

Egg size in the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia, Canada

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The Least Sandpiper was studied on Sable Island, Canada, in 1975 and 1976. Culmen length and egg measurements are greater there than in northern Manitoba. Egg dimensions vary greatly among females, and egg size varies slightly with female size. Egg size in initial and replacement clutches does not differ systematically. Egg length tends to increase slightly over the laying sequence. The significance of constant clutch size and low variation in egg size within clutches of shorebirds is discussed.

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Introduction

Knowledge of natural history of calidridine sandpipers has been extended greatly in recent years, through studies in Alaska, Canada, Greenland, Spitsbergen, Scandinavia and the Soviet Union (Flint 1973, Pitelka et al. 1974, and references in those papers). Nevertheless, detailed information on most species is lacking, and even such widespread species as the Least Sandpiper, *Calidris minutilla* (Vieill.), remain virtually unstudied.

I studied behaviour and ecology of the Least Sandpiper on Sable Island, Nova Scotia, in the summers of 1975 and 1976. In this paper I summarize and discuss data on egg and clutch size in this and related species. Data on the main features of the nesting cycle, habitat, parental care and male display flights will be published separately (Miller unpubl.).

Methods

Field work was carried out on Sable Island, Nova Scotia (43°53'N 59°55'W), from 17 May to 23 July, 1975 and from 14 May to 3 August, 1976. I mist-netted some birds but caught most on their nests, with a simple drop

trap. Culmen length and egg dimensions were measured to the nearest 0.1 mm with vernier calipers. Further information on field methods is in Miller (1977).

Results

The normal definitive clutch size for *C. minutilla* on Sable Island is four eggs (Tab. 1). This is true of both replacement and initial clutches. Two of the four sub-normal clutches (of two and three) were replacement clutches. One female laid a first clutch of three and a replacement clutch of four eggs.

C. minutilla has a greater culmen length and longer and broader eggs on Sable Island than in northern Ma-

Tab. 1. Clutch size in *C. minutilla* on Sable Island.

Year(s)	Definitive clutch size			
	1	2	3	4
1975	0	0	0	26
1976	0	1	3	27
Both	0	1	3	53

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Tab. 2. Summary of descriptive statistics for culmen length and egg size of *C. minutilla* on Sable Island and elsewhere^a.

	Culmen length (mm)		Egg measurements (mm)	
	male	female	length	breadth
Sable Is., N.S. (this study)	17.8±0.09 (37)	19.5±0.13 (33)	29.1±0.03 (209)	21.2±0.06 (209)
Churchill, Man. (Jehl 1970, Jehl and Smith 1970)	17.4±0.11 (45)	18.9±0.12 (43)	28.6 ^b ±0.12 (88)	20.5±0.09 (88)
California, British Columbia and Alaska (Page 1974)	17.0 ^c ±0.08 (43)	18.7 ^c ±0.12 (46)	—	—
Magdalen Is., P.Q. (Philipp 1925)	—	—	29.5 (25)	21.8 (25)
<i>P</i> of difference between means, Sable Is. and Churchill ^d	<0.01	<0.01	<0.001	<0.001

^a Measurements are listed as $\bar{Y} \pm s_y (N)$, except for the Magdalen Islands, which are simply $\bar{Y} (N)$.

^b Mistakenly listed as "38.6" by Jehl and Smith (1970: 45).

^c Measurements from museum specimens, without correction for changes in length due to drying.

^d Two-tailed *P*-estimates are listed (by *t*-tests).

nitoba, but smaller eggs than on the Magdalen Islands, Quebec (Tab. 2).

The descriptive statistics for egg dimensions, summarized in Tab. 2, refer to all eggs measured. For scolopacids this is probably representative, since as a rule they have a definitive clutch of four eggs of similar size, which smooths out variation in egg dimensions among

females. Variation in egg dimensions among females is highly significant [by one-way analysis of variance, $P < 0.001$ for length (L), breadth (B) and "volume" ($L \cdot B^2$)]. These variations are fairly consistent within and between breeding seasons (Fig. 1).

