

POLYANDRY, REPLACEMENT CLUTCHES,
AND SITE TENACITY IN THE RED PHALAROPE
(*Phalaropus fulicarius*) AT BARROW, ALASKA

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It has been commonly stated that phalaropes have a polyandrous breeding system (Mayr, 1939; Welty, 1962). This has been assumed because all incubation and brood rearing duties are performed by males, potentially freeing females to seek out new mates and lay additional clutches. However, conclusive evidence for polyandry exists only for the Northern Phalarope (*Lobipes lobatus*) (Hildén and Vuolanto, 1972; Raner, 1972). Presently no conclusive evidence exists for polyandry in either the Wilson's Phalarope (*Steganopus tricolor*) or the Red Phalarope (*Phalaropus fulicarius*) (Höhn, 1967, 1971; Johns, 1969; Howe, 1975a; Kistchinski, 1975). Only Hildén and Vuolanto (1972) have published information on site tenacity, philopatry, and replacement laying in Northern Phalaropes. In this paper, we present data on multiple clutches and site tenacity in the Red Phalarope and briefly discuss the relationship of these topics to their social system. Detailed data on the behavior and pair bond of the Red Phalarope will appear in a separate publication.

STUDY AREA

Field work was conducted approximately 4 km south of the Naval Arctic Research Laboratory (NARL) near Barrow, Alaska (71°17'N, 156°47'W). Much of the Barrow area consists of polygonized ground which produces a "fine-grained mosaic" (MacLean, 1973) of dry and flooded terrain. The most productive habitats in this area are the low-lying, moist areas of polygon troughs and wet tundra (Pitelka et al., 1974), and it is in such areas that Red Phalaropes feed, nest, and rear their young.

Since we were interested primarily in conducting intensive behavioral observations, we selected a relatively small area of low-center polygons (0.67 km²) that had supported a moderate concentration of phalarope nests in 1974 (9.0 nests/km²). Even more phalaropes nested here in 1975 (24.0 nests/km²). In addition, we located approximately 90% of all phalarope nests in an adjoining 0.36 km² of marsh. The overall nesting density in 1975 was 44.6 nests/km². Our study area is perennially one of the first low-lying sections near NARL to become free from snow. It lies leeward of a regularly-traveled road. Dust from the road settles on the snow, decreasing albedo, and hastening snow melt.

Ponds dotted our entire study area. Some existed only during spring run-off; others were permanent. Most permanent ponds were less than 100 m². The largest pond covered approximately 5,000 m². All ponds were shallow; maximum pond depth was 19 cm. Phalaropes fed extensively at shallow (1-2 cm) pond edges.

The Barrow vegetation has been described well by Britton (1957). Our study area was comprised largely of sedges, which were short (height: 5-10 cm) and did not hinder our observations.

METHODS

In order to identify the birds associated with each nest, members of a pair were color banded prior to the completion of the clutch. Birds were captured with a 2.4-m diameter hoop, strung with mist netting. Birds were stalked until the hoop could be thrown over them. Red Phalaropes are quite tame and very mobile. Stalking generally required 30 min per bird, although some birds were caught within 10 min and others could never be approached close enough for capture. This technique required considerable caution and patience, but proved effective. The hoop net provides the investigator with mobility, a feature lacking in the horizontal mist net (Johns, 1963). Incubating males were captured with a 25-cm diameter hoop, strung with mist netting and attached to a mouse trap. The trap was designed to capture the bird as it settled on the eggs. Captured birds were banded above the tarsal joint with three plastic colored bands and one aluminum USFWS band, two bands per leg. Nests were located by flushing males from the nest sites and by following incubating males or laying females to the nest.

Observations were made on banded birds, both with and without binoculars. Blinds were not used because the birds were easily observed, without apparent disturbance, at a distance of about 10 m. Behavioral notes were recorded on tape or in field notebooks.

Nelson (1972) has defined a pair bond as "the special relationship between members of a pair which facilitates co-operation in one or more phase of the breeding cycle." The existence of a pair bond between a male and a female is generally inferred from the presence of certain unique behavior patterns between these individuals. For our Red Phalaropes, we used the presence of "pushing" displays (Bengtson, 1968), close association over several days and aggressive behavior patterns oriented towards individuals outside but not within the pair, as confirmation of the existence of a pair bond. Many, but not all, pairs were observed during repeated copulations.

