of the first egg of the replacement clutch averaged 15 days (SD = 1.6). Hockey (1983) reported an interval of 22 days for the African Black Oystercatcher (*H. moquini*), and Glutz et al. (1975) noted a range of 8–15 days for *H. ostralegus*.

CLUTCH SIZE

Geographic variation in clutch size. Clutch size averaged 2.41 for museum clutches. Clutches of two and three eggs occurred at similar frequencies, while one-egg clutches were few and four-egg clutches were extremely rare (Table 3).

The frequency distribution of clutch size, mean clutch size, and variance in clutch size did not vary significantly among regions. Other published field estimates of clutch size agree with the museum estimates summarized in Table 3 (L'Hyver 1985).

Seasonal trends in clutch size were investigated by comparing collection dates for clutches of different size. There was no significant seasonal trend in clutch size within any of the five regions (Table 4) but, within each region, three-egg clutches were collected slightly later in the season than were two-egg clutches (about five days later, excepting CS).

Local variation in clutch size. The size of 39 clutches noted by Burger around southern Vancouver Island did not differ significantly from the BC museum sample (Table 5).

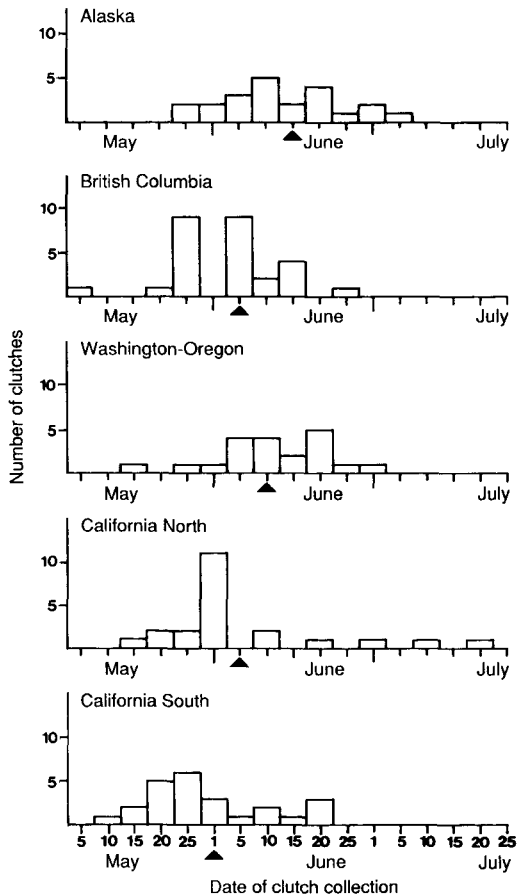Clutch size on Cleland Island averaged 2.06

FIGURE 2. Frequency histograms for dates of clutch collection by region. The triangles mark the intervals containing the median collection date for each region.
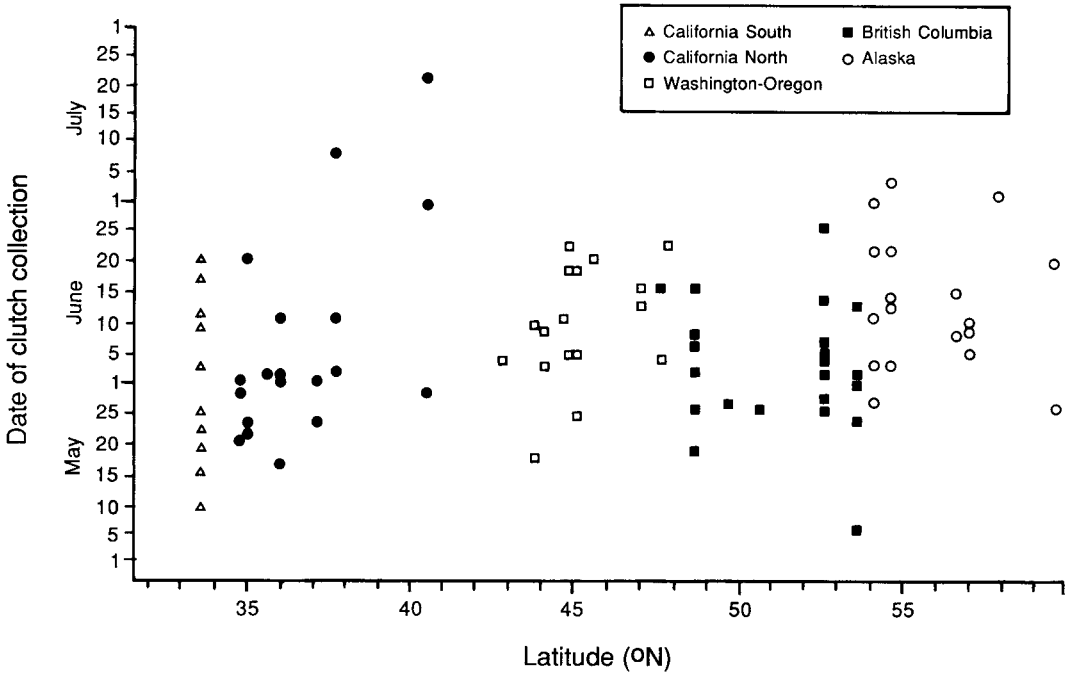
FIGURE 3.   Relationship of the date of clutch collection to latitude.

and did not vary significantly across the years 1970–1983 (Table 5). However the yearly estimates are not independent samples since many birds bred repeatedly on the island over that period. Clutch size on Cleland Island differed significantly from both the southern Vancouver Island field sample and the BC museum sample. Cleland Island had a higher proportion of two-relative to three-egg clutches; four-egg clutches have never been noted there.

