

BREEDING BIOLOGY OF THE WILSON'S PHALAROPE IN NORTH DAKOTA

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INTRODUCTION

Recent investigations have increased our knowledge about the breeding biology of the Red Phalarope, *Phalaropus fulicarius*, (Bengtson, 1968; Höhn, 1971; Kistchinski, 1975; Schamel and Tracy, 1977; Mayfield, a,b), the Northern Phalarope, *P. lobatus*, (Höhn, 1968, 1971; Hildén and Vuolanto, 1972; Raner, 1972), and Wilson's Phalarope, *P. tricolor*, (Höhn, 1967; Johns, 1969; Howe, 1975a,b). In particular, sequential polyandry has been documented in the Red Phalarope and Northern Phalarope by field studies of marked individuals (Hildén and Vuolanto, 1972; Raner, 1972; Schamel and Tracy, 1977). Here I present information on Wilson's Phalarope concerning size dimorphism, breeding chronology, relative aggressiveness of the sexes, clutch size, laying behavior, nest distribution, and egg predation. The three species are compared when possible. Although I did not investigate polyandry in Wilson's Phalarope, behavioral similarities with the other phalaropes suggest that some females may also lay eggs in the nests of more than one male.

STUDY AREA AND METHODS

Wilson's Phalaropes were studied from 12 May to 26 June 1975, at the Audubon National Wildlife Refuge, McLean Co., ND. The refuge includes 5,967 ha around Lake Audubon and approximately 190 islands in the lake. Phalaropes nest near sloughs on the mainland and on many of the islands. Cultivated fields, seeded pasture (*Bromus inermis*, *Agropyron* sp., *Poa* sp.) and mixed-grass prairie (mainly *Stipa viridula*, *Koeleria cristata*) surround the lake; the islands are covered by prairie and pasture grasses (see also Stewart and Kantrud, 1972; Whitman and Wali, 1975).

My efforts were concentrated on a 5.2-ha island about 1.4 km from shore (T148N; R82W, Sect. 31). The island has three low hills and several shore areas with cattails (*Typha* sp.) and willows (*Salix interior*) where the phalaropes fed.

Adults of both sexes were caught at feeding areas with a horizontal mist net (Johns, 1963), and on nests with a spring-released trap (Schamel and Tracy, 1977), a drop net (Sowls, 1949), and a flush net (Kagarise, 1978). I captured six females and 17 males, weighed them with a "Pesola" scale (± 0.5 g), and measured their wing length (± 3.0 mm). I marked the birds with "Safflag" wing tags (Cronin and Sherman, 1976; Vehrencamp, 1976), metal leg bands, and either colored plastic or "Safflag" leg bands.

Nests were found by observing males' activities and by walking around the island, flushing birds from their nests. Nests were marked with 0.3 m stakes placed 1–2 m away, and were checked every 1–4 days.

TABLE I.
Phalarope dimorphism in winglength and weight.

