Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland

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An isolated, colour-ringed coastal population was studied for seven years. The first individuals arrived each year, some already paired, in late May and commenced egg-laying about one week later; old birds arrived and nested earlier than yearlings. Rapid growth of oocytes took only 3—4 days, and the laying interval averaged 26.5 hours. Successive polyandry was recorded several times. Factors involved in the timing of breeding and in nest site selection are discussed. Incubation usually took 17—18.5 days and was shorter towards the end of the season. The development of young, movements of broods and parental care are described. Males started to moult during incubation. Females departed earlier than males, soon after hatching of the first broods. The Finnish population migrates to the southeast, over the continent of Europe.

1. Introduction

Phalaropes are small swimming waders, which are grouped into their own family Phalaropodidae in the big order Charadriiformes. They are characterized especially by many anatomical and behavioural features related to their adaptation for a swimming mode of life as well as to the reversed roles of the sexes. The female is bigger and more brightly coloured than the male and she is also the dominant partner in courtship behaviour; the male incubates and takes care of the young.

The family includes three species: the Grey Phalarope *Phalaropus fulicarius* (called Red Phalarope in America) and the Red-necked Phalarope *Ph. lobatus* (called Northern Phalarope in America), both circumpolarly holarctic, breeding mainly in the tundra zone and wintering on the open sea of tropical oceans; also Wilson's Phalarope *Ph. tricolor* breeding in the central parts of North America and wintering on inland waters of South America. As a result of the classical study by TINBERGEN (1935) in Green-

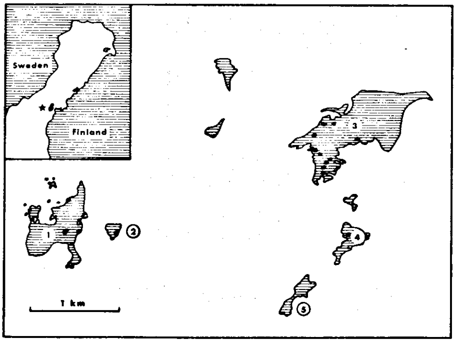

FIG. 1. The island group of Norrskär: 1 = W.Norrskär, 2 = Fletagrund, 3 = E.Norrskär, 4 = Revgrund, 5 = Synnertsberg. The black dots indicate pools. The geographical location of the study area is shown on the inset.

land, the best known of the three species is the Red-necked Phalarope. Additional information has been published, especially by HÖHN (1968, 1971), but many details of the biology of this species remain incompletely known or even misinterpreted. The breeding biology and behaviour of the Grey Phalarope has been described by MANNICHE (1910), BENGTSON (1968) and HÖHN (1971), that of Wilson's Phalarope by HÖHN (1967) and JOHNS (1969). HÖHN (1965, 1969) has reviewed the biology of all Phalarope species.

This paper reports part of a population study on the Red-necked Phalarope, carried out during seven summers on the west coast of Finland at the southern border of the species' range. It concerns only the breeding biology; behaviour and population dynamics will be reported later.

2. Study area and methods

2.1. Study area. The field observations were carried out in the island group of Norrskär (63° 15'N, 20° 38'E) in the outer archipelago of the Quarken Straits, the narrowest portion of the Gulf of Bothnia. The study area is very isolated, surrounded by open sea on all sides; the nearest islands are Rönnskär, 15 km southeast, and Raippaluoto 25 km east. The Swedish coast lies about 50 km northwest (Fig. 1).

Norrskär is the southernmost permanent breeding locality of the Red-necked Phalarope in Finland. It is separated from other permanent breeding grounds of the species (on the coast near Oulu and in the Scandinavian fjeld area) by distances of about 300 km. However, breeding has occurred in the intervening areas, the nearest on Rönnskär in 1959—60 (O. Hildén).

The island group of Norrskär consists of two larger islands, Western and Eastern Norrskär, and six small islets (Fig. 1). Of these, W. Norrskär is the only permanent breeding place of Phalaropes, but nesting has been recorded occasianolly on the nearby islet Fletagrund, and in 1971 also on Synnertsberg and probably Revgrund, and 1972 probably on E. Norrskär.

W. Norrskär has an area of 28 ha but is only 8 m high. It consists partly of sand and stones and partly of bedrock, but is mainly covered by sparse vegetation (see VALOVIRTA 1937). Trees are completely absent, and even low juniper bushes grow only in a small area in the central part of the island. The low height of the vegetation is due partly to grazing by sheep, which were kept on the island until recently. Somewhat more luxuriant meadows are found along the shores, especially in the western parts of the island. Small coves and ponds frequented by Phalaropes are formed on low shores. They vary in size according to the water level. The most important feeding site is the largest pond in the interior of the island, the Central Pond, which is no longer connected to the sea. It is about 50 m in diameter and has low, swampy shores. In early summer it is deep and aquatic vegetation scarce, but later the water level falls and about half the surface becomes covered by sedges. In the rocky southwestern part of the island is a lighthouse and pilot station together with

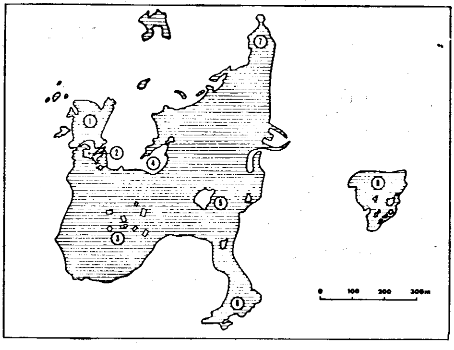

FIG. 2. Localities on W.Norrskär mentioned in the text: 1 = Tern Cape, 2 = Lagoon, 3 = lighthouse with surrounding dwellings, 4 = Bay, 5 = Central Pond, 6 = South Cape, 7 = North Cape, 8 = Fletagrund.

the homes of their personnel. The locality names used in the text are shown in Fig. 2.

In addition to Phalaropes, a number of other bird species breed abundantly on W. Norrskär. In the following list, the numbers of pairs of the most numerous species breeding in 1966—72 are presented. (For a more detailed review of the birds of Norrskär, see Hildén & Vuolanto 1968.)

Anas platyrhynchos	1— 6
A. acuta	1— 4
A. clypeata	0— 4
Aythya marila	19— 29
A. fuligula	1— 9
Melanitta fusca	4— 11
Somateria mollissima	12— 20
Mergus merganser	3— 6
M. serrator	20— 30
Charadrius hiaticula	13— 22
Arenaria interpres	30— 40
Tringa totanus	16— 23
Philomachus pugnax	0— 7
Larus canus	2— 5
Sterna paradisaea	95—110
Riparia riparia	4— 10
Delichon urbica	5— 15
Oenanthe oenanthe	3— 9
Motacilla alba	7— 14

Among these, the Arctic Tern *Sterna paradisaea* and the Turnstone *Arenaria interpres* are particularly important to the Phalaropes, the former influencing their habitat selection (p. 64), the latter taking eggs.

Fletagrund lies about 300 m east of W. Norrskär. It is a small islet of rock and gravel with two fairly large ponds and several small rock pools. Its most numerous breeding birds are *Sterna paradisaea* (22—30 pairs), *Somateria mollissima* (15—20), *Cepphus grylle* (8—17), *Larus canus* (5—8), *Melanitta fusca* (4—8) and *Arenaria interpres* (5—6). E.Norrskär is the largest island of the group, almost 2 km in diameter. Although Phalaropes usually do not nest there, they favour the island especially before breeding, since its numerous shallow ponds and lagoons are rich in invertebrate food.

2.2. Methods. In every year except 1968, field work commenced in late May on arrival of the Phalaropes and was continued until mid-July when all young were hatched. The observation periods in the various years were as follows:

1966	23 May	to	2 July	41	days in total
1967	26 May	to	15 July	50	„
1968	18 June	to	30 June	13	„
1969	27 May	to	10 July	45	„
1970	25 May	to	16 July	53	„
1971	25 May	to	17 July	54	„
1972	31 May	to	14 July	45	„

Of the authors, Vuolanto did most of the field work and preliminary treatment of the data for his licenciate thesis, whereas Hildén planned and directed the work and prepared the final manuscript for publication.

Observation of Phalaropes is very easy due to their tameness. A stationary observer can watch birds without disturbing them at a distance of only a few meters; egg laying, for instance, has been observed at close range without the use of a hide. On the other hand, the activity of the birds, e.g. when repeatedly flying from one place to another, often complicates observation. The nests are easy to find as soon as incubation has started, but during egg-laying to search for them is time-consuming and requires much experience. Within the study area, all nests which were subsequently successful were found in the years of study, 35 of them during egg-laying and 36 during incubation. Only 2—3 nests, destroyed at an early stage, were missed.

For individual recognition, as many birds as possible were marked with coloured rings in addition to numbered aluminium rings. All but two incubating males were captured at their nests by a trap of the type described by, among others, Bohlken (1934) and Rittinghaus (1956). In addition, traps supplied with long arms and placed in shallow water at favoured feeding sites of Phalaropes were used successfully. Altogether 21 adult ♂♂ and 15 ♀♀ were colour-ringed in the course of the study. Also, all but six young hatched, or 108 in total, were marked with coloured rings, nestlings within each brood with the same combination of colours.

2.3. Individual differences in appearance. The sexes are easy to distinguish in the field. The best identification features of the female are the larger size and brighter colours, especially the distinct rusty-brown V-figure on the slate-gray back. The back pattern of the male is more diffuse and paler yellowish in colour.

Small differences of plumage often make it possible to recognize individuals even without seeing their colour-rings. This is easier for males, as pointed out by Tinbergen (1935) and Höhn (1968). The most striking variations are found in the shape of the throat patch, the extent and brightness of the red at the sides of the neck, the colour of the front of the neck, its thickness, the general darkness of the plumage and the colouring of the feathers of the rear part of the back, which in some individuals are fringed with white. Some males are almost as pale in summer as in winter plumage. Individual differences in females are similar but less conspicuous. The colouring of the neck (i.e. presence or absence of downward extensions

Table 1. Arrivals of Red-necked Phalaropes in different parts of Finland. Only localities where the species is more or less annual as a passage migrant are included in the table.

Locality			Earliest	Average	Latest	Years	Collected by
Aspskär	60°15′N	26°25′E	20 May	24 May	30 May	8	A. Vuorjoki, etc
Helsinki	60°10′N	25°00′E	19 May	24 May	30 May	13	O. Hildén & L. Laine
Pori	61°30′N	21°35′E	19 May	25 May	2 June	16	A. Kaukola
Valassaaret	63°25′N	21°05′E	19 May	25 May	1 June	14	O. Hildén
Kokkola	63°50′N	23°05′E	16 May	25 May	3 June	18	R. Casén & H. Hongell
Kajaani	64°15′N	27°45′E	19 May	22 May	29 May	7	P. Helo
Oulu	65°00′N	25°30′E	19 May	25 May	3 June	14	J. Siira
Kemi	65°45′N	24°35′E	17 May	25 May	29 May	8	P. Rauhala

of the white throat patch, the distribution and patterning of red and grey, etc.) and of the back feathers are the best features for individual recognition. These marks were found to be constant in individuals from year to year, and thus are not related to the age of the birds. Confirmation of this is provided by the fact that one-year-old birds do not differ from older ones in appearance, and they similarly show a wide variation in colouring. According to Kozlova (1961) one-year-old birds are distinguishable from adults by having ochre-coloured margins to their upper wing-coverts in early summer, but we have not noticed this difference at Norrskär.

