

## FIELD STUDIES OF WILSON'S PHALAROPE

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ONE of the most interesting yet least adequately studied common avian species in the Western Hemisphere is Wilson's Phalarope (*Steganopus tricolor*). Of particular significance is the fact that phalarope females are larger and more colorful than are the males. Also the female courtship behavior is more aggressive, while the relatively drab and retiring male builds the nest (Höhn, 1967), incubates the eggs, and broods the young. Under exceptional circumstances the female may assist in incubation of eggs and care of young (see Cole, 1943; Dixon, 1943). In connection with the reversed parental behavior of phalaropes, the male alone develops the paired incubation patches more typical of brooding females in other species (Bailey, 1952) (Figures 1, 2). As relatively high levels of both prolactin and androgenic hormones are necessary to develop the incubation patch (Johns and Pfeiffer, 1963), overwhelming evidence shows sex reversal to be grounded in the birds' physiology.

A number of papers have been written on phalarope behavior, but until recently no laboratory research has been conducted to determine the possible hormonal causes of these behavioral and physiological peculiarities, nor has any comprehensive paper been published that utilizes a behavioral approach to their study. Since Tinbergen's (1936) detailed paper on the Northern Phalarope (*Lobipes lobatus*) in east Greenland, most published accounts have been terse general statements of a descriptive nature in textbooks and field guides. A recent exception to this is Höhn's (1967) paper, to which the present paper is largely a supplement, which reports many notable field observations on the breeding biology and behavior of Wilson's Phalaropes.

During the springs of 1961 and 1962 I spent several months capturing Wilson's and Northern Phalaropes on the grassy ponds of the National Bison Range and the Nine-Pipe National Wildlife Refuge north of Missoula, Montana for experiments being conducted at the University of Montana (Johns and Pfeiffer, 1963; Johns, 1964). Some ponds were trapped consistently while others nearby were left undisturbed for daily observations and occasional photography. Additional confirmatory observations were made almost daily at undisturbed ponds in Turnbull National Wildlife Refuge near Cheney, Washington, during the springs of 1965, 1966, and 1967. During these months I accumulated data that in some cases support and in others cast doubt on earlier published statements.

As it was important to our research to obtain a large number of phalaropes before they departed for their winter range in South America, we

TABLE 1  
 PHALAROPE SEX RATIOS IN NINE-PIPE AND TURNBULL NATIONAL WILDLIFE REFUGES

	Male	Female	Ratio
27 April-19 May	72	194	0.37 : 1
20 May-31 May	895	1,827	0.49 : 1
1 June-15 June	207	987	0.21 : 1
16 June-30 June	320	181	1.76 : 1

started watching the breeding grounds for them several weeks before the first birds generally arrive. Wilson's Phalaropes usually appear on the breeding grounds of western Montana and eastern Washington during the first week of May. Actual first sightings are 1 May 1961 and 7 May 1962 on Nine-Pipe National Wildlife Refuge in Montana, and 6 May 1965 and 27 April 1966 on Turnbull National Wildlife Refuge in Washington. These earliest arrivals were predominantly females.

In many censuses taken prior to 15 June, females consistently outnumbered the males. After this date the reverse became true (see Table 1). During the first week or two after arrival on the breeding grounds, the relatively high female to male ratio reflects the females earlier arrival. The relative increase in the number of males between 20 and 31 May probably reflects a gradual influx of males from the south. As the males are incubating from 1 to 10 June (nests with eggs are seldom reported before the last week of May), counts show a decrease in their numbers. Finally, during the last half of June, counts show a seeming surplus of males for the first time. This results from the tendency of female phalaropes to gather in essentially unisexual flocks and leave for the wintering grounds while many of the males are still brooding. Clearly extreme caution must be used during the incubation period if any significance is to be attached to observed sex ratios. In spite of the normal bias in sex counts, considerable evidence suggests that female phalaropes do indeed outnumber males (Bent, 1927: 29), although possibly not to the extent indicated by Table 1.

#### MATING RELATIONSHIP

Tied very closely to the question of sex ratio in phalaropes is the question of polyandry. Some authors state categorically that phalarope females commonly practice polyandry (Cruickshank and Cruickshank, 1958: 152; Welty, 1962: 233). Hall (1960: 215) even goes so far as to state in regard to the Wilson's Phalarope that "it is then not uncommon for a female to have two mates and two separate families which are cared for by the humble males." No source or explanation is given for this statement.