Initial and replacement clutches on Cleland Island were similar in size (Table 6). Individual females tended to lay initial and replacement

clutches of the same size ($n = 4$): one female laid two successive two-egg clutches; two laid two successive three-egg clutches; and one female replaced a three- with a two-egg clutch. Nol et al. (1984) found that initial and replacement clutches were similar in size in *H. palliatus* too. If a female *H. ostralegus* loses a first egg to predation soon after laying she may move to another scrape and only lay the remaining eggs in that clutch (Harris 1967). We observed no such behavior in *H. bachmani*.

Individual females also tended to lay initial clutches of similar size in 1982 and 1983: seven

TABLE 2.   Comparison of initiation dates for first clutches on Cleland Island and initiation/collection dates for nearby areas in British Columbia and Washington.

	Initiation/collection dates					
Sample/location	Earliest	Latest	Range (days)	Median	$\bar{x} \pm SD$	n
Cleland Is. (1982)[a]	13 May	26 June	44	29 May	2 June ± 11.0	24
Cleland Is. (1983)[a]	10 May	4 July	55	1 June	30 May ± 12.8	32
BC Museum sample[a]	5 May	25 June	51	1 June	2 June ± 9.4	34
Mandarte Is. and Race Rocks[b]	7 May	30 May	24	20 May	21 May ± 5.7	17
Destruction Is., Washington[c]	ca. 22 May	ca. 19 June	ca. 29	ca. 31 May	ca. 3 June	25

[a] Dates of clutch initiation on Cleland Island and collection dates in the BC museum sample did not differ significantly from one another (one-way ANOVA: $F_s = 0.57$; df = 2, 87; $P > 0.05$).
[b] Data from Fig. 10 of Drent et al. (1964) (48°38'N, 123°17'W).
[c] Data from Fig. 2 of Nysewander (1977) (47°41'N, 124°29'W).

TABLE 3. Summary of clutch size in different regions, based on museum eggshell collections.[a]

Region	Clutch size					
	1	2	3	4	$\bar{x} \pm SD$	n
Alaska	3	13	11	2	2.41 ± 0.780	29
British Columbia[b]	6	14	17	0	2.30 ± 0.740	37
Washington–Oregon	0	7	12	1	2.70 ± 0.571	20
California North	1	10	11	1	2.52 ± 0.665	23
California South	4	12	10	0	2.23 ± 0.710	26
All regions	14	56	61	4	2.41 ± 0.715	135

[a] There were no significant differences ($P > 0.05$) among regions in the frequency distribution of clutch size ($G_{adj} = 12.6$, df = 12), mean clutch size (by Hochberg's GT-2 method: GT-2 estimates ranged from 0.39 to 2.23, with df = 130) or variance in clutch size (F_{max} approximation test: $F_{max} = 1.87$, df = 4).
[b] Campbell et al. (1990), using data in the British Columbia Nest Records Scheme, reported a range of 1–5 eggs ($\bar{x} = 2.10$, SD = 0.722). This large sample ($n = 1,371$) does not differ significantly from ours ($G_{adj} = 3.9$, df = 4, $P > 0.05$), though it presumably contains a greater proportion of incomplete clutches, plus large clutches resulting from bigamy (Glutz et al. 1975, Hale 1980, Nethersole-Thompson and Nethersole-Thompson 1986).

females laid two-egg clutches and three females laid three-egg clutches; six females laid clutches of different size in the two years.

Finally, we investigated seasonal trends in clutch size by comparing mean laying dates for initial clutches of different size. In 1982, three-egg clutches were laid significantly earlier than two-egg clutches; a similar trend in 1983 was not significant (Table 7). These trends are opposite to those summarized in Table 4.

DISCUSSION

Timing and length of the nesting season. Food is generally thought to be the most important ultimate factor underlying the timing of nesting for seasonally breeding species of birds (Lack 1966, 1968; Daan et al. 1988). For example, the strong seasonal fluctuations in food availability in medium- and high-latitude terrestrial ecosystems may have promoted the evolution of breeding times so that eggs hatch when food is abundant (e.g., Holmes 1966). Food can also be proximately important to adults by contributing directly to egg formation or providing maintenance energy during egg formation. Thus, availability of food to adults can determine when breeding starts (Högstedt 1974). Neither of these generalizations can readily explain why many shorebird species breed when and for as long as they do, however (e.g., Pienkowski 1984, Gratto and Cooke 1987, Guillou and Debenay 1988), and this applies to our observations on *H. bachmani*. As a working hypothesis we suggest that this species' intertidal food shows moderate and ill-defined seasonal peaks in productivity (but see Dare [1977] on *H. ostralegus*). If this is so then the start of *H. bachmani* nesting is probably not directly tied to food supplies either proximately or ultimately. Instead, nesting should begin early to

