

## LATITUDINAL TRENDS IN BREEDING RED PHALAROPES

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**Abstract.**—Despite earlier arrival on breeding grounds further south, there is no significant prolongation of the laying period there. This is caused by a pronounced delay (10–13 d) between arrival and egg-laying. Farther north, this delay is minimal (2 d). The length of the egg-laying period seems relatively fixed; we found no significant differences with respect to latitude. Instead of responding to phenologically very late summers with abbreviated laying periods and significantly smaller clutch sizes, Red Phalaropes simply fail to nest (Mayfield 1978). We found a strong (though not significant) trend towards slightly larger clutches farther north. This trend is apparently not an artifact of partial predation. Greater nest attendance farther north is probably a key factor in the noted trends of slightly shorter incubation duration and a decline in incubator weight during incubation.

### TENDENCIAS LATITUDINALES EN LA REPRODUCCIÓN DE *PHALAROPUS FULICARIA*

**Sinopsis.**—El hecho de llegar más temprano al extremo sur de las áreas en donde se reproduce el Falarope Rojo (*Phalaropus fulicaria*) no extiende significativamente su periodo reproductivo. Los falaropes que se reproducen en estas áreas toman de 10–13 d, entre su llegada y la puesta de huevos, mientras que las aves que se encuentran más al norte retardan su puesta tan solo 2 d. El largo del periodo de puesta de huevos, parece ser fijo; no encontramos diferencias en poblaciones de diferentes latitudes. En veranos tardíos, los falaropes no anidan, en vez de responder a estos con periodos más breves en la puesta de huevos y camadas más pequeñas (Mayfield 1978). Encontramos una tendencia (aunque no fue significativa) a camadas ligeramente más grandes en el norte. Esta tendencia aparentemente no es un artefacto de la depredación. Notamos una mayor reducción de peso en los adultos incubando en el norte y un periodo de incubación más corto. Probablemente el lapso mayor de tiempo que dedican estas aves a incubar, que las del sur, sea la razón de esta tendencia.

Northern nesting birds face climatic problems of short, cool summers and unpredictable weather (Holmes 1971, Mayfield 1978). The breeding bird is thus presented with logistical difficulties in timing of arrival, laying and incubation. Such influences may be exacerbated as birds travel further north.

The effect of latitude on breeding parameters should be clearly exhibited by Red Phalaropes (*Phalaropus fulicaria*), which nest over a 20° latitudinal range, from subarctic Alaska (60°N) to high arctic Canada (80°N) (Mayfield 1979). Red Phalaropes typically nest in low-lying tundra, the last terrestrial habitat to become snow free (Pitelka et al. 1974), which may abbreviate their nesting season further. Neither sex is territorial, thus arrival times should be more related to egg-laying than in species that establish breeding territories. We would expect a brief interval between arrival and laying to be advantageous at all latitudes. Laying should be postponed in cold springs (Lofts and Murton 1968)

and termination of laying may be hastened by cold weather during the summer. Thus, a compression of the breeding season may occur at high latitudes. Weather factors may also influence clutch size. Kistchinski (1975) reported an increased incidence of small clutches in Red Phalaropes during a phenologically late year.

Because the male Red Phalarope is the sole incubator, incubation dynamics may vary more than in species where both sexes incubate. The male may need to spend more time incubating in a colder, more northern climate (Kendeigh 1940) and lost foraging time may result in lowered body mass (Sherry et al. 1980). Alternatively, the male may devote enough time foraging to maintain body weight at the expense of slowed chick growth and, therefore, prolonged incubation (Romanoff 1934).

#### STUDY AREA

We collected data on breeding Red Phalaropes near Barrow, Alaska (71°17'N, 156°47'W) 1973–1975 and at Cape Espenberg, Alaska (66°30'N, 163°30'W) 1976–1979. We documented Red Phalarope arrival on our study areas for 2 yrs at Barrow and 1 yr at Cape Espenberg.

Both study sites consisted of low-lying tundra marshes dominated by *Carex aquatilis*. Seasonal and permanent ponds were present at both sites. The Barrow site was located in an ancient, drained lake basin, where permafrost relief patterns of low-center and high-center polygons were present. Cape Espenberg lacks strongly polygonized ground, but does have many parallel series of eroded dune ridges, interspersed with small ponds and pools. The study area at Barrow was approximately 1 km<sup>2</sup>, while at Cape Espenberg, it was 0.25 km<sup>2</sup>.