2.4. Population at Norrskär. According to local lighthouse keepers and pilots Red-necked Phalaropes have "always" nested at Norrskär. The population was found in 1959 by O. Hildén who visited Norrskär during bird census work in the archipelago. Both in 1959 and 1960 four males were observed showing alarm behaviour and some young were found. The annual numbers of resident Phalaropes at Norrskär in recent summers have been as follows:

	Breeding pairs	Excess birds	Total population
1966	3	1 ♂	7
1967	6	—	12
1968	5	3 ♀♀	13
1969	10	2 ♀♀	22
1970	19	1 ♂, 1 ♀	40
1971	16	12♂♂, 6♀♀	50
1972	9	10♂♂, 7♀♀	35

The figures for 1971 and 1972 are not quite exact due to the large population and large numbers of non-breeding birds. The possibility remains that some of the "excess birds", which were observed only occasionally at W. Norrskär, may have nested somewhere outside the study area.

3. Arrival and pair formation

3.1. Arrival at the breeding grounds. The spring migration of the Red-necked Phalarope is very rapid. The first individuals are seen at about the same time, late May, throughout the whole of Finland including Norrskär (Table 1). Long series of arrival data are lacking from Lapland, but the few observations available confirm the picture given above: e.g. Enontekiö 30 May 1909 (Suomalainen 1912) and 24 May 1910 (Munsterhjelm 1911), Muonio 28 May 1905, 23 May 1913 and 31 May 1915 (Montell 1917). The same period of arrivals, from mid-May to early June, is reported throughout the species' breeding range: e.g. from the USSR (Dement'ev & Gladkov 1969), Norway (Haftorn 1971), Scotland (Baxter & Rintoul 1953, Bannerman 1961), Iceland (Timmermann 1949), Greenland (Salomonsen 1950, 1967) and Alaska (Bent 1927, Höhn 1968).

The date of the first sighting at Norrskär during five springs varied by only three days, between 26 and 29 May. The bulk of the population arrives soon thereafter at the turn of the month but in each year except 1966 some birds did not arrive until mid-June or even the end of that month. A more detailed analysis of the arrivals of Phalaropes at Norrskär is given in Table 2.

Old birds that had bred previously

TABLE 2. Arrivals of Red-necked Phalaropes at Norrskär in 1966—72. Daily observations include only new birds (not recorded before), except in a few cases when the total number is mentioned.

1966:	29 May	2♀♀+3♂♂	including 2 pairs
	2 June	1♀+1♂	a pair
1967:	27 May	4♀♀+3♂♂	including 1 pair
	28 May	1♀+1♂	a pair
	15 June	1♀+1♂	a pair
	after 15 June	1♂	
1969:	27 May	5 birds	observed by R. Hudd
	28 May	6♀♀+2♂♂	including those above
	29 May	1♀+1♂	a pair
	31 May	1♂	
	3 June	1♀+1♂	a pair
	1—3 June	4♀♀+1♂	
	5 June	1♀	
	5—7 June	2♂♂	
	11 June	1♂	
	about 25 June	1♂	
1970:	27 May	1 bird	
	28 May	2♀♀+2♂♂	including one pair
	30 May	4♀♀+2♂♂	»
	1 June	1♀+2♂♂	
	2 June	1♀+1♂	a pair
	3 June	2♂♂	
	4 June	2♀♀+2♂♂	including one pair
	5 June	1♀	
	7—12 June	5♀♀+4♂♂	
	12 June	2♂♂	
	12—15 June	2♂♂	
	after 15 June	2♂♂	
	18 June	1♀	a non-breeding yearling
1971:	26 May	3♀♀+2♂♂	including 2 pairs
	27 May	3♀♀+4♂♂	
	28 May	16 in total	including some passage migrants
	29 May	c. 30 in total	including some passage migrants
	30 May	c. 35 in total	including some passage migrants
	2 June	1♀+1♂	
	3 June	1♀+1♂	
	10 June	1♂	
	16 June	1♀+1♂	a pair
	29 June	1♀+1♂	a pair
	5 July	1♂	a yearling with an injured leg
1972:	(20 May	2 birds	at E.Norrskär, Jalonen & Lehtinen)
	(25 May	about 40 birds	at E.Norrskär, Jalonen & Lehtinen)
	31 May	2♀♀+2♂♂	2 pairs (first day of observation)
	1 June	11 birds identified	

in the area generally arrived earlier than one-year-old birds, as in most other bird species so far studied. The following tabulation shows the arrival periods of 28 colour-ringed birds of known age (ad. = at least 2 years old, juv. = 1 year old):

Before 3 June	3 to 13 June	After 13 June
14 ad. 2 juv.	3 ad. 4 juv.	0 ad. 5 juv.

Of birds that had bred at least once before in the area 82 % arrived before 3 June, whereas 82 % of one-year-old birds arrived on or after this date. Thus late arrivals are very likely to be young birds, which are also seen frequently outside the species' breeding range throughout the summer (e.g. KOZLOVA 1961, v. HAARTMAN et al. 1963—66, DEMENT'EV & GLADKOV 1969).

During the first few days after arrival Phalaropes stay most of the time in flocks at some favoured sites. Such places on W.Norrskär are the Central Pond, the end of the Bay and the Lagoon. However, they also spend much time on E.Norrskär, especially during spells of cold weather when very few are seen on W.Norrskär. This must be due to better feeding conditions on E.Norrskär, where several ponds with brownish, rapidly warming water support many food animals at this time of the year.

There is no clear difference in the dates of arrival of the two sexes at Norrskär. However, TINBERGEN (1935) concluded on the basis of previous literature that females appear at breeding grounds before males. The same is maintained by BAXTER & RINTOUL (1953), BANNERMAN (1961) and DEMENT'EV

& GLADKOV (1969). Similarly, females began to arrive about one week before males in the study area of HÖHN (1968) in Alaska. All Grey Phalaropes seen close enough to be sexed by HÖHN (1971) on their first day of arrival in Canada were females. HÖHN (1967) and JOHNS (1969) also report that in Wilson's Phalarope females arrive somewhat earlier than males.

The discrepancy between our observations and those mentioned above may have arisen because Phalaropes often congregate in favourable feeding areas after arrival but before dispersing to their breeding grounds. In Iceland (TIMMERMANN 1949) and Greenland (SALOMONSEN 1950), for instance, Red-necked Phalaropes stay in large flocks in coastal bays and delta areas until their nesting ponds inland are free of ice. The same behaviour has been noted in the Karigasniemi area, Finnish Lapland, where dozens of Phalaropes congregate each spring at the eastern, early melting end of Lake Passjärvi before they disperse to the surrounding marshes (O. Hildén, unpubl.). In these cases the sexes naturally appear at actual nesting sites simultaneously, although the females may be slightly earlier in arrival in the general area. This may also apply in our study area where E.Norrskär is the most frequented place during the first few days. Hence it is quite possible that some difference between the arrival dates of the sexes would have been recorded if daily observations had been made on E.Norrskär.

3.2. Pair formation. Almost half the birds were already paired when first observed on W.Norrskär. The same was reported by TIMMERMANN (1949) from Iceland. Hence some pair formation must occur either during migration or in the areas where the birds gather prior to nesting. The first alternative seems improbable, considering the strong site tenacity of both sexes, according to our observations (to be reported in another paper). If pairing commonly took place on passage, reduced tenacity to a former breeding ground would be shown by at least one of the sexes (cf. SOIKKELI 1967); but this was not so in the Norrskär population. Consenquently, birds which arrive paired on W.Norrskär must have paired somewhere nearby, probably on E.Norrskär. Pairing before arrival at the nesting sites is typical of many arctic bird species which are adapted to the short breeding season available, and gives birds the opportunity to start nesting immediately after occupying their breeding grounds (e.g. BARRY 1970).

Those individuals which are not paired on arrival at Norrskär usually form pair bonds within one or two days. Some exceptions to this rule have been recorded, however. The longest period between arrival and pairing was 10 days (although potential partners were available all the time).

4. Nest site selection

4.1. Location of nests. The nest sites in different years are shown in Fig. 3. Four areas were much more favoured than others: (1) the surroundings of the Central Pond, (2) Tern Cape, (3) the shore meadows of the Bay, and (4) the surroundings of the small pond on the eastern shore. Outside these main areas some nests were found at the South Cape, on Fletagrund and (in 1971 only) on Synnertsberg.

The distribution of nests varied considerably from year to year. In 1967, for instance, four out of six nests were concentrated near the Central Pond, whereas in 1966, 1968 and 1969 the nests were very scattered with only one at the Central Pond. In 1970 and 1971, the first nests were situated at Tern Cape and later ones near the Central Pond. The fourth site was colonized in 1971 and 1972. Annual differences in the distribution of nests were clearly con-

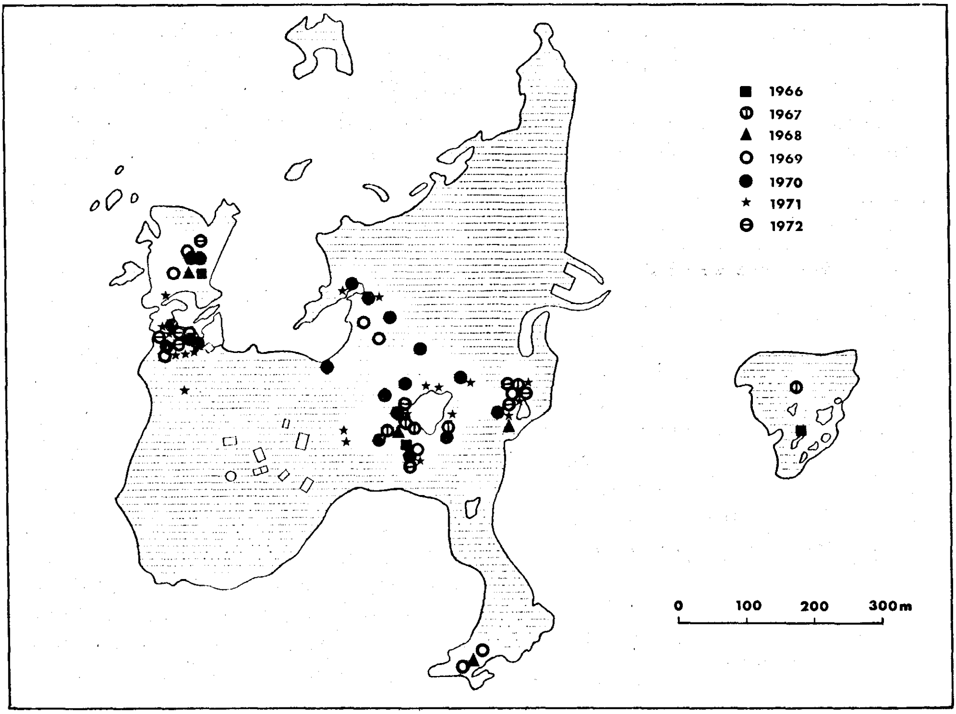

FIG. 3. Location of Phalarope nests at Norrskär in 1966—72.

nected with differences in the feeding areas favoured before and during egg-laying. In 1966 and 1967, Phalaropes frequented the Central Pond much more than in 1969—72, when the Lagoon and Bay were their most favoured feeding sites. This was due to annual differences in the occurrence of food animals, caused by variable weather conditions, variations of water level and temperature differences between sea and fresh water in the Central Pond.

