OBSERVATIONS ON THE BREEDING BIOLOGY OF WILSON'S PHALAROPE (*STEGANOPUS TRICOLOR*) IN CENTRAL ALBERTA

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Since the publication of Bent's "Life histories of North American shore birds" (1927), only minor references to Wilson's Phalarope have appeared in the periodical literature. Books on the avifaunas of certain states published since then have generally added only distributional information, though Roberts (1932) and Gabrielson and Jewett (1940) give glimpses of its life history and Randall's contribution (1961) on this bird does somewhat more than this.

The study reported here was carried out in the Edmonton district of Alberta, Canada, in the breeding seasons of 1962 to 1964, inclusive, but includes some observations made in the spring of 1963 near Missoula, Montana. It developed from a study of the endocrinology of this species, initiated in 1961, which was expanded to include observations of behavior when I realized the fragmentary state of knowledge of the life history of this species.

Breeding Range and Habitats in Alberta

The A.O.U. Check-list (1957) gives the northern breeding limits of Wilson's Phalarope in this area as central Alberta, citing the localities Belvedere and Rochester; the more northern of these is 60 miles north of Edmonton. Breeding does, however, extend into the Peace River district, where Soper (1949: 247) found downy young near Grande Prairie, a locality 120 miles more northerly that Edmonton. Almost certainly these birds breed still farther north, because Wilson's Phalaropes have been seen in June near the Little Buffalo River in Wood Buffalo Park (Soper, 1942: 55) about 400 miles north of Edmonton.

In Alberta breeding occurs not only in the farming country of the aspen grove parklands, but also on the shores of muskeg lakes in the more northern, mixed forest zone. Here this bird, otherwise typical of the Upper Austral Life Zone, invades the Canadian Zone to some depth.

In both types of country I have found that nesting areas of the phalarope are almost invariably also breeding grounds of the Black Tern (*Chlidonias niger*). The only exception to this was an islet on Lake Miquelon (about 30 miles east of Edmonton) where, in 1964, five phalarope nests were found and where Common Terns (*Sterna hirundo*) also nested. This Black Tern—Wilson's Phalarope association may be due to similar food requirements of these two birds, terns taking insects on the

wing and phalaropes securing the aquatic larval forms of many of the same prey species.

(Lovenskiold [1964: 208] writing of the Red Phalarope in Spitzbergen states that when breeding it often seeks the protection of Arctic Terns [*Sterna paradisaea*], nesting in the middle of or near their breeding colonies, though he also cites circumstantial evidence that terns in one case punctured phalarope eggs. Black Tern colonies are much looser than those of the Arctic Tern so that protection, while it may well be a factor in the Common Tern–Wilson's Phalarope association noted, is probably only a minor factor in the Black Tern–phalarope association. The fact is that Black Terns nest on almost every sizeable slough in the Edmonton district, including those which phalaropes also use. To my mind this argues for common ecological factors such as food and type of cover.)

The breeding habitats are shallow sloughs with a marginal vegetation of grasses and short sedges or portions of lake shore with this type of vegetation. Waters in which a belt of tall cattails or sedges leaves no open grassy margins are not used as breeding areas though the birds may appear on them during the spring migration. (Some features of the breeding colony shown later in Figure 4 may appear to contradict this, but in the "collective feeding" areas shown on this figure the water was very shallow and a number of small weed grown islets were present.)

In dry years the smaller, shallow sloughs may dry out in the spring and become useless for phalaropes. Thus, in the dry summer of 1964, many breeding sites used in previous years held no phalaropes. There was, however, no noticeable reduction in the breeding population of the district, because there was more breeding on the shores of larger and deeper sloughs and lakes than previously. The smaller breeding sloughs are often very close to farms and they may be near highways with heavy traffic. In the farming country the nests sites are in hay meadows or pasture, 50 to 100 yards from the water's edge, or occasionally on islets in lakes, much nearer to open water, among rough grass. The birds breed in small colonies of from two to eight pairs.