The length and breadth of eggs are not correlated significantly (see Fig. 1). Egg length is more variable

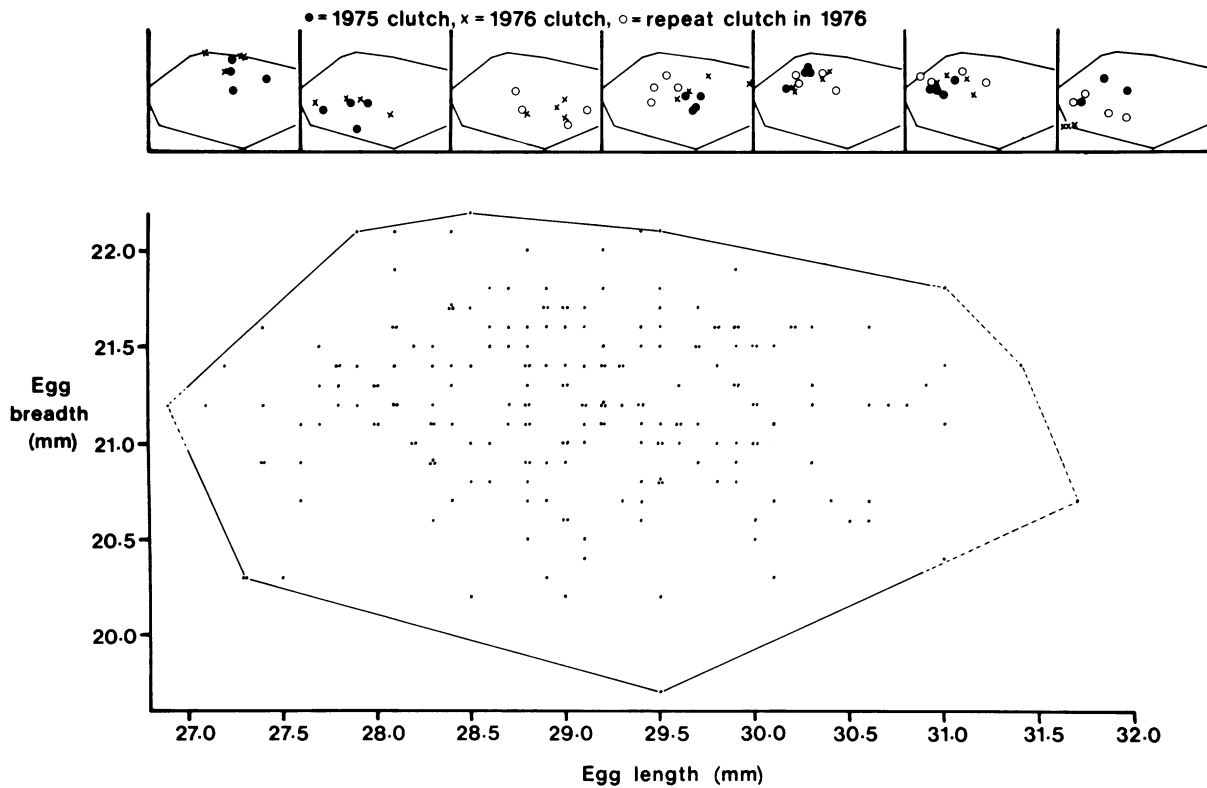


Fig. 1. Bivariate plot of egg breadth against egg length. Outlying values are joined by a solid or dashed line. That portion of the polygon's perimeter which is solid corresponds to the portion shown in each of the small diagrams, above. In the latter are depicted egg sizes of seven females, each of which laid two or more clutches. Eggs in a single clutch have the same kind of symbol.

Tab. 3. Summary of the results of simple linear (least-squares) regression of egg dimensions on culmen length of females of *C. minutilla* on Sable Island.