permit re-nesting following predation and to provide chicks with a long summer season for growth and development (shorebirds have high metabolic rates and maximal energy needs of oystercatchers occur near the time of fledging; Hockey 1984, Kersten and Piersma 1987, McNab 1988). These factors may account for the moderate and unsystematic geographic variation that we observed, which is about the same as for *H. os-*
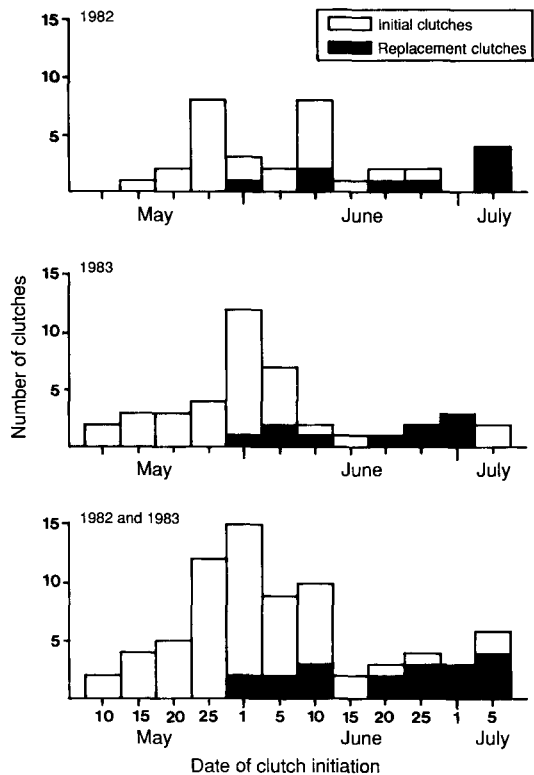

FIGURE 4. Frequency histograms for dates of clutch initiation on Cleland Island in 1982 and 1983.

TABLE 4. Relationship of clutch size to collection date within regions, based on museum eggshell collections.[a]

Region	Two-egg clutches		Three-egg clutches	
	$\bar{x} \pm$ SD	n	$\bar{x} \pm$ SD	n
Alaska	10 June ± 10.9	11	15 June ± 10.4	10
British Columbia	30 May ± 9.1	13	3 June ± 10.2	17
Washington–Oregon	8 June ± 11.7	7	14 June ± 10.6	12
California North	2 June ± 16.3	9	7 June ± 17.8	11
California South	29 May ± 13.5	11	28 May ± 11.5	10
All regions	2 June ± 12.7	51	7 June ± 13.4	60

[a] All comparisons within regions were insignificant ($P > 0.05$) by Student's t-test.

tralegus—about 0.5 day's delay in breeding per degree of increasing latitude (Väisänen 1977).

Inland populations of *H. ostralegus* nest far earlier than nearby coastal populations because of earlier food availability inland to pre-laying females (Heppleston 1972, Greenhalgh 1973, Väisänen 1977, Wilson 1978, Briggs 1984, Beintema et al. 1985, Nol 1989; see also Goutner 1985; a similar trend occurs in some plover species: Briggs 1983, Pienkowski 1984). *H. bachmani* has a much narrower range of nesting habitats but it appears that nesting on the exposed outer coast (e.g., Cleland Island; Destruction Island, Washington) begins about a week later than in the San Juan Islands and Strait of Juan de Fuca (Table 2; Nysewander 1977). This apparent difference should be investigated in more detail, as it may provide a critical test of our hypothesis that seasonal food availability does not proximately influence the start of breeding.

Geographic variation in timing of breeding cannot be extrapolated across oystercatcher species because of large ecological and life-history differences among them (Maclean 1972, Nol 1984). Consider the difference in timing of breeding between *H. bachmani* and the Pacific subspecies of American Oystercatcher (*H. palliatus frazari*), for example: collection dates for 78 clutches of the latter, from Baja California, averaged 9 May (median = 15 May, SD = 21.0; see Appendix), about 20 days earlier than the former in southern California yet separated by only a few degrees of latitude. Even greater differences characterize the two New Zealand oystercatcher species *H. ostralegus* and *H. unicolor,* which often nest syntopically yet breed about two months apart in both allopatry and sympatry (Baker 1974). Differences like these undoubtedly reflect fundamental differences in the species' adaptive suites so it would be untenable and unprofitable to consider them as simple extrapolations from intraspecific trends.

