

## EGG DIMENSIONS AND NEONATAL MASS OF SHOREBIRDS

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**ABSTRACT.**—Eggs of 10 species of shorebirds (Charadriidae, Scolopacidae, Phalaropodinae) collected at Churchill, Manitoba, were measured and artificially incubated. Neonates were weighed within 6 h of hatching. This paper reports variation in egg size and neonate mass among clutches, and the relationship between egg dimensions and neonate mass. Coefficients of variation were 4 to 9% for egg volume and 6 to 15% for neonate mass. In most species, a significant proportion (48–84%) of the variance in egg volume could be attributed to differences between clutches. Neonate mass was significantly related to egg size in six of nine species.

Coefficients of variation in the volume of eggs within populations of shorebirds (Charadriidae, Scolopacidae, and their allies) are on the order of 4 to 7% (Väisänen et al. 1972, Väisänen 1977). Much of this variation arises from differences in the sizes of eggs laid by different females, which are detected as between-clutch variation (e.g., Väisänen et al. 1972, Miller 1979, Baker and Cadman 1980). The relationship between the sizes of eggs and neonates has been described for many species of birds, including some members of Charadriiformes (e.g., Ricklefs et al. 1978, Lundberg and Väisänen 1979, Lloyd 1979), but not for shorebirds. Because shorebird chicks must feed themselves shortly after hatching, often in cold environments, larger size, more advanced developmental state, and greater energy reserves of neonates presumably carry a selective premium, all else being equal. Indeed, the relative egg size (percent adult mass) of shorebirds is large compared to most other groups of birds (Rahn et al. 1975). If egg size is under strong selection (i.e., most unfavorable genes have been removed), variation within populations must be either nongenetic in origin or compensated by variation in other, balancing traits that are correlated with egg size (e.g., Rose 1982). The large variance between clutches found in most populations suggests genetic variation in egg size, although age and developmental effects have not been ruled out.

As a step towards understanding the evolution of large egg size in shorebirds, and interpreting variation in egg size among birds in general, I report here on variation in egg size and neonate mass among clutches, and on the relationship between egg size and neonate mass in 10 species of shorebirds at Churchill, Manitoba.

### MATERIALS AND METHODS

Ten species were included in this study: Lesser Golden-Plover (*Pluvialis dominica*); Semipalmated Plover (*Charadrius semipalmatus*);

Whimbrel (*Numenius phaeopus*); Hudsonian Godwit (*Limosa haemastica*); Lesser Yellowlegs (*Tringa flavipes*); Stilt Sandpiper (*Calidris himantopus*); Short-billed Dowitcher (*Limnodromus griseus*); Dunlin (*Calidris alpina*); Least Sandpiper (*C. minutilla*); Red-necked Phalarope (*Phalaropus lobatus*). These were the species most readily available in the study area and, fortuitously, represent much of the variation in size and habits among arctic shorebirds.

Clutches were collected at various stages of incubation from wet and dry tundra habitats to the east of Churchill, Manitoba (50°N, 94°W), during mid- and late June 1979. Eggs were marked with indelible ink and their lengths (*L*) and breadths (*B*) were measured to the nearest 0.1 mm with dial calipers. I used the product of the length and the square of breadth ( $LB^2$ ) as an index to volume (Väisänen 1969, Väisänen et al. 1972). Regressions of volume on  $LB^2$  had coefficients of determination of between 88 and 98% in eight species of waders studied by Väisänen (1977). Eggs were incubated in a small incubator (Hovabator, Inc.) at 37°C and approximately 60% relative humidity. Neonates were individually marked and weighed soon after hatching, usually within 6 h. I could match neonates to their eggs unambiguously in most cases. Where there was doubt, the data were omitted from the pertinent analyses.

Additional data on lengths and breadths of eggs in 5 clutches of Hudsonian Godwits, 8 clutches of Whimbrels, 7 clutches of Short-billed Dowitchers, 24 clutches of Least Sandpipers, and 33 clutches of Stilt Sandpipers (all from the Churchill area) were generously provided by J. R. Jehl. I analyzed these measurements separately, rather than pooling them with my data, because neonatal masses were not available. I used the SAS statistical package (Helwig and Council 1979), primarily the MEANS and GLM procedures, to analyze the data. Univariate statistics presented are the

mean ( $\bar{x}$ ), standard deviation (SD), standard error of the mean (SE), and coefficient of variation (CV). The statistical significance of differences between the CVs was based upon a value of  $F$  calculated as the square of the ratio of the larger to the smaller (Lewontin 1966). The statistical significance of a range of CVs was based on the  $F_{\max}$  test (Sokal and Rohlf 1969:371). Variance among clutches in egg dimensions and neonate mass was determined by a one-way analysis of variance (ANOVA) with clutch as the main effect.

