

The breeding biology of Red-necked Phalaropes *Phalaropus lobatus* at Nome, Alaska

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Red-necked Phalaropes *Phalaropus lobatus* were studied near Nome, Alaska during 1993-1995. Adult females were significantly larger than males in body size, but the difference was small (ca. 2.6-4.8%). Phalaropes arrived in the first week of May, and initiated clutches in the first week of June. There was little annual variation in the timing of breeding or other aspects of fecundity. The majority of clutches contained four eggs (88.7%, n=62), and nest success varied from 29.2-70.8%. Repeatability was lower for egg volume (29.0%, mean \pm SD= 5.85 \pm 0.69 cm³, n=232 eggs in 61 nests) than chick mass (50.1%, 4.13 \pm 0.31 g, n=68 chicks in 20 nests). Male phalaropes had nest attendance rates of 81.3%, and their flushing distance and behaviour was unaffected by the stage of incubation. Return rates of young (2.9%, n=34) and adults (females 11.1%, n=18; males 17.3%, n=52) were low. Red-necked Phalaropes breeding at Nome had similar morphometrics, fecundity, and demography as other populations in Alaska, Canada and Finland. The low adult return rates in this species suggest that breeding site-fidelity is weak. If so, gene flow may prevent the development of subpopulations that are adapted to local conditions.

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INTRODUCTION

Red-necked Phalaropes *Phalaropus lobatus* are an arctic-nesting shorebird with a holarctic breeding distribution. Like other phalarope species, they are facultatively polyandrous and exhibit sex-role reversal. Females compete for mates and do not defend a territory; males provide all parental care to eggs and young. The breeding biology of Red-necked Phalaropes have been studied previously in several areas, including Finland (Hildén and Vuolanto 1972), Canada (La Pérouse Bay, Reynolds 1987) and Alaska (Cape Espenberg, Schamel and Tracy 1991; Wales, Erckmann 1981; Seward Peninsula, Kessel 1989). I examined the breeding biology of phalaropes as part of an ongoing study of two other sandpiper species. In this paper, I summarize data on the morphometrics, fecundity and demography of phalaropes breeding at Nome, Alaska, and compare these values to populations at other sites.

METHODS

Red-necked Phalaropes were studied at a 4 km² study site, 21 km east of Nome, Alaska (64°20'N, 164°56'W)

during May-July in 1993-1995. Most nest searching effort was conducted in the dry habitats that sandpipers used for nesting. Phalaropes prefer wetter areas (Rodrigues 1994), but these habitats were not intensively searched. Workers found phalarope nests opportunistically by observing males flushing away from their nests. Some nests were probably missed because I sometimes encountered young broods of unknown origin during the late breeding season. Most nests were found after males started incubation, but a few nests were found during laying. It was not possible to determine which birds were paired or which female had laid the clutch because I did not conduct behavioural observations. All nests were marked with a line of small sticks and a wooden stake 10 m from the nestcup.

Date of clutch initiation was estimated by back-dating from laying, stage of incubation or hatch. To estimate stage of incubation, I floated the eggs in water and compared egg buoyancy to a reference curve based on sandpipers (cf. Van Passen *et al.* 1984, B.K. Sandercock, unpubl.). To back-date from hatch, I assumed a laying rate of one egg per day and an incubation period of 19 days (Hildén and Vuolanto 1972, Reynolds 1987). I revisited nests every 3-7 days to monitor their success, and to check if the male was in

attendance. The presence of young or small shell fragments indicated the nest was successful.

During nest visits, I noted whether the male was present or absent. If the male was absent, I handled 1-2 eggs to determine their relative temperature. I assumed the male had flushed during my approach if the eggs were warm (Erckmann 1981), and that the male was on an incubation break if the eggs were cold. If the male was observed, I recorded his flushing distance and whether he flew away or remained near the nest after flushing.

Adult phalaropes were captured in the early and late breeding season with mist nets or walk-in traps placed over the nest. Hatching young were captured at the nest, and all birds were banded with one numbered metal band on the upper leg. Female phalaropes usually had brighter plumage than males, but there was some overlap between the sexes (cf. Reynolds 1987). I sexed birds by the colouration of the plumage on the head and neck. A white supercilium was connected to a rufous neck patch in males whereas the two areas were separated by dark grey neck feathers in females (Paulson 1993). I recorded the following morphometrics for all age classes: exposed culmen, tarsus bone, flattened wing chord and body mass.