Dependent variable ^a	Regression equation	r ²	F _s	d.f.	
Egg breadth (B)	B = 78.60 + 0.32 culmen	0.03	1.04	1,40	0.25 < P < 0.50
Egg length (L)	L = 83.06 + 1.69 culmen	0.14	6.46	1,40	0.01 < P < 0.025
"Volume" = L · B ²	V = 30.14 + 1.13 culmen	0.13	5.90	1,40	0.01 < P < 0.025

^a The dependent variables are the totals for each clutch, obtained by adding the appropriate dimensions for all eggs within each clutch.

than is breadth, coefficients of variation being 3.1% and 2.0%, respectively.

Egg size is related directly to the size of the laying female. Females with longer bills tended to lay longer and more voluminous eggs (Tab. 3). No paternal or seasonal influences upon egg dimensions were detected through stepwise multiple regression, using culmen length of mate and the date of clutch completion as additional independent variables.

Egg size varies systematically with laying order in many bird species. Eggs in scolopacid clutches are uniform in size and shape (Norton 1970), but I predicted an increase in egg dimensions over the laying sequence for two reasons. First, Väisänen et al. (1972) documented such a trend for egg length in three species of scolopacids. Second, those authors reported that females of the Temminck's Stint, *Calidris temminckii*, lay larger eggs in their second clutch, of which they take care (the male takes charge of the first clutch and brood (Hildén 1965, 1975, Kokhanov 1973). This is compatible with general theory which predicts that females should invest most heavily in offspring which they, rather than their mates, care for. It further suggests that scolopacids may invest differentially in eggs, despite their fixed clutch size. Because an increase in egg size over the laying sequence was predicted, one-tailed statistical tests are used in the following analyses.

Tab. 5. Relationship of egg size to laying order within 13 clutches of *C. minutilla* on Sable Island (L = length, B = breadth, L · B² = "volume").

		Size of eggs relative to those laid earlier (E) and later (La) within each clutch					
		<E	=E	>E	<La	=La	>La
Laying order of egg	L	—	—	—	4	0	9
	1 B	—	—	—	9	1	3
	L · B ²	—	—	—	7	0	6
	L	4	0	0	6	0	1
	2 B	1	0	3	3	2	2
	L · B ²	2	0	2	6	0	1
	L	8	0	10	6	1	1
	3 B	8	3	7	2	0	6
	L · B ²	6	0	12	2	0	6
	L	7	1	24	—	—	—
	4 B	20	4	8	—	—	—
	L · B ²	15	0	17	—	—	—
Column totals	L	19 ^a	1	34 ^a	16	1	11
	B	29	7	18	14	3	11
	L · B ²	23	0	31	15	0	13

^a Cumulative binomial *P* (one-tailed) for this distribution (19:34) = 0.027. All other comparisons of column totals show *P* (one-tailed) > 0 · 10.

Tab. 4. Relationship of egg dimensions to order of laying for *C. minutilla* on Sable Island: descriptive statistics for pooled data^a.

		Variable			N
		Length (mm) (L)	Breadth (mm) (B)	"Volume" (cc) (L · B ²)	
Position of egg in laying sequence	1	28.8 ± 0.26	20.9 ± 0.35	12.6 ± 0.42	6
	2	28.2 ± 0.34	21.2 ± 0.38	12.7 ± 0.46	4
	3	29.0 ± 0.36	21.2 ± 0.12	13.0 ± 0.15	9
	4	29.2 ± 0.24	21.1 ± 0.17	13.0 ± 0.21	11
	1-2-3	28.8 ± 0.11	21.2 ± 0.07	12.9 ± 0.09	44
	1-2	28.6 ^b ± 0.13	21.1 ± 0.11	12.8 ± 0.14	25
	3-4	29.1 ^b ± 0.20	21.1 ± 0.11	13.0 ± 0.13	20

^a Measurements are listed as $\bar{Y} \pm s_y$.

^b One-way analyses of variance were performed to test the hypothesis that eggs laid third and fourth are larger than those laid first and second; only the variable length showed a significant difference: F_s = 3.74, d.f. = 1,43, 0.025 < P (one-tailed) < 0.05.

Tab. 6. Size of eggs and intervals between initial and replacement clutches, for five females of *C. minutilla* on Sable Island (all retained the same mates for the replacement clutches; B = breadth, L = length).