Aerial chases referred to in this paper were similar to those described by Howe (1975b) for Wilson's Phalaropes. We considered aerial chases to be any flight of three or more birds where: (1) both sexes are present and (2) one bird is pursued by the others. The pursued bird may be either male or female. The sex ratio in all aerial chases was recorded. Since these records were made opportunistically, the number of flights observed on different days cannot be compared.

A census plot, 250 × 980 m (24.5 ha), was staked out in prime phalarope habitat within the study area. Perpendicular to the 980 m side, lines were staked at 65 m intervals, the minimum visibility distance in dense fog. Counts were made while walking along these 16 lines. All phalaropes whether flying or on the tundra within 33 m of either side of these lines were counted (except lines 1 and 16, where only one side was included). Birds were identified by sex and breeding status when possible (pairs, singles, incubating males). Except during extremely poor weather, the plot was walked every other day between 1400 and 1700, Alaska Daylight Time.

Counts on this plot began 11 June and ended 4 July. Sex ratio information prior to 11 June comes from field notes from the same area.

Most data presented here were collected from 7 June through 7 July 1975. Information from the summers of 1973 and 1974 is based upon the field notes of Douglas Schamel. J. Peter Myers, University of California at Berkeley, kindly provided sightings of banded phalaropes in 1976.

RESULTS

Polyandry. In 1975, we color banded eight pairs of Red Phalaropes before clutch completion and three pairs after clutch completion. Based upon arrival and laying dates, it would have been impossible for any of these 11 pairs to have completed additional clutches in the Barrow area prior to their capture. Four of the females from these pairs exhibited serial polyandry, each producing clutches for two different males in succession (Fig. 1). Time between the laying of the last egg of the first clutch and the first egg of the second clutch was very short (3-5 days) (Fig. 2). The mean distance between successive nests was 378 m (range: 65-1,080 m). All four of the polyandrous females formed their second pair bonds during a brief period in which unmated males occurred in the local population (Fig. 2). At no time during the egg laying period in 1973 or 1974 did males appear to outnumber females in the study area. In these two years all aerial chases observed contained more females than males. In 1975 we documented the presence of unmated males in our study area by two methods: (1) a direct count of the sexes from transects (Fig. 2) and (2) the sex ratio counts of birds involved in aerial chases (Table 1). The results of these two techniques are complementary. The sex ratio was essentially unity when the birds first arrived. By 10 June, there were more males than females, a situation that persisted until 17 June. Females C, D and E (Fig. 2) deposited the last egg of their first clutch during the early morning hours of 17 June. By that afternoon, the sex ratio was essentially unity (Fig. 2 and Table 1). Only two of these three females obtained second mates. Female C formed her second pair bond, and stopped associating with her first mate, prior to the deposition of the fourth egg of her first clutch. Unfortunately, we do not have comparable observations on Female D or E. The large influx of females in early July corresponds to their postbreeding flocking and departure.

The incubation behavior of the male makes it possible for the female to form a new pair bond before the completion of the first clutch. The male increases attentiveness at the nest (lining the nest cup, maintaining the grass canopy over the nest, sitting on the eggs) from the first through the last egg. Incubation may begin after the deposition of the third egg. Two males captured one day prior to clutch completion had fully developed brood patches. Thus, the female is frequently alone just before the completion of the clutch. Mayfield (in prep.) found these same trends in Red Phalaropes on Bathurst Island, Canada. The male beginning