RESULTS AND DISCUSSION

In the three years of this study, 175 Red-necked Phalaropes (74 young, 101 adults) were captured and 63 nests were monitored. Sample sizes vary below because complete information was not available for all birds and nests.

Morphometrics of adult phalaropes

Table 1. Morphometrics of adult female and male Red-necked Phalaropes. Overall, there was a significant difference in body size between the sexes (MANOVA, Wilk's $\lambda=0.42$, $F_{4,78}=27.2$, $P<0.0001$).

	Culmen (mm) Mean \pm sd	Tarsus (mm) Mean \pm sd	Wing (mm) Mean \pm sd	Mass (g) Mean \pm sd	n
—	22.8 \pm 1.0	21.9 \pm 1.7	115.9 \pm 3.1	37.2 \pm 3.5	30
—	22.2 \pm 1.0	21.3 \pm 1.2	110.5 \pm 3.1	31.7 \pm 2.5	71
Stats	$F_{1,99}=7.8$, $P<0.01$	$F_{1,83}=3.5$, $P=0.06$	$F_{1,99}=62.4$, $P<0.001$	$F_{1,98}=78.2$, $P<0.001$	

The mean estimates of exposed culmen, tarsus length and wing chord of Red-necked Phalaropes at Nome (Table 1) were close to values reported for wintering birds in California (Rubega 1996). Females were significantly larger than males in most measures of body size, but the average differences between the sexes were small (2.6-4.8%, Table 1). Rubega (1996) also found evidence of reversed sexual size dimorphism, but concluded that morphometrics were not adequate for discriminating between the sexes.

Fecundity

Timing of arrival, laying and hatching: Red-necked Phalaropes were one of the first birds to arrive each year at Nome; first sightings were usually during the second week of May (Table 2). The earliest records of arrival for other areas of the Seward Peninsula range from 7-8 May (Kessel 1989). There was no annual variation in the date of clutch initiation; mean date of clutch initiation was in the first week of June in all years (Table 2). Despite some variation among sites in latitude, egg-laying starts in early June for most study populations (63°N, Hildén and Vuolanto 1972; 58°N, Reynolds 1987, 64-66°N, Kessel 1989, 64°N, this study).

Some of the variability in the dates of clutch initiation was due to uncertainty in my estimation techniques. Stage of incubation could be determined from egg flotation with an accuracy of $\pm 2-3$ days (B.K. Sandercock, unpubl.). Similarly, back-dating from hatch has an accuracy of $\pm 1-2$ days because length of incubation is variable and declines as the season progresses in Red-necked Phalaropes (mean=17-18.5 days, $n=20$, Hildén and Vuolanto 1972; mean=18.7 days, $n=47$, Reynolds 1987; mean=21.5 days, $n=30$, Kessel 1989; 22 days, $n=1$, this study). Dates of hatching were easily determined, and most nests produced young in late June (Table 2).

Table 2. Timing of reproduction of Red-necked Phalaropes at Nome, Alaska.

	Date of first sighting	Date of laying		n	Date of hatching		n
		Mean \pm sd	Range		Mean \pm sd	Range	
1993	14 May	2 Jun \pm 4.3	27 May - 8 Jun	8	16 Jun		1
1994	12 May	3 Jun \pm 7.0	20 May - 11 Jun	23	20 Jun \pm 5.2	16 Jun - 1 Jul	7
1995	14 May	4 Jun \pm 6.7	25 May - 18 Jun	22	26 Jun \pm 7.8	16 Jun - 13 Jul	16
Stats		$H_2=16.4$, $P=0.97^\dagger$			$H_2=4.6$, $P=0.09^\dagger$		

[†] Kruskal-Wallis test (c^2 approximation).

Clutch size and nest success: There was little variation in clutch size. Almost 90% of the nests contained four eggs (Table 3), a rate comparable to other sites (96%, n=25, Höhn 1968; 99%, n=71, Hildén and Vuolanto 1972; 92%, n=243, Reynolds 1987; ca. 85%, n=101, Kessel 1989). The events that led to clutches of less than four eggs in this study are unclear. Partial nest predation is rare at Nome (B.K. Sandercock, unpubl.), but clutches of 2-3 eggs may have been renests or second clutches with a new male (Reynolds 1987). Females were not observed intensively enough during laying to determine if this was the case.