Female	Interval (days) ^a	Mean egg dimensions (mm)				% vol 2 relative to vol. 1 ^b
		clutch 1		clutch 2		
		\bar{B}	\bar{L}	\bar{B}	\bar{L}	
75-11	9	21.4	28.5	21.4	28.6	100.5
75-05	17	21.3	29.8	21.3	28.6	95.8
75-13 ^c	7	20.3	27.4	20.8	28.0	129.5
75-17	7	21.4	28.3	21.5	28.2	100.7
75-06	7	20.7	29.7	20.7	29.6	99.5
Column means	9.4	21.1	28.7	21.1	28.6	105.2

^a Interval between the loss of the initial clutch and completion of the replacement clutch.

^b The figures in this column represent the total volume of the replacement clutches relative to that of the initial clutches. They were computed as $100 (\bar{L}_2 \cdot \bar{B}_2^2) / (\bar{L}_1 \cdot \bar{B}_1^2)$, which is equivalent to the expression used by Soikkeli (1967: 174).

^c The definitive size of the first clutch of this female was three eggs; all other records are of four-egg clutches.

Descriptive statistics for pooled data on all eggs are summarized in Tab. 4. Eggs laid first or second in a clutch are about 0.5 mm shorter than eggs laid third or fourth, but the first and last pairs of eggs do not differ significantly in breadth or "volume" (Tab. 4). It is more strictly correct to compare relative egg size within clutches, since egg size varies among females. To assess this, I ranked each egg according to whether it was smaller than, equal to or larger than eggs laid earlier or later in the same clutch. The results summarized in Tab. 5 show that eggs tend to be longer than those laid earlier in the same clutch. There are six possible comparisons of column totals in Tab. 4, namely columns 1 vs. 3, and 4 vs. 6, for each of the three variables. Five of these comparisons agree with the hypothesis (one-tailed cumulative binomial $P = 0.11$).

Egg size did not change systematically between initial and replacement clutches of individual females (Tab. 6). Female 75-13 laid much larger eggs in her replacement clutch than in her first clutch, whereas eggs of other females showed little change.

One female chick banded in 1975 nested on Sable Island in 1976. Her eggs were about the same size as those of females known to be older (i.e. banded as adults in 1975). The yearling's four eggs averaged 29.8 ± 0.16 mm long and 21.2 ± 0.10 mm broad (values are $\bar{Y} \pm s_y$).

Discussion

Ecogeographic variation in reproductive investment by birds occurs strikingly in clutch size, number of clutches and egg size. Patterns of parental care are also impor-

tant, but are harder to measure. In shorebirds, clutch size and number of clutches are almost invariant across most species and in a broad range of ecological situations. Below I review these conservative features of shorebird biology and suggest reasons for them, and suggest which aspects of shorebird reproduction may exhibit greater plasticity.

Clutch size in waders

All species of northern scolopacids except one (the Snipe-billed Godwit, *Limnodromus semiplamatus*) have a definitive clutch size of four eggs, and this is the maximal clutch size occurring regularly in any species in the Charadrii. *C. minutilla* on Sable Island conforms to this pattern. There are few competing explanations of this remarkable conservatism. MacLean (1972) points out that many temperate or tropical species in the Charadrii have a definitive clutch size of fewer than four, which agrees with a general trend for species at high latitudes to have larger clutches than do their non-migratory tropical relatives. This may account for why low-latitude scolopacids have a reduced clutch size, but it does not explain why the maximal clutch size of their high-latitude relatives is four and almost invariably so. MacLean (1972) and Safriel (1975) reject the suggestion that scolopacids have four eggs because they cannot cover any more than that number. In his paper on the Semipalmated Sandpiper, *Calidris pusilla*, Safriel (1975) proposes that the upper limit to clutch size is set by the abilities of the parents to watch over and brood many chicks. He augmented some broods experimentally so that each contained five chicks, and found that fewer birds fledged from them than from normal broods with four chicks. He attributed this to the increased feeding area covered by large broods, which exposed them to greater risk of detection by predators, and made it difficult for the attending parent to monitor movements of chicks and to protect them from predators. This explanation fails to account for the universality of a definitive clutch size of four eggs among species of scolopacids which differ greatly in the roles of the sexes in the rearing of the brood, and which are exposed to a wide range of conditions of pressure from predators, food patchiness and food availability. For example, *C. minutilla* on Sable Island conforms to the typical calidridine pattern, yet its breeding season is about twice as long as at Churchill, Manitoba (Miller 1977), and until recent historic times its breeding success was affected by predation very little (the Herring Gull, *Larus argentatus*, started to nest on Sable Island only around 1920; Lock 1973: 6f). In addition, there seems to be no reason why mated adults of *C. pusilla* could not split up a larger brood and each care for one part, as sometimes occurs in related species (Williamson 1946, Tuck 1972). Yet Safriel notes (p. 704) that females "desert the family and leave them soon after hatching".