TABLE 5. Summary of clutch sizes on Cleland Island (1970–1983), in southern Vancouver Island sample, and in museum sample from British Columbia.[a]

Sample	Clutch size					
	1	2	3	4	$\bar{x} \pm$ SD	n
Cleland Is.						
1970[b]	14	38	9	0	1.92 ± 0.614	61
1971[b]	8	26	14	0	2.12 ± 0.672	48
1972[b]	11	34	13	0	2.03 ± 0.648	58
1976[c]	11	25	18	0	2.13 ± 0.728	54
1977[c]	12	38	10	0	1.97 ± 0.610	60
1978[c]	5	15	9	0	2.14 ± 0.693	29
1982	2	24	11	0	2.24 ± 0.548	37
1983	8	19	11	0	2.08 ± 0.712	38
All years	71	219	95	0	2.06 ± 0.655	385
Southern Vancouver Is.	4	9	26	0	2.56 ± 0.680	39
Museum sample	6	14	17	0	2.30 ± 0.740	37

[a] Across years for Cleland Island, $G_{adj} = 15.9$, df = 14, $P > 0.05$; between Cleland Island (all years) and southern Vancouver Island, $G_{adj} = 26.9$, df = 2, $P < 0.001$; between Cleland Island (all years) and museum sample, $G_{adj} = 7.2$, df = 2, $P < 0.05$; between southern Vancouver Island and museum sample, $G_{adj} = 3.2$, df = 2, $P > 0.05$.
[b] Data from Hartwick (1974).
[c] Data from Groves (1984).

TABLE 6. Comparison of clutch size for initial and replacement clutches on Cleland Island.[a]

Sample	Clutch size				
	1	2	3	$\bar{x} \pm$ SD	n
1982					
Initial	2	11	7	2.25 ± 0.639	20
Replacement	1	6	1	2.00 ± 0.535	8
1983					
Initial	6	15	8	2.07 ± 0.704	29
Replacement	2	7	4	2.15 ± 0.689	13
All initial	8	26	15	2.14 ± 0.677	49
All replacement	3	13	5	2.10 ± 0.625	21

[a] For 1982 and 1983 combined, initial and replacement clutches did not differ in size ($G_{adj} = 0.47$, df = 2, $P > 0.05$).

At northern latitudes relatively brief and synchronized nesting periods of birds occur because of the late spring, the brevity of the growing season, the lack of replacement clutches, and the onset of harsh autumn weather (Nol et al. 1984, Pienkowski 1984). Duration of the breeding season of *H. bachmani* does not differ systematically between Alaska and southern California, however, which is in keeping with our suggestion that food supply does not have an important direct effect on breeding phenology. A proximate factor that could influence the end of nesting is the onset of post-breeding moult (Lack 1966, 1968; Pienkowski 1984; Beintema et al. 1985); an ultimate one is reduced viability of late-season chicks. Martinez et al. (1983) and Goutner (1985) noted that the nesting season of *H. ostralegus* in southern Europe is about as long as in northern Europe even though in southern Europe it commences much earlier.

CLUTCH SIZE

Geographic variation in clutch size. Most information on geographic variation in avian clutch size comes from passerines. Such variation can be pronounced (e.g., Yom-Tov and Hilborn 1981), but is not always reflected in simple north-south trends (Lack 1947, Väisänen 1977, Slagsvold 1982). Some bird species show no or only slight increases in clutch size with latitude but they are in the minority (Klomp 1970, Payne 1976, Väisänen 1978, Møller 1984, Pienkowski 1984).

In contrast to *H. moquini* (Summers and Cooper 1977) and *H. bachmani,* both *H. ostralegus* (Glutz et al. 1975, Bianki 1977, Väisänen 1977) and the two North American subspecies *H. p.*

TABLE 7. Relationship of clutch size to laying date for initial clutches on Cleland Island.

Year	Clutch size	Date of clutch initiation		
		$\bar{x} \pm$ SD	Median	n
1982[a]	2	4 June ± 11.2	1 June	10
	3	16 May ± 1.9	17 May	5
1983[b]	2	2 June ± 16.1	2 June	10
	3	22 May ± 3.3	23 May	6

[a] By Student's t-test, $t_s = 3.50$, df = 13, $P < 0.01$; by median test, $\chi^2 = 8.00$, df = 1, $P = 0.047$.
[b] As for footnote a: $t_s = 1.78$, df = 14, $P > 0.05$; $\chi^2 = 4.00$, df = 1, $P = 0.46$.

palliatus and *H. p. frazari* show geographic variation in clutch size. In the latter there is a difference of about 0.3 eggs for 10 degrees of latitude from Mexico to Virginia (Nol et al. 1984). We can only speculate on why such geographic variation exists: a rich and predictable food supply would permit breeding oystercatchers to lay more eggs, to incubate more eggs (see Kålås and Løfaldli 1987), and to raise more or higher-quality young. High predation pressure on nests or chicks would favor low investment per nest and per egg/chick; in addition, it is easier for parents to protect few young from predators (Safriel 1967; Heppleston 1972; Walters 1982, 1984; Briggs 1984; Groves 1984; Nol 1984). It is unlikely that this constellation of interacting factors would result in similar patterns within and across species (Lack 1947, Koenig 1984, Pienkowski 1984; see also Mayo 1980). In any case, the trends for oystercatchers are so weak in comparison with those noted for many passerines that it would seem to be more relevant to focus on the relative uniformity of the patterns, rather than on differences among them. We suggest that this strong uniformity is related to ancestral features that characterize all oystercatcher species. These are shared parental roles (see Purdy and Miller 1988) and the parent-offspring relationship, which resist substantial evolutionary change because of their complexity (van Rhijn 1991); basic "adaptive" features like clutch size may be limited in a general sense by parental working capacity (including vigilance) within this complex behavioral suite (MacLean 1972, Glutz et al. 1975, Nol 1989; see also Swennen et al. [1989]).