From food samples and field observations we conclude that Phalaropes feed predominantly on the larvae as well as hatching and swarming adults of Chironomidae in the Bay and Lagoon, whereas the principal food items in freshwater ponds consist of Trichopteran larvae, water fleas, tadpoles, water spiders and collembolans. The availability of these food animals obviously regulates the choice of feeding areas and thus influences nest site selection.

Nests are sometimes very close to each other. The shortest distances between nests at Norrskär were 2, 3 and 5 metres. This probably explains the clutches of 5, 7, 8, and even 12 eggs mentioned in literature (BENT 1927, CONGREVE & FREME 1930, TIMMERMANN 1949): they are shared nests of two or three pairs, not proof of simultaneous polygyny as erroneously believed.

In most arctic areas Red-necked Phalaropes usually inhabit marshes with small ponds. They nest in wet places on moss or among sedges close to the water line, often on hummocks surrounded by water (e.g. BENT 1927, SALOMONSEN 1950, KOZLOVA 1961, HÖHN 1965, V. HAART-

MAN et al. 1963—66, DEMENT'EV & GLADKOV 1969, HAFTORN 1971). At Norrskär, the nest sites were markedly different. Most nests lay at a considerable distance from water, as shown in the tabulation below:

Metres from the water line	0—1	1—5	5—20	20—50	>50
Number of nests	4	14	21	26	9

Another difference is that nests on dry soil (sand, gravel, dry meadow) outnumbered those in moist sites: 55 v. 15, respectively (four nests could not be classified). Nests were always located in patches of low or sparse vegetational cover from which the incubating birds could watch the surroundings. Usually the nest lies almost exposed; in the course of incubation, however, it may become concealed by growing vegetation. The predominant plants around nests were as follows:

Grasses (*Festuca ovina, F. rubra, Deschampsia flexuosa, Puccinellia sp.*):	31	cases
Eleocharis uniglumis	21	„
Sedges (*Carex nigra, C. glareosa*)	10	„
Others (*Trifolium repens, Potentilla anserina, Empetrum sp.*)	6	„

The preference for drier nest sites at Norrskär may result from the very restricted areas of suitable wet meadows available on W.Norrskär, namely on the west shore and, later, around the Central Pond (when the water level falls). However, it may also be an adaptation to variations in sea level. During heavy rainfall the water level in freshwater ponds rises sufficiently to threaten nests located near the shoreline only occasionally, but on an island nesting close to the sea shore could be hazardous. A parallel case is offered by the Arctic Tern: in Lapland it nests inland on small hummocks surrounded by water, but on the sea coast farther away from the shore, usually beyond the reach of high water.

4.2. Nesting in tern colonies. All nest sites of Phalaropes on Norrskär (except those in the interior of the island) were located in or near colonies of Arctic Terns. This alone does not prove any real social attraction to terns; there are eight colonies of Arctic Terns along the shores of the island, many of them without nesting Phalaropes. Thus the Tern-Phalarope association could exist simply because terns nest in every place suitable for Phalaropes! Some facts, however, indicate that the presence of terns is an important factor influencing nest site selection by the species.

First, Phalaropes nesting in tern colonies react to calls of the terns by leaving the nest as soon as they hear the first alarm. In this respect they react in the same way as those species showing a strong association with larids (cf. BERGMAN 1964). Second, in Finnish Lapland, Phalaropes are clearly attracted socially to terns: although they commonly nest near ponds without terns, the highest nesting densities are always found near those ponds inhabited by a pair of Arctic Terns (O. Hildén, unpublished records from the Karigasniemi area). In the study area of RANER (1972) in Swedish Lapland, these two species invariably occurred together at the same ponds. Similarly, Grey Phalaropes studied by LØVENSKIOLD (1964) and BENGTSON (1968) bred in or near colonies of Arctic Terns, and Wilson's Phalaropes studied by HÖHN (1967) nested in colonies of Black Terns *Chlidonias niger*. Third, most other waders and ducks of the outer archipelago are known for their tendencies to nest in larid colonies. (The Turnstone and the Tufted Duck *Aythya fuligula* are the best known examples.) This habit originally evolved from the effective protection against enemies that larids provide (e.g. BERGMAN 1957, KOSKIMIES 1957, HILDÉN 1964 and 1965 b). The same association seems to have evolved also in the Red-necked Phalarope.

On the other hand, many authors do not mention that Red-necked Phalaropes prefer to nest in the company of terns. Possibly this tendency has not yet evolved everywhere within the species' range; it is also less marked than in many other species, as indicated by regular nesting outside tern colonies.

5. Egg-laying

5.1. Laying period. Fig. 4 summarizes the dates of laying of first eggs in those nests where this could be determined with an accuracy of one or two days. About half the nests were found during the egg-laying period; in other cases the onset of laying was estimated from the date of hatching by allowing for the length of the egg-laying and incubation periods.

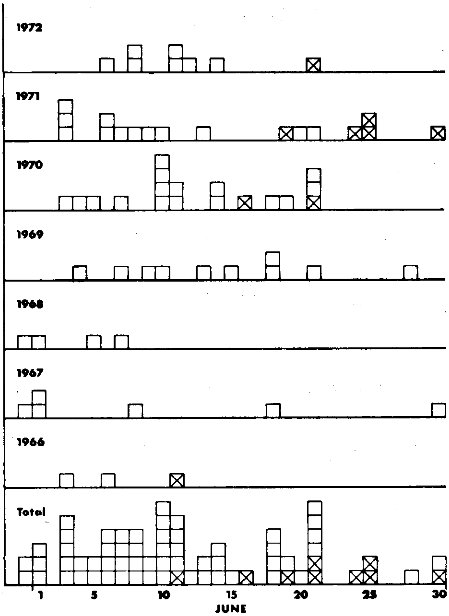

FIG. 4. Periods of egg-laying in the Red-necked Phalarope at Norrskär in 1966—72. Each square represents the date of the first egg in those nests where it could be determined with an accuracy of 1—2 days. Crossed squares refer to replacement or second clutches.

Egg-laying commenced each year between 31 May and 6 June, i.e. within a single week. This precise onset of the breeding season is typical for arctic and subarctic birds and is an adaptation to the short summer. On the other hand, another common adaptation of most northern species, namely a short laying period for the whole population, is not evident in the nesting of Phalaropes at Norrskär. Only in 1966 and 1968, when the observations referred to 3 and 4 clutches respectively, were these started within as little as 8—9 days. In other years the laying period was strikingly prolonged, lasting until late June, without any clear peak. This is due partly to laying of replacement and second clutches (see p. 69), partly to the late arrival of some birds.The seven years' data include layings during a one month period, from 31 May to 30 June.

About the same laying period, from early June to early July, has been reported everywhere within the species' range; the earliest known clutches were

TABLE 3. The date of egg-laying in relation to age in Red-necked Phalaropes.

	First-breeders [1]	Older breeders [2]	Birds of unknown age [3]
Material	8 ♂♂ 2 ♀♀	36 ♂♂ 13 ♀♀	20 ♂♂ 12 ♀♀
Laying period	10 to 21 June	31 May to 21 June	31 May to 30 June
Mean date of laying	14 June	7 June	13 June

[1] Ringed as young and controlled while breeding the following year (one female two years later).

[2] Ringed birds controlled after having bred at least once in earlier years.

[3] Birds ringed for the first time at the nest.

TABLE 4. The influence of the age of both mates on the date of egg-laying in Red-necked Phalarope pairs (cf. the text).

	Both mates old	Old and young	Both mates young
Material (pairs)	10	11	3
Laying period	31 May to 11 June	6 to 21 June	3 to 21 June
Mean date of laying	5 June	11 June	12 June

laid in late May, the latest in mid-July (BENT 1927, NICHOLSON 1930, WITHERBY et al. 1948, TIMMERMAN 1949, SALOMONSEN 1950, 1967, BANNERMAN 1961, KOZLOVA 1961, HÖHN 1965, HAFTORN 1971).

As expected from their earlier arrival, adult birds (at least 2 years old) lay about one week earlier, on average, than young birds breeding for the first time (Table 3). The difference is highly significant ($t = 4.248, P < 0.001$). The long laying period of birds of unknown age implies the presence of both adults and young in this category, but the late mean date of laying suggests a high proportion of first-breeders. Actually, the presence of older breeders among those of unknown age is probably confined to the start of the study when the whole population was of unknown age; the new, unringed birds of later years have been almost exclusively young. This idea is supported by the fact that all birds banded in the first year of ringing were relatively early breeders: the three males ringed in 1966 incubated nests in which the first eggs were laid on 3, 6 and 11 June respectively, and the two females ringed in 1967 (when the ringing of females started) commenced laying on 31 May and 1 June respectively. When these five birds are excluded, the mean date of laying for the remaining 27 birds of unknown age is 14 June, exactly the same as for definite first-breeders.

A delay in the onset of egg-laying by first-breeders is common in birds in general (e.g. LACK 1966, 1968, SOIKKELI 1967, GROSSKOPF 1970, NORTON 1972). Besides later arrival, this may result from young birds, who have less experience, taking somewhat longer to build up their food reserves, to occupy territories and to form pair bonds.

In Table 4 the influence of the age of both mates on the nesting date of the pair has been tested. As practically all birds of unknown age are probably one-year-olds (the five birds of 1966—67 excluded), they have been combined with individuals, known from ringing to be young.

In pairs consisting of a first-breeding and an older bird, the date of egg-laying is determined mainly by the younger mate. The difference in nesting date between pairs of two old birds and pairs of one old and one young bird is highly significant ($t = 3.517, P < 0.005$). This is in contrast to the Redshank *Tringa totanus,* in which the date of breeding is determined by the older mate of a pair: pairs in which one mate is young and the other old are about as early as pairs in which both mates are old breeders (GROSSKOPF 1970). It seems possible that different factors are responsible for the later nesting of young birds in both species. After arrival Redshanks spend some weeks at the breeding grounds before they begin to nest. Consequently, the earlier nesting of old birds is probably not attributable to their earlier arrival but to their better knowledge of the breeding grounds, their attachment to the former territory and their better experience in general (GROSSKOPF 1970). If a young and inexperienced Redshank pairs with an older bird, it shares all the advantages gained by the experience of its mate and may thus reach readiness for breeding synchronously with the older bird. In the Red-necked Phalarope, however, birds commence breeding almost immediately after arrival, and thus young birds are late in nesting mainly because they arrive late. Hence for a young bird to mate with an older bird cannot accelerate its nesting activities appreciably.