The most compelling explanation for the conservative definitive clutch size of four similar-sized pyriform eggs lies in its optimal configuration in minimizing the rate of heat loss when uncovered [Norton (1970: 45), Nethersole-Thompson (1973: 75) notes perceptively that wader species which regularly lay definitive clutches of less than four eggs tend to lay eggs of more ovate than pyriform shape, thus maintaining much surface contact among eggs in a clutch]. Eggs which are cooled frequently have slower development and may hatch asynchronously, and such cooling is much more pronounced in subnormal small clutches than in those of normal size (Norton 1970: 29, Frost and Siegfried 1977). These explanations are applicable to calidridines throughout their range, including Sable Island, and not just in northern regions where there is a danger of freezing injury to uncovered eggs. [Norton (1973: 56) refers to his unpublished data on low supercooling points of fresh eggs of *Calidris* species, and to resistance to chilling injury of older eggs, in support of this view.]

Because of stabilizing selection for thermal reasons on a definitive clutch size of four eggs, the ways in which shorebirds can increase their reproductive output are restricted (see Graul 1973, and Emlen and Oring 1977). Shorebirds can increase investment in one clutch of four eggs more easily than they can lay a second clutch of four eggs, so in response to food abundance they should produce larger and richer eggs. Published observations support this prediction. Skeel (1976) reported that eggs of the Whimbrel, *Numenius phaeopus*, were larger in an early spring than in a late spring. In the Lapwing, *Vanellus vanellus*, eggs are heavier on arable farmland than on natural grassland, perhaps because of differences in the availability of food, especially earthworms, to laying females (Murton and Westwood 1974). Major geographic trends in egg size in waders (e.g. Tuck 1972: 190, Väisänen 1977) are due partly to geographic differences in the size of adult birds (Väisänen et al. 1972, Väisänen 1977, this study), but may be modified further by regional or year-to-year variation in food availability [parenthetically it should be noted that the large size of eggs of *C. minutilla* on Sable Island does not agree with Väisänen's (1977) observation of small egg size in the southernmost breeding population of the Dunlin, *Calidris alpina*].

Egg dimensions

Females of *C. minutilla* show strong individual variation in egg size, and these individual differences were consistent within and between years. Both trends have been documented for related species (Väisänen et al. 1972). Age of females may contribute to this variation, though eggs of one yearling female of *C. minutilla* were as large as eggs from older females. The same has been noted for the Snowy Plover, *Charadrius alexandrinus* (Rittinghaus, cited by Väisänen et al. 1972: p. 40).

There are no systematic differences in size of eggs

from first and replacement clutches of waders. In *C. minutilla* and the Black-tailed Godwit, *Limosa limosa*, eggs in first and replacement clutches differ little in size (this study, and van Balen, cited by Haverschmidt 1963: 47). In contrast, eggs in replacement clutches of *C. alpina* tend to be narrower, longer and less voluminous than those in first clutches (Soikkeli 1967, Väisänen et al. 1972), and eggs in replacement clutches of *V. vanellus* are smaller than those in first clutches (Heim, cited by Väisänen 1977: 22).