Phalarope nest success was not monitored in 1993. More nests were unsuccessful in 1994 than in 1995 (Table 3). In 1994, two partially incubated clutches were abandoned immediately after the nest was found, which was unusual because the male was not captured in either case. There was a higher predation rate in 1994 than 1995 although predator and microtine numbers were similar in both years (B.K. Sandercock, pers. obs.). Some variation in rates of nest loss may have been due to individual predators learning to use the nest stakes to find eggs.

Table 3. Clutch size and nest success of Red-necked Phalaropes at Nome, Alaska.

	Clutch size			Hatched	Fate of the clutches			n
	2	3	4		Depred-ated	Aban-doned	Unknown	
1993	-	13.3%	86.6%	33.0%	-	-	66.7%	15
1994	-	-	100.0%	29.2%	58.3%	8.3%	4.2%	24
1995	4.3%	17.4%	78.3%	70.8%	29.1%	-	-	24
Pooled	1.6%	9.7%	88.7%	46.0%	33.3%	3.1%	17.4%	63 [†]
Stats	---			G ₃ =7.9, P=0.005 [§]				

[†] One clutch was depredated before final clutch size was determined.

[§] Hatched vs. unsuccessful nests. Nests found in 1993 or of unknown fate were excluded.

Egg size and chick size: Measurements of Red-necked Phalarope eggs and young at Nome (Tables 4 & 5) were within the range of previously reported values (egg length 27.9-31.0 mm, egg width 20.0-21.0 mm, Reynolds 1987; hatchling mass, mean=3.9 g, n=86, Hildén and Vuolanto 1972). The legs of phalarope young were well-developed at hatching (chick tarsi were 85% of adult length, Tables 5 vs. 1), which is typical of nidifugous birds.

I found no evidence for annual variation in size of eggs or young (Tables 4 & 5). There were significant differences among females in egg size, but surprisingly, the repeatability of phalarope egg volume was low (Table 4). Variation in egg size is usually greater

among- than within-females, thus the repeatability (and heritability) of egg size is high in many birds (Boag and van Noordwijk 1987). Shorebirds that lay multiple clutches lay eggs that are small in relation to female body size (including phalaropes, Sæther *et al.* 1986). A higher degree of within-female variation in egg size might also be expected if individuals laying multiple clutches are energetically stressed in these species. Alternatively, phalarope egg size may not be a good indicator of egg reserves (*sensu* Williams 1994). The repeatability of measurements of chick size was higher (Table 5), and the variation in egg volume may have been due to components that have little effect on size of the young at hatching.

Table 4. Annual variation in the egg size of Red-necked Phalaropes. A nested ANOVA was used to analyse egg size variation because eggs within a clutch are not independent observations.

	Length (mm)	Width (mm)	Volume (cm ³) [†]	number of eggs, nests
	Mean \pm sd	Mean \pm sd	Mean \pm sd	
1993	29.4 \pm 1.1	20.5 \pm 0.5	5.84 \pm 0.43	54, 14
1994	29.3 \pm 3.3	20.2 \pm 3.0	5.82 \pm 0.97	91, 23
1995	29.4 \pm 1.2	20.6 \pm 0.6	5.90 \pm 0.41	87, 24
Pooled	29.4 \pm 2.2	20.5 \pm 1.9	5.85 \pm 0.69	232, 61
Repeatability [§]	14.1%	6.8%	29.0%	
Year	F _{2,59} =0.12, P=0.88	F _{2,59} =0.79, P=0.46	F _{2,59} =0.12, P=0.89	
Female (Year)	F _{58,171} =1.7, P<0.01	F _{58,171} =1.3, P=0.11	F _{58,171} =2.6, P<0.001	

[†] Volume = kLW² (Hoyt 1979), where k=0.47 in most shorebirds (B.K. Sandercock, unpubl.).

[§] Amount of variation in egg size explained by differences among females.

Table 5. Annual variation in the size of hatching Red-necked Phalaropes. See Table 4 for details of analysis.

	Culmen (mm)	Tarsus (mm)	Mass (g)	number of young, nests
	Mean \pm sd	Mean \pm sd	Mean \pm sd	
1993	7.35 \pm 0.26	18.1 \pm 0.55	3.95 \pm 0.24	4, 1
1994	7.87 \pm 0.36	18.3 \pm 0.78	3.99 \pm 0.33	26, 7 [†]
1995	7.79 \pm 0.52	18.2 \pm 0.74	4.24 \pm 0.24	35, 12
Pooled	7.77 \pm 0.47	18.2 \pm 0.74	4.13 \pm 0.31	68, 20
Repeatability	61.5%	54.6%	50.1%	
Year	$F_{2,16}=0.76, P=0.48$	$F_{2,16}=0.07, P=0.93$	$F_{2,17}=0.19, P=0.17$	
Female (Year)	$F_{16,45}=6.5, P<0.001$	$F_{16,45}=5.6, P<0.001$	$F_{17,46}=5.8, P<0.001$	

[†] One brood of four young were weighed only.