The following tabulation lists the laying dates of individually marked females breeding in at least two consecutive years within the area.

♀ No.	Year	First egg laid
1	1967	1 June
	1968	31 May
	1969	4 June
3	1969	15 June
	1970	18 June (2nd clutch)
	1971	3 June
	1972	11 June
5	1969	21 June
	1970	4 and 21 June (2nd clutch)
	1971	3 and 25 June (2nd clutch)
	1972	8 June
7	1970	21 June
	1971	9 and 21 June (2nd clutch)
	1972	8 and 21 June (2nd clutch)
9	1970	3 June
	1971	3 June

Females 3 and 7 and probably also 1 were already "old" breeders in the first year of breeding included in the table; females 5 and 9 were of unknown age. The onset of egg-laying was similar from year to year in females 1 and 9, likewise in females 5 and 7 if the first year is excluded. (It is possible that the first year's delayed laying date refers to a second clutch or (♀5) to breeding for the first time.) The laying dates of female 3 show greater annual variation. Though small, the material suggests that the onset of egg-laying of an individual varies less in different years than that of the population in general. If so, the laying date must be partially determined on a genetic basis or by a circannual rhythm initiated on the date the bird was hatched.

5.2. Interrelations between the dates of arrival and egg-laying. After arrival, birds wait for some time before laying, partly to restore their condition after the long migratory journey, partly because time is needed for occupation of a territory, pair formation, courtship, nest-building and other activities preceding egg-laying. In the population of Dunlin *Calidris alpina,* studied by Soikkeli (1967) on the Finnish coast between 1962 and 1966, birds arrived between 8 and 14 April and egg-laying started between 24 April and 4 May, i.e. 14 to 24 days later. The period between arrival and onset of egg-laying tends to be shorter the later the species arrives, as shown in Table 5 for some Finnish waders.

In the Red-necked Phalarope the

Table 5. Period between arrival and onset of egg-laying in some Finnish waders (data from v. Haartman et al. 1963—66).

Species	Mean annual arrival date of first individuals		Time between arrival and egg-laying
Vanellus vanellus	Helsinki	23 March	About four weeks
Numenius arquata	Helsinki	8 April	About three weeks
Tringa ochropus	Helsinki	11 April	About three weeks
Charadrius hiaticula	Pori	12 April	About three weeks
Charadrius dubius	Helsinki	20 April	About two weeks
Tringa hypoleucos	Helsinki	27 April	About two weeks
Tringa glareola	Häme	30 April	About two weeks
Calidris temminckii	Kokkola	15 May	About two weeks
Tringa erythropus	Muonio	16 May	About one week

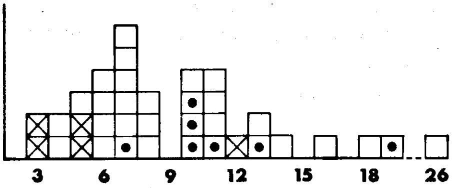

FIG. 5. Time intervals between arrival and laying of the first egg of individually marked female Red-necked Phalaropes at Norrskär. Crossed squares refer to 1967 (warm weather at the time of arrival), and squares with a dot inside to 1969 (cold weather at the time of arrival); cf. the temperature curves in Fig. 6.

period between arrival and onset of egg-laying is shorter than in any other Finnish wader species so far studied in detail. In the five years at Norrskär, the time from the first sighting to the laying of the first egg amounted to only 4 to 9 (average 6.6) days. Although the species is later in arrival than any other breeding bird on Norrskär, its young are among the first to hatch (excluding some early nesting duck species). Other northern wader species arriving late seem also to commence egg-laying as rapidly after arrival as the Red-necked Phalarope, although the data are still scanty. Besides the Spotted Redshank *Tringa erythropus,* mentioned in Table 5, such species include the Dotterel *Eudromias morinellus* (in 1969 the first two birds arrived at Värriötunturi, eastern Lapland, on 30 May, and the first egg was laid on 6 June, PULLIAINEN 1971) and the Broad-billed Sandpiper *Limicola falcinellus* (time difference between arrival and onset of egg-laying at Karigasniemi about one week; O. Hildén unpubl.).

It was stated earlier (p. 62) that pair formation takes place almost immediately after arrival, but the very rapid onset of egg-laying also presupposes that development of eggs in the ovaries must start at the same time. This is only possible in favourable weather conditions when food is plentiful, and cold weather delays the egg formation (cf. p. 72). Fig. 5 summarizes our data on the time difference between arrival and laying of the first egg of individually marked females. In favourable conditions females needed only 3 to 4 days to form the first egg, but sometimes more than 10 days elapsed before they were ready for egg-laying (in these cases even pair formation was delayed, p. 62). Besides variation in weather conditions, this may result from individual physiological differences, perhaps because some females were in poor condition at the time of arrival.

In Wilson's Phalarope, males arrive with fully active testes, whereas females are not in laying condition (HÖHN 1967). This difference from the Red-necked Phalarope may be connected with the earlier arrival of Wilson's Phalarope, in early to mid-May, and its more southern distribution.

5.3. Laying interval. The interval between the laying of successive eggs in 11 precise measurements was 24—30 (average 26.5) hours. In 5 more cases it was 23—28.5, 23—29, 23.5—26.5, 25.5—27.5, 26—30, and twice it was at most 23.5 and 24 hours. Some additional, less exact observations yield estimates of less than 30 hours, except in one case of at least 38 hours.

On one occasion, when we flushed a female from its nest as it was laying the third egg (24 hours after the second egg), the bird did not return until the next day, which resulted in an abnormally prolonged laying interval of 49 hours. The full clutch consisted of four eggs, which shows that the bird did not lay its third egg elsewhere.

Thus egg-laying in the Red-necked Phalarope takes place daily, at intervals averaging little more than 24 hours. This period is shorter than in other small waders so far studied, except the Common Snipe *Capella gallinago.* This may be due in part to the small size of Phalarope eggs in relation to the weight of the female. The mean weight of a female Red-necked

TABLE 6. Influence of the date of nest failure on remating and replacement nesting in the Red-necked Phalarope at Norrskär.

Male No./ Year	Date of nest failure	Days from the onset of incubation	Remating of the male	First egg of the replacement clutch
♂—/1966	17 June	11	17 June	—
♂ 3/1966	24 June	10	24 June	—
♂ 8/1967	15 July	15	?	?[1]
♂ 8/1968	23 June	14	23 June	—
♂ 12/1969	7 July	17	—	—
♂ 13/1969	9 July	14	—	—
♂ 14/1969	10 July	9	—	—
♂ 19/1970	18 June	2	18 June	21 June
♂ 19/1970	10 July	19	—	—
♂ 26/1970	8 July	17	—	—
♂ 27/1970	8 July	17	—	—
♂ 10/1971	26 June	15	27 June	—
♂ 16/1971	10 June	3	—	—[2]
♂ 25/1971	21 June	11	21 June	25 June
♂ 28/1971	21 June	6	21 June	24 June
♂ 36/1971	25 June	4	25 June	—
♂—/1971	6 July	3	?	?[3]
♂ 11/1972	18 June	8	18 June	21—22 June[4]

[1] The observations were concluded on 15 July.
[2] The male disappeared the day after nest failure.
[3] The male was not colour-ringed and thus could not be identified.
[4] The replacement clutch was found on 25 June, when the bird was already incubating four eggs.

Phalarope is 38 g (24 weighings at Norrskär), and the fresh weight of each egg averages 6.3 g (SCHÖNWETTER 1960—66); thus a complete clutch of 4 eggs represents only 66 % of the female's weight. In the Common Snipe, too, the corresponding ratio is low, 68 %, but in species with a longer laying interval it is much higher: e.g. in Temminck's Stint *Calidris temminckii* 82 % and Dunlin 90 % (the mean laying intervals are 31 hours and 36 hours respectively, O. Hildén unpubl., SOIKKELI 1967). There are exceptions, however, from this correlation between the relative clutch weight and the laying interval. The Turnstone, for instance, has eggs as relatively light as those of the Red-necked Phalarope and Common Snipe (the ratio is 65 %, using a mean weight of 111 g for 32 females weighed at Norrskär, S. Vuolanto unpubl.); yet the laying interval of the species amounts to about 40 hours (BERGMAN 1946, S. Vuolanto unpubl.). Hence other factors, such as differences in the availability of food for the female during egg-laying and the size of the bird (larger species tend to have longer laying intervals), must be involved in the varying interval between egg-laying in different species.

TINBERGEN (1935) recorded a time of 58 hours between the laying of the first and third eggs. HÖHN (1967, 1968) reports that the interval at which eggs are laid is either 24 or 48 hours both in Wilson's and Red-necked Phalaropes, but as he checked the nests only once a day this conclusion is not justified. In all four nests followed by RANER (1972) the eggs were laid daily and the clutches thus completed in four days.

5.4. Replacement and second clutches, polygamy. A female Phalarope may lay two clutches in the same season if a mate is available after the laying of the first clutch. This situation occurs if (1) a nest is destroyed and the male (not necessarily the original) again reaches a peak of sexual activity, or (2) there are excess males in the population. The former cases are replacement clutches, the latter true second clutches associated with successive polyandry.

Replacement nests. In the course of our study, 18 Phalarope nests were destroyed during incubation. In only four cases did nest failure result in the laying of a replacement clutch. In another five cases, when nests were lost in June, males remated and copulated repeatedly, but no replacement clutches were laid. That pair formation and copulation do not always result in laying of a substitute clutch may be associated with lowered hormonal activity of females. When the nests were lost in July (8 cases), after the termination of the normal laying season, males did not mate again although females were still present. Presumably by that date the hormonal activity of males had also declined and so inhibited pair formation. The intervals between nest failure and the onset of laying of a replacement clutch were 3 days (twice), 4 days and 3—4 days (Table 6).

Of the four cases of renesting, the male once mated with the same female as earlier in the season and twice with a new one; in the fourth case the female was not colour-ringed and thus could not be individually identified. Females of replacement clutches may, of course, be birds which had not laid eggs previously that season (late arriving or excess individuals). Our data include one such case, and TINBERGEN (1935) observed one instance in Greenland. As regards reproductive output of the species, it is important to note that females may replace not only their own but any destroyed clutches. In this way a male which lost its clutch may father a new one, even though its former mate has disappeared or lost its sexual potency.

Previous records of replacement nesting by Red-necked Phalaropes are scarce. Late nests have often been assumed to be repeat clutches of pairs which lost their first nests (e.g. GLADSTONE 1907, v. HAARTMAN et al. 1963—66, RANER 1972), but only TINBERGEN (1935) observed that the substitute clutch could be laid by a new female. In Wilson's Phalarope replacement clutches are possible, to judge from one female shot as late as 18 June with an enlarged ovary and oviduct (HÖHN 1967).