#### METHODS

Information in this paper is based upon our own data, as well as those of other observers. We standardized definitions, to make the various observations comparable. "Arrival" is defined as the first sighting of Red Phalaropes on the study area. "Incubation period" is defined as the period between the laying of the last egg and the hatching of the last egg (Mayfield 1979). "Laying period" is defined as the period between the laying of the first egg of the first clutch and the first egg of the last clutch in the population; it shows the span of nest initiation.

We estimated weight loss of incubating males by constructing a graph of bird weight vs. number of days into incubation at the time of capture. The latter figure was determined by knowing the date of nest initiation or back-dating from hatching. Erckmann's (1981) estimates of weight loss are based upon recaptures of individual birds. In both our study and Erckmann's (1981), birds were weighed to the nearest 0.1 g with a Pesola scale. Birds were captured by nest traps and/or hoop nets (Schamel and Tracy 1977).

We located nests by watching the behavior of the pair during nest

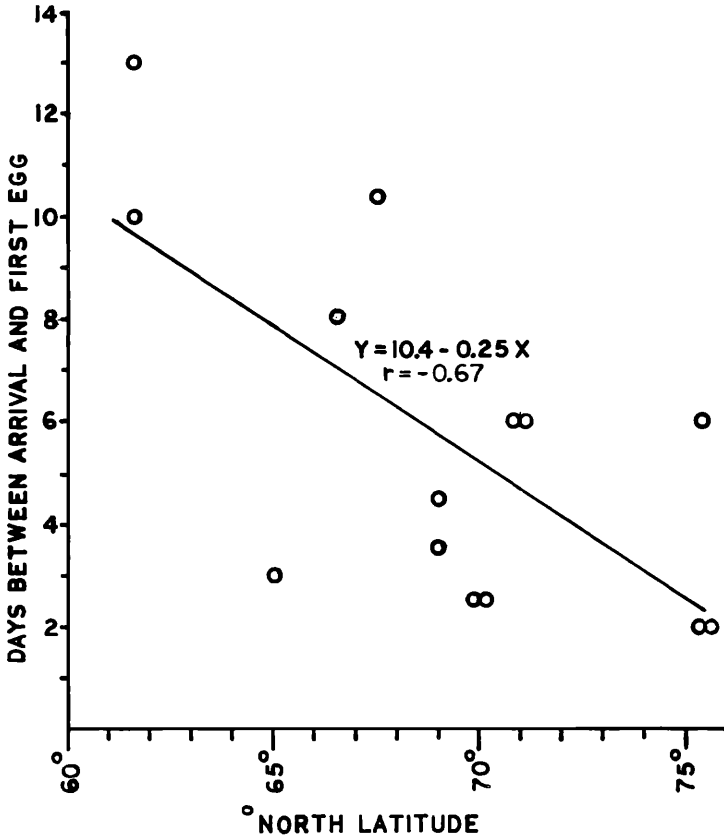


FIGURE 1. Latitudinal differences in the arrival/egg-laying interval in Red Phalaropes. Data are from Brandt (1943) and C. P. Dau (pers. comm.) (61°30'N), Sutton (1932) (65°N), this paper (66°30'N and 71°17'N), Kistchinski (1975) (67°30'N), Parmelee et al. (1967) (69°N), P. D. Martin (pers. comm.) (70°N), and Mayfield (1979 and pers. comm.) (75°45'N). Circles indicate individual data points.

searching, by following foraging males back to their nests, and by flushing males from nests while we walked through the study area. During the nesting season, we spent 9–12 h each day in the study area.

A time/activity budget was constructed by observing color-banded incubating males over several days. Bird activity was monitored over a 24 h period from distances of 10–30 m. All activities were timed with a stop-watch. These data were used to estimate nest attentiveness.