Relationships between neonate mass and egg volume were determined by linear regression of both original measurements and log-transformed values. The slope of the logarithmic regression ( $b$ ) defines the allometric relationship between measurements  $Y$  and  $X$ , according to the expression  $Y = aX^b$ . Values of  $b$  significantly greater than or less than 1 indicate departure from linearity or direct proportionality between increase in neonate mass and increase in egg volume. The slope of the arithmetic regression ( $b$ ) in the expression  $Y = a + bX$  represents the grams of increase in neonate mass per cubic centimeter increase in egg volume index. Regressions were calculated over the sample as a whole for each species, although the similarity of egg dimensions within clutches suggests that measurements of individual eggs are not independently distributed and therefore that sample sizes used for statistical inference may be inflated. Regressions also were calculated within clutches, using an analysis of covariance in which the effects were clutch and  $LB^2$ . By entering clutch as the first effect, differences between clutches are removed and the regression of mass upon volume expresses their relationship within clutches.

## RESULTS

Univariate statistics for the egg volume index ( $LB^2$ ) and neonate mass are presented in Table 1. Coefficients of variation in volume index differed significantly among species and ranged from 4.2 to 9.1% ( $F_{\max} = 4.6$ ,  $P < 0.05$ ). CV's of neonate mass also differed significantly, with a range of 5.9 to 15.1% ( $F_{\max} = 6.6$ ,  $P < 0.01$ ). The largest CVs belonged to the two largest species, Whimbrel (15.1%) and Hudsonian Godwit (12.0%). Among the remaining species (dowitcher excluded), CVs did not differ significantly.

In all species except the Lesser Yellowlegs, the CV among neonate masses exceeded that among egg volume indices; the squares of the ratios of CVs ( $F$ -values) significantly exceeded 1 ( $P < 0.05$ ) in five of nine species (dowitcher excluded): Semipalmated Plover (3.47),

Whimbrel (4.52), Hudsonian Godwit (2.62), Dunlin (2.44), and Least Sandpiper (2.15).

Analyses of variance in egg volume indices and neonate masses within and among clutches are also presented in Table 1. Much of the variation in egg volume index and neonate mass was related to differences in the averages of eggs and neonates between clutches. The mass of the neonate varied significantly among clutches in five species ( $R^2$ , 50–89%), but not in the Whimbrel, Lesser Yellowlegs, Least Sandpiper, and Northern Phalarope ( $R^2 < 50\%$ ). The coefficient of determination among clutches in neonate mass was not clearly related to values of  $R^2$  for the volume index of the egg.

In most species of birds, large eggs produce large chicks, and shorebirds are consistent with this general pattern. I calculated the regression of the log of neonate mass against the log of  $LB^2$  to determine the relationship between neonate size and egg size (Table 2). The relationship was significant in all species except the Lesser Yellowlegs, Least Sandpiper, and Northern Phalarope. For the significant relationships,  $R^2$  varied between 21 and 75%. The slopes ( $b$ ) of the significant regressions varied between 0.69 (0.30 SE) in the Dunlin and 1.45 (0.27 SE) in the Whimbrel. Except for the Dunlin, all the slopes exceeded 1, but none significantly so ( $t$ -test, where  $t = [b - 1]/s_b$  with  $n - 2$  degrees of freedom). Although within some species large eggs may produce disproportionately large chicks ( $b > 1$ ), my samples of neonates were too small to quantify the relationship with much precision.

Because the relationship between neonate mass and egg volume index may result in part from differences among clutches, I performed a second analysis of variance with clutch as a main effect in order to determine the relationship of neonate size to egg size within clutches. The logarithmic regressions were significant only for the Whimbrel ( $F[1,12] = 9.42$ ,  $P = 0.01$ ,  $b = 1.58 \pm 0.51$  SE) and Stilt Sandpiper ( $F[1,15] = 20.49$ ,  $P < 0.001$ ,  $b = 0.89 \pm 0.20$  SE), although they were close to being significant for the Semipalmated Plover ( $P = 0.068$ ) and Northern Phalarope ( $P = 0.056$ ). Significant arithmetic regressions were: Semipalmated Plover ( $F[1,15] = 4.83$ ,  $P = 0.044$ ,  $b = 0.43 \pm 0.20$  SE); Whimbrel ( $F[1,12] = 6.69$ ,  $P = 0.024$ ,  $b = 0.59 \pm 0.23$ ); Stilt Sandpiper ( $F[1,15] = 21.61$ ,  $P < 0.001$ ,  $b = 0.31 \pm 0.07$ ); and Northern Phalarope ( $F[1,12] = 4.54$ ,  $P = 0.055$ ,  $b = 0.31 \pm 0.15$ ).