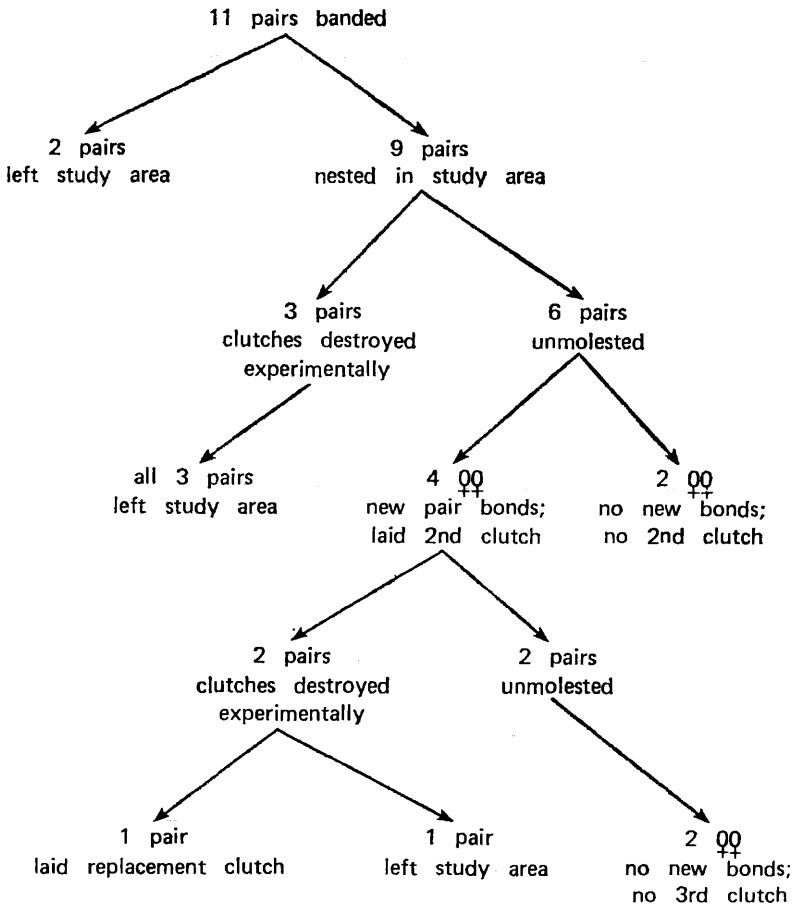


FIGURE 1. Histories of 11 pairs of Red Phalaropes marked prior to or immediately following the completion of the first nest, 1975.

incubation may not be threatened by cuckoldry in the last egg, provided he inseminates the female and maintains the pair bond for at least 4 hr after the laying of the penultimate egg (Lofts and Murton, 1973). However, more data are needed to clarify this topic.

The pair bond may remain intact for a variable amount of time. As described above, a pair may stop associating even before their clutch is complete. However, pairs may associate after clutch completion. Of 40 nests under periodic observation, a minimum of 20 incubating males were observed in pair bond associations with females at least 1 day after clutch completion. Seven of these associations involved females that had produced the clutch, a situation that is probable for the other birds, as well. In only one case (described below) was a male known to associate with a female that had not laid his clutch. Bonds were maintained an