	Winglength, mm		Weight, g	
	$\bar{x} \pm SD$ (n)	Male \bar{x} /female \bar{x}	$\bar{x} \pm SD$ (n)	Male \bar{x} /female \bar{x}
Red Phalarope	Male: ¹ 130.6 \pm — ⁷ (55)	¹ 0.94, ⁶ 0.94	¹ 48.9 \pm — (54)	¹ 0.80, ⁴ 0.83, ⁶ 0.86
	⁶ 123.7 \pm — (9)		⁴ 50.8 \pm 4.3 (69)	
Northern Phalarope	Female: ¹ 138.4 \pm — (21)	¹ 0.94, ⁶ 0.94	¹ 60.8 \pm — (19)	¹ 0.80, ⁴ 0.83, ⁶ 0.86
	⁶ 131.2 \pm — (8)		⁴ 61.0 \pm 5.3 (51)	
Wilson's Phalarope	Male: ² 105.1 \pm — (11)	² 0.95, ⁶ 0.98	⁶ 62.2 \pm — (8)	⁶ 0.84
	⁶ 105.5 \pm — (2)		⁶ 35.0 \pm — (2)	
Wilson's Phalarope	Female: ² 110.2 \pm — (11)	² 0.95, ⁶ 0.98	⁶ 41.5 \pm — (2)	⁶ 0.84
	⁶ 108.0 \pm — (2)		⁵ 50.1 \pm 5.2 (100)	
Wilson's Phalarope	Male: ⁵ 121.8 \pm 23.4 (97)	⁵ 0.91, ³ 0.93	³ 51.7 \pm 2.6 (17)	⁵ 0.74, ³ 0.71
	³ 127.2 \pm 2.7 (17)		⁵ 68.0 \pm 8.4 (53)	
Wilson's Phalarope	Female: ⁵ 134.0 \pm 36.4 (50)	⁵ 0.91, ³ 0.93	³ 72.5 \pm 5.5 (5)	⁵ 0.74, ³ 0.71
	³ 137.4 \pm 2.3 (5)			

Data from: ¹ Schamel, unpubl., ² Ridgway, 1919, ³ the present study, ⁴ Kischinski, 1975, ⁵ Höhn, 1967, ⁶ Parmalee et al., 1967. ⁷ a — indicates that standard deviation could not be calculated from the literature source.

RESULTS

A. *Sexual Dimorphism*

Among phalaropes and certain other species in the Charadriiformes (e.g., some calidridine sandpipers, Pitelka et al., 1974), females are larger and heavier than males. The sexual differences were significant in the Wilson's Phalaropes I studied (Table 1, Mann-Whitney U Tests, $P < .05$); however, I could not statistically test data from other sources. In all three species the male/female body weight ratio is less than the male/female winglength ratio, perhaps due to the females' production of eggs, because the birds were weighed during the breeding season (see also Lack, 1968, p. 219).

B. *Chronology of Breeding*

Wilson's Phalaropes on the islands began nesting 1-2 weeks later than those on the mainland (Table 2), possibly because temperatures or food levels were lower on the exposed islands. On the study island, eggs were laid from at least 25 May through 15 June (Fig. 1). Additional data on the timing of reproduction in Red, Northern, and Wilson's phalaropes were provided by Höhn (1967, 1968), Hildén and Vuolanto (1972), Raner (1972), Howe (1975a), Kistchinski (1975) and Mayfield (a,b).

TABLE 2.
Breeding chronology in 1975 for Wilson's Phalaropes on the Audubon National Wildlife Refuge.¹

	Mainland ²	Island
Aerial chases in flocks of 10-15 birds	?-18 May	?-30 May
Copulations	15-23 May	28 May-4 June
Pairs, nests, male distraction displays	15-23 May	24 May-20 June
Large flocks of 15-25 birds	25 May-26 June	none seen

¹ Dates are approximate because observations were not made in both areas every day, nor at the beginning and end of the breeding period. ² After 23 May few observations were made on the mainland.

C. *Social Interactions*

In courting flocks, I saw females defend males by threatening other females; males often repulsed females but rarely other males (see also Höhn, 1971; Howe, 1975a,b). The agonistic behavior I observed was like that Howe (1975b) described, so I will use his terminology. Höhn (1967) and Johns (1969) also discussed courtship among Wilson's Phalaropes.