Second clutches. In 1966 and 1970, there was an excess male in the population at Norrskär. In both cases this male mated with the first female freed from its original mate (after laying its first clutch). Consequently, these females produced two successive clutches, which were incubated by different males. In 1971, there were about six excess males in the population. Three of them succeeded in mating with females which had laid one clutch already, and which therefore produced a second clutch later. The time difference between the two clutches, calculated from the date of the last egg of the first clutch to the first egg of the second clutch, was in two cases exactly 9 and 22 days and in three other cases about 5, 6 and 19 days. In 1972, no second clutches were laid in spite of the presence of about 3 excess males (in this year non-breeding occurred commonly).

STRESEMANN (1927—34, p. 331) already referred to the possible polyandry of the Red-necked Phalarope: "Bei *Phalaropus* machen die Weibchen oft 2 oder mehr Gelege in geringer Entfernung voneinander und überlassen deren Bebrütung je einem Männchen." The conclusion was, however, based on some rather vague observations of Wilson's Phalarope (in BENT 1927), which did not in fact prove polygamy even in this species. TINBERGEN (1935) considered polyandry in the Red-necked Phalarope possible, but not very probable. NETHERSOLE-THOMPSON (1951) mentioned one case of supposed biandry: two sets of eggs, identical in type, within ten yards of one another and a trio of a female and two males on a nearby pool. Höhn (1967, 1970) accepts no definite evidence for polyandry in this species. Raner (1972) was the first to prove polyandry in the Red-necked Phalarope: in a small colony (4 ♀♀, 6 ♂♂) of colour-ringed birds in Northern Sweden, two females produced second clutches with the aid of the excess males. In both cases the second clutch was started 6 days after completion of the first clutch. In Wilson's Phalarope, Höhn (1967) and Johns (1969) could find no evidence of polyandry, contrary to some earlier statements, probably based on inadequate or misinterpreted observations. In the Grey Phalarope, no observations indicating polyandry are known (Höhn 1967).

Our observations show that successive polyandry is a normal phenomenon in the Red-necked Phalarope, provided that there are excess males in the population. It is, of course, of biological value as all males in the population may father a clutch by this means. As stated earlier, remating with a new male and eventual laying of a second clutch may also be caused by the failure of the first nest; in principle, this could also be considered as successive polyandry. Simultaneous polyandry is, from our observations, impossible in the Red-necked Phalarope, because an excess male accompanying a pair badly disturbs normal courtship behaviour and is frequently chased away by either the male or the female.

In the Dotterel, which also shows sex reversal in breeding activities, similar cases of successive polyandry have been reported (Nethersole-Thompson 1951, Franke 1953, Pulliainen 1971). It is likely to occur also in the Spotted Redshank, the third northern wader in which the male almost exclusively incubates and takes care of the young, to judge from one observation in Swedish Lapland (Raner 1972). The polygamy of Temminck's Stint is of a somewhat more advanced form, each female mating successively with two males and laying two clutches within a period of ten days, but then incubating the second clutch herself (Hildén 1965a, 1970). Recently, observations indicating the occurrence of similar behaviour in the Sanderling *Crocethia alba* have been made in North America (Parmelee 1970).

In most other wader species both sexes share incubation and females may even help in tending young; normally this prevents the occurrence of successive polyandry for the breeding season is too short to permit laying a second clutch after leaving the young of the first. However, occasional cases have been reported, e.g. in the Dunlin (Soikkeli 1967). In the Ringed Plover *Charadrius hiaticula,* some pairs may raise two successful broods in one season (Laven 1940, Bub 1962), at least in non-Arctic breeding areas. In a few wader species with prolonged breeding seasons, e.g. the Woodcock *Scolopax rusticola* and Common Snipe, laying of two clutches is common even though the female attends the young of both broods. Whether the laying of two clutches in these species may be associated with polyandry is not known.

There are in literature several observations of supposed polygyny in the Red-necked Phalarope (reviewed by Höhn 1965). This is, however, possible only in the case of replacement nesting, when the male of a destroyed nest mates with a new female (see p. 70). Simultaneous polygyny is as impossible as simultaneous polyandry, due to intolerance between birds (see p. 70). Theoretically, successive polygyny not caused by nest failure would be possible, as the male maintains its courtship behaviour for a few days after the onset of incubation and often tries to copulate with several females successively. However, this behaviour never results in pair formation

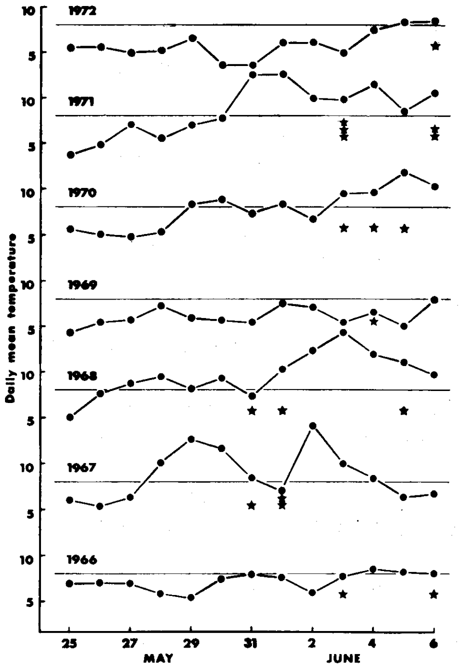

FIG. 6. Daily mean temperatures at Norrskär between 25 May and 6 June, 1966—72, and the onset of egg-laying in the Red-necked Phalarope (each clutch marked with a star). The critical mean temperatures of 8°C are indicated by solid lines.

and laying of a new clutch. Moreover, polygyny in a species like the Red-necked Phalarope would be biologically disadvantageous, as only males incubate and thus are unable to care for more than one clutch. The continued sexual behaviour of males at the beginning of incubation, mentioned above, obviously explains the observations which have been misinterpreted as proof of polygyny (e.g. CONGREVE & FREME 1930). In several wader species casual polygyny has been definitely proved, usually in the form of one male simultaneously mated to two females, which may both lay eggs in a single nest (see the review by NETHERSOLE-THOMPSON 1951).

5.5. Timing of the breeding season. In most birds, annual variations in the onset of egg-laying are mainly correlated with differences in spring temperatures; an increase in temperature during the critical period when birds are physiologically ready for breeding is followed by egg-laying some days later. Among waders, for instance, this has been demonstrated in the Kentish Plover *Charadrius alexandrinus* (RITTINGHAUS 1956), Redshank (GROSSKOPF 1958) and Dunlin (SOIKKELI 1967).

In the Red-necked Phalarope, too, the small annual differences in the onset of egg-laying are correlated with differences in temperatures in late May and early June. Fig. 6 presents the daily mean temperatures at Norrskär for the period 25 May—6 June and the dates of first eggs. In both springs of early nesting, 1967 and 1968, there was a distinct rise in mean temperature in the last days of May, whereas in the other springs the temperature rise took place more slowly and some days later. The critical daily mean temperature seems to be about 8°C: as soon as this level is reached,

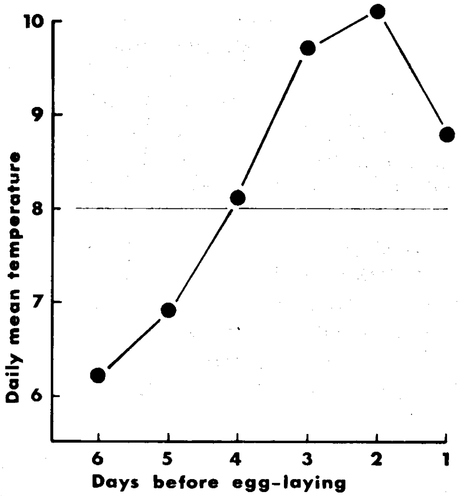

FIG. 7. Daily mean temperatures at Norrskär for six days preceding the onset of egg-laying of each Red-necked Phalarope clutch commenced between 31 May and 6 June 1966—72 (n = 18). The critical mean temperature of 8°C is indicated by a solid line.

egg-laying starts 3—4 days later. This is also illustrated by Fig. 7, which shows the mean temperatures of days preceding the laying of the first egg; a marked rise occurs 3—4 days before the onset of egg-laying. The same period, 3—4 days, was recorded between nest failure and the onset of replacement laying (p. 70).

This period of only 3—4 days needed for rapid growth of oocytes in Red-necked Phalaropes may appear short when compared with small passerines, for instance, which need 4—5 days to form eggs. However, in other small waders studied, the period of egg-formation seems almost as short as in the Red-necked Phalarope. Laying of a replacement clutch begins in the Dunlin within 3 (Heldt 1966) or 4 days (Soikkeli 1967), Kentish Plover 4—7 (Rittinghaus 1956), Ringed Plover 5—6 (Laven 1940) and Redshank about 6 days (Grosskopf 1958) after nest failure.

The rise in temperature may influence Phalaropes directly, by increasing their hormonal activity, or indirectly by affecting the availability of food. In our opinion, it acts in both ways. A sudden rise in temperature is followed immediately by a conspicuous increase in courtship activities. For example, in 1970 the weather was very cold and windy during the first few days after the arrival of the Phalaropes; only a few birds visited W.Norrskär occasionally and no courtship was observed. But on the very first warm and calm day, 30 May, when the maximum temperature reached 10.4°C, nine Phalaropes congregated on the Central Pond where they courted, copulated repeatedly and chased each other excitedly.

A rise in temperature also causes simultaneous warming of water in shallow bays and so brings forth a sudden increase in food supply. The first mass emergence of the early swarming chironomid *Tanytarsus gracilentus* takes place on the first warm days at the turn of May—June (cf. Paasivirta 1972). On such days enormous numbers of these small insects occur both on the water surface and on the shores. Phalaropes, like many other waders and passerines, then feed almost exclusively on them. This superabundant food evidently triggers rapid development of eggs in the ovaries of females.

It seems likely that both the arrival date and the onset of breeding in the Red-necked Phalarope are adapted ultimately to the time of occurrence of Chironomidae. Before the emergence of adult chironomids there are very few suitable food animals for Phalaropes, so earlier arrival would certainly be hazardous for them. The very concise arrival period of the species in the last days of May matches the beginning of mass availability of chironomids, and this abundant source of food allows nesting to start almost immediately. Later in June and July, food is no longer a critical factor, because many species of Chironomidae replace *Tanytarsus gracilentus* and numbers of water fleas, tadpoles, insect larvae, etc. soon develop in shallow waters.

The proximate factor responsible for the termination of egg-laying is obviously the decreasing activity of the sex hormones in birds (see p. 70). But the ultimate factors are more obscure. It seems most unlikely that the food available for adults on the breeding grounds limits the breeding season. At the turn of June—July when the last clutches are laid, and even later in July, insect food is very plentiful and could provide females with enough food for egg production. Most likely the termination of egg-laying is correlated adaptively with the date of southward migration. Adult waders start their departures very early in summer, and since the timing of migration has evolved through natural selection, this early departure must have some survival value. Before they leave, adult Phalaropes build up their energy reserves for the long migratory journey, and most of them also begin to moult (see p. 80). The departure of females from Norrskär begins at the turn of June—July, i.e. at the time the last clutches are laid, that of males about mid-July as soon as they leave the broods. Later nesting would thus delay departure, which might result in higher mortality.