## DISCUSSION

Samples of eggs collected in this study had average volumes and coefficients of variation

TABLE 1. Statistical distributions of sizes of eggs and neonates, and analysis of variation within and between clutches, of shorebirds at Churchill, Manitoba.

Species and measurement <sup>a</sup>	n	Statistics <sup>b</sup>			ANOVA <sup>c</sup>		
		$\bar{x}$	SD	CV	df	P	R <sup>2</sup>
<b>Lesser Golden-Plover</b>							
LB <sup>2</sup>	24	51.79	3.35	6.47	5,18	<0.001	0.81
Mass	14	18.30	1.66	9.08	4,9	0.014	0.72
<b>Semipalmated Plover</b>							
LB <sup>2</sup>	24	18.51	0.96	5.18	5,18	<0.001	0.84
Mass	22	6.41	0.62	9.65	5,16	<0.001	0.73
<b>Whimbrel</b>							
LB <sup>2</sup>	24	90.33	6.42	7.11	5,18	0.002	0.63
LB <sup>2</sup>	27 <sup>d</sup>	95.70	8.67	9.06	7,19	<0.001	0.84
Mass	19	32.38	4.89	15.11	5,13	0.202	0.40
<b>Hudsonian Godwit</b>							
LB <sup>2</sup>	16	69.15	5.14	7.44	3,12	<0.001	0.78
LB <sup>2</sup>	18 <sup>d</sup>	73.52	4.21	5.73	4,13	0.062	0.48
Mass	16	22.99	2.77	12.04	4,10	0.001	0.89
<b>Lesser Yellowlegs</b>							
LB <sup>2</sup>	22	34.72	2.91	8.38	5,16	<0.001	0.80
Mass	18	11.97	0.96	8.04	5,12	0.101	0.50
<b>Stilt Sandpiper</b>							
LB <sup>2</sup>	26	23.73	1.00	4.22	7,18	0.365	0.31
LB <sup>2</sup>	127 <sup>d</sup>	23.79	1.39	5.86	32,94	<0.001	0.75
Mass	22	8.15	0.48	5.90	5,16	0.033	0.50
<b>Short-billed Dowitcher</b>							
LB <sup>2</sup>	26 <sup>d</sup>	35.76	2.64	7.37	6,19	<0.001	0.76
Mass	3	11.47	0.64	5.61	—	—	—
<b>Dunlin</b>							
LB <sup>2</sup>	26	22.85	1.37	5.98	6,19	<0.001	0.71
Mass	22	7.47	0.70	9.35	6,15	0.048	0.53
<b>Least Sandpiper</b>							
LB <sup>2</sup>	25	11.89	0.61	5.12	6,18	0.043	0.48
LB <sup>2</sup>	90 <sup>d</sup>	12.36	0.81	6.56	23,66	<0.001	0.62
Mass	16	4.06	0.31	7.51	5,10	0.488	0.32
<b>Northern Phalarope</b>							
LB <sup>2</sup>	24	11.82	0.77	6.48	5,18	<0.001	0.72
Mass	19	4.00	0.32	7.91	5,13	0.354	0.32

<sup>a</sup> LB<sup>2</sup> in cubic centimeters; mass in grams.

<sup>b</sup> n = number of eggs in sample, SD = standard deviation, CV = coefficient of variation.

<sup>c</sup> df = degrees of freedom (clutches, eggs within clutches), P = probability of F ≥ 1, R<sup>2</sup> = coefficient of determination.

<sup>d</sup> Measurements provided by J. R. Jehl.

in volume similar to the samples collected from the same area by: Jehl and Smith (1970) for the Whimbrel, Hudsonian Godwit, Short-billed Dowitcher, and Least Sandpiper; Jehl (1973) for the Stilt Sandpiper; and Hagar (1966) for the Hudsonian Godwit. Jehl (1973) reported the average mass of nine chicks of the Stilt Sandpiper less than 24 h old as 8.1 g, which is very close to the average of 8.15 g obtained for 22 incubator-hatched chicks in this study. The average mass of 16 Hudsonian Godwit chicks hatched in this study ( $\bar{x}$  = 23.0 g) was similar to the value of 23.4 g for 10 chicks weighed by Jehl and Smith (1970).