As pairs began to appear at feeding areas, I observed both males and females threatening conspecifics. For example, on 17 May the male and

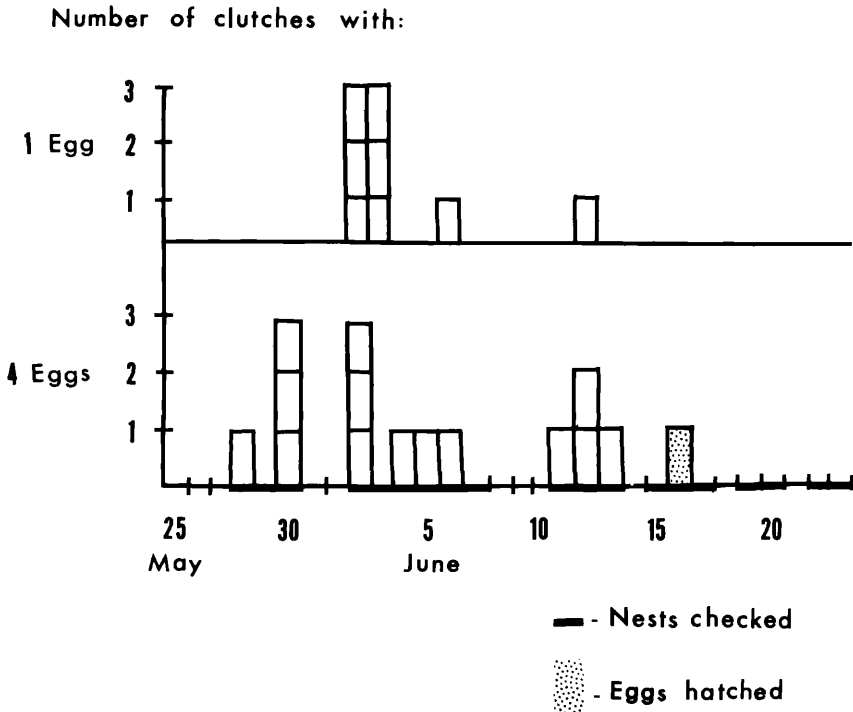


FIGURE 1. Dates on which 23 clutches were found on the study island. The upper graph indicates when eight clutches were begun (date inferred if nest found with 2-3 eggs, assuming one egg laid/day). The lower graph shows when 15 completed clutches were found, initiation date unknown.

female of one pair repeatedly threatened (Head Retracted, Head Forward, and Flying Threats) the male and female of another pair. On 18 May I saw a paired male run and fly after another paired male without obvious interaction between the two females. I watched a fight between two males on 30 May, but did not see its beginning or possible cause. One male struck at another with its wings and bill in midair and on the ground. Howe (1975a) and Höhn (1967) also noted that newly paired males become more aggressive and begin defending their mates against other birds.

Throughout copulation and egg-laying, paired males and females continued to repulse unpaired conspecifics. For example, two different females defended their mates against other females on 5 and 6 June. On 5 June both members of a marked pair known to be laying chased a female that attempted to court the paired male. On 23 May a solitary female approached a copulating pair and was chased by both the male and female; on 28 May only the male of a similarly disturbed pair chased a male intruder. In contrast, Bengtson (1968) suggested that Red Phal-

rope females, but not males, were hostile toward nearby females during precopulatory behavior.

By the time males were incubating, very few threats by paired females occurred (see also Howe, 1975a). However, males now repulsed females that approached or courted them at feeding areas and their nests (see also Höhn, 1967; Howe, 1975a). I observed unmarked, probably incubating males being courted by females in feeding areas; males rejected these attentions with Head Forward and Flying Threats and pecks. Similar female courtship of incubating or brooding males has been reported for the other phalaropes (Tinbergen, 1935; Bengtson, 1968; Hildén and Vuolanto, 1972; Kistchinski, 1975; Schamel and Tracy, 1977; Mayfield, a,b).

D. Clutch Size, Interval between Eggs, and Post-laying Behavior

Clutch size.—Eighteen of the 19 complete nests (i.e., receiving no additional eggs) contained four eggs. In two of these 18 nests, one egg had been removed and partially consumed about 1 m away; single eggs disappeared from two other nests during incubation. Such partial predation may account for the occasional 1–3 egg clutches reported previously (Bent, 1927; Höhn, 1967, 1968; Hildén and Vuolanto, 1972; Kistchinski, 1975; Mayfield, a,b). Consistently smaller clutches occur in arctic tundra regions or during particularly harsh summers in the Red Phalarope (Kistchinski, 1975).