Observations During the Breeding Season

Arrival in spring.—Randall (1961: 205), whose experience relates mainly to Alberta, gives the end of April as the time of arrival for western Canada. For the Edmonton district, however, early to mid-May is the period in which most first sightings fall. This is evident from the following first records: (from the diaries of the late W. Rowan) 21 May 1924, 15 May 1925, 7 May 1927, 12 May 1936, 16 May 1939, and 9 May 1940;

TABLE 1

WEIGHTS AND MEASUREMENTS OF ADULT WILSON'S PHALAROPES COLLECTED NEAR EDMONTON, ALBERTA, MAY TO MID-JULY, 1962–64

	Males			*Females*		
Measurement	*N*	*Mean and range*	*Standard error*	*N*	*Mean and range*	*Standard error*
Body weight (g)	100	50.17 (30–64)	0.524	53	68.09 (55–85)[1]	1.160
Length of bill (mm)	94	31.00 (28–34)	0.467	49	33.85 (30–38)	0.224
Length of tarsus (mm)	97	31.54 (28–35)	0.151	50	34.08 (30–38)	0.703
Length of wing (mm)	97	121.8 (115–133)	2.38	50	134.0 (124–143)	5.15

[1] One female weighed only 34 grams.

(personal observations) 19 May 1949, 9 May 1954, 21 May 1956, 18 May 1961, 13 May 1962, 5 May 1963, and 2 May 1964.

Bent (1927: 29) stated that the first arrivals are usually females, followed later by mixed flocks of both sexes. Here, however, both sexes are represented in the first arrivals of the season. This is possibly related to the fact that this area is near the northern limit of the breeding range. On a spring visit to the Missoula district of Montana in 1963 (almost 500 miles farther south), I saw females only on 3 and 4 May; males were not seen until 5 May. On this date they were still greatly outnumbered by females, as they were up to 8 May, when I left Montana. This would suggest that females are the first to migrate northwards but that those continuing toward more northern areas slow down sufficiently so that some of the males catch up with them. In the Edmonton district, also, females at first outnumber males.

The testicular, ovarian, and oviduct cycles.—Figure 1 is a graphic representation of the weights of both testes of 96 male Wilson's Phalaropes collected between the spring arrival and 22 July, 1962 to 1964, inclusive. Table 1 gives body weights and various measurements for these birds. Testicular weights range from a maximum of 350–435 mg, reached by most birds in mid to late May, to a minimum of 3–8 mg in mid-July. Thus at the usual time of arrival of the males in the Edmonton district, the testes are about at their largest. Microscopic sections of some of the testes collected in 1962 indicated spermatogenesis up to the end of May, i.e., during the period when testicular weights are generally 200 mg or higher.