In *C. minutilla*, egg size varies directly with size of the laying female. Väisänen et al. (1972) also report significant positive correlations between egg size and female size in several shorebird species which are normally monogamous. Their data on *C. alpina* show $r^2 = 0.13$ for bill length with egg volume, which is identical to my figure for *C. minutilla*. This is statistically significant in both cases, but it is clear that the greatest proportion of the variance remains unexplained.

Ordering of egg size

Two factors constrain differential investment (as estimated by size) in eggs according to laying order. Heat loss of an exposed clutch is least when the four eggs are in extensive physical contact with one another, and this is achieved best when they are of similar size and pyriform shape. Second, hatching synchrony is important in allowing chicks to leave the nest together, so eggs which start to develop at about the same time should be of similar size in order to have similar development times (see below). Eggs laid last in clutches of *C. minutilla* tend to be longer than those laid first, as Väisänen et al. (1972) found for related species. A similar trend may prevail in the Common Snipe, *Capella gallinago* (Tuck 1972: 191). Also, eggs laid last in clutches of the Wattled Jacana, *Jacana jacana*, and the Piping Plover, *Charadrius melodus*, tend to be the largest (Wilcox 1959, Osborne and Bourne 1977). The single reported exception for waders appears to be the African Black Oystercatcher, *Haematopus moquini*, whose two eggs do not differ in size (Summers and Cooper 1977). The general trend toward last-laid eggs being larger than earlier eggs may reflect a response to the lower rate of loss of clutches which are complete and are being incubated nearly constantly: last-laid eggs are less likely to be preyed upon so may merit more investment. High predation rates on incomplete clutches have been reported for several shorebird species (Lind 1961, Harris 1967, Soikkeli 1967, Miller unpubl.). However, ordering of egg size according to laying sequence is widespread in birds (see Howe 1976, and included references), and a more universal explanation should be sought. In his study of grackles, Howe (1976: 1204) suggests that "higher provisioning in the last egg enhances the competitive position of the chick most disadvantaged by hatching sequence", since the egg which is laid last usually hatches last. Scolopacid chicks which hatch last are

younger and weaker than their siblings when they leave the nest together, a disadvantage which could be reduced if late-hatching chicks come from large, well provisioned eggs. This explanation rests on two assumptions: (1) that egg size and chick size at hatching are positively correlated; and (2) that eggs tend to hatch in the order they were laid. The first assumption is well documented (e.g. Davis 1975, Bowen 1976). My data concerning the second assumption are few: the last-laid eggs in two clutches of *C. minutilla* were the last to hatch. The same has been noted for related species (Parmelee et al. 1967, Nettleship 1974). As a general rule, hatching order follows laying order in waders (Lind 1961: 106ff, Bolotnikov et al. 1973, Hussell and Page 1976), though there are some reported exceptions (Parmelee et al. 1968, Parmelee 1970). Nevertheless, it seems that shorebird eggs laid last tend to hatch last, as required if Howe's (1976) interpretation is applicable.

Disadvantages to hatching last can be reduced if last-laid eggs hatch most quickly, and this is the rule for shorebirds (Williamson 1946, Lind 1961: 108f, Nethersole-Thompson 1973: 96, 100, Rubinstein 1973; but see Bolotnikov et al. 1973).

In summary, ordering of egg size such that large eggs are laid last is widespread in shorebirds. However, the size differences among eggs in a shorebird clutch are very slight compared with those in other bird species (Howe 1976, and included references), and result in virtually equal investment in each offspring. Constraints to egg-size variation, and hence to differential investment in offspring, are probably set partly by selection for extensive surface contact among eggs, for hatching synchrony and for synchrony in maturation of siblings. Because of limits to clutch size and to variation in parental investment in offspring, shorebirds have a very conservative reproductive pattern. Shorebirds probably exhibit major ecogeographic variation and species differences in reproductive patterns *after* hatching, e.g. in the duration, assiduousness and sexual division of parental care, but these are known poorly at present (Miller unpubl.).

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