The success of eggs and young in relation to the date of breeding is another factor, which may have affected the evolution of the date of termination of breeding. As will be shown in a later paper, the survival of late clutches is poor due mainly to predation by Turnstones. In addition, the few young hatched from late clutches are not able to start their southward migration until mid-August. By this time, the food supply may already have declined, at least in the more northern breeding areas. Thus, a prolonged breeding season might increase both the mortality of adults and the losses of eggs and young.

6. Incubation period

6.1.Clutch size. Our data from Norrskär include 71 completed clutches of the Red-necked Phalarope, 70 of them of 4 and one of 3 eggs. Occasional clutches of 3 eggs have also been reported from other areas, but probably at least some of them were the result of loss to predators or laying of one egg outside the nest (cf. SOIKKELI 1967). According to BENT (1927), some clutches of 5 or 7 eggs are known, and CONGREVE & FREME (1930) found two clutches with 8 eggs. All these cases probably represent shared nests of two pairs (cf. p. 63).

6.2. Onset of incubation. Males start to incubate during the egg-laying period. Some males make short visits to the nest as soon as the first egg is laid, others after the second or third egg. Gradually the visits to the nest become more frequent and longer. Male 5, for instance, which on 2 June 1967 had 2 eggs in its nest, visited the nest only once during 8 hours of continuous observation and stayed there 5 minutes. The following evening, when the nest contained 3 eggs, this bird spent periods of about 15 minutes on the nest every hour. The male studied by TINBERGEN (1935), which lost its first clutch, started incubation of the replacement clutch soon after the first egg was laid. Immediately after laying of the fourth egg, periods on and off the nest are of about equal duration (15 to 30 minutes), but by the following day periods of incubation already exceed those spent off the nest. After this, periods away from the nest gradually get shorter, to less than 10 minutes per hour, but occasional long interruptions in incubation may still occur. Fig. 8 shows the incubation rhythms at three nests in the early phases of incubation. The observations made by TINBERGEN (1935) on the beginning of the incubation are rather similar.

According to some old observations,

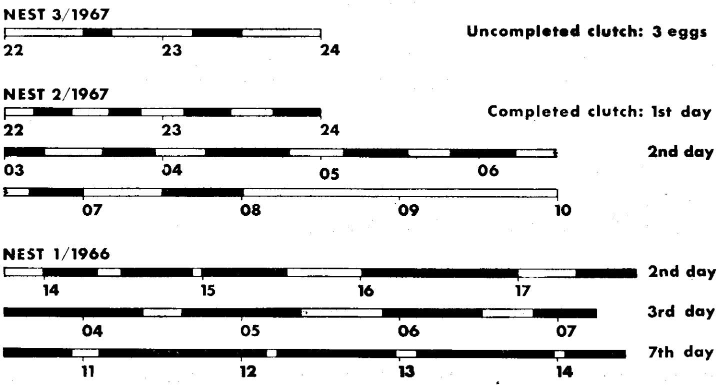

FIG. 8. Incubation rhythm in three nests of the Red-necked Phalarope at Norrskär during the first days of incubation. Black bars indicate periods on, and white bars off the nest.

TABLE 7. Length of incubation period in relation to the time of year in the Red-necked Phalarope.

Date of laying	Before 8 June	8 to 14 June	After 14 June
Number of clutches	7	12	7
Extreme values	17.3—20.7	17—19	16.8—19
Mean	19.0	18.0	17.4

even female Red-necked Phalaropes may incubate (BENT 1927), but this could not be confirmed by later workers (TINBERGEN 1935, HÖHN 1965, 1968 and 1971, RANER 1972). None of our extensive observations at Norrskär indicate that females incubate, even occasionally.

6.3. Length of incubation. We have data for 20 nests on the exact duration of the incubation period, calculated from laying of the last egg to hatching of the last young. It varied from 16.8 to 20.7 days (average 17—18.5 days in 77 % of all cases). Variations in the length of the incubation period may be caused in part by annual and seasonal differences in air temperature and food supply, the latter influencing the time needed by the male for feeding. The two longest incubation periods were recorded in 1967 and concerned early clutches laid at the beginning of June. June of that year was the coolest June during our whole study period, and may have retarded the development of eggs (cf. BEER 1964). SOIKKELI (1967) noticed the shortest incubation periods in late nests of Dunlin; he related this to higher air temperatures and drying of the nest sites. In the Mallard *Anas platyrhynchos,* HESS (1972) demonstrated a clear decrease in the mean incubation time from March to June, as a result of the direct influence of increasing air temperature. On the other hand, since cold weather retards the growth of food for Phalaropes, it may also have delayed incubation in 1967 by increasing the time males needed to spend feeding.

Table 7 summarizes our observations of the incubation period in relation to the date of egg-laying. Seven less precise measurements are included using the mean of the extreme values (e.g. between 17—19 = 18.0). A clear trend is shown of reduction in the incubation period towards the end of the breeding season. The difference in incubation period between the earliest (group 1) and later (groups 2 and 3) nests is highly significant (group 1/group 2: $t = 4.271$, $P < 0.001$; group 1/group 3: $t = 4.908$, $P < 0.001$).

On one occasion, the incubation period was lengthened to 23 days because of an accident to the male. The bird was entangled in a fishing net on the second day of incubation, 7 June 1971, and hurt its leg and wing; it was incapable of flight for 1—2 days. However, it resumed incubating after about 2—3 days. This exceptional case has not been included above.

Previous data on the incubation period of the Red-necked Phalarope are scattered and based on sporadic observations; in most cases incubation took 18—20 days (e.g. TINBERGEN 1935, HÖHN 1965). The commonest incubation period (17—18.5 days) recorded by us is the shortest known among waders. Data on the normal incubation period of the other Phalarope species are scarce and partly contradictory. According to HÖHN (1967, 1969), it is 20—21 days in Wilson's Phalarope, whereas JOHNS (1969) recorded periods ranging from 16 to 21 days in the field and 15 to 18 days for ten eggs placed in an incubator. For the Grey Phalarope, observations range from 15 days (WORTH 1940) to 23—24 days (SALOMONSEN 1950). Probably all three Phalarope species have very short incubation periods. In all other small waders

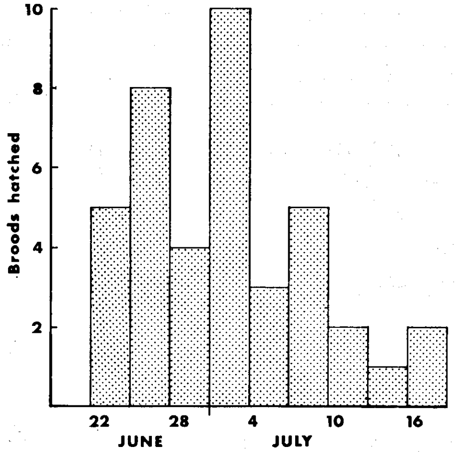

FIG. 9. Hatching dates in the Red-necked Phalarope at Norrskär in 1966—72 presented in periods of three days (n = 40).

so far studied, incubation lasts more than 20 days: e.g. in Temminck's Stint 21 (O. Hildén, unpubl.), Dunlin 22 (HELDT 1966, HOLMES 1966, SOIKKELI 1967, NORTON 1972), Common Sandpiper 22 (v. HAARTMAN et al. 1963—66), Redshank 23—24 (GROSSKOPF 1970), Ringed Plover 24 (LAVEN 1940) and Kentish Plover 26 days (RITTINGHAUS 1956), on average.

If the eggs are addled, the male may continue incubation far beyond the normal period. In two such cases at Norrskär, incubation lasted 26 and 30 days; two other clutches were collected after incubations of 24 and 31 days.

7. Brood period

7.1. Hatching and development of young. The hatching period fell between the following dates in the seven years of the study:

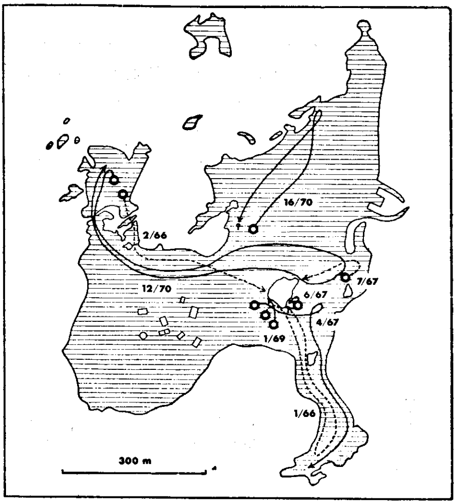

FIG. 10. Examples of the movements of Phalarope broods at Norrskär. Open circles refer to the nest sites, and the tips of the arrows to the final spots where the broods settled. (The broods are numbered according to the accompanying male and year.)

1966	24 June to	27 June,	4 days	(n= 2)
1967	24 June to	8 July,	14 „	(n= 4)
1968	22 June to	27 June,	6 „	(n= 3)
1969	25 June to	8 July,	13 „	(n= 6)
1970	24 June to	10 July,	16 „	(n=13)
1971	26 June to	16 July,	21 „	(n= 9)
1972	30 June to	2 July,	3 „	(n= 2)
Range	22 June to	16 July,	24 days	(n=39)

Hatching commenced each year about at the same date in late June, usually between 22 and 26 June, as expected from the synchrony in the onset of leying (see p. 65). The end of the hatching period, however, varied considerably in relation to the number of nests and the success of the latest clutches. As shown in Fig. 9, which combines the hatching data for different years, hatching occurred steadily from 22 June to 9 July, but from this date

TABLE 8. Time of hatching of the last young in 37 nests of the Red-necked Phalarope.

Hrs	00—03	03—06	06—09	09—12	12—15	15—18	18—21	21—24
Cases	4	4	8	7	3	6	2	3

TABLE 9. The daily distances moved at Norrskär by Red-necked Phalarope broods of different ages. Only distances of 50 m or more are considered.

♂ No./Year	Age of the brood (days): the distance moved (metres) on this day					
♂ 1/1966	1:50,	7:700				
1967	4:300					
1969	1:50					
1970	6:150					
1971	—					
♂ 2/1966	4:400					
♂ 4/1967	1:200,	4:300				
♂ 6/1967	—					
1968	3:300					
1969	2:300,	7:200				
1970	2:250,	5:300,	7:200,	9:100		
♂ 7/1967	1:100,	5:250				
♂ 8/1969	1:100,	4:100,	7:100			
♂ 9/1969	1:50,	3:150				
1970	3:150,	4:200,	5:600,	6:250,	8:150	
♂ 11/1970	4:200,	11:550				
♂ 12/1970	3:150,	4:250,	5:400,	9:500		
♂ 13/1970	3:100,	4:300,	5:100,	6:350,	7:250	
♂ 16/1970	2:100,	6:200,	7:200,	8:250,	9:250,	10:200
♂ 17/1970	3:200,	4:200,	5:200,	8:300		
♂ 20/1970	3:150,	6:550,	9:150			
♂ 24/1970	3:250					
♂ 25/1970	1:100,	2:250,	3:250			

onward only five clutches were hatched. By the end of June, 44 % and before 10 July 90 % of the young had hatched.