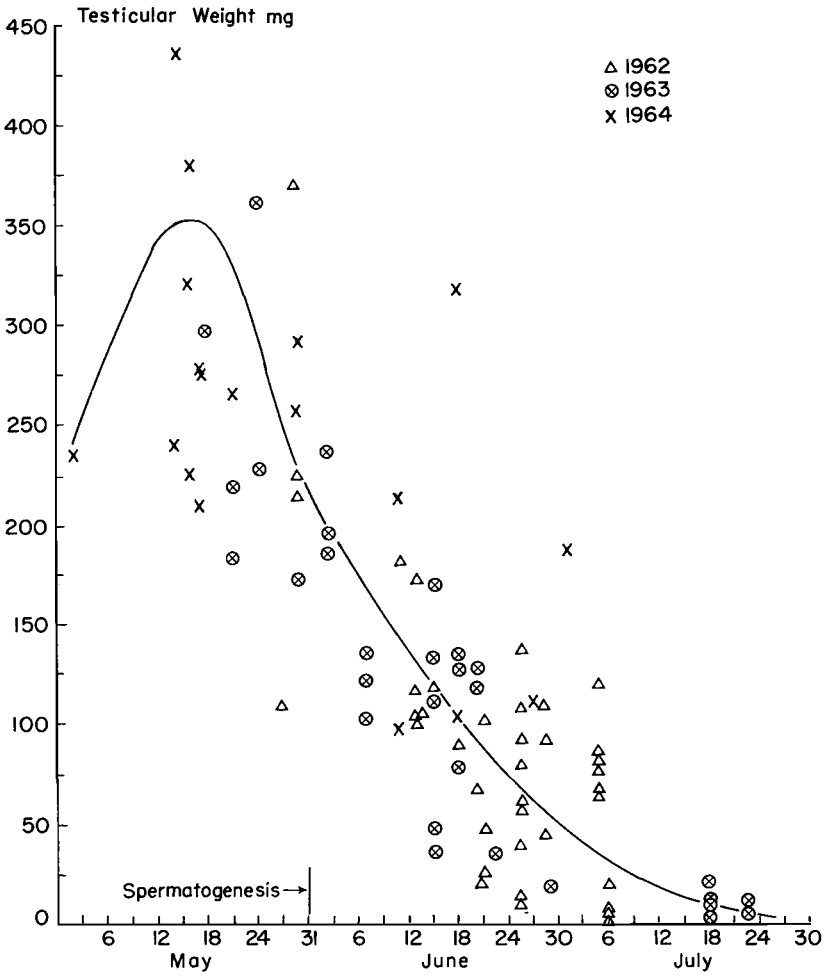

Figure 1. Seasonal cycle of testicular weight for Wilson's Phalaropes in three successive breeding seasons, 1962–64.

Figure 2 shows the weight of the ovary and of the oviduct of 55 female Wilson's Phalaropes collected between the spring arrival and 26 June of the same years (see Table 1 for body weights and measurements). Ovarian weights range from 25–40 mg, very early and late in the breeding season, to almost 5 g when they contain fully enlarged, yolk-filled ova. The weight of the oviduct, which reflects the secretion of estrogens, ranges from 40–60 mg to about 1.6 g (with 4.88 g recorded in one case). Maximal weights were recorded for both structures between 17 and 31 May,