A Wilson's Phalarope nest with eight eggs was found outside the study area on 12 June. A male flushed from the area but it may not have been his nest. Based on similarities in shape, color, and length, four eggs appeared to have been laid by one female and four by another. However, I did not investigate egg variability within clutches and cannot be certain that one female did not lay all eight eggs. Occasional nests with more than four eggs have been reported for phalaropes (Bent, 1927; Congreve and Freme, 1930; Hildén and Vuolanto, 1972; Kistchinski, 1975; Mayfield, b). These nests suggest either simultaneous polygyny, the sharing of a single nest by multiple pairs, or nest parasitism.

Laying interval.—One marked female laid her third and fourth eggs between 1000 and 1100 on two consecutive days, with 24.4–24.8 hr between eggs. This female and another laying her first egg were on the nest a mean of 24 min (range = 10–32 min, maximum values because the actual moment of laying was not known). Previously reported mean intervals between consecutive eggs for Northern, Red, and Wilson's phalaropes are: 26.5 hr ($n = 11$, Hildén and Vuolanto, 1972), 23.4 hr ($n = 18$, Mayfield a, b), and 26.4 hr ($n = 3$, Howe, 1975a), respectively. In the latter two studies, females were on nests a mean of 14.2 min ($n = 5$) and 13.8 min ($n = 5$), respectively, while laying.

Post-laying behavior.—I did not make frequent observations of pairs at nests, but did watch an unusual interaction between one male and female. The female had laid her fourth egg 7 min previously,

and both birds were within 1 m of the nest. The female walked through and around the nest, giving barely audible calls. When the male approached, the female walked toward him and then returned to the nest. The male went into the nest, remained there for several seconds, and both then flew to the shore. This interaction may have related to the beginning of male incubation, which generally commences when the third egg is laid (Howe, 1975a).

On the study island one marked female continued to defend her marked mate with Flying Threats for 1.5 hr after completing the clutch. I saw the pair together twice the next day, once feeding and once walking in the grass near their nest, but did not see the female thereafter. I could not find any of the other three banded females after their clutches were completed or destroyed by predators. In all three phalarope species most pairs separate after laying and females gradually leave nesting areas to join feeding flocks; only males incubate and later brood the chicks. The length of time females remain near nesting males apparently depends on the species, locality, and availability of unmated males (Höhn, 1967, 1971; Bengtson, 1968; Johns, 1969; Hildén and Vuolanto, 1972; Howe, 1975a; Kistchinski, 1975; Schamel and Tracy, 1977; Mayfield, b).

E. Nest distribution

On the northern part of the island most nests were probably found; the rest of the area was searched less carefully. Nest density on the north lobe (3.5 ha) was 1 nest/0.17 ha. Howe (1975a) reported an average density of only one nesting male Wilson's Phalarope per 14.3 ha in his non-island study site. Comparable data for the other species are: Red Phalarope—1 pair/0.05–1.1 ha (Kistchinski, 1975), 1 pair/2.2–4.2 ha (Schamel and Tracy, 1977), and 1 pair/20.4–62.4 ha (Mayfield, b); Northern Phalarope—1 pair/1.5–9.3 ha (Hildén and Vuolanto, 1972), and 1 pair/0.2–0.3 ha (Kistchinski, 1975). The high density of nests I found may relate to the small area of the study island. However, the island may also have been preferred by phalaropes for some reason, because nests were less numerous on nearby islands of a similar size.

On the northern lobe, most of the 20 nests were clustered in three areas. The mean distance between neighboring nests was 24 m ($n = 20$, range = 7.3–73 m); two nests were only 7 m apart. Kistchinski (1975) reported that most Red Phalarope nests were 40–80 m apart; Mayfield (b) found no nests of the species closer than 35 m. Occasional phalarope nests as close as 2–6 m have been noted (Höhn, 1967, 1971; Parmalee et al., 1967; Hildén and Vuolanto, 1972; Howe, 1975a; Kistchinski, 1975).