#### RESULTS AND DISCUSSION

*Interval between arrival and egg-laying.*—The interval between arrival on the breeding grounds and the laying of the first egg in a population

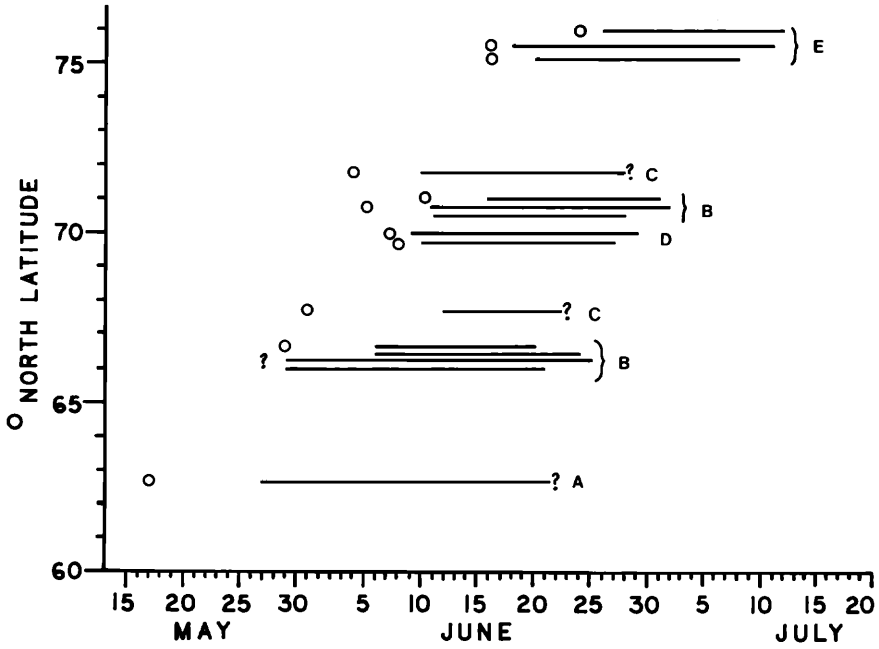


FIGURE 2. Latitudinal differences in arrival and egg-laying period in Red Phalaropes. Data from: A) Brandt (1943), B) this study, C) Kistchinski (1975), D) P. D. Martin (pers. comm.), E) Mayfield (1979 and pers. comm.). Circle indicates arrival of birds on study site; line shows the period of initiation of nests; best guesses by authors are indicated by “?”.

is inversely correlated with latitude ( $r = -0.67$ ,  $t = 3.05$ ,  $df = 12$ ,  $0.01 < P < 0.02$ , Fig. 1). The greatest interval (13 d) was recorded at the most southern location (Hooper Bay, Alaska; C. P. Dau, pers. comm.); the shortest interval (2 d) was reported at the most northern site (Bathurst Island, Canada; Mayfield 1979 and pers. comm.).

The delay farther south is not caused by nesting habitat availability, for snow melt either coincides with arrival (Brandt 1943) or precedes it (our observations at Espenberg). Another possible explanation for the delay is that arriving birds need to replenish energy reserves before nesting. We see no reason why phalaropes which settle further south should be in poorer condition than those birds that continue to migrate several hundred miles further north. Indeed, we would expect the opposite. Two early arriving males captured prior to the onset of incubation at Espenberg were 2–3 g heavier than birds captured during early incubation. At Barrow, five preincubation males were 2–3 g lighter than birds entering incubation.

More likely, the delay between arrival and laying farther south is caused by hormonal control of laying or environmental constraints, such

as food availability. We found a month difference in arrival times and in the onset of laying when comparing the southernmost and northernmost breeding sites (Fig. 2). This suggests that the onset of laying is cued by local events in the environment and/or genetic differences between latitudinal subpopulations. In contrast to our data, Väisänen (1977) found no latitudinal delay in the onset of laying in Red-necked Phalaropes (*Phalaropus lobatus*) and only a 5 d delay in mean laying dates farther north. Red-backed Sandpipers (*Calidris alpina*; a territorial species) delayed arrival and egg laying farther north and showed an arrival/egg-laying compression (Holmes 1971).

