The Condor 99:389–396

SOURCES OF VARIATION IN CLUTCH SIZE, EGG SIZE AND CLUTCH COMPLETION DATES OF SEMIPALMATED PLOVERS IN CHURCHILL, MANITOBA[1]

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Abstract. Variation in clutch size, egg size and clutch completion dates was studied in a population of Semipalmated Plovers (*Charadrius semipalmatus*) over 5 summers in Churchill, Manitoba. Clutch size variation was greatest in 1992, a year of unusually low summer temperatures, with almost 25% of clutches containing less than four eggs. More eggs were left unhatched in the nest in 1992 than in any other year. Clutch completion dates were negatively correlated with the average temperature during the pre-laying period. Synchrony of nesting was greatest in 1994, the warmest year. Egg volume and mass were not reduced as a result of the cold summer, and the variation in egg volume and mass attributable to differences among females was similar and significant in all years. Repeatabilities of all egg measurements were high. Egg volume was moderately correlated with female body mass but not with female wing length nor female condition (mass/wing length), a result consistent with that found in other shorebirds. Egg size did not vary consistently with laying order, suggesting strong selection for uniformity in egg size within a clutch.

Key words: egg size, clutch size, clutch completion dates, Charadrius semipalmatus, *Semipalmated Plover, shorebirds, variability, repeatability, female size, climate.*

INTRODUCTION

Among shorebirds there is little variation in clutch size, apparently because there is strong stabilizing selection for the modal clutch size (Mayo 1980, Walters 1984). Variation is primarily latitudinal: females of species in temperate and arctic zones lay four-egg clutches, whereas females of species nesting closer to the equator tend to lay three eggs or sometimes two (Walters 1984). Furthermore, intraspecific variation in clutch size also is extremely low, both within and among years (Szekely et al. 1994), and there is little information available on what factors might alter clutch size in shorebirds (Mayo 1980).

Egg size in shorebirds also is relatively invariant with low coefficients of variation of 5–7% (Miller 1979, Ricklefs 1984). In temperate and arctic-nesting species, four uniform, pyriform eggs are laid and thought to have evolved to maximize the efficiency of incubation heat transfer (Norton 1973, Miller 1979). Eggs of fully precocial shorebirds do not appear to become progressively larger or smaller with laying sequence (Nol and Lambert 1984, Slagsvold et al. 1984, Lank et al. 1985). Significant differences between females in egg size have been documented in a number of species, and this source of variance is generally much greater than any other source, including geographic variation (Väisänen 1977, Galbraith 1988, Grant 1991). These large differences among females may be the result of genetic differences or environmental effects. Heritability of egg size has been inferred through use of repeatability analyses for several species of European shorebirds (Väisänen et al. 1972), but mother-daughter regressions are difficult to obtain, in part because of low natal philopatry (Thompson et al. 1994). Although female size appears to explain some variation in egg size, particularly among populations (Väisänen 1977), the extent to which egg size reflects female condition or structural size remains unclear (Grant 1991).

Variation in clutch and egg size might not be detected under the usual conditions in which temperate and arctic shorebirds are studied. That is, variation in these traits might only occur during especially extreme conditions when individuals are stressed and unable to produce four eggs of similar size and shape. Long-term studies of

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[1] Received 10 May 1996. Accepted 17 December 1996.

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shorebirds are rare and the documentation of breeding during extremely cold conditions is poor because arctic-breeding shorebirds may fail to breed as a result of further shortening of their short breeding seasons (Pitelka et al. 1974, Mayfield 1978, Gratto-Trevor 1991).