In none of my studies have I come across any evidence of polyandry

in Wilson's Phalarope. Actually the usual surplus of females suggests monogamy or polygyny to be the usual relationship. As Mayr (1939) states, polyandry normally indicates a surplus of males, which has not been shown for phalaropes in any published count. It is, of course, possible that spinster colonies exist, and that many of the females seen during the breeding season are actually unmated, but this seems unlikely as dozens of flocked female phalaropes examined during the spring of 1962 all proved to be sexually mature. These birds, sacrificed during the last week of May or the first week of June after most eggs are normally laid, had greatly enlarged ovarian follicles and frequently eggs in the oviducts. If such spinster colonies exist, contrary to the usual situation for bachelor colonies of other avian species, the individuals are sexually mature and must compete actively earlier in the season for the available males. During the early weeks of May one commonly sees a single male actively pursued by several females. Much scuffling occurs among the females for these apparently too few males, which should tend to prevent a female from mating with more than one male. The case against polyandry is further strengthened by Höhn's (1967) observation that ovaries of Wilson's Phalaropes sacrificed early during the breeding season never contain more than four follicles with a greater diameter than 5 mm. This corresponds with the usual single clutch of four eggs and rules out the deposition of more than one clutch per female.

The more probable condition is promiscuity. Tinbergen (1936) states that a Northern Phalarope male will copulate with a second female if one visits him. I have seen incubating male Wilson's Phalaropes fly to nearby open water and copulate with one of the numerous females gathered there, but whether or not these were acts of mated pairs could not be told because none of the females were marked for field identification and I never saw a female visit a male at the nest site. This last tends to substantiate the claim that the female does not normally assist in incubation duties (McIlhenny, 1940; Van Tyne and Berger, 1959: 273).

The aggressive and competitive courtship behavior of female Wilson's Phalaropes on the breeding grounds indicates that pair bonds usually are not yet formed when they arrive. Additional evidence for this is the sex ratios during different parts of the breeding season. Earliest arrivals are preponderantly females, as Tinbergen (1958) also noted for the Northern Phalarope. In addition to separate arrival dates, Pitelka (1959) presents evidence that female Northern Phalaropes also leave the breeding grounds earlier than do the males. The earliest male arrivals on the breeding grounds of western Montana and eastern Washington do not yet have incubation patches (Figures 1, 2), which develop only after endogenous levels of prolactin and testosterone are sufficiently high (Johns and Pfeiffer,



Figure 1. Ventral apertia of Wilson's Phalarope male immediately after arrival on the breeding grounds (note the dark down feathers between the contour feathers which have been pushed aside to show the area where the incubation patches will develop later).

1963). Although spermatogenesis is already in progress on arrival, probably endogenous male sex hormone titers are not yet high because increased vascularity of the incubation patch is not yet apparent, nor is courtship response behavior as readily elicited by the female.

Courtship activity by both male and female phalaropes seems essentially under the control of androgenic hormones as it is in other birds (Noble



Figure 2. Incubation patches on male Wilson's Phalarope at the height of the breeding season (mean dimension at this time is  $44 \times 15$  mm).

and Wurm, 1940). Dyrenfurth and Höhn (1963) have shown these hormones to be in higher concentration in female phalaropes than in males, which probably causes the female to be the more active in courtship. The evidence contradicts Lack's (1940) statement that Wilson's Phalaropes usually pair while still in migratory flocks enroute to the breeding grounds. While Höhn (1967) is probably correct that pairing occurs both enroute to and after arrival on the breeding grounds, my studies show that most Wilson's Phalaropes arrive on the breeding grounds unmated, and that mating usually occurs between the 1st and 20th of May.

#### COURTSHIP BEHAVIOR

Immediately after arrival courtship behavior increases gradually in intensity for a week or two, reaching a peak about mid-May. At this time it is common to see solitary males swimming nervously along the edges of grassy ponds pursued by several females. Often one female seems to be dominant or to have already formed a pair bond with the male. This female usually follows the male more closely and manages to stay between him and the other females. Occasionally, if another female approaches too closely, the dominant female attacks and drives her away. The winner then remains in Höhn's (1967) "head down" posture while uttering twice each second a low-pitched "pittera, pittera, pittera." The male usually watches attentively from several feet away or swims about aimlessly and nervously nearby.

Only once have I seen a male take part in one of these scuffles. I had watched a pair of phalaropes swim back and forth along 300 feet of grassy shoreline for about an hour in the hope that the male would eventually lead me to the nest. Soon a strange female approached too closely and was attacked by the first female. The fighting that followed continued for about 4 minutes with the female participants alternately landing on each other's back to peck furiously at the back of her opponent's head. This fighting occurred in the water and was unusual in that the female being attacked never seemed to offer any defense. Gradually the bottom bird sank lower until only her head and neck appeared stretched above the water. At this stage the lower female flew up to land on the back of her temporarily victorious opponent. The process of alternately landing on one another's back continued for some time, with the male on two different occasions swimming close in to peck furiously and indiscriminately at both females. Höhn (1967) states that actual fighting between females is rare and describes one battle in which the antagonists faced one another in midair while attempting to stab one another with their bills. Although neither combatant visibly appeared to be winning, eventually the less colorful interloping female quit the battle to fly off some 30 feet. At this rela-

tively short distance she was free from the aggressions of the mated female and was once again allowed to follow along discretely (albeit hopefully) in the background. In all respects except duration and intensity of the head pecking, the fighting between these two females appeared superficially similar to normal heterosexual copulation.