Nest attendance and male behaviour: Rates of nest attendance increased during incubation, and males were present on 81.3% of all nest visits (Table 6). Erckmann (1981) used telemetry to monitor Red-necked Phalarope nests, but also recorded a mean nest attendance rate of 77.7%. Males captured at different stages of incubation did not differ in body mass (Table 6). Similarly, Erckmann (1981) recaptured males and found little change in body mass during incubation. Rates of nest attendance and mass loss in Red-necked Phalarope are comparable to other shorebirds that are uniparental incubators (Carter and Montgomerie 1985).

Parental investment theory predicts that parental effort should increase as incubation progresses because

clutch value increases with offspring age (Montgomerie and Weatherhead 1988). I found that the flushing distance and behaviour of male phalaropes was not affected by stage of incubation (Table 6), although males observed in late incubation tended to flush at shorter distances. In general, male Red-necked Phalaropes defended their clutches only weakly: they usually flew away when an observer approached the nest (see also Höhn 1968), and if they remained in the vicinity of the nest, they rarely vocalized or displayed. Many shorebirds attempt to deflect predators from their eggs or young but species with uniparental care are less aggressive, possibly because distraction displays are riskier for a single parent (Larsen *et al.* 1996).

Table 6. Nest attendance, body mass, and behaviour of male Red-necked Phalaropes in relation to stage of incubation. n is number of nest visits or number of males captured.

Days of incubation	% of visits male was present		Male mass (g)		Flushing distance		% of visits male stayed near nest	
		n	Mean \pm sd	n	Mean \pm sd	n		n
1-7	75.8%	132	31.4 \pm 2.1	21	5.1 \pm 5.8	56	28.0%	50
8-14	85.7%	49	31.9 \pm 2.8	9	4.2 \pm 2.9	17	41.2%	17
15-19+	87.4%	87	31.0 \pm 3.1	4	4.1 \pm 2.6	23	36.0%	25
Pooled	81.3%	268	31.3 \pm 2.3	40 [†]	4.7 \pm 2.6	96	32.6%	92
Stats	$G_2=5.5, P=0.07$		$H_2=0.11, P=0.95^s$		$H_2=0.07, P=0.96^s$		$G_2=1.2, P=0.56$	

[†] Includes six males for which stage of incubation was unknown.

^s Kruskal-Wallis test (c^2 approximation).

Natal philopatry and adult return rates

Thirty-four young were banded in the first two years of the study (4 in 1993, 30 in 1994), but only one bird (2.9%, a yearling female) was recaptured in a subsequent year. Natal philopatry of Red-necked Phalaropes usually ranges from 4-10%, and yearling breeders of both sexes have been reported from other sites (Colwell *et al.* 1988, Schamel and Tracy 1991). The return rate of adult females at Nome (11.1%, n=18) was lower than males (17.3%, n=52; $G_1=0.41, P=0.52$), probably because males were more likely to be trapped on a nest. Return rates of adult phalaropes are higher at other sites (38%, La Perouse Bay; 50%, Cape Espenberg; Colwell *et al.* 1988). The return rates of phalaropes at Nome should be treated as minimum

estimates because only 15-25% of the total population was trapped, and an individual's probability of recapture was low.

SUMMARY

Red-necked Phalaropes breeding at Nome did not differ from populations at other sites in their morphometrics, fecundity or demography. Lack of geographical variation is somewhat surprising, given that this species has quite a wide breeding distribution. Phalaropes

depend on ephemeral sites to breed, and have a mating system where neither sex is territorial (female access polyandry, Reynolds 1987). The return rates of adult phalaropes are low compared to most territorial shorebirds (Colwell *et al.* 1988, Schamel and Tracy 1991), and may indicate high breeding dispersal. Molecular data support this notion: Haig *et al.* (1997) found that the genetic differentiation among Red-necked Phalaropes is relatively low, and that there is no evidence of the subpopulation structure found in other shorebirds (e.g. Dunlin, *Calidris alpina*, Wenink *et al.* 1996). Gene flow should retard adaptation to local conditions, and may explain why Red-necked Phalarope populations are homogeneous in their breeding biology.

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