F. Egg and Chick Predation

Predation rate.—The survival of 23 Wilson's Phalarope clutches on the island was lower than that reported for other phalaropes. All eggs disappeared from 22 of 23 nests (96%), and only 2 (3%) of 80 eggs laid

eventually hatched. One clutch on another island probably produced chicks because the marked male was still in the area, giving distraction displays (as described by Höhn, 1967) 24 days after I found the nest. At four nests, single eggs disappeared before the remainder of the clutch was destroyed. Except for these partial predations, all eggs were taken, the nest structure was not disturbed, and no shells were left in the area. Four males deserted two or three days after I discovered their nests; all eggs eventually vanished from these nests too.

Earlier reports of nest failure among phalaropes indicate variable clutch survival between areas and years, although none incurred as intense predation as those I observed. Data on the frequency of nest destruction for the three species are: Red Phalarope—0 of 8 to 14 of 18 (78%) (Mayfield, a,b); Northern Phalarope—9 of 11 (81%) (Höhn, 1968), 18 of 56 (32%) (Hildén and Vuolanto, 1972) and 1 of 4 (25%) (Jehl, 1971); Wilson's Phalarope—6 of 7 (85%) (Höhn, 1967).

Potential predators.—Only one predation attempt was observed (on 16 June), when I noticed a male Wilson's Phalarope fluttering and calling around a 0.5 m long Garter Snake (*Thamnophis* sp.) that had a chick in its mouth. The snake dropped the chick at my approach. Garter Snakes also probably preyed on some phalaropes' eggs, leaving an intact nest and no shell fragments. Birds (e.g., perhaps Red-winged Blackbirds, *Agelaius phoeniceus*) may have taken single eggs from nests, as suggested by puncture holes in the shells; avian predators may also consume the eggs of the other phalaropes (Höhn, 1967, 1968; Hildén and Vuolanto, 1972; Kistchinski, 1975; Mayfield, b). Other evidence suggested that small mammals frequented the island and may have destroyed some Wilson's Phalarope nests. At least one Canada Goose (*Branta canadensis*) and four duck nests were also destroyed; usually these nests were ripped apart and smashed shells were scattered around the nest. Such sign is typical of Striped Skunk (*Mephitis mephitis*) and Raccoon (*Procyon lotor*) predation (Rearden, 1951). I found Raccoon fur near one duck nest, and a track of a skunk or Badger (*Taxidea taxus*) along the shore.

Factors related to intense predation.—Two factors may have caused the intense egg predation on the study island. First, Wilson's Phalarope nests were dense compared to breeding conditions in other studies. Tinbergen et al. (1967) showed that experimental plots of "crowded" camouflaged eggs incurred a higher loss from crow predation than less crowded plots. Pitelka et al. (1974) also suggested that calidrine sandpipers with "clumped dispersion patterns" and high nesting densities suffer greater nest losses than more isolated species. The large number of nesting pairs and the discrete area to be searched may have made the small island especially attractive to predators. Second, my activities could have attracted predators to nests (but see Willis, 1973; Anderson and Storer, 1976). Birds and diurnal mammals may have found nests when I flushed males and females, or I may have disturbed the nests' camouflaging vegetation while trapping. Nocturnal mammals may have followed my trails to nests.

Behavior of pairs after nest predation or desertion.—None of the 16 males and four females marked on the island were seen after their clutches were destroyed by predators. From 17 to 23 June I searched about 100 other islands within 3 km of the study island but could not locate any marked birds; perhaps they left the lake and joined flocks on the mainland.