*Length of the laying period.*—We expected to find a shorter laying period and greater variability farther north. Comparing only sites with three or more years of data (Espenberg, Barrow, and Bathurst), we found no significant differences in variability of the laying period (Bartlett's test,  $\chi^2 = 3.19$ ,  $df = 2$ ,  $0.10 < P < 0.25$ ). Although the longest mean laying period occurred at the most southerly site, Espenberg (Table 1), we found no significant differences between means (ANOVA,  $F = 0.44$ ,  $P > 0.50$ ). The longer laying period for 2 yrs at Espenberg was caused by one pair nesting 5–6 d earlier than the rest of the population. Such asynchrony of nest initiation was not seen in Barrow.

Examining within-site variation, we found that phenologically early years tend to have slightly (1–2 d) longer laying periods than late years. The briefest laying periods at Barrow and Bathurst (Mayfield 1979) corresponded to the latest arrival of phalaropes. This relationship was not found at Espenberg.

Only years when egg-laying occurred were included in the Bathurst analysis. Mayfield (1978) reported no nesting birds in his study area in 2 of 7 yrs. It appears that if egg laying occurs at all in a population, the duration of the laying period is unaffected by latitude. Holmes (1971) and Väisänen (1977) noted only a slight shortening of the laying period in Red-backed Sandpipers farther north. Red-necked Phalaropes showed no latitudinal differences in northern Europe (Väisänen 1977).

*Clutch size.*—Like other arctic nesting shorebirds, Red Phalaropes are determinate layers with a modal clutch size of four eggs. Clutches containing fewer than four eggs are more common during phenologically late summers (Kistchinski 1975) and later in the breeding season (Soikeli 1967). Potentially colder and less predictable weather at higher latitudes may lead to smaller mean clutch sizes and greater variability in clutch size farther north.

Comparing Espenberg, Barrow, and Bathurst only, we found no significant difference in clutch size among these sites (heterogeneity  $\chi^2 = 8.75$ ,  $df = 4$ ,  $0.05 < P < 0.10$ ). Had the null hypothesis been rejected it would have been because of larger clutch sizes farther north (Table 1), contrary to our prediction. Variances were not homogeneous (Bartlett's test,  $\chi^2 = 16.95$ ,  $df = 4$ ,  $P < 0.001$ ). Clutch size variation was not significantly different between Espenberg and Barrow ( $F = 1.22$ ,  $0.2 <$

TABLE 1. Comparison of breeding events of Red Phalaropes at three sites, sample sizes in parentheses.

Event	Espenberg, AK (66°30'N)	Barrow (71°N)	Bathurst (75°30'N) <sup>1</sup>
Mean delay between arrival-laying (d)	8 (1)	6 (2)	3.3 (3)
Range	—	—	2-6
Mean length of laying period (d)	22.0 ± 6.2 <sup>2</sup> (4)	18.7 ± 3.1 (3)	19.3 ± 3.2 (3)
Range	15-29	16-22	17-23
Clutch size	3.7 ± 0.7 (78)	3.8 ± 0.6 (97)	3.9 ± 0.4 (37)
Range	1-4	1-4	3-5
Mean incubation period (d)	20.1 ± 2.7 (7)	19.7 ± 1.2 (8)	18.3 ± 0.6 (3)
Range	17-24	18-21	18-19
Mean nesting success	75% (56)	54% (46)	33% (36)
Range	60-93%	45-73%	17-100%

<sup>1</sup> Data from Mayfield 1979 and pers. comm.

<sup>2</sup> Plus/minus one standard deviation.

$P < 0.5$ ), but was significantly different between Espenberg and Bathurst ( $F = 3.13$ ,  $P < 0.001$ ) and between Barrow and Bathurst ( $F = 2.56$ ,  $0.002 < P < 0.005$ ). The variance at Bathurst was smaller than farther south.

It is possible that partial predation of clutches may have contributed to a smaller clutch size and higher variability farther south. But we find no evidence to support such a contention. Predatory activity seems to be more intense farther north (Table 1) and partial predation is apparently rare. Mayfield (1979) did not report partial predation and we observed it at only 2 of 175 clutches (1%). In addition, we found no correlation between clutch size and predator activity, as measured by percent of clutches lost to predation ( $r = 0.080$ ,  $t = 0.21$ ,  $df = 7$ ,  $P > 0.5$ ).