In this study we report on annual variation in clutch size and the degree of variation both between and within females for egg size, egg mass and clutch completion dates in the Semipalmated Plover, *Charadrius semipalmatus,* a shorebird breeding in the arctic and subarctic that we have studied for five breeding seasons in Churchill, Manitoba, Canada. We tested two predictions about patterns of variation in egg size based on the hypothesis that the ability of females to lay eggs is related to food availability on the breeding grounds: (1) variation among females in egg size should be different in the unusually cold summer of 1992 than in warm or average summers because late breeding will either increase or reduce the differences accrued among females before arrival on the breeding grounds, and (2) intraclutch variation in egg size should be highest in poor climatic years and lowest in warm years because Semipalmated Plovers may reduce the energy allocated to some eggs in response to the poor breeding conditions (Horsfall 1984, Järvinen and Ylimaunu 1986, Murphy 1994). We also examined nesting synchrony. We expected increased breeding synchrony in the cold summer of 1992 if females that opted to breed did so over a shorter time frame because of the delay in appropriate conditions early in the laying period. By contrast, decreased breeding synchrony may occur if the poor breeding conditions enhanced the difference between "good" and "poor" quality birds. We used birds recaptured in successive years to analyze repeatability of egg characters. We also tested whether there is a relationship between female size or mass and egg volume, as an explanation for differences among females in the volume of eggs laid.

METHODS AND STUDY AREA

STUDY SITE

Semipalmated Plovers were studied in Churchill, Manitoba (58° 45'N, 95° 04'W) in 1988, and 1992 through 1995. The area comprised about 384 km^2 of roads, tundra, boreal forest, lakes, and gravel ridges. Most plovers nested wherever there was a moderately large expanse of gravel ($\bar{x}$ = 2.6 ha, see Rippin Armstrong and Nol 1993). Most nests were in depressions in the gravel, although some were placed directly on tundra or mudflats. All nests in the Churchill area were accessible by motor vehicle and were within 30 km of the town of Churchill. Nests were visited every two to three days during incubation and monitored from a distance by observing the incubating adult. Nests were visited every 12–24 hr just prior to and during the hatching of the plover's precocial young.

EGG MEASUREMENTS

We measured and weighed eggs from most nests in the study area in all years. Egg masses usually were recorded during the first week of incubation and measured using a Pesola spring balance to an accuracy of 0.1 g. Egg volume was calculated using the equation: $[(0.4482 \cdot \text{egg length} \cdot \text{egg width}^2) - 0.269]/1{,}000$, assuming that egg shape of Semipalmated Plovers is similar to the shape of eggs in Common Ringed Plovers *(C. hiaticula,* Väisänen 1977). Egg length and width were measured at the widest point, using calipers to an accuracy of 0.01 mm. Incubation was assumed to begin the day the fourth egg was laid; if nests were found only after clutch completion we back-dated from the date of hatch by using a 24-day incubation period (determined from 7 nests in 1993, $\bar{x} \pm$ SD: 24.4 ± 0.92). Clutch size and the number of eggs left unhatched were recorded for each nest. Hatching success is defined as the proportion of nests where at least one egg hatched.

MONITORING ADULTS

Adults were captured at the nests with walk-in nest traps during the last half of incubation (days 12–24 to avoid potential desertion) and were weighed to the nearest 0.1 g using a Pesola spring balance. Tarsus and bill lengths were measured to the nearest 0.01 mm, whereas wing length was measured to the nearest 1 mm. We examined the relationship between female size and egg size by using the egg data from the year in which we first trapped the female, and using each female only once in the analysis.

WEATHER VARIABLES AND NESTING CHRONOLOGY

Average daily air temperatures were obtained for the years 1981 to 1995 from the Environ-

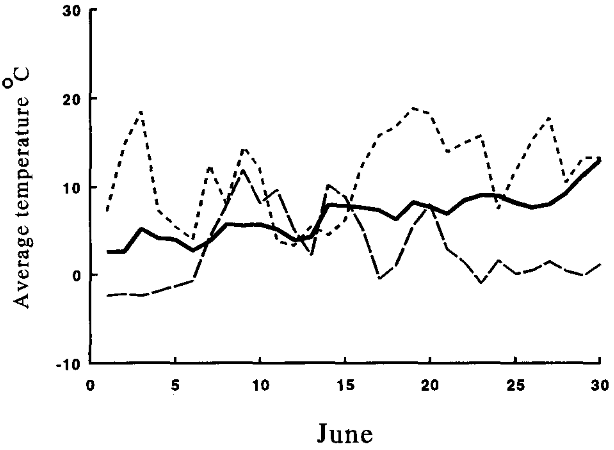

FIGURE 1. Average daily temperatures (°C) during June in Churchill, Manitoba. Solid line indicates mean for the years 1981 to 1995, long dashes are average daily temperatures for 1992 and short dashes are average daily temperatures for 1994. For both 1992 and 1994 temperatures during the period 1–7 June are significantly different than the long-term average ($P < 0.001$).