Variability in the mass of neonates was generally greater than the variability among egg volumes; CVs of the two measures were positively correlated, but not significantly so

(Spearman rank correlation coefficient  $r_s$  = 0.52,  $P > 0.05$ ). Within a sample, increased variation in neonate mass over that of egg volume could be caused by several factors. First, not all chicks were weighed at the same length of time after hatching. All were fully dried out and their down fluffed up before they were weighed, but some, especially those which hatched overnight, remained up to 6 h longer in the incubator, during which period they lost an unknown amount of mass. Second, neonate mass may be determined by yolk size, rather than total egg contents, which may be more variable than egg volume. Third, embryos may differ in the manner in which they utilize egg contents, perhaps hatching with more or less yolk, more or less accumulated body fat, or at a greater or lesser stage of development (see,

TABLE 2. Relationship between neonatal mass and egg volume index in shorebirds at Churchill, Manitoba.

Species and type of regression <sup>a</sup>	Statistics <sup>b</sup>					
	df	F	P	R <sup>2</sup>	b	s <sub>b</sub>
<b>Lesser Golden-Plover</b>						
Logarithmic	1,12	5.73	0.034	0.32	1.01	0.42
Arithmetic	1,12	6.79	0.023	0.36	0.33	0.13
<b>Semipalmated Plover</b>						
Logarithmic	1,20	24.01	<0.001	0.55	1.37	0.28
Arithmetic	1,20	27.61	<0.001	0.60	0.48	0.09
<b>Whimbrel</b>						
Logarithmic	1,17	28.07	<0.001	0.62	1.45	0.27
Arithmetic	1,17	21.28	0.002	0.56	0.55	0.12
<b>Hudsonian Godwit</b>						
Logarithmic	1,10	30.50	<0.001	0.75	1.29	0.23
Arithmetic	1,10	30.68	<0.001	0.75	0.42	0.08
<b>Lesser Yellowlegs</b>						
Logarithmic	1,14	0.78	0.393	0.05	—	—
Arithmetic	1,14	0.99	0.337	0.07	—	—
<b>Stilt Sandpiper</b>						
Logarithmic	1,20	27.07	<0.001	0.58	1.04	0.20
Arithmetic	1,20	28.48	<0.001	0.59	0.36	0.07
<b>Dunlin</b>						
Logarithmic	1,20	5.22	0.030	0.21	0.69	0.30
Arithmetic	1,20	4.80	0.040	0.19	0.21	0.10
<b>Least Sandpiper</b>						
Logarithmic	1,14	2.47	0.139	0.15	—	—
Arithmetic	1,14	2.62	0.128	0.16	—	—
<b>Northern Phalarope</b>						
Logarithmic	1,17	3.76	0.069	0.18	—	—
Arithmetic	1,17	3.27	0.071	0.18	—	—

<sup>a</sup> Logarithmic,  $\log(Y) = a + b \log(X)$ ; arithmetic,  $Y = a + bX$ ; where  $Y$  is neonate mass and  $X$  is egg volume index.

<sup>b</sup> df = degrees of freedom (effect, error),  $F$  = ratio of model mean square to error mean square,  $P$  = probability of  $F \geq 1$ ,  $R^2$  = coefficient of determination,  $b$  = slope of regression,  $s_b$  = standard error of slope.

for example, Ricklefs et al. 1978). These relationships can be resolved only by further study.

A large proportion of the variation in egg dimensions resulted from differences among clutches. In addition to the data presented here, this has been demonstrated for the American Oystercatcher (*Haematopus palliatus*; Baker and Cadman 1980), Least Sandpiper on Sable Island, Newfoundland (Miller 1979), the Dunlin and Greater Golden-Plover (*Pluvialis aprinaria*) in Norway (data of Innes 1980 analyzed in this study). Väisänen et al. (1972) analyzed variation in egg volumes ( $LB^2$ ) in five species of shorebirds with respect to female, clutches of the same female, and eggs within clutches. The percentage of variation due to each of these effects ranged between 45 and 77% for females, 0 and 21% for clutches of the same female, and 19 and 41% for eggs within clutches. Hence, variation among clutches reflects the primarily different characteristic dimensions of eggs laid by each female (see also Miller 1979). Other significant effects detected by Väisänen et al.

(1972) were position in laying sequence, sequence of clutch within years, and year.