Hatching occurs at all times of the day (Table 8). The apparent preponderance of hatching between 06 and 18 hrs is not significant ($\chi^2 = 3.27$, $P > 0.1$). Hatching of the whole brood takes 4—12 (average 8) hours ($n = 9$). These data do not include clutches in which the full number of eggs did not hatch.

The period during which the young stay in the nest depends on the time of hatching. If the last young hatched in the morning, the brood left the nest within 3 to 6 hours, but if hatching occurred later in the afternoon or towards evening the young spent their first night in the nest. This seems to be a general rule among waders.

Young broods stay on dry soil and/or on mud along the waterline. Most broods moved over long distances, up to several hundred metres a day, usually over dry sandy areas, before settling in a rather restricted locality. Some broods, however, stayed throughout their development within a restricted area near the nest. Table 9 and Fig. 10 show the movements of those broods for which the data are most accurate. (Distances shorter than 50 metres a day are excluded from the table, but broods might have moved around extensively without leaving the same general locality.)

The most favoured site for broods on W.Norrskär is the Central Pond, where as many as seven males attending young have been observed at the same time. Never have small young been seen swimming, in spite of their concentration at the water's edge. In this respect their behaviour at Norrskär differs from that of Lapland: in the Karigasniemi area, for instance, Phalarope broods usually haunt wet sedges bordering marsh ponds, often in places with several centimetres of water, and even newly-hatched young have been observed swimming behind the male across an open pond like ducklings (O. Hildén unpubl.). Probably the difference in behaviour is adaptive, since on the coast swimming in seawater could be fatal for small young because of waves. In Wilson's Phalarope, young are able to swim when only one hour old (JOHNS 1969).

Newly hatched young, before leaving the nest, weigh 3.2—4.8 (average 3.9) g (n = 86). The weights of four young less than 24 hours old weighed by HÖHN (1968) were 3.6—4.0 g. We have only a few data on the weight increase of the young, mainly during the first five days after hatching, since they are almost impossible to find after this age. The results are presented in Fig. 11. Compared with those of the Dunlin (SOIKKELI 1967, Fig. 5), young of the Red-necked Phalarope increase in weight much faster. This is shown in the tabulation below, which presents the mean weights in relation to the initial weight (= 1) of the young of both species.

Age (in days)	0	3	5	9
Dunlin	1	1.3	1.9	3.2
Red-necked Phalarope	1	1.8	2.6	4.7

No observations of the age at which young are capable of flying have been made, because of their very secretive behaviour. According to HÖHN (1965), young of the Red-necked Phalarope fly in about 20 days. Curiously enough, no young of this age have been seen at Norrskär, even though many of them returned to the area the following years.

7.2. *Parental care.* The male broods its newly-hatched young at short intervals, and continuously at night from about 21 to 03 hrs. More detailed observations could not be made because of difficulties in following the broods in rank vegetation. When 4—5 days old, the young are no longer brooded regularly by day, except during cold and rainy weather. This conclusion is based on observations that beyond that age young are extremely difficult to find, and that the male no longer accompanies its brood on land but begins to feed on nearby water. From this stage onwards, alarm produced by approaching enemies is intense only at night when the male still broods the young; by day the male merely flies a few times around any intruder which approaches the brood and then alights farther off. When the young are about ten days of age, the male gives the alarm only at night; when about two weeks old the young are left completely alone.

In the Grey Phalarope also, young have to care for themselves at an early age and the male usually feeds more than a hundred metres from the brood (BENGTSON 1968). As in the Red-necked Phalarope, the male stops giving alarm calls about one week before the young are able to fly (MANNICHE 1910).

As noted above, several broods of Red-necked Phalaropes often keep close to each other, so that groups of several males showing alarm behaviour are often seen. The same has been reported by

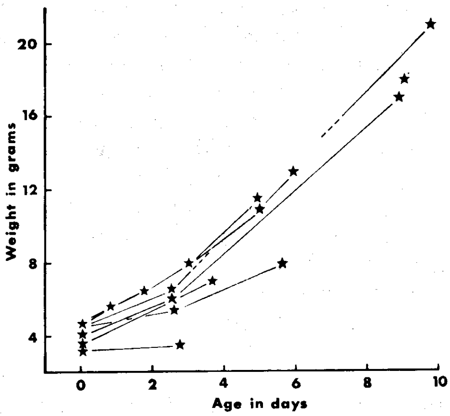

FIG. 11. Development of body weight in eight Red-necked Phalarope young during the first 10 days of life.

SALOMONSEN (1950) and, for Wilson's Phalarope, by JOHNS (1969). On one occasion we were able to establish that a single male brooded young belonging to two broods (in the presence of the second male), but probably this kind of social care of young occurs more commonly, as in the Dunlin (SOIKKELI 1967). It is also possible that a male which has lost its own brood adopts foreign young. In Wilson's Phalarope, this has been recorded in captivity: downy young taken to the laboratory were brooded by a male which was not their father but which had young of the same age when it was captured (HÖHN 1967). Adoption of young is known to occur occasionally in Dunlin (SOIKKELI 1967), and is reported in the Kentish Plover (RITTINGHAUS 1961), Ringed Plover (S. Vuolanto, unpubl.) and Dotterel (PULLIAINEN 1970). Presumably both brooding and adoption of strange young, which increases breeding success, occur commonly among waders, especially in species which nest in semi-colonies.

In about half the occasions recorded in 1966—1970, the female as well as the male was seen to show alarm near the nest at the time of hatching. Of six individually marked females showing this behaviour, four had laid the clutch in question, while two others were foreign. On two occasions two, and once even four, females were observed close to a nest at the time of hatching, all of them calling anxiously. TINBERGEN (1935) and HÖHN (1968) also mention observations of females showing alarm while accompanying broods. This situation gives the impression that both male and female tend the young. This is in fact the opinion of some authors (COLE 1943, HAFTORN 1957; see also records cited by HÖHN 1965). However, careful observations of the birds' behaviour require a different interpretation. When alarmed the male tries vigorously to drive away the female, pursuing and attacking her persistently. If a person is standing by a newly-hatched brood which is apparently tended by both parents, the male finally spends more time chasing the female than giving alarm calls around the observer! The female yields to the attacks of the male, and may even hide herself in a juniper shrub for a while, but returns over and over again to the brood. On one occasion, the female accompanied the brood for two days, and when attacked by the male, she performed courtship nesting. On another occasion, four females which were gathered around a newly-hatched brood tried to invite the male to copulate with them; after a while, the male in fact copulated briefly with one of the females. The behaviour of the male, female and young were watched also in situations in which the parent birds no longer showed alarm at the presence of an observer. In such cases, the female never participated in brooding the young, although she often walked quite close to them.

These observations show clearly that females accompanying newly-hatched broods are interested not in the young, but solely in the male. At the time of hatching, many females still exhibit sexual activity. This is shown, for instance, in regular remating with males which have lost their clutches as late as the end of June (see p. 70). This sexual activity continually seeks ways in which to be fulfilled. A male which has lost its nest is a biologically valuable object of this drive. But, additionally, males which at the time of hatching of their young behave conspicuously and call anxiously (in contrast to their skulking and indifferent behaviour during incubation) may attract females intent on pairing, which leads to the peculiar behaviour described above. This may thus be considered as misdirected instinctive behaviour, lacking biological significance. — In 1971—72 when non-breeding males were present throughout the breeding season, this type of behaviour by females was not recorded.

Similar behaviour of females towards males tending young may occur in the other Phalarope species, too. Thus among the Grey Phalaropes studied by BENGTSON (1968) on Spitzbergen, females were often seen courting males attending broods but they never took care of the young; if a strange female approached the young, the male drove her away rather abruptly. Observations of both parents attending the brood, reported in literature (see HÖHN 1965), very probably refer to similar cases. In Wilson's Phalarope, males tending young are joined occasionally by females (JOHNS 1969).

8. Onset of the postnuptial moult

Immediately after the onset of incubation, the red neck patch of some males starts changing to white from both above and below. At the same time the neck begins to look ruffled, and the bird is often seen pecking at it with its bill. As early as 10 June 1966, an unmistakable change in the colouration of male 2 was noticed, and red neck feathers were also found around the nest cup of male 1. In general, a careful search around the nest at the end of incubation often reveals some dropped neck feathers. The moult of males does not, however, proceed farther on the breeding grounds, and many retain their plumage throughout the whole incubation period, especially the palest individuals which from the start look almost like birds in winter plumage (see p. 59).

The start of moult in females seems to be later than in males. We have only one observation of a moulting female at Norrskär: on 10 July 1967 female 2 already had a partly white neck, and the streaks on her back were broader and paler than before, nearly grey instead of rusty brown in colour. All other females maintained their colouring unchanged until their departure.

According to previous records, the postnuptial moult starts on the breeding grounds (SALOMONSEN 1950) or in July (BENT 1927, BANNERMAN 1961, KOZLOVA 1961). Differences between sexes are not reported. KOZLOVA (1961) states that the Red-necked Phalarope has a prolonged moult which is not completed until they reach the wintering grounds, where birds arrive partly in winter plumage.

9. Post-breeding departure

Table 10 summarizes our data on the departures of adult Phalaropes from Norrskär, as well as observations of passage migrants. The females start their southward migration soon after hatching of the first broods, i.e. in the last days of June. By mid-July, when observations were concluded, most females had left the area. The males start their departures within a few days after leaving the brood and thus before the young are able to fly, i.e. approximately two weeks after the females, about 10 July. By mid-July, only a few males have left the island group. Males that have lost their clutch or brood, however, may depart earlier; in 1972, for instance, all males except those tending young had disappeared by 7 July.

There seem to be local differences in the time of departure of females from breeding grounds. Most handbooks, as well as HÖHN (1965) and GABRIELSSON & LINCOLN (1959, according to HÖHN 1971), state that females gather in flocks shortly after incubation has started and leave their breeding grounds soon afterwards. However, according to SALOMONSEN (1950) in Greenland and HÖHN (1968) in Alaska, females do not start to depart until the time of hatching, i.e. at the turn of June—July, which agrees well with our observations. Not a single female disappeared from Norrskär before the first young were hatched. Local

Table 10. Departures of Red-necked Phalaropes from Norrskär in 1966—72: a summary of observations.