ment Canada weather station in Churchill. Semipalmated Plovers arrive in Churchill at the end of May and the first week of June and they commence laying in early to mid-June and incubate eggs in June and early July. Chicks fledge by late July to early August.

DATA ANALYSIS

For among-year comparisons an average egg mass and egg volume for each nest was calculated. To determine the amount of variation attributable to differences among and within females in a single year, we used a Model II one-way analysis of variance (Sokal and Rohlf 1995) which calculates the percent variation as the variance component due to differences among females divided by the total variance in the model (using the VARCOMP procedure, SAS Institute 1990). The within-female variation in egg measurements and clutch completion dates is the remainder, once the among female component is removed. We did not statistically evaluate this component of variance. Repeatability of egg measurements was determined by calculating the intraclass correlation coefficient (Falconer 1981) for females that laid eggs in two or three successive years in the study area.

RESULTS

WEATHER

Average temperatures during the period after arrival (1 June) but before egg-laying were lower in 1992 than during the period 1981–1995 (Fig. 1), and it was the coldest summer on record in 40 years (Churchill Weather Office). Temperatures in 1992 reached average after 7 June but again plummeted to below the 15-year average after 15 June. In 1994, temperatures during June were 7°C higher than the 15-year mean in the same two periods (first and third weeks, Fig. 1). Temperatures during June in 1988, 1993 and 1995 were not significantly different than the 15-yr average (not shown).

CLUTCH COMPLETION DATES AND BREEDING SYNCHRONY

Clutch completion dates were almost perfectly negatively correlated with the average temperature in the first week of June ($r = -0.95$, $n = 5$, $P = 0.01$), with earliest completion in 1994 and latest in 1992 (Table 1). Breeding synchrony, as measured by the standard deviation in clutch completion dates (small values indicating greater synchrony), was greatest in 1994, the year with the earliest mean completion dates, and the least in 1993, one of the three years with intermediate clutch completion dates.

CLUTCH SIZE AND HATCHING SUCCESS

Clutch size was significantly less in 1992 than in all other years where, in general, few birds laid less than four eggs (Fisher's exact tests: 1992 vs. 1988, $P = 0.024$, 1992 vs 1993 and 1994 (same clutch size in both latter years), P

TABLE 1. Mean (± SE) date of clutch completion, breeding synchrony, and egg size, volume and mass during five breeding seasons in Churchill, Manitoba. Sample sizes are in parentheses.

	1988	1992	1993	1994	1995
Clutch completion**	June 16 ± 0.6 (44)	June 19 ± 1.2 (13)	June 13 ± 0.7 (44)	June 10 ± 0.3 (49)	June 13 ± 0.4 (37)
T(°C) 1–7 June	8.1	1.84	10.4	16.3	8.1
Breeding synchrony (SD)	3.71	4.15	4.58	2.12	2.21
Egg length* (mm)	32.4 ± 0.2 (48)	32.6 ± 0.3 (24)	32.7 ± 0.1 (44)	33.1 ± 0.1 (39)	32.7 ± 0.2 (32)
Egg width** (mm)	22.8 ± 0.1 (48)	24.1 ± 0.1 (24)	23.9 ± 0.1 (44)	23.9 ± 0.1 (39)	23.8 ± 0.1 (32)
Egg volume** (cm^3)	7.2 ± 0.1 (48)	7.8 ± 0.1 (24)	7.9 ± 0.1 (51)	7.9 ± 0.1 (39)	7.7 ± 0.1 (32)
Egg mass** (g)	8.7 ± 0.1 (48)	9.3 ± 0.1 (13)	9.2 ± 0.1 (44)	9.4 ± 0.1 (39)	9.4 ± 0.1 (30)

* $P < 0.02$, ** $P < 0.001$ (one-way ANOVA). For each egg measurement, 1988 is different than all others (Tukey's multiple comparisons tests).