*Incubation duration.*—Incubation duration was slightly shorter farther north (Fig. 3) ( $r = -0.45$ ,  $t = 2.72$ ,  $df = 29$ ,  $0.01 < P < 0.02$ ). Incubating males at Barrow lost weight whereas those farther south, at Cape Espenberg, did not (Fig. 4). We noted a significant decline in 2 of 3 yrs at Barrow (1973:  $r = -0.64$ ,  $t = 2.66$ ,  $df = 10$ ,  $0.02 < P < 0.05$ ; 1974:  $r = -0.58$ ,  $t = 3.12$ ,  $df = 19$ ,  $0.001 < P < 0.01$ ). We noted a similar, but not significant, decline in 1975 ( $r = -0.40$ ,  $t = 1.30$ ,  $df = 9$ ,  $0.2 < P < 0.5$ ). This decline represented an average loss in body weight of 13.5% in 1973 and 10.0% in 1974, when projected over the entire incubation period. Similarly, Erckmann (1981) found a significant weight loss in incubating males at Cambridge Bay, Canada (69°N) (10% loss,  $P = 0.05$ ) and a nearly significant loss in the Arctic National Wildlife Range in northeastern Alaska (70°N) (14% loss,  $P = 0.08$ ). In contrast, we found no significant weight change in incubating males at Espenberg (Fig. 4) ( $r = 0.13$ ,  $t = 0.48$ ,  $df = 14$ ,  $P > 0.5$ ). At Wales, Alaska (66°N),

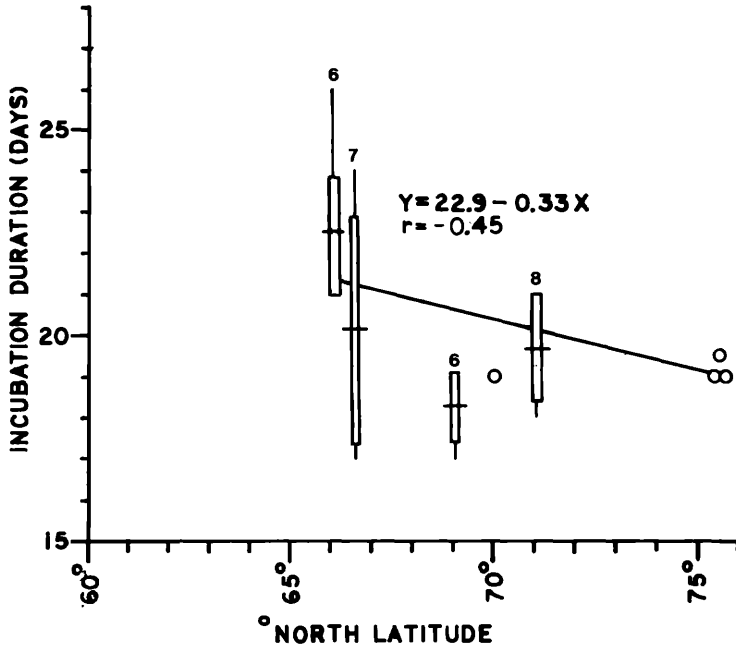


FIGURE 3. Latitudinal differences in incubation duration in Red Phalaropes. Values given are: mean (horizontal line), SD (block), range (vertical line), and sample size.

Erckmann (1981) found no significant weight change in incubating males during two seasons ( $r = 0.13$ ,  $df = 72$ ,  $P > 0.25$ ). Incubating males are able to maintain body weight in the southern part of their range, but apparently cannot maintain weight at higher latitudes.

Male weight change during incubation seems to be related to nest attentiveness. We estimated that incubating males spent 85% of their time at the nest at Barrow, compared to Erckmann's (1981) estimate of 83% at the Arctic National Wildlife Range. Farther south, at Wales, Alaska, he found 70% nest attentiveness. The shorter time allocated for foraging farther north apparently renders the incubating bird incapable of maintaining body weight. Prey density and incubator effectiveness in foraging are important considerations with respect to incubator weight change, but we have no data on these.