Seasonal trends in clutch size. Seasonal declines in clutch size occur in many bird species (Klomp 1970), including the oystercatchers *H. p. palliatus* in Virginia (Nol 1984, Nol et al. 1984, Nol 1989), Blackish Oystercatcher (*H. ater*) in

Argentina (Nol 1984), and European *H. ostralegus* (Väisänen 1977). In *H. p. palliatus* the seasonal decline results from a preponderance of small replacement clutches (mean clutch size of 2.29, compared with 2.78 for initial clutches; Nol et al. 1984, Nol 1989). No such decline occurs in *H. moquini,* a species in which initial and replacement clutches are of the same size (Hockey 1983). Other reported weak seasonal declines in shorebird clutch size could be due to differences between initial and replacement clutches (Klomp 1970, Pienkowski 1984; but see Summers and Hockey 1980).

In our study *H. bachmani* on Cleland Island showed a statistically significant but weak decline in clutch size in 1982 but not 1983; this was not due to a preponderance of replacement clutches later in the season for these were the same size as initial clutches. As in our study, Harris (1967) noted a weak seasonal decline in clutch size in European *H. ostralegus* even though initial and replacement clutches were equal in size (but see Väisänen 1969). Many other factors could effect a seasonal decline, such as increased nest predation (late-season nesters might invest less in nest defense), differences between early and late breeders in age or experience (Klomp 1970, Winkler and Walters 1983), or individual/genetical differences between early and late breeders (Lack 1947, Toft et al. 1984). Interestingly, the museum samples for *H. bachmani* suggested a trend towards *increasing* clutch size later in the season, possibly because of a collecting bias towards incomplete clutches early in the season.

Individuality and Ecological Variation. We obtained few data on individual female *H. bachmani* but those data suggest strong individuality in clutch size and nesting date. Consistent differences separate individual female *H. p. palliatus* and *H. moquini* (Hockey 1983, Nol et al. 1984). Differences among individuals have profound effects on reproductive ecology generally (Lack 1947), especially in long-lived species (e.g., Ollason and Dunnet 1988). Indeed, in *H. p. palliatus,* individual differences are the single most important cause of variation in nesting date and clutch size (Nol et al. 1984; see also Thompson et al. 1986). Mounting evidence points to substantial heritability of non-morphological characters such as clutch size and laying date in birds (Boag and van Noordwijk 1987, van Noordwijk 1987). This subject merits attention for shorebirds, especially long-lived sedentary species like oystercatchers.

Spatiotemporal ecological variation underlies some of our observations on *H. bachmani,* such as on differences in breeding dates between inner and outer coastal areas. Year-to-year ecological fluctuations are central to understanding reproductive patterns (Boyce and Perrins 1987). Year-to-year variation in reproductive ecology is becoming well documented for birds (e.g., Harris 1967, Erikstad et al. 1985, Pratt and Winkler 1985, Thompson et al. 1986, Nol 1989, Watson 1989), and has emerged as an important ecological principle (Wiens 1989). We noted only minor year-to-year variations in clutch size on Cleland Island, in contrast to other species with sibling competition and brood-reduction strategies (Lack 1947, Groves 1984, Nol et al. 1984). Spatial variation on various scales likewise affects many facets of shorebird breeding biology and individual specialization (e.g., Hockey 1982; Hockey and Underhill 1984; Safriel 1985; Galbraith 1988; Watson 1988, 1989; Lauro and Burger 1989; Leopold et al. 1989).

CONCLUDING COMMENTS

We have documented geographic variation in the timing of nesting across the range of *H. bachmani.* The variation is similar in extent and pattern to that reported for European *H. ostralegus* but is far less than typically reported for noncoastal species. We detected no general patterns of geographic variation in clutch size, however, as is typical of shorebirds (Maclean 1972, Cramp 1983; but see Mayo 1980). Observed local differences such as the absence of four-egg clutches on Cleland Island may reflect chance effects (e.g., absence of those rare genotypes that produce large clutches), which result in patchy and adaptively meaningless genetic population structure. Social stimulation under high breeding density (see Nol et al. 1984) or local adaptation to high predation pressure there (e.g., from gulls on Cleland Island) are unlikely explanations.

We feel that detailed baseline studies on parental behavior/energetics, demography, and trophic ecology, with special reference to heritability, individuality and spatiotemporal ecological variations (including climate), will offer most insight into the evolutionary ecology of oystercatcher reproduction. Some of this research needs to be long-term to embrace ecological vari-

ation over a period that is long relative to the species' reproductive life-span (Boyce and Perrins 1987, Newton 1989).

ACKNOWLEDGMENTS

LITERATURE CITED

BAKER, A. J. 1974. Ecological and behavioural evidence for the systematic status of New Zealand oystercatchers (Charadriiformes: Haematopodidae). R. Ont. Mus. Life Sci. Contrib. 96.