Höhn (1967) states that he saw Wilson's Phalaropes copulate only "while standing in shallow water or even on dry land." Probably copulation occurs wherever the participants find themselves at the time of stimulation. Of 53 copulations recorded in my field notes over 5 years, 37 took place while swimming. In these cases the male lit on the swimming female's back and pecked lightly at the top of her head for the 2 to 4 seconds of the act. Head-pecking during copulation apparently does not occur in the Northern Phalarope (Tinbergen, 1936).

#### FEEDING HABITS

Wilson's Phalaropes' usual feeding method is to swim or walk along the shoreline of shallow grassy ponds and pick insects and crustaceans from the surface. On occasion they may reach down into the water as far as the head and neck allow; they appear to be incapable of submerging completely. Sometimes in their progress they make short forays onto shore, where I have seen them pick insect eggs from sedges and grasses and make short hops into the air to catch flying insects.

The unique "spinning" method of feeding so often reported for phalaropes is apparently employed most often in the early morning. Höhn (1967) believes that Wilson's Phalarope spins less often than other phalarope species for he saw it only once in three seasons of study. In my five seasons hardly a day passed that I did not witness spinning, mostly between 05:00 and 07:00. The practice is greatly curtailed later in the day. Often in the early morning 10 to 20 birds of both sexes may be seen turning in tight circles of not more than 8 inches diameter while busily picking the crustaceans and insects their actions bring to the surface.

The spinning is reported to create currents that stir up otherwise motionless and hidden insect larvae. Tinbergen (1936) suggests their spinning occurs only in the morning after a cold night because the aquatic insects are sluggish in the cooler water. Nonetheless I have seen Wilson's Phalaropes spin at all hours of the day, and in deep as well as in shallow water. I have motion pictures of adult phalaropes in captivity walking in circles in shallow pans of warm, clear water containing brine shrimp (*Artemia salinas*) which were clearly visible, and I have photographed 2-day to 4-week-old incubator-hatched Wilson's Phalarope chicks performing the same way on dry ground while feeding on bits of egg yolk (Figure 4). This behavior by incubator-hatched chicks with no previous visual



Figure 3. Incubator-hatched Wilson's Phalarope chick (1 hour old).

contact with other phalaropes confirms Höhn's (1967) suggestion that spinning is an innate behavior. He describes what he calls "spin walking" in captive young that possibly could have learned it from adult birds before capture. Its occurrence in incubator-hatched chicks proves it to be inherent.

#### LAYING AND INCUBATION

The incubator-hatched chicks were part of an experiment to determine whether phalaropes are determinate or indeterminate layers, as well as to



Figure 4. Incubator-hatched (12 gm) Wilson's Phalarope chick 16 days old picking egg yolk from the water after performing the inherent "spinning" movement usually associated with swimming adult birds.

resolve differences of opinion in the literature on the incubation period. On 4 June 1961 at 19:00 I found a Wilson's Phalarope nest with an apparently incomplete clutch of three eggs. The following morning at 06:00 the nest contained four eggs. One of these eggs was then removed carefully without disturbing the nest or nest site. This removal did not stimulate the female to replace the missing egg and normal incubation by the male was soon in progress. A slight modification of this experiment by removing the third egg deposited in another nest was followed by deposition of only one more egg, and a later check showed that the male successfully incubated a clutch of only three eggs. This evidence clearly shows Wilson's Phalarope to be a determinate layer.

The removed eggs in both instances were placed in an incubator at 103°F where they hatched after 16 days. I have recorded for four naturally incubated nests periods ranging from 16 to 21 days, though possibly my daily visits disturbed the male's incubation pattern enough to alter the normal rate of development. Eight other artificially incubated eggs taken from four separate nests before the male began incubation required incubation periods between 15 and 18 days. This is somewhat shorter than the 22 days suggested by Höhn (1967) for Wilson's Phalaropes, and it corresponds more closely to the 15-day incubation period Worth (1940) quotes for the Red Phalarope and the 20-day period Hall (1960) indicates for Northern Phalaropes.