= 0.007; 1992 vs. 1995, $P = 0.004$, Table 2). In 1992 about 25% of all females laid fewer than four eggs. In six replacement clutches found in 1994 ($n = 1$) and 1995 ($n = 5$), one contained three eggs (16.6%). Dates of clutch completion were 9 days earlier in 1992, than dates of completion of the six replacement clutches from 1994 and 1995 ($\bar{x}$ ± SD, 28 June ± 4 days, Table 1).

The proportion of the total clutch that hatched was significantly lower in 1992 than other years, with most nests hatching only 3 of 4 eggs (Fisher's exact test; 1992 vs. all other years, $P < 0.001$, Table 2). Unhatched eggs were left unattended in the nest.

EGG SIZE

Egg length and egg width had the lowest phenotypic correlations ($r = 0.28$, $n = 146$, $P < 0.001$), whereas egg mass was strongly correlated with volume ($r = 0.82$, $n = 144$, $P < 0.001$). Eggs in 1988 were significantly lighter, shorter and less voluminous than eggs found in all other years (Table 1, Tukey's multiple comparison test, $P < 0.05$). Egg volume or mass did not vary significantly among the years 1992 to 1995 (Tukey's test, $P > 0.05$). For eggs of known laying order, we found no significant effect of laying order for width, mass, volume, or length (Table 3).

TABLE 2. Clutch sizes and number hatched in each of five years.

	Clutch size			Number hatched			
Year	2	3	4	1	2	3	4
1988		2	46		1	2	28
1992	1	6	22	1		8	2
1993		1	48		2	7	17
1994		1	46			3	35
1995			37			1	23

SOURCES OF VARIATION AND REPEATABILITY

All egg measurements except egg width in 1995 varied significantly among females (Table 4). However, there was no consistent pattern related to spring temperature: in the cold year of 1992 there were significant differences among females for width, volume, mass, and length, and the magnitude of these differences were at least as high as in some other years (Table 4). The remaining variance (subtracting percentage of variance in Table 4 from 100) that represents the within-clutch variance also was not greater in 1992 than in any other year (Table 4). For 13 females for which we have data from successive years (average 2.3 years), we calculated repeatability, which provides an upper estimate of heritability (Falconer 1981). For all egg characters this value was high (above 0.67, Table 5).

FEMALE SIZE

Female mass was moderately correlated with egg volume ($r = 0.51$, $n = 37$, $P < 0.002$), a stronger correlation than that found between egg volume and female condition ($r = 0.40$, $n = 35$, $P = 0.03$, where female condition equals mass/wing length, Galbraith 1988), or between egg volume and wing length ($r = 0.33$, $n = 35$,

TABLE 3. Effect of egg order on length, width, volume and mass of eggs from seven females.

	Egg order				F statistic for effect of:	
	1	2	3	4	Female	Egg order
Length (mm)	33.04	33.13	33.03	33.68	12.16**	2.43
Width (mm)	23.58	23.73	23.69	23.51	5.36*	0.64
Volume (cm^3)	8.66	8.79	8.74	8.78	7.77**	0.35
Mass (g)	9.16	9.16	9.30	9.13	4.49*	0.35

* $P < 0.01$, ** $P < 0.001$.

$P = 0.053$). Partial correlations using female mass and female condition revealed that only female mass varied significantly with egg volume (significance of partial correlations; female mass: $t_{29} = 2.03$, $P = 0.05$, female condition: $t_{29} = 1.01$, $P = 0.32$), indicating that eggs are larger from larger females, not from those of better condition.

We compared the body size of females at nests in 1992 with those captured in 1993 through 1995. There was no significant difference in any measurement for female size between 1992 and all other years, except that culmen length was significantly longer for females that bred in other years than for those that bred in 1992 ($\bar{x}$ ± SE, culmen (mm), 1992: 11.2 ± 0.2, $n = 8$, other years combined: 11.8 ± 0.1, $n = 66$, $P = 0.003$).