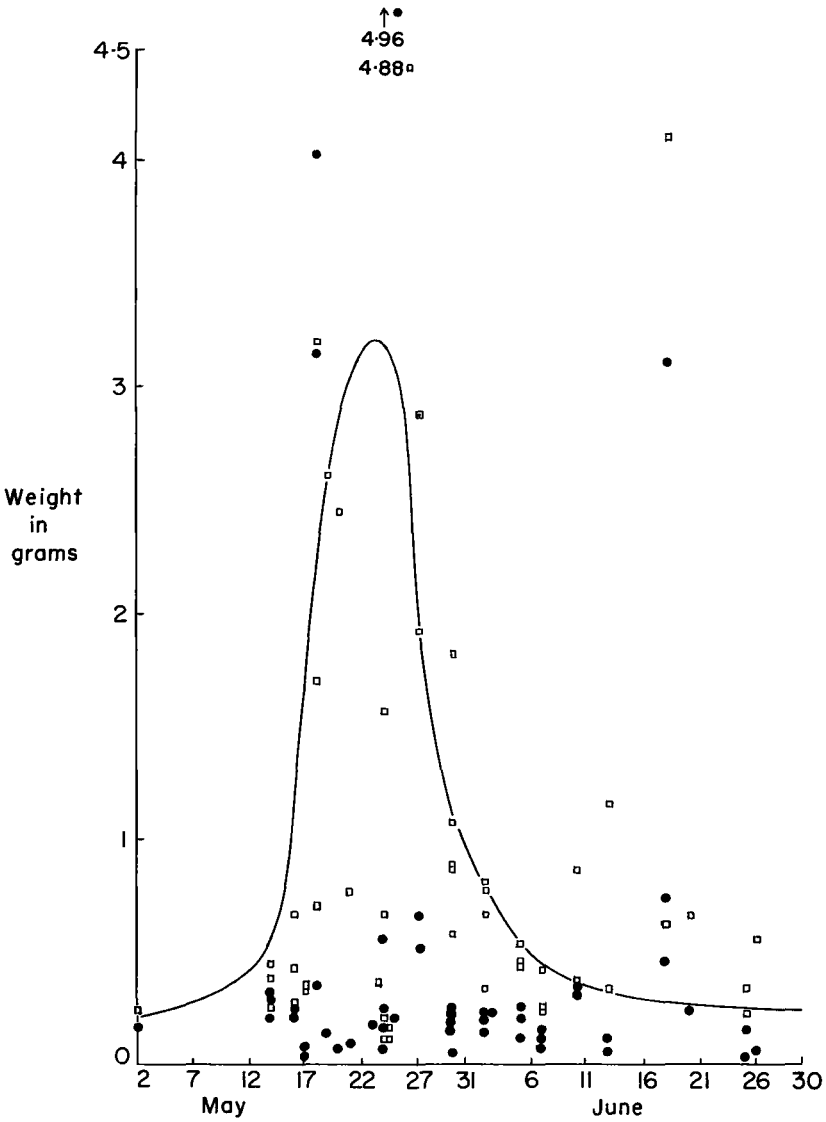

Figure 2. Seasonal cycle of weight of the ovary (black dots) and oviducts (open squares) of Wilson's Phalaropes in three successive breeding seasons, 1962–64. The line represents the weight cycle of the oviduct.

with the exception of one bird which had an enlarged ovary and oviduct on 18 June. Perhaps this represents a second clutch laid in replacement of a lost first clutch. Thus, males appear to arrive with fully activated testes and most females are evidently not yet in laying condition on arrival.

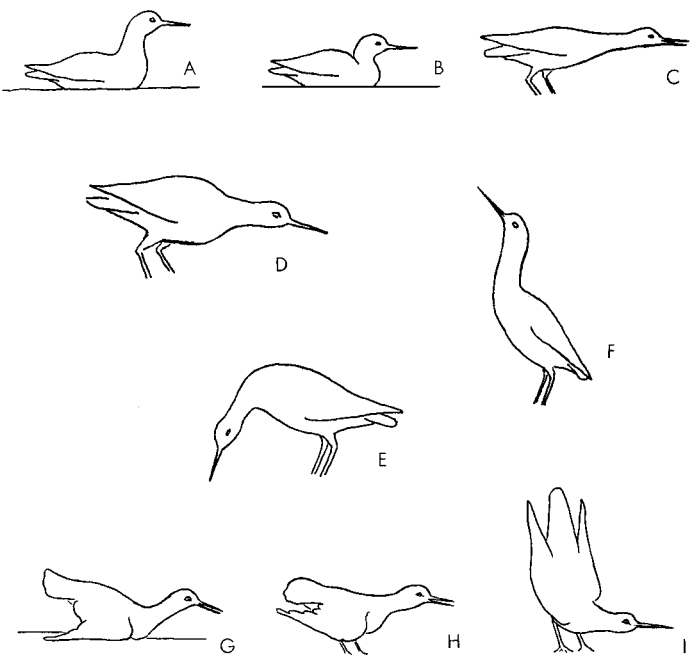

Figure 3. Displays and postures of Wilson's Phalaropes. A, normal swimming posture; B, Head Down threat; C, Head Forward threat; D, Bowing display of female (rarely seen); E, Head Down precopulatory posture; F, Head Up precopulatory posture; G, distraction display of male disturbed from nest; H, usual form of distraction display; I, distraction display of one male with downy young.

Pair formation.—In view of the slightly earlier northward migration of females it is evident that pairing does not take place on the wintering grounds but must occur while the birds are on passage or soon after their arrival on the breeding grounds. Since birds on passage have been observed going through actions interpreted as being likely to lead to pair formation (see below), and since, even in the northern area, small flocks of females with few or no males are seen early in the season, pairing in fact occurs at both periods mentioned.

The observations to be described first were made on 5 May 1963, in Montana, of birds which were probably still on passage since they were seen on a pond which is not a breeding area. Eight females and one male phalarope were swimming on a small reed-fringed pond (see Figure 3, A, for normal swimming posture). One female kept close to the male and whenever another female approached the pair, the first female lowered her head onto her shoulders in what I call the "Head Down" pose (Figure

3, B) and swam "purposefully" toward the intruder. When one to two feet from the intruder, the defending female took wing and flew a very short distance, with her legs dangling, towards the intruding female. This always caused the latter to flush. A very short chase of a few yards followed, and the original female then returned to the immediate vicinity of the male. She was clearly defending the vicinity of the male and not any particular segment of the pond, because the pair gradually moved along the pond while repeated encounters of this nature took place. It also seems evident that the Head Down pose is a threat posture, being preparatory to a forward lunge with the beak, accompanied by a horizontal extension of the neck. When females threaten others while walking they extend the head forwards and may partially open the bill; this I call the "Head Forward" pose (Figure 3, C). I also noticed at least twice that when the defending female referred to above approached the male particularly closely, he chased her for a foot or two, swimming fast and with raised wings. This may indicate that the pair bond between these two birds was still in a formative stage.