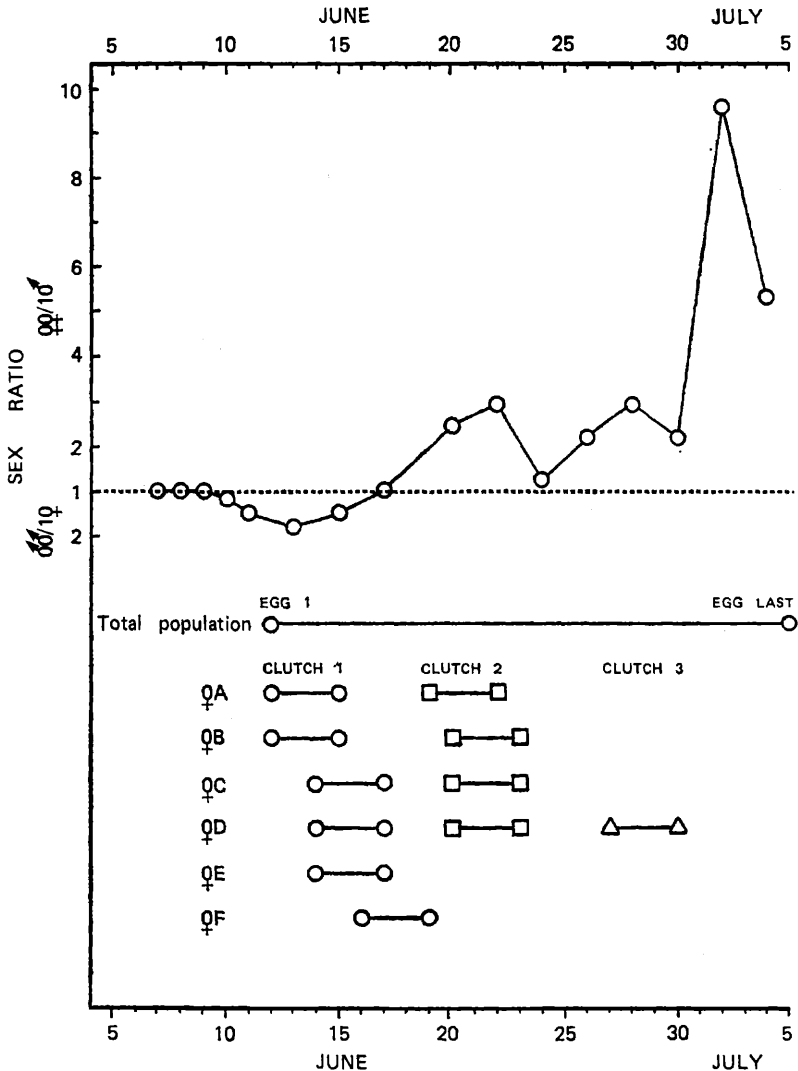


FIGURE 2. The relationship of sex ratios from census transects to the initiation of successive clutches, 1975.

average of 4 days (range: 1-13 days) after clutch completion. During this time, the female remained near the nest, usually within 10-100 m. She joined the male during his frequent feeding bouts away from the nest. Occasional copulations occurred at these times, some at least 3 days after clutch completion. Females were last seen associating with their incubating males on 2 July, which was also the date of the last known nest initiation in our study area.

TABLE 1.
Sex ratios in aerial chases of the Red Phalarope, 1975.

Date	Number of aerial chases having:		
	Extra males	Equal no. both sexes	Extra females
7-9 June	—	—	—
9-11	7	1	1
12-14	16	—	—
15-17	8	—	—
18-20	—	—	5
21-23	—	—	10
24-26	—	—	3
27-29	—	—	6
30-2 July	—	—	9
3-5 July	—	—	—

Although a female may form a pair bond with a second male, this does not necessarily mean that the bond with her first mate is broken. Four days after completing a clutch for her second mate, Female C returned to her first nest. She accompanied this incubating male during his feeding bouts over the next 4 days. Their bond was either still intact or was easily reformed.

Pair bonds may occasionally be broken by intruding females. We witnessed the displacement of Female B from her second mate on 30 June, 7 days after the completion of the clutch. The aggressor was an unbanded female. After displacing Female B, she formed a pair bond (pushing, feeding together, associating; however, no copulations noted) which did not lead to a clutch of eggs. This female was subsequently captured and banded. She remained paired with the male through 2 July, while he continued to incubate. On 2 July, the male died in a freak accident. The female then left the area. The male had been captured after pairing with Female B and 3.5 days prior to the laying of the first egg of the clutch. At this time, he had no sign of a brood patch. It is unlikely that he had been paired with any female in 1975 prior to pairing with Female B.

Replacement laying. We found evidence suggesting one case of replacement laying in 1975 (Fig. 1). Female D was known to have laid two clutches, one each for two different males. The second clutch was destroyed experimentally within a few hours of its completion. Eight days later the male associated with the destroyed clutch was discovered incubating a four-egg clutch 84 m from the destroyed nest. The male and Female D were still associating as a pair. It is very likely that Female D laid the replacement clutch. The time between the laying of the last egg of the second clutch

and the first egg of the third clutch was not more than four days. If Female D laid all three clutches, she produced 152% of her body weight in eggs in 17 days (clutch 1 = 30.8 g; clutch 2 = 31.8 g; clutch 3 = 31.1 g; pre-laying weight of this female = 68.1 g).