At Barrow, we found incubation duration to be inversely correlated to the date of nest initiation ( $r = -0.84$ ,  $t = 3.80$ ,  $df = 6$ ,  $0.001 < P < 0.01$ ). Nests initiated late in the season had the shortest incubation period. This hastens the hatch of clutches initiated late in the season which may be advantageous to avoid late summer storms. The seasonal difference in incubation duration also tends to synchronize population hatching dates which may be a mechanism to avoid predation on young.

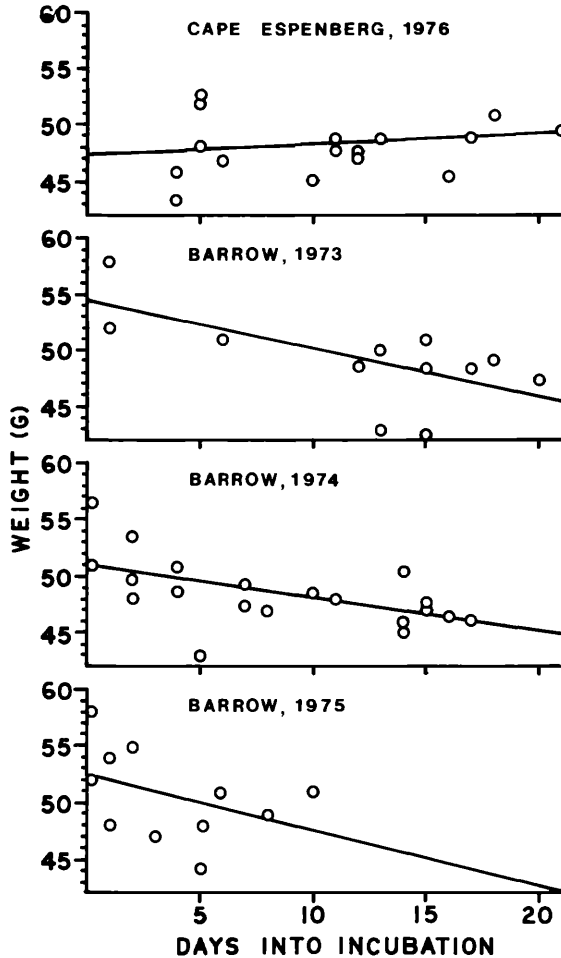


FIGURE 4. Weight change in Red Phalarope males during incubation at Cape Espenberg and Barrow, Alaska.

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## LITERATURE CITED

- BRANDT, H. 1943. Alaska bird trails. Bird Research Found., Cleveland, Ohio.
- ERCKMANN, W. J., JR. 1981. The evolution of sex-role reversal and monogamy in shorebirds. Ph.D. diss., Univ. Wash., Seattle.
- HOLMES, R. T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93-99.
- KENDEIGH, S. C. 1940. Factors affecting length of incubation. Auk 57:499-513.
- KISTCHINSKI, A. A. 1975. Breeding biology and behaviour of the Grey Phalarope *Phalaropus fulicarius* in East Siberia. Ibis 117:285-301.
- LOFTS, B., AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool. (Lond.) 155:327-394.
- MAYFIELD, H. F. 1978. Undependable breeding conditions in the Red Phalarope. Auk 95:590-592.
- . 1979. Red Phalaropes breeding on Bathurst Island. Living Bird 17:7-39.
- PARMELEE, D. F., H. A. STEPHENS, AND R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. Nat. Mus. Can. Bull. 222:1-229.
- PITELKA, F. A., R. T. HOLMES, AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. Amer. Zool. 14:185-204.
- ROMANOFF, A. L. 1934. Study of artificial incubation of game birds. I. Temperature requirements for pheasant and quail eggs. II. Humidity requirements for pheasant and quail eggs. Bull. Cornell Univ. Agr. Exp. Sta. No. 616:1-39.
- SCHAMEL, D., AND D. TRACY. 1977. Polyandry, replacement clutches, and site tenacity in the Red Phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. Bird-Banding 48:314-324.
- SHERRY, D. F., N. MROSOVSKY, AND J. A. HOGAN. 1980. Weight loss and anorexia during incubation in birds. J. Comp. Physiol. Psychol. 94:89-98.
- SOIKKELI, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4:158-198.
- SUTTON, G. M. 1932. The birds of Southampton Island. Mem. Carnegie Mus. Vol. 12. Part II. Section 2.
- 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.

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