I placed a stuffed male and female Wilson's Phalarope on the shore and watched developments through binoculars. One of the unmated females swam towards the mounts, then walked up the shore toward them, and, after going into the Head Forward threat pose, struck the mounted female with her beak. The bird then remained inactive for about 10 minutes and then once more attacked the female mount. After this second attack, it stood with its back to the mount, turned its head over its back, settled the beak among the shoulder feathers, and appeared to go to sleep. This was, however, evidently not true sleep but probably a displacement phenomenon, perhaps due to frustration over the bird's inability to force the immobile female into flight; the bird's nictitating membrane moved repeatedly during this false sleeping. Such pseudo-sleeping has been observed in several other species (Cornwell and Bartonex, 1963). When the mounts were picked up, I found that one glass eye had been dislodged.

Similar episodes in which females repeatedly defended, by threat and short pursuit flights, the vicinity of their males from other females were seen later that season on 21, 23, 25, and 29 May 1963, in Alberta, and in the following spring on 12, 16, 19, 25, 30, and 31 May; an episode of this type observed 25 May 1923 is described by Roberts (1932: 534). Throughout this early phase the males, which later do show occasional aggressive behavior towards other males, act with apparent unconcern and merely occasionally, as noted above, repel a female which tries to get too close to them. One episode of repulsion of a female by a male, observed on 20 May 1964, is worth describing. A male was seen to threaten a

female, causing her to fly away a few feet. Three times subsequently this female tried to approach the male, walking towards him with her head partially lowered towards the shoulders, and each time the male responded with the Head Forward threat at which the female turned and flew a few feet away.

My interpretation of this behavior is that a female will select a certain male, the latter during this phase showing no interest in other birds of either sex but usually busying himself with feeding. The female will keep close to the male selected, turning other females away from him by threats and actual attacks. Though males initially seem at times to "resent" the closeness of the female, they eventually accept her as a companion to whom sexual advances will be directed at a later date. When a pair of phalaropes pass by another pair, the female of the latter may threaten or attack the intruding female but not the strange male. Another observation which emphasizes the active part played by the females in pair formation is that early in the season when a male moves either on foot or on the wing he is always followed by the female but he does not follow her. In 1964, I first recorded a male repeatedly following his female, when both were walking about, on 25 May. Before that it was always the female that followed.

Real fights between females are rare, in contrast to the situation in the Northern Phalarope (*Lobipes lobatus*) which Brandt (1943: 150) described as fighting by the hour (however, in seven weeks of observations of breeding Northern Phalaropes, in 1965, I saw only momentary conflicts). The most definite, but short-lived, fight of female Wilson's Phalaropes I observed took place on 22 May 1963, when a strange female flew in to land beside a pair and immediately attacked the female of the pair. Both females then hovered, facing one another, beak to beak, and appeared to be attempting to stab one another as they fluttered with dangling legs. The intruder very soon desisted and took off.

Only once did I see a female attack another when no male was present and this is also my only observation suggesting territorial behavior in this species. On 23 May 1963, a female occupying a very small pond by herself chased off another female which tried to land on it. Thereupon I placed a stuffed female in this pond but the bird originally present, though it returned and appeared to see the mount, made no gestures directed towards the mount.

There seems to be an epigamic display of females, used in association with pair formation, but I only observed it on two occasions. On 10 June 1963 both members of a pair of phalaropes were feeding as they went wading along a lake shore, gradually approaching another female. After the male had passed the strange female she ran after him and

then postured with the head lowered, the neck extended forward, the chest depressed, and the breast feathers puffed out. The term "Bowing" (Figure 3, D) is suggested for this female display. Only the last two features distinguish this posture from the Head Forward threat. The male took no apparent notice and moved along feeding as he went in a direction which took him close to his mate once more. The second, similar observation was made on 25 May 1964. Both members of a pair of phalaropes were preening when another male walked past. The female several times Bowed at the passing male.