DISCUSSION

CLUTCH SIZE

When weather conditions on the breeding grounds are very poor, shorebirds may abandon breeding entirely (Mayfield 1978, Gratto-Trevor 1991), but rarely has a reduction in clutch size been reported (Kistchinski 1975). We found reduced clutch sizes and greater abandonment of eggs before hatching was complete in 1992, a year significantly colder than any in the past 15 years. Clutch size in 1992 was similar to that found in replacement clutches in 1994 and 1995, although our sample for replacement clutches was quite small. The reduction in clutch size in 1992 could be interpreted as a simple response to the later nesting that occurred in that year. Nest completion dates for replacement clutches were 9 days later than completion dates in 1992, so that the decline in clutch size is probably a facultative response to low temperatures and their impact on the food supply for females prior to egg-laying. The mechanism for a reduction in clutch size in shorebirds has not been examined but may include follicular resorption, as reported for arctic-breeding geese (Barry 1962, Raveling 1978, Hamann et al. 1986). A similar reduction in clutch size also was seen in 1992 for Common Eiders (*Somateria mollissima*) breeding near the Churchill study site (Robertson 1995).

A reduction in clutch size could be interpreted as an adaptive response to reduce brood size. The time spent brooding in Semipalmated Plovers appears to be a function of brood size as parents of three or four chicks spend twice as much time brooding during the first 5 days after hatching as do parents of one or two chicks (Sullivan Blanken and Nol, unpubl. data). In 1992, incubating parents also abandoned eggs more frequently in the nest during hatching than in other years, probably due to the continual near freezing temperatures at the time of hatching. This form of brood reduction also would result

TABLE 4. The percentage of variance attributable to differences among females and its significance for four egg-characteristics measured in each of five years.

Year	Length	Width	Volume	Mass
1988	74.3***	61.7***	70.2***	30.3**
1992	16.2*	64.2***	61.2***	75.5***
1993	51.5***	73.9***	73.0***	77.1***
1994	46.9***	55.9***	62.3***	67.1***
1995	55.3***	4.1	65.2***	54.1***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 5. Repeatability and significance for egg length, width, volume and mass, and clutch completion dates from 28 females measured in multiple years (total: eggs, 56 female years; date, 54 female years).

	Repeatability
Egg length	0.72
Egg width	0.68
Egg volume	0.67
Egg mass	0.68
Clutch completion dates	0

All egg variables significant at $P < 0.001$.

in fewer demands on brooding adults during periods when low temperatures would force adults to feed more frequently to meet their own energy requirements.

EGG SIZE

Given the very uniform clutch sizes of all arctic-nesting shorebirds, a reduction in egg size might have been expected over a reduction in clutch-size in response to the poor conditions in 1992. Egg size is moderately correlated with female mass, but not with female condition. Females that bred in 1992 were not significantly lighter after laying then females that bred in other years, a result consistent with the lack of variation in egg size in the years 1992 to 1995. This relationship between female mass and egg size is similar to that reported for other precocial shorebirds (R^2 = 0 to 35%, Väisänen et al. 1972, Miller 1979, Bergstrom 1988), although in Northern Lapwings (*Vanellus vanellus*) condition, rather than structural size, appeared to influence egg size (Galbraith 1988). The surprising lack of effect of female condition on egg size in our study suggests that females may reach some threshold mass to lay eggs, beyond which variation among females results in little or no increase in egg volume. It also is possible that mass and condition prior to laying explains much of the variation in egg volume among females. This explanation would be similar to the findings for arctic-nesting geese except that variation in clutch size, rather than egg size was strongly explained by the condition of females upon arrival at the breeding grounds (Ankney and MacInnes 1978). Unfortunately it is extremely difficult to catch plovers (and most other shorebirds) prior to laying so that this suggestion will be difficult to assess.