BEINTEMA, A. J., R. J. BEINTEMA-HIETBRINK, AND G.J.D.M. MÜSKENS. 1985. A shift in the timing of breeding in meadow birds. Ardea 73:83–89.

BIANKI, V. V. 1977. Gulls, shorebirds and alcids of Kandalaksha Bay. Israel Program for Scientific Translations, Jerusalem, Israel.

BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics, p. 45–78. In F. Cooke and P. A. Buckley [eds.], Avian genetics: a population and ecological approach. Academic Press, Orlando, FL.

BOYCE, M. S., AND C. M. PERRINS. 1987. Optimizing Great Tit clutch size in a fluctuating environment. Ecology 68:142–153.

BRIGGS, K. 1983. The distribution and reproduction of Ringed Plovers breeding coastally and inland in north-west England. Bird Study 31:222–228.

BRIGGS, K. 1984. The breeding ecology of coastal and inland oystercatchers in north Lancashire. Bird Study 31:141–147.

CAMPBELL, B., AND E. LACK [EDS.]. 1985. A dictionary of birds. Buteo Books, Vermillion, SD.

CAMPBELL, R. W., N. K. DAWE, I. McTAGGART-COWAN, J. M. COOPER, G. W. KAISER, AND M.M.C. McNALL. 1990. The birds of British Columbia. Vol. 2: diurnal birds of prey through woodpeckers. Royal British Columbia Museum, Victoria, British Columbia.

CRAMP, S. [ED.]. 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic, Vol. 3: waders to gulls. Oxford Univ. Press, Oxford, England.

DAAN, S., C. DIJKSTRA, R. DRENT, AND T. MEIJER. 1988. Food supply and the annual timing of avian reproduction, p. 392–407. In H. Ouellet [ed.], Acta XIX Congr. Intern. Ornithol., Vol. 1. National Mus. Canada, Univ. Ottawa Press, Ottawa, Ontario.

DARE, P. J. 1977. Seasonal changes in body weight of oystercatchers Haematopus ostralegus. Ibis 119: 494–506.

DRENT, R., G. F. VAN TETS, F. TOMPA, AND K. VERMEER. 1964. The breeding birds of Mandarte Island, British Columbia. Can. Field-Nat. 78:208–263.

ELEY, T. J., JR. 1976. Extension of the breeding range of the Black Oystercatcher in Alaska. Condor 78: 115.

ERIKSTAD, K. E., H. C. PEDERSEN, AND J. B. STEEN. 1985. Clutch size and egg size variation in Willow Grouse Lagopus l. lagopus. Ornis Scand. 16:88–94.

GABRIELSON, I. N., AND F. C. LINCOLN. 1959. The birds of Alaska. Stackpole, Harrisburg, PA.

GALBRAITH, H. 1988. Effects of agriculture on the breeding ecology of lapwings Vanellus vanellus. J. Appl. Ecol. 25:487–503.

GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER, AND E. BEZZEL [EDS.]. 1975. Handbuch der Vögel Mitteleuropas, Vol. 6, Charadriiformes, Part 1. Akademie Verlagsgesellschaft, Wiesbaden, West Germany.

GOUTNER, V. 1985. Timing of laying of oystercatchers (Haematopus ostralegus) in the Evros Delta. Vogelwelt 107:187–188.

GRATTO, C. L., AND F. COOKE. 1987. Geographic variation in the breeding biology of the Semipalmated Sandpiper. Ornis Scand. 18:233–235.

GREENHALGH, M. P. 1973. A comparison of breeding success of the oystercatcher between inland and coastal areas in N. W. England. Naturalist (Leeds) 926:87–88.

GROVES, S. 1984. Chick growth, sibling rivalry, and chick production in American Black Oystercatchers. Auk 101:525–531.

GUILLOU, J. J., AND J. P. DEBENAY. 1988. Les tannes, marais ouverts de la côte Sénégalaise. Présentation du milieu et de l'avifaune. Régime alimentaire des limicoles nicheurs et paléarctiques. Alauda 56:92–112.

HALE, W. G. 1980. Waders. Collins, London, England.

HARRIS, M. P. 1967. The biology of oystercatchers Haematopus ostralegus on Skokholm Island, S. Wales. Ibis 109:180–193.

HARRIS, M. P. 1969. Effect of laying date on chick production in oystercatchers and Herring Gulls. Brit. Birds 62:70–75.

HARTWICK, E. B. 1974. Breeding ecology of the Black Oystercatcher (Haematopus bachmani Audubon). Syesis 7:83–92.

HAYMAN, P., MARCHANT, J., AND PRATER, T. 1986. Shorebirds: an identification guide to the waders of the world. Croom Helm, London, England.

HEPPLESTON, P. B. 1972. The comparative breeding

ecology of oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. J. Anim. Ecol. 41:23–51.

HOCKEY, P.A.R. 1982. Adaptiveness of nest site selection and egg coloration in the African Black Oystercatcher *Haematopus moquini*. Behav. Ecol. Sociobiol. 11:117–123.

HOCKEY, P.A.R. 1983. Aspects of the breeding biology of the African Black Oystercatcher. Ostrich 54:26–35.