Bowing is possibly the posture referred to by Randall (1961: 205) when he described females, after pursuit flights (see below), as running back and forth before the male with lowered head and outstretched neck. It seems also to have been involved in E. W. Nelson's report (see Bent, 1927: 29) of the only "demonstration" he observed during pairing, which he described as "a kind of solemn bowing of the head and body; but sometimes, with the head lowered and thrust forward, they will run back and forth in front of the object of their regard, or again a pair may often be seen to salute each other by alternately bowing or lowering their heads." This last, alternate bowing, is a behavior I have never seen. Since in these observations females other than the displaying one were also present, I cannot be sure that the bowings described were different from the Head Forward threat display or from the poses which may precede copulation as described below. At any rate, from the rarity of its occurrence in my own observations and from Nelson's remark that he found these phalaropes "very undemonstrative toward each other . . . quite unlike the usual manner among birds" it must be concluded that mating or "epigamic" display, other than that used as an immediate prelude to coitus, is but feebly developed in this species.

Pursuit flights.—During the breeding season one frequently observes flights in which a male phalarope is followed by two or more females. These flights are always initiated by a male taking wing, with his mate or, at any rate, the nearest female following him, to be joined by a varying number of other females. The greatest number of females I have seen following one male in flight is seven. The females follow every twist and turn executed by the male and during these flights the birds (it is impossible to be sure of which sex) at times give their usual nasal call but in a somewhat abbreviated form; very often, however, the whole flight is silent. It usually lasts a few minutes and sometimes takes the birds far enough for one to lose sight of them even with binoculars. A constant feature towards the end of flights is that the male, before landing, slows his wing beats and, with the outer portion of the wing only, executes a rapid, almost quivering, motion; the motion of at least the outer part of

the wings is reminiscent of the normal flight of the Spotted Sandpiper (*Actitis macularia*). On only two occasions was I able to see what took place when the birds landed after a pursuit flight. On the first occasion one of the females at once set about chasing away the others individually. On the other, the male, which had been followed by only two females, was followed by them as he dodged about among the tufts of grass; he was soon out of my sight. It seems that these flights occur only about the time that the males begin incubation. Thus, in 1962, the first pursuit flight was seen on 25 May, while on 4 June, a nest with four eggs was found in the locality. In 1963, I noted these flights at another locality from 22 May onward and the downy young of two broods were found here on 12 June; allowing a 20-day incubation period, laying would have begun about 22 May. In 1964, the only observation of such a flight, on 3 June, was made after egg laying had taken place. Pursuit flights may depend on an excess of females over males in a given locality. In the 1962 and 1964 breeding seasons I recorded pursuit flights only on two days, but, in 1963, when most of my observing was done at a group of pools where seven females and three males (only two of which were later found with young) spent the breeding season, I recorded pursuit flights on six days between 22 May and 4 June. These pursuit flights have also been observed by others, including Randall (1961: 205), Salt and Wilk (1958: 191), C. Grant (cited by Amadon, 1959: 533), P. B. Peabody (cited in Bent, 1927: 29), and by Bent himself.

The quivering of the male's wing tips may be homologous with whirring wing beats described for female Red Phalaropes (*Phalaropus fulicarius*) by Manniche (1910: 153) and Andrew (1955) during actions preceding copulation, and for the Northern Phalarope by Tinbergen (1935: 5, 9) as part of the female's territorial flights and in males when they rise and hover over the female as a prelude to copulation. In Wilson's Phalarope the quivering wing beats do not, however, give rise to any noise.

Precopulatory behavior and copulation.—Since pair formation in Wilson's Phalarope seems to be the result of female initiative and since we tend to believe that in the phalaropes the usual roles of the sexes are largely reversed, it is of interest to determine which sex in fact initiates copulatory activities. In the Red Phalarope there are only two published observations of mating. In Manniche's account (1910: 154) the female was apparently more active during the prelude whereas in the observation by Andrew (1955: 546) mating took place without prelude. In the Northern Phalarope, Tinbergen (1935: 9) described an invitatory pose assumed by the female on the water and, in all his observations of consumated copulations, such were initiated by the female; he also observed attempts at coitus initiated by the male which the female rejected (Tin-

bergen, 1935: 6). Congreve and Freme (1930: 223) have described actual coitus of a male first with one then with another female in this species.