We rejected our prediction that among-female differences in egg characteristics would account for an either greater or lesser amount of total variation in years when breeding is delayed, because in the cold breeding season of 1992 the variation attributable to differences among females and the within-clutch variation were comparable to those found in other years. Thus, differences in egg characteristics among females are maintained despite delays in laying, and account for greater than 65% of the variance. This value is similar to that found for at least 10 other species of shorebirds (e.g., Väisänen et al. 1972, Nol and Lambert 1984, Grant 1991). Because of the consistency of this measure across shorebirds nesting in different environments, it is tempting to conclude that the additive genetic component (i.e., heritability) probably accounts for most of the repeatability (Moss and Watson 1982) that we also documented. In another precocial species, the American Coot *Fulica americana,* egg size appears to vary independently of environmental quality (Arnold 1994). Given that heritable individual differences among females probably account for most of the variation in egg size in Semipalmated Plovers, it is then not surprising that in 1992 the magnitude of these effects was similar to that found in other years.

The adaptive value of within-clutch variation in egg size has been documented for many altricial species (Slagsvold et al. 1984). Although precocial species do not feed their young, intraclutch variation in egg size may still be adaptive (Leblanc 1987, Grant 1991, Friedl 1993). We did not find any significant effect of egg order on egg size in Semipalmated Plovers, although the sample size for nests with complete information to control for variation among females was relatively small (n = 7). We have no reason to presume that a significant effect would be found with a larger sample size, in part because within-clutch variation did not seem to vary across years, and no other study has documented an effect of egg-order on egg volume or mass in shorebirds (Miller 1979, Cairns 1982, Lank et al. 1985). These results suggest that there is strong stabilizing selection to minimize intraclutch variation in egg size in shorebirds, and possibly other birds as well (Jover et al. 1993).

CLUTCH COMPLETION DATES

The greatest breeding synchrony occurred in 1994 with the earliest dates of clutch completion, the warmest temperatures, and presumably the earlier activity of invertebrate prey (Lank et al. 1985). A year with the greatest food availability for Western Gulls (*Larus occidentalis*) also resulted in the greatest breeding synchrony (Sydeman and Emslie 1992). In general, good weather and its effects on prey availability probably reduce the effects of differences in quality among individuals on the timing of laying.

We found no repeatability for standardized clutch completion dates, so special environmental variance, that is variance arising from temporary or localized circumstances (Falconer 1981, e.g., weather, habitat quality), accounts for all variation in this measure in Semipalmated Plovers. This result contrasts with results from other precocial (Velvet Scoters *Melanitta fusca*, Koskimies 1957; Mallards *Anas platyrhynchos*, Batt and Prince 1979; Snow Geese *Anser caerulescens*, Findlay and Cooke 1982) and semiprecocial species (American Oystercatcher *Haematopus palliatus*, Nol et al. 1984) that show significant repeatability for breeding dates. The timing of breeding in Semipalmated Plovers may be under strong directional selection (Price et al. 1988) because the arctic breeding season is short, and female investment in the clutch is large (clutch mass = 78% of female body mass). Although we lack sufficient data to examine directly the fitness correlates of early breeding, early breeding necessarily increases the opportunity for laying replacement clutches after loss to predation (Lank et al. 1985) and other sources of mortality. The average breeding dates for the population in Churchill appear to be determined primarily by the temperature during the pre-laying period.

Later clutch-completion dates in response to low temperatures in 1992 suggest that Semipalmated Plovers rely on food ingested during the laying period for laying eggs. However, more information on female mass prior to egg-laying, the relative feeding rates of males and females during the pre-laying period, and detailed information of the physiology of egg production in arctic shorebirds (Arnold and Rohwer 1991, Williams 1994) is required before we can be confident in this interpretation.

ACKNOWLEDGMENTS

We thank the Northern Scientific Training Grant program for funding the following students: A. Rippin Armstrong, S. Board, K. Kilpatrick, A. Smith, and L. Flynn. This research was supported in part by NSERC grants to E. Nol. Facilities for the preparation of this manuscript were provided by the National Biological Service in Corvallis, OR. D. Mehlmann and J. Plissner provided comments on an earlier version of the manuscript, and T. Williams, D. Lank, D. Schamel, and B. Sandercock of Simon Fraser University provided helpful discussion. Two anonymous reviewers also provided useful comments.

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