HOCKEY, P.A.R. 1984. Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. Ardea 72:111–117.

HOCKEY, P.A.R., AND L. G. UNDERHILL. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. S. Afr. J. Zool. 19:1–11.

HÖGSTEDT, G. 1974. Length of the pre-laying period in the Lapwing *Vanellus vanellus* L. in relation to its food resources. Ornis Scand. 5:1–4.

HOLMES, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3–46.

KÅLÅS, J. A., AND L. LØFALDLI. 1987. Clutch size in the Dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? Ornis Scand. 18:316–319.

KERSTEN, M., AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea 75:175–187.

KLOMP, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1–24.

KOENIG, W. D. 1984. Geographic variation in clutch size in the Northern Flicker (*Colaptes auratus*): support for Ashmole's hypothesis. Auk 101:698–706.

LACK, D. 1947. The significance of clutch-size. Parts I and II. Ibis 89:302–352.

LACK, D. 1948. The significance of clutch-size. Part III. —Some interspecific comparisons. Ibis 90:25–45.

LACK D. 1966. Population studies of birds. Clarendon Press, Oxford, England.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.

LAURO, B., AND J. BURGER. 1989. Nest-site selection of American Oystercatchers (*Haematopus palliatus*) in salt marshes. Auk 106:185–192.

LEOPOLD, M. F., C. SWENNEN, AND L.L.M. DE BRUIJN. 1989. Experiments on selection of feeding site and food size in oystercatchers, *Haematopus ostralegus*, of different social status. Neth. J. Sea Res. 23:333–346.

L'HYVER, M.-A. 1985. Intraspecific variability in nesting phenology, clutch size and egg size in the Black Oystercatcher *Haematopus bachmani*. M.S.thesis, Univ. Victoria, Victoria, British Columbia.

MACLEAN, G. L. 1972. Clutch size and evolution in the Charadrii. Auk 89:299–324.

MCNAB, B. K. 1988. Food habits and the basal rate of metabolism in birds. Oecologia 77:343–349.

MCNAIR, D. B. 1985. A comparison of oology and nest record card data in evaluating the reproductive biology of Lark Sparrows, *Chondestes grammacus*. Southwest. Nat. 30:213–224.

MCNAIR, D. B. 1987. Egg data slips—are they useful for information on egg-laying dates and clutch size? Condor 89:369–376.

MARTINEZ, A., A. MOTIS, E. MATHEU, AND F. LLIMONA. 1983. Data on the breeding biology of the Oystercatcher *Haematopus ostralegus* L. in the Ebro Delta. Ardea 71:229–234.

MAYO, O. 1980. Variance in clutch size. Experientia 36:1061–1062.

MILLER, E. H., AND J. M. COOPER. 1991. Field heritability estimates for a shorebird: culmen, egg size, and laying date in the Least Sandpiper (*Calidris minutilla*). Unpubl. ms.

MØLLER, A. P. 1984. Geographical trends in breeding parameters of swallows *Hirundo rustica* and House Martins *Delichon urbica*. Ornis Scand. 15:43–54.

MURTON, R. K., AND N. J. WESTWOOD. 1977. Avian breeding cycles. Clarendon Press, Oxford, England.

NETHERSOLE-THOMPSON, D., AND M. NETHERSOLE-THOMPSON. 1986. Waders: their breeding, haunts and watchers. T. and A. D. Poyser, Calton, England.

NEWTON, I. 1989. Introduction, p. 1–11. *In* I. Newton [ed.], Lifetime reproduction in birds. Academic Press, London, England.

NOL, E. 1984. Reproductive strategies of the oystercatchers (Aves Haematopodidae). Ph.D.diss., Univ. Toronto, Toronto, Ontario.

NOL, E. 1989. Food supply and reproductive performance of the American Oystercatcher in Virginia. Condor 91:429–435.

NOL, E., A. J. BAKER, AND M. D. CADMAN. 1984. Clutch initiation dates, clutch size, and egg size of the American Oystercatcher in Virginia. Auk 101: 855–867.

NYSEWANDER, D. R. 1977. Reproductive success of the Black Oystercatcher in Washington State. M.S.thesis, Univ. Washington, Seattle.

OLLASON, J. C., AND G. M. DUNNET. 1988. Variation in breeding success in Fulmars, p. 263–278. *In* T. H. Clutton-Brock [ed.], Reproductive success: studies of individual variation in contrasting breeding systems. Univ. Chicago Press, Chicago.

PAYNE, R. B. 1976. The clutch size and number of eggs of Brown-headed Cowbirds: effects of latitude and breeding season. Condor 78:337–342.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

PIENKOWSKI, M. W. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. J. Zool. 202:183–214.

PRATT, H. M., AND D. W. WINKLER. 1985. Clutch size, timing of laying, and reproductive success in a colony of Great Blue Herons and Great Egrets. Auk 102:49–63.

PRICE, T., M. KIRKPATRICK, AND S. J. ARNOLD. 1988. Directional selection and the evolution of breeding date in birds. Science 240:798–799.