Our first evidence for replacement laying involved a nest-trapped and color banded incubating male in 1973. The same day the male was captured, a lone female was hoop-netted and marked about 80 m from this nest. The incubating male was subsequently seen associating, in an apparent pair bond, with this female during feeding bouts. Four days later, the nest was destroyed by a predator. The two birds remained together and initiated another nest 3 days later, 90 m from the destroyed nest. This nest ultimately contained three eggs, only one of which hatched. One egg was infertile and the other was abandoned, although the embryo was well developed. This female may have produced both clutches for the male or only the second. The important feature, however, is that she replaced a lost clutch for an incubating male.

Site tenacity and philopatry. Red Phalaropes at Barrow showed a low degree of site tenacity (return of adults) and philopatry (return of young). Seven of 90 banded males (7.8%) were seen on the study area in succeeding years (Table 2). One of these males was seen during three summers. Its 1974 nest was 175 m from the 1973 nest site. Although it did not nest on the study area in 1975, this bird was seen paired in mid-June and was found freshly killed

TABLE 2.
Banding and recovery records of adult and young Red Phalaropes.

Age, sex	1974			1975			1976		
	No. return	No. possible ¹	%	No. return	No. possible ¹	%	No. return	No. possible ¹	%
Adult									
Males	2	11	18.1	2	35	5.7	4	44	9.1
Females	—	5	—	—	8	—	—	17	—
Young									
Local chicks	1	38	2.6	—	43	—	—	12	—
Others ²	—	—	—	—	21	—	—	—	—

¹Number of banded birds on study area previous year.

²Young-of-the-year captured after fledging.

(from flying into a power line) in mid-July (J. P. Myers, pers. comm.). In 1975, a second male initiated a nest 197 m from its 1974 nest. Of 30 banded females, none returned to the study area. One chick of 93 banded (1.1%), a male, returned as a yearling. It nested within 110 m of the site where it hatched.

DISCUSSION

A prerequisite for polyandry seems to be the local availability of unmated males (Mayr, 1939). In other documented cases of polyandry in phalaropes (Hildén and Vuolanto, 1972; Raner, 1972), excess males were noted. Excess males were recorded in local populations of polyandrous Spotted Sandpipers (*Actitis macularia*) (Hays, 1972; Oring and Knudson, 1972) and European Dunlins (*Calidris alpina schinzii*) (Soikkeli, 1967). In contrast, studies of breeding Wilson's Phalaropes have reported excess females in the populations (Höhn, 1967; Johns, 1969; Howe, 1975b), and polyandry has not been documented in this species. The sex ratio in Red Phalaropes is not always skewed towards males. Data from 1973 and 1974 at Barrow indicate parity or excess females. Polyandry was not suspected in either of these two years. In all the above cases of polyandry, except Raner (1972), replacement clutches were also found.

One of the contributing features of the "rapid multi-clutch system" (Graul, 1973) of the Red Phalarope is their flexible pair bond. The main function of the pair bond in the Red Phalarope seems to be the procurement of eggs (for the male) or an egg and brood tender (for the female). When unmated males were available, pair bonds were frequently not actively maintained after clutch completion, or even earlier. When single males were not present locally, many females maintained pair bonds with their incubating males for as long as two weeks after the laying of the last egg. Copulations observed after the clutch was completed probably served to maintain the pair bond. Competition for paired males took place, as indicated by extra females in the aerial chases, which were noted through 2 July (Table 1). We observed this competition leading to the formation of a new pair bond only once. However, the importance of this process should not be underestimated. Although this behavior gave no evident benefit to the female in this case, had the male lost his eggs to predation, the new female may well have been able to lay a replacement clutch. Howe (1975b) suggested that the most persistent females in these aerial chases may be the most sexually mature and, thus, most efficient mates. Although he never observed the displacement of a paired female, Howe (1975b) acknowledged its possibility. We found that, when excess males prevailed locally, competition for females occurred in aerial chases (Table 1 and Gillandt, 1974). Competition for mates and maintenance of pair bonds in Red Phalaropes terminated by the end of the nest initiation period.