#### PARENTAL CARE

One problem when keeping phalarope chicks in the laboratory is providing enough fresh water for drinking while preventing chicks from dying of heat loss from wet plumage. This I accomplished by filling the water container with small glass marbles; the chicks could drink from between the marbles, and they remained dry when they stumbled and fell on the surface. This appears at first to be an anomalous situation, as the location of typical nest sites suggests that an early ability to swim would be mandatory for phalarope chicks in the wild. Often nests are built on a slightly elevated grassy hummock completely surrounded by water, which the precocial chicks must swim across. Several times I have noted such nests containing a full clutch of eggs one day and nothing but a few shell fragments the following morning. Apparently the brooding male leads his chicks from the nest site to nearby feeding grounds within a few hours after they hatch.

To verify this early ability to swim, I placed incubator-hatched chicks on a large rock entirely surrounded by water. Chicks only 1 hour old (Figure 3) voluntarily waded into the water and swam buoyantly to shore. Feather wetting seemed to cause no undue body heat loss so long as the



chick entered the water purposefully and swam high on the surface. Mortality occurred only when a chick stumbled and fell into the water and wet the upper body surfaces.

While searching phalarope-inhabited meadows for recently hatched chicks often several agitated male birds will circle one almost within arm's length. This is particularly true after most of the males have finished incubating and are still brooding. If one stops moving for a few minutes, the birds will usually soon fly off a short distance. Only occasionally are the males joined by females, and these appear to be little disturbed and soon depart. Probably the males alight some distance from their concealed chicks and slip quietly back to them through the vegetation. This is their usual tactic when returning to the nest. While watching from a blind at the nest I have repeatedly seen undisturbed males fly straight from the nest, but in returning they typically light some 30 feet away and creep stealthily back to the nest under cover of vegetation.

#### LATE SUMMER BEHAVIOR PATTERNS

A peculiar behavior pattern of Wilson Phalaropes late in the breeding season is the swift and erratic flight of small flocks of three to eight females over the breeding grounds while the males are still incubating or brooding. The birds are in such close formation that their wing tips may be heard striking together. Around and around, or back and forth between adjacent ponds, first skimming low over the grass tops, then shooting up quickly to several hundred feet above ground, they fly in this seeming game of chase while first one bird and then another takes over the role of leader. During the entire flight all members keep up a constant call which can be described phonetically as "puttera, puttera, puttera," and can be reasonably duplicated by a low-pitched tongue vibration against the palate while exhaling.

Occasionally these flocks land in water or on dry land to engage in what appears to be halfhearted battle. Infrequently a male bird may join the flight and perform in a similar manner, but always soon loses interest and returns to nesting duties. These strangely competitive flights suggest a possible degree of late summer gonadal recrudescence such as has been found in some other avian species (Marshall, 1952). Whatever its physiological cause, this behavior becomes commoner as summer progresses, until in early July the females begin to leave in small flocks.

The departure from northwestern Montana and northeastern Washington seems to be in small and essentially unisexual flocks. Gradually the number of females on the breeding grounds diminishes until their numbers are exceeded by the males who remain behind to complete their brooding activities. It is of interest that Höhn (1967) reports that in central Al-

berta female phalaropes "leave the nesting areas long before the eggs hatch." The earlier departure of females from Alberta than from Montana or Washington may be related to the greater migratory distance.

After the early departure of most female phalaropes, rather large flocks of drab adult males and juvenile birds of both sexes may be seen feeding on grassy inland ponds. Even these mixed flocks leave the breeding grounds in late summer or early fall while the weather is still dependably warm. A daily search of the ponds of Nine-Pipe National Wildlife Refuge during the late summer of 1962 revealed that the last straggler had left the refuge by 24 August.

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#### SUMMARY

In northwestern Montana and northeastern Washington Wilson's Phalarope females arrive on the breeding grounds before the males and normally outnumber the males. Monogamy or promiscuity is the usual mating relationship.

The female appears to be a determinate layer whose parental obligation ceases with deposition of the usual four eggs in the nest. Copulation is performed most often while afloat with the male perched lightly on the female's back. Light head pecking by the male often accompanies this act. Incubation performed solely by the male requires between 15 and 18 days, exceptionally as long as 21 days. The precocial, nidifugous chicks leave the nest area a few hours after hatching and are able to swim when 1 hour old.

The often reported spinning habit of phalaropes in water, while appearing to be a useful feeding mechanism, is performed under varied conditions and is an inherent behavior pattern displayed by incubator-hatched chicks with no previous contact with adult birds, even in the absence of water deep enough for swimming.

Adult birds display certain behavioral patterns during late summer indicative of the fall gonadal recrudescence observed in some other avian species. This behavior is commoner in females and becomes more apparent just before their essentially unisexual flock departure for the south.

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