PURDY, M. A. 1985. Parental behaviour and role

differentiation in the Black Oystercatcher *Haematopus bachmani*. M.S.thesis, Univ. Victoria, Victoria, British Columbia.

PURDY, M. A., AND E. H. MILLER. 1988. Time budget and parental behavior of breeding American Black Oystercatchers (*Haematopus bachmani*) in British Columbia. Can. J. Zool. 66:1742–1751.

RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.

ROHLF, F. J. 1988. BIOM: a package of statistical programs to accompany the text Biometry. Applied Biostatistics, Inc., Setauket, NY.

SAFRIEL, U. 1967. Population and food study of the Oystercatcher. Ph.D.diss., Oxford Univ. Oxford, England.

SAFRIEL, U. N. 1985. 'Diet dimorphism' within an Oystercatcher *Haematopus ostralegus* population—adaptive significance and effects on recent distribution dynamics. Ibis 127:287–305.

SAS INSTITUTE, INC. 1985a. SAS user's guide: basics, version 5 edition. SAS Institute, Inc., Cary, NC.

SAS INSTITUTE, INC. 1985b. SAS user's guide: statistics, version 5 edition. SAS Institute, Inc., Cary, NC.

SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54:159–169.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second ed. W. H. Freeman, San Francisco.

SUMMERS, R. W., AND J. COOPER. 1977. The population, ecology and conservation of the Black Oystercatcher *Haematopus moquini*. Ostrich 48:28–40.

SUMMERS, R. W., AND P. A. R. HOCKEY. 1980. Breeding biology of the White-fronted Plover in the south-western Cape, South Africa. J. Nat. Hist. 14:433–445.

SWENNEN, C., M. F. LEOPOLD, AND L. L. M. DE BRUIJN. 1989. Time-stressed oystercatchers, *Haematopus ostralegus*, can increase their intake rate. Anim. Behav. 38:8–22.

THOMPSON, D. B. A., P. S. THOMPSON, AND D. NETHERSOLE-THOMPSON. 1986. Timing of breeding and breeding performance in a population of Greenshanks (*Tringa nebularia*). J. Anim. Ecol. 55: 181–199.

TOFT, C. A., D. L. TRAUGER, AND H. W. MURDY. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Aythya*, Anatidae), and a proposed evolutionary explanation. J. Anim. Ecol. 53: 75–92.

VÄISÄNEN, R. A. 1969. Evolution of the Ringed Plover (*Charadrius hiaticula* L.) during the last hundred years in Europe: a new method based on egg dimensions. Ann. Acad. Sci. Fenn. (A, IV) 149:1–90.

VÄISÄNEN, R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. Ann. Zool. Fenn. 14:1–25.

VÄISÄNEN, R. A. 1978. Egg and clutch sizes in four passerine species in northern Finland. Ornis Fenn. 55:60–68.

VAN NOORDWIJK, A. J. 1987. Quantitative ecological genetics of Great Tits, p. 363–380. *In* F. Cooke and P. A. Buckley [eds.], Avian genetics: a population and ecological approach. Academic Press, Orlando, FL.

VAN RHIJN, J. G. 1991. The Ruff: individuality in a gregarious wading bird. T. and A. D. Poyser, London, England.

WALTERS, J. R. 1982. Parental behavior in lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. Evolution 36:1030–1040.

WALTERS, J. R. 1984. The evolution of parental behavior and clutch size in shorebirds, p. 243–288. *In* J. Burger and B. L. Olla [eds.], Behavior of marine animals, Vol. 5. Plenum Press, London, England.

WATSON, A. 1988. Dotterel *Charadrius morinellus* numbers in relation to human impact in Scotland. Biol. Cons. 43:245–256.

WATSON, A. 1989. Dotterel populations and spacing on three Scottish areas in 1967–86. Ornis Fenn. 66:85–99.

WIENS, J. A. 1989. The ecology of bird communities, Vol. 2: processes and variations. Cambridge Univ. Press, Cambridge, England.

WILSON, J. R. 1978. Agricultural influences on waders nesting on the South Uist machair. Bird Study 25:198–206.

WINKLER, D. W., AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds, p. 33–68. *In* R. F. Johnston [ed.], Current ornithology, Vol. 1. Plenum, New York.

YOM-TOV, Y., AND R. HILBORN. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia 48:234–243.

APPENDIX

COLLECTIONS USED IN THE STUDY

The number of clutches examined in each institution (collections available as of December 1982) is indicated in parentheses: *H. bachmani,* followed by *H. palliatus frazari**. For details on catalog numbers and clutch sizes, see L'Hyver (1985).

American Museum of Natural History (2, 6*), California Academy of Sciences (2, 9*), Carnegie Museum of Natural History (1), Cowan Vertebrate Museum (3), Field Museum (3, 4*), Museum of Vertebrate Zoology (7), National Museum of Canada (3), National Museum of Natural History (13, 1*), Royal British Columbia Museum (5), Royal Ontario Museum (6), San Bernardino County Museum (11, 7*), Santa Barbara Museum of Natural History (8, 2*), University of Puget Sound (9, 4*), Western Foundation of Vertebrate Zoology (62, 52*).