Brief or variable pair bonds prevail in serially polyandrous shorebirds. Gillandt (1974) and Kistchinski (1975), both of whom suspected polyandry in Red Phalaropes, found the bonds to break after laying was completed. Spotted Sandpipers have brief (Hays, 1972) or unstable (Oring and Knudson, 1972) bonds. Females may begin incubation with the laying of the last egg or may display for several days after clutch completion (Oring and Knudson, 1972). Some female Mountain Plovers (*Eupoda montana*) terminate initial pair bonds when males begin incubation (Graul, 1973). In contrast,

polyandrous European Dunlins do not leave their first mate until the eggs have hatched (Soikkeli, 1967).

Variable pair bonds seem to provide advantages for Red Phalaropes. If unmated males are available after the completion of a clutch, females may be able to attempt an additional clutch. When such males are not available, females may either maintain or terminate their pair bond. Termination is selected for if the probability of finding a new mate is greater than [probability of losing the first clutch to, for example, predation] \times [probability of successful renesting, in the event of the loss of the first clutch]. Otherwise, pair bond maintenance may be most beneficial. Females involved in aerial chases may be late arrivals seeking a mate for their first clutch or birds from the local population or other areas attempting to lay a second or third clutch. Males should generally benefit from pair bond maintenance, unless females attract predators, compete for food or lower male feeding efficiency. However, when more males than females occur locally, unmated males must rely upon the termination of existing pair bonds in order to obtain clutches. The same is true for males that have lost clutches and are no longer paired. These males benefit most, initially, by the termination of pair bonds. After they have formed a pair bond, they benefit most by maintenance, until the female is no longer capable of laying a replacement clutch. Then, initiation of a new pair bond would be most beneficial.

The return rate of adult male Red Phalaropes, although much lower than the other polyandrous and monogamous shorebirds reviewed, shows a tendency for some birds to return each year. The fact that no female Red Phalaropes returned suggests even less site tenacity for them than for males. Isolated populations of Northern Phalaropes (Hildén and Vuolanto, 1972) and Spotted Sandpipers (Hays, 1972; Oring and Knudson, 1972) have shown strong site tenacity (>50% return). Graul (1973) reported that 50% of the male Mountain Plovers returned to his study area. He found that more males than females returned. Soikkeli's (1970) usually monogamous European Dunlins showed a 73% return rate and more than 50% of Holmes' (1971) strictly monogamous Western Sandpipers (*Calidris mauri*) returned to his study area. The return rate of young Red Phalaropes, about one-seventh that of adult males, is comparable to young European Dunlins (Soikkeli, 1970) and Western Sandpipers (Holmes, 1971). The low level of return of Red Phalaropes probably complements the variable mating system of these birds. Instead of being "tied" to an area, they are free to seek the best areas for breeding, an opportunistic adaptation suggested by Pitelka et al. (1974). Those birds returning to the same area to breed are probably able to settle earlier and, potentially, nest earlier, if the habitat is available. This has the advantage of lengthening the potential laying period. The low rate of return suggests that variability in habitat availability is considerable and outweighs the advantages of returning to the same area.

The Red Phalarope provides an excellent example of the transition from monogamy to serial polyandry, as described by Pitelka

et al. (1974) for *Calidris* sandpipers. They predicted that serial polyandry could evolve from either replacement laying in a monogamous species or from female emancipation at the first nest, with a potential opportunity to lay additional clutches. Red Phalaropes appear to go both ways. The female is released from incubation duties but remains with a male unless the opportunity for laying a set of eggs for another male arises.

SUMMARY

Four instances of serial polyandry were documented in a small group of color banded Red Phalaropes near Barrow, Alaska. A prerequisite for polyandry seems to be the local availability of unmated males (Mayr, 1939). All four females formed their second pair bonds during a brief period in which unmated males occurred in the area. Replacement laying was also found and may involve the original and/or new females. One of the contributing features of the "rapid multi-clutch system" (Graul, 1973) of the Red Phalarope is their flexible pair bond. The pair bond may end before clutch completion or persist for nearly two weeks after the laying of the last egg at a nest. The return rate of adult male Red Phalaropes, although much lower than other polyandrous and monogamous shorebirds, shows a tendency for some birds to return each year. These birds provide an example of the transition from monogamy to serial polygamy, as described by Pitelka et al. (1974).

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