In spite of frequent observations from early morning to evening, during the short period when Wilson's Phalaropes copulate, I cannot with certainty describe a typical action sequence; there was much variability in the actions. One general feature, however, which emerges clearly, is that although Northern Phalaropes copulate while swimming on water, as noted by Tinbergen (1935: 9), Gordon (1921), and B. Hantzsch (cited in Tinbergen, 1935: 9) and in 14 observations of copulation in this species made by myself, Wilson's Phalaropes do so while standing in shallow water or even on dry land. F. Pitelka (pers. comm.) informs me that he has seen many copulations of Red Phalaropes both in water and on land.

(Lovenskiold [1964: 208] states flatly that Red Phalaropes mate on dry land while Northern Phalaropes do so on water.)

The following observations were made in 1963. On 18 May, I suddenly noticed a fluttering among some Wilson's Phalaropes on a lake shore. Binoculars revealed a male standing with raised and fluttering wings on the back of a female who was also standing. Gradually he lowered his tail towards the female's back but jumped off without actually touching the female's body with his own. Even when, for moments, the male's wings were closed, the female supported his weight with apparent ease. Later a male without any other preliminary action raised his wings and started quivering them as if about to hover onto the back of a nearby female which, however, moved aside. On 25 May, a male made several "purposive" runs (without assuming a threat posture) towards a nearby female but the female in each case flushed and fluttered a foot or two out of the way.

On 30 May, I suddenly noticed a male standing rigid in a striking pose with lowered head, the "Head Down" precopulatory posture of Figure 3, E. The female ran to his side; the male tripped about so as to stand just behind the female, raised his wings, and started to flutter them and seemed about to mount while the female lowered her rump. The male, however, did not mount, and the female, after twitching her tail from side to side, moved on. Not long after, a feeding male approached a female and both for some seconds stood in this Head Down pose. The male then raised his head and stood for some moments immobile with a very elongated neck, the "Head Up" pose of Figure 3, F. Then he moved first to the side and then to the rear of the female, raised his wings, fluttered them, and hovered on to her back where, however, he remained only momentarily; both birds resumed feeding after the male dismounted.

In 1964 several relevant observations were made. On 16 May I saw

a pair walking along and feeding in shallow water. The male walked to the side of the female, dipped his bill into the water and drew it back towards himself a few times and, then, in an only partially erect pose, walked around the female which half raised her head and seemed to puff out her neck, somewhat as in the alarm posture which normally precedes taking wing. The male then spread his wings, fluttered them, and hovered onto the back of the female which lowered her body somewhat. The male lowered his rump onto the female's back and for a full 30 seconds made apparent copulatory movements without, however, as far as I could tell, manouvering his tail beneath the female's. The male then hopped off the female's back and the female flew away and was immediately followed by the male.

On the same day I saw a male, which without preliminaries, fluttered his wings and mounted. While the copulation or attempted copulation was in progress another male threatened the pair in the Head Forward pose and was then chased away by the female which had just been mounted.

On 25 May both members of a pair were seen to raise their necks momentarily, whereupon the male started to flutter his wings and actually raised himself above the water; the female approached him, lowered her head somewhat, and puffed out her neck, but the male landed beside, not upon, the female. Once more he went through the same motions whereupon both resumed feeding.

It appears that, whereas the full copulatory sequence includes the preliminary, rigid and apparently ecstatic Head Down and Head Up poses, copulation may start without any specific preliminary action, being simply initiated by the male starting to flutter his wings before raising himself onto the female's back.

Aggressive behavior of males.—A noticeable feature is that, while early in the season male Wilson's Phalaropes show aggressive behavior only towards females in apparent self defense when females press their company too closely upon them, they show apparently unprovoked aggression later in the breeding season. Thus, on 1 June 1964, I saw a male chase away first one then another female and occasionally a male would briefly chase another that approached it "too" closely in feeding. Actual fights between males were, however, never seen and the rare antagonistic actions between males clearly had no territorial significance and seemed to indicate no more than momentary "irritation" at the proximity of another bird. Such encounters were in any case much rarer than threats and chases among females.