Females		
1966:	26 June	♀1 disappeared
1967:	26 June	2 ♀♀ as passage migrants
	28 June	♀1, ♀2 and ♀3 disappeared, the other 3 ♀♀ present to the end of the observation period (15 July)
1969:	29 June	4 ♀♀ departed, 6 ♀♀ still present
	3 July	additional 4 ♀♀ departed, the remaining 2 ♀♀ still present on 10 July when the observation was concluded
1970:	27 June	some ♀♀ disappeared, exact number of those still present impossible to obtain due to the large population
	3 July	2 ♀♀ were seen to migrate SE, about 15 ♀♀ still present
	5 July	5 ♀♀ recorded (= about 15 ♀♀ departed)
	6 July	only 2 ♀♀ left
	8 to 15 July	1 ♀ still present
1971:	2 July	only 2 ♀♀ left (= about 20 departed)
1972:	7 July	all ♀♀ except one disappeared
	11 July	last ♀ seen
Males		
1967:	9 July	♂1 disappeared (young hatched on 24 June)
	10 July	4 ♂♂ as passage migrants
1969:	10 July	all breeding ♂♂ still present on the last observation day
1970:	3 July	♂23 was recorded for the last time (the bird ceased to incubate about 28 June)
	9 July	♂10 departed (two days earlier the bird was still incubating its sterile eggs)
	11 July	♂16, ♂20 and ♂1 departed (young hatched on 1 July, 24 June and 26 June respectively)
1971:	11 June	♂16 disappeared after the destruction of the nest on 10 June
1972:	7 July	only males attending broods left, other ♂♂ departed

variations in the date of departure of females appear to be characteristic of Phalaropes in general. Thus in the Grey Phalarope in Alaska, females usually leave their breeding ground soon after egg-laying (Höhn 1971), but Bengtson (1968) saw females still in the breeding areas in Spitzbergen up to the end of July; Løvenskiold (1964) also reported this from Spitzbergen. In Wilson's Phalarope, females departed earlier from Alberta than from Montana or Washington (Höhn 1967, Johns 1969).

Two main factors may be responsible for these local differences in time of departure of female Phalaropes: (1) the food supply on the breeding grounds and (2) the length of the migratory journey. A limited food supply may cause females to depart early, to move to a more favourable area to build up their fat deposits for migration. An early departure also reduces competition for food with males and young, which may also be of importance. If food is abundant, however, staying at the nesting grounds until the young hatch is probably more advantageous, since some females are able to lay second clutches for males which have lost their nests or arrived late (see p. 70). Longer migratory journeys, on the other hand, associated with later arrival and later onset of egg-laying, may force females to depart at an earlier stage of the breeding cycle from the northernmost breeding areas.

The migration of adult Red-necked Phalaropes is very rapid, as shown by two ringing recoveries. Male 7, which on 15 July 1967 (the last day of observation) was still tending its young at Norrskär, was recovered on 18 August at Odessa, USSR, 2000 km SE (Stén

1969). A female ringed during spring migration, on 28 May 1965, at Valassaaret (30 km NE of Norrskär), was shot in July 1965 at Volgograd, USSR, 1900 km SE (STÉN 1968).

The migration of juvenile Phalaropes takes place later and probably more slowly. This is indicated also by Finnish ringing recoveries. A juvenile, ringed as a nestling in Utsjoki, Finnish Lapland, on 9 July 1957, was shot on 20 September near Saratov, USSR, 2240 km SE (NORDSTRÖM 1959). Another juvenile was ringed as a passage migrant at Tauvo, Finnish west coast, on 11 August 1961, and shot near Leningrad, USSR, on 20 September, 660 km SE (NORDSTRÖM 1963). The great majority of all observations of Red-necked Phalaropes in Finland during autumn migration are made in August and early September (v. HAARTMAN et al. 1963—66), and evidently most of them refer to juvenile birds.

The ringing recoveries quoted above show that the migration of the Finnish population is directed towards the southeast, over the continent of Europe and not along the coasts like the migration of some wader species (cf. HÖHN 1966). The wintering areas are supposed to be in the Arabian Sea (v. HAARTMAN et al. 1963—66).

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Summary

1. The study was carried out in 1966—72 on the west coast of Finland where the southernmost permanent Finnish population of Red-necked Phalaropes (7 to 50 birds annually) breeds. Most adult birds and all young hatched were colour-ringed. Small differences in the plumage were also used for individual identification.

2. The first Phalaropes arrived in the study area each year in the last days of May and the bulk of population soon thereafter, but young birds often appeared through the whole of June. No difference between the sexes was detected in the time of arrival on the breeding island. Almost half the birds were already paired when first observed, and unpaired birds usually formed pair bonds within one or two days.

3. The nests were confined to four main areas, but their distribution varied considerably from year to year, as a result of annual differences in the birds' favoured feeding sites. The nests lay farther from water and on drier ground than in arctic areas, and most were placed in or near colonies of Arctic Terns.

4. Egg-laying commenced each year between 31 May and 6 June, soon after arrival, but there was no clear peak; the last clutches were not laid until the end of June. Old birds which had bred before, nested about one week ahead of first-breeding birds; in pairs consisting of a first-breeding and an older individual, the date of egg-laying was determined mainly by the younger mate. Eggs were laid at a mean interval of 26.5 hours.

5. A female Phalarope may lay two clutches in the same season if (1) a nest is destroyed and the male is able to remate (4 cases observed), or (2) there are excess males in the population (5 cases observed). This "successive polyandry" is of biological value as it increases the reproductive output of the species.

6. The precise onset of breeding is adapted ultimately to the mass emergence of Chironomidae at the turn of May—June. Small annual differences are correlated with differences in temperature: when the daily mean temperature reached about 8°C, egg-laying followed 3—4 days later. The termination of egg-laying may be adaptively correlated with the date of southward migration.

7. Of 71 completed clutches, 70 consisted of 4 and only 1 of 3 eggs. The male starts to incubate with increasing intensity after the laying of the first to third egg. The incubation period is shorter than in other small waders, being 16.8—20.7 (usually 17—18.5) days. It is shorter, on average, towards the end of the season, probably because of the rising air temperature.

8. The young hatch between 22 June—16 July. A newly hatched young bird weighs 3.9 g on average; at the age of 9 days its weight has already increased almost fivefold. Some broods move more than several hundred metres a day, others keep within a restricted area throughout their development; never have young been recorded swimming. During the first days of life they are continuously tended by the male, but after 4—5 days it begins to feed at or on nearby water and broods the young only at night; when about two weeks old the young are left alone. Not only the male but also the female may show alarm behaviour near the brood, but observations show that she is interested not in the young but solely in the male.

9. As soon as incubation has commenced, some males start to moult their neck feathers, but the moult does not proceed farther on the breeding grounds. Only one moulting female was observed in the study area.

10. The departure of females started in the last days of June, soon after hatching of the first broods, and by mid-July most females had left the area. Males departed later, within a few days of leaving the brood, the first about 10 July. Local variations in the date of departure of females may be due to (1) the food supply on the breeding grounds, and (2) the length of the migratory journey. On the basis of ringing recoveries, Finnish Red-necked Phalaropes are believed to migrate to the southeast over the European continent.

Selostus: **Vesipääskyn *Phalaropus lobatus* pesimäbiologiasta Suomessa.**

1. Tutkimus on suoritettu 1966—72 Merenkurkun eteläreunalla sijaitsevalla Norrskärin saarella, jolla pesii Suomen eteläisin pysyvä vesipääskykanta (vuosittain 7—50 yks.). Pääosa emolinnuista ja kaikki poikaset on värirengastettu. Eräät yksilöt on tunnistettu myös yksilöllisten värierojen perusteella.

2. Ensimmäiset vesipääskyt saapuvat Norrskärille täsmällisesti toukokuun loppupäivinä ja kannan pääosa muutaman päivän kuluessa tämän jälkeen, mutta yksittäisiä nuoria lintuja ilmestyy saarelle usein kesäkuun loppuun asti. Sukupuolten välillä ei ole todettu eroa saapumisajoissa. Lähes puolet linnuista on pariutuneita jo saapuessaan, ja pääosa lopuista pariutuu 1—2 päivän kuluessa.

3. Pesät ovat keskittyneet neljälle pääalueelle, mutta niiden sijainti on vaihdellut vuosittain melkoisesti lintujen suosimien ruokailupaikkojen mukaan. Pesäpaikat sijaitsevat kauempana rannasta ja kuivemmilla paikoilla kuin Lapissa, yleensä lapintiirayhdyskunnissa.

4. Muninta on alkanut vuosittain täsmällisesti 31.5.—6.6., hyvin pian saapumisen jälkeen, mutta huippu on epämääräinen ja viimeiset pesyeet on munittu vasta kesäkuun loppupäivinä. Vanhat yksilöt pesivät keskimäärin n. viikkoa aikaisemmin kuin ensi kertaa pesivät linnut; vanhan ja nuoren linnun muodostamissa pareissa pesintäaika määräytyy lähinnä nuoremman mukaan. Muninta tapahtuu keskimäärin 26.5 tunnin välein.

5. Naaras voi munia kaksi pesyettä samana kesänä, jos (1) jokin koiraista menettää pesyeensä ja pariutuu uudelleen (4 tapausta) tai (2) kannassa on ylimääräisiä koiraita (5 tapausta). Tällainen perättäispolyandria lisää tietenkin lajin lisääntymiskykyä.

6. Munintakauden täsmällinen alku on ilmeisesti ajoittunut surviaissääskien massaparveiluun touko—kesäkuun vaihteessa. Pienet vuosittaiset erot johtuvat selvästi eroista lämpötiloissa: kun vuorokauden keskilämpö nousee n. 8 asteeseen, muninta alkaa 3—4 päivän kuluttua. Pesimäkauden päättyminen taas lienee sopeutunut muuttomatkalle lähtöön.

7. Täysilukuisista pesyeistä 70 on ollut nelimunaisia ja vain 1 kolmimunainen. Koiras alkaa hautoa vähittäin 1.—3. munan jälkeen. Hautomisaika on lyhyempi kuin muiden pikkukahlaajien: 16.8—20.7, useimmiten 17—18.5 vrk. Se lyhenee keskimäärin kauden loppua kohden, ilmeisesti ilman lämpenemisen takia.

8. Poikaset kuoriutuvat 22.6—16.7. Vastakuoriutunut poikanen painaa keskimäärin 3.9 g, ja 9 vrk:n iässä sen paino on jo lähes viisinkertaistunut. Eräät poikueet vaeltavat jopa satoja metrejä päivässä, toiset pysyvät suppealla alueella koko kehityksensä ajan; poikasten ei ole koskaan todettu uivan. Koiras kulkee poikastensa kanssa vain 4—5 ensimmäistä päivää ja pysyttelee sen jälkeen päivisin kauempana poikueesta uimassa; se hylkää poikaset n. 2 viikon ikäisinä. Usein on myös varoitteleva naaras nähty poikueen mukana, mutta havaintojen mukaan se on kiinnostunut vain koiraasta eikä poikasista.

9. Heti haudonnan alettua eräiden koiraiden kaulan höyhenys rupeaa vaihtumaan, mut-

ta sulkasato ei edisty pesimäpaikoilla alkua pitemmälle. Naaraista vain yhden sulkasato on todettu alkaneeksi Norrskärillä.

10. Naaraitten poismuutto alkaa ensimmäisten poikueiden kuoriutumisen aikoihin kesäkuun lopulla, ja heinäkuun puoliväliin mennessä useimmat naaraat ovat kadonneet. Koiraat lähtevät myöhemmin, muutaman päivän kuluttua poikueesta erottuaan, ensimmäiset n. 10.7. Alueellisten erojen naaraiden poismuuton ajankohdassa otaksutaan johtuvan (1) ravintotilanteesta pesimäpaikoilla ja (2) muuttomatkan pituudesta. Muutamat rengaslöydöt osoittavat Suomen vesipääskyjen muuttavan Euroopan manteren poikki kaakkoon.

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