One male whose nest was accidentally stepped on was seen feeding on the island almost two weeks later; he ran at an approaching female and then continued feeding. Another male deserted his nest after being trapped and did not flush or give distraction displays (see Höhn, 1967) in its vicinity. He was seen feeding and flying overhead for the next week and then disappeared. A second deserting male may have renested on the south lobe of the island. This marked male was found a week after deserting, giving distraction displays and chasing courting females as if he were incubating. Although he remained there for at least another week, I could not find his nest.

DISCUSSION

My observations and those of Howe (1975a,b) indicate that female Wilson's Phalaropes are more aggressive than males during courtship, while males become more defensive during egg-laying and incubation. Although certain physiological factors suggested by Howe (1975a) may mediate the level of female aggression, they cannot account for the evolution of the change or explain why males become more aggressive. I suggest that changes in relative aggressiveness are responses to different selective pressures on males and females.

Females apparently compete for males in courting flocks and continue defending their mates during copulation and egg-laying. Most females do not associate with their mates after completing clutches; however, Schamel and Tracy (1977) found that some female Red Phalaropes remain paired and may produce replacement clutches under certain conditions. Unpaired females compete with paired females for this opportunity.

A male's "coyness" during courtship may reflect his selection of a superior mate or rejection of all females until conditions are most suitable for nesting. After pairing, males would gain by chasing unpaired males from their female's vicinity if intruders try to mate with the female. I did not see marked, paired birds copulating with unpaired birds, but Congreve and Freme (1930), Tinbergen (1935), Höhn (1968, 1971) and Johns (1969) observed occasional, apparently promiscuous matings among unmarked phalaropes. Also, incubating or brooding males may repulse late-courting females because they interfere with incubation (see also Graul, 1973). Such females may be seeking potential mates, that is, males that will either leave their clutches (see also Parmalee and Payne, 1973), or that have recently lost their clutches (Hildén and Vuolanto, 1972; Schamel and Tracy, 1977). Finally, incubating males may defend their clutches against other females attempting to lay in their nests. If

incubating males have not fertilized the additional eggs, they should be selected to defend against females that try to parasitize their parental care. Reports of 5–8 egg clutches might indicate that parasitism occasionally occurs.

The similarity of size, color, and behavioral dimorphisms among the phalaropes suggests that, like Red and Northern phalaropes, Wilson's Phalaropes are facultatively polyandrous. Polyandry has been found among phalaropes when unpaired males were available after first clutches had been laid (Hildén and Vuolanto, 1972; Raner, 1972; Schamel and Tracy, 1977). Also, food and weather conditions probably must remain suitable for later clutches. On the study island, no marked females paired with a second male, although some females may have bred elsewhere after leaving the island. I did not determine if any "extra" males were available but males that had lost clutches were present. Thus, a shortage of males apparently would not have prevented polyandrous matings on the island. However, because nesting occurred 1–2 weeks later on the island, and because destroyed clutches were not replaced, environmental conditions may have made late clutches unfeasible in 1975. Nevertheless, additional studies of Wilson's Phalaropes may document polyandrous matings when unpaired males occur locally and late clutches are likely to survive.

SUMMARY

Nesting Wilson's Phalaropes were studied on an island in Lake Audubon, ND. Adults were caught on their nests, weighed, measured, and marked for field identification. Like Red and Northern phalaropes, Wilson's Phalaropes I measured were dimorphic in weight and wing-length. Males appeared to be more aggressive toward conspecifics of both sexes when paired or incubating than during courtship. Eggs were laid from the end of May through the middle of June; egg deposition on the mainland occurred 1–2 weeks earlier. Complete clutches contained four eggs, except for one eight-egg clutch probably resulting from two females. The density of nests was 1/0.17 ha, high compared to other phalaropes and the Wilson's Phalarope in other places. All eggs disappeared from 22 of 23 nests on the island, probably taken by Garter Snakes, small birds, Raccoons, or skunks. The high nest density, discrete area of the island, and my study techniques may have contributed to the high egg predation. The possible significance of relative male and female aggression, post-laying behavior, and unusually large clutches are discussed.

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