Few studies have related egg dimensions to the characteristics of the female parent. Väisänen et al. (1972) found small but significant correlations between egg volume and female mass in the Dunlin ( $R^2 = 0.08$ ), Common Redshank (*Tringa totanus*; 0.07), and the Common Ringed Plover (*Charadrius hiaticula*; 0.15), but not Temminck's Stint (*Calidris temminckii*) or the Red-necked Phalarope. In addition, egg volume in the Dunlin was correlated with wing length ( $R^2 = 0.18$ ) and bill length (0.13). Miller (1979) found that the volume of eggs of the Least Sandpiper was correlated with the length of the culmen of the female ( $R^2 = 0.14$ ). I analyzed Innes' (1980) data on egg dimensions (clutch means) and female dimensions for 10 clutches of Dunlin in Norway. The multiple regression of egg volume on the mass and wing length of the female adult revealed that volume was significantly related to female mass only ( $F[1,8] = 5.68$ ,  $P = 0.044$ ), with a slope of  $0.153 \text{ cc}^3 \cdot \text{g}^{-1}$  (0.064 SE). In general, egg size appears to be positively related to certain measurements of the size of the female parent, although the explained variation in egg dimensions appears to be consistently less than 20%. Furthermore, the anatomical connections between these measurements and egg size has not been determined.

In shorebirds, as in other species having precocial young, the size of the neonate is correlated, often strongly so, with the volume of the egg. In this study, six significant correlations had coefficients of determination of 19 to 75%. The percentage of variance explained by arithmetic and logarithmic regression differed by 6% or less. For three of six species with significant regressions, the logarithmic slopes were substantially, but not significantly, greater than one. If larger samples prove these trends to be real, then larger eggs would produce disproportionately larger neonates, as found in the Laughing Gull (*Larus atricilla*) by Ricklefs et al. (1978). The slopes of the arithmetic regression have to be multiplied by approximately 1.8 in order to convert the egg volume index to grams of fresh mass (Hoyt 1979). These slopes indicate that each additional gram of fresh egg mass results in between 0.4 g (Dunlin) and 1.0 g (Whimbrel) increase in neonate mass. In spite of the reduced variation in egg volume index within clutches, significant relationships between volume and neonate mass were found in four species, suggesting that egg-size differences within clutches have similar consequences for neonate mass as do differences between clutches. The relationship of neonate mass and egg size has been examined in char-

adriiforms other than shorebirds. Lloyd (1979) determined that, in the Razorbill (*Alca torda*), neonate mass and egg volume were related, with coefficients of determination of 29 and 66% in two years ( $n = 45, 25, P < 0.001$ ). Lundberg and Väisänen (1979) found a similar relationship in the Common Black-headed Gull (*Larus ridibundus*;  $R^2 = 0.59$ ). The slope of the linear regression between neonate mass and egg volume was  $0.83 \text{ g} \cdot \text{cm}^{-3}$ . In the Laughing Gull, linear relationships between neonate mass and egg mass had slopes of  $0.92 \text{ g} \cdot \text{g}^{-1}$  (yolk sac included) or  $0.72$  (yolk sac excluded; Ricklefs et al. 1978).

The information discussed above yields the following conclusions concerning egg variation in shorebirds. The standard deviation in egg volume is approximately 6% of the mean, perhaps with some differences among species. Approximately 50 to 80% of the variation in egg volume may be attributed to differences among females and probably has a strong genetic component, although relatively little of this variation (<20%) is related to measurements of female size.

The percentage of variation in neonate mass distributed between clutches varies widely between about 30 and 90%. The within-clutch variation ranged between CVs of 4.6% and 13.5%, with six of the nine species in this study falling between 6.2 and 8.5%. The low extremes were the Hudsonian Godwit, in which most neonate variation was distributed among clutches, and the Stilt Sandpiper, which had low variability in neonate mass in the sample as a whole. Most of the variation in neonate mass in the extremely high species, the Whimbrel, occurred within clutches. Neonate mass is directly related to egg size, but values of  $R^2$  vary widely between perhaps 20 and 75%. The variation in quality of the chick related to mass is unknown as is the effect of this variation on the survival and future fecundity of the individual.

This study supplements previous work in documenting levels of variation in egg size and neonate mass within populations of shorebirds, confirming that a large part of the variation is associated with differences between clutches and, probably, between females, and demonstrating that neonate mass is related to egg size both within the samples and within clutches. Further work is required to determine whether species differ in overall egg-size variability, apportionment of variability within and between clutches, and the relationship of egg size to neonate mass and quality. Studies are also needed to determine the consequence of egg size, hence neonate size, for postnatal growth and survival of both the chicks and the female parent.

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