Nest building and egg laying.—It was only in 1964 that I was fortunate enough to find three phalarope nests before the clutches were complete. Wilson's Phalaropes are not as tame as the more northern species so that,

TABLE 2
NUMBER OF EGGS IN THREE NESTS IN 1964

	Date							
Nest	*30 May*	*31 May*	*1 June*	*2 June*	*3 June*	*4 June*	*5 June*	*6 June*
A	0	0	1	1	2	3[1]		
B	1	2	2	3	4	4		
C					2	n.o.[2]	n.o.[2]	4

[1] No further eggs were laid at nest A.
[2] No observations made.

unlike observers of the latter, I was unable to watch them nest building. However, from 28 May onwards pairs were seen landing in areas of short grass about 100 yards from the water. Two females were flushed from empty scrapes at two different sites, so presumably two different birds were involved. One was watched returning to the scrape and by the early afternoon of that day the first egg had been laid. On 9 June, three birds, a pair and an extra female, were flushed from the grass near a scrape. One female was particularly "reluctant" to leave, and a new scrape was found where she had hesitated.

The scrapes are simply circular depressions in the ground, quite bare of vegetation. At least the first egg is laid before there is any lining. The above observations suggest that the scrapes are made by the females, though, as recorded by Tinbergen (1935: 10) for the Northern Phalarope, the male may take part in their formation as well. The lining of the nest with dead grass, as a result of which the nest proper is built, is probably done by the male Wilson's Phalarope, as was the case in a pair of Northern Phalaropes observed by Tinbergen (1935: 12) and in the Red Phalarope observed by Manniche (1910: 154) and Brandt (1943: 396). On 2 June 1964, I flushed a male from a nest containing one egg, laid the day before. I found that a small amount of grass lining had been laid in the cup. In another nest the lining was almost complete by the time two eggs had been laid. Bent (1927: 29) stated that he saw a male Wilson's Phalarope building a nest. The average nest is a cupped mass of dead grass, two inches thick. Randall (1961: 205) observed an interesting variant from the normal nest. He found a dozen nests built among dwarf birch in a grassy muskeg inundated by water up to a foot. The nests were on platforms of twigs, dry grass, and moss, built up to a level of six inches above the water.

Wilson's Phalaropes, like the northern species, make several scrapes, selecting one of them in which to lay the eggs. In two of three nests observed in 1964, I found a scrape within six feet of the nest and in the third, two scrapes were found within this distance of the nest. The time

of day of egg laying was ascertained for one egg only, laid on 30 May, sometime between 0900 and 1300 hours. The intervals at which eggs were laid in three nests are summarized in Table 2. In the case of Nest A, an approximate 48-hour interval occurred between the laying of the first and second eggs and, in the case of Nest B, between the second and third eggs. The only comparable observations of phalaropes are those made on one pair of Northern Phalaropes by Tinbergen (1935: 13) where the first three eggs were laid at 24-hour intervals and the last, 24 or 48 hours later (the observer was unable to visit the nest site on the day following the laying of the third egg).

The normal clutch of Wilson's Phalaropes consists of four eggs. Bent (1927: 31) says this species "almost invariably lays four eggs, rarely only three." Randall (1961: 205) found only two sets of three eggs and one set of six eggs which he attributed to two females. In my experience, clutches of three only are not so rare. I have found 3 nests with only three eggs out of a total of 15 nests. Of the sets of three, one was followed through the whole laying period, while the other two were checked repeatedly, and it was ascertained that no further eggs were laid and that the male was, in fact, incubating.

Incubation and hatching.—It is generally accepted that only the male Wilson's Phalarope incubates and develops an incubation patch. In a series of females collected between the spring arrival of the species (early to mid-May) and mid-July, in four successive years, an incubation patch was never found in a female whereas it was present on all males collected after about 1 June. Once the full set of eggs had been laid I only once found a female on the nest, on 11 June, this nest having been incubated since 5 June. Since my notes give no details beyond stating that the bird "feigned injury" it is possible that a slip of the pen was involved in recording the bird's sex.

Distraction display by females disturbed from the nest during the egg-laying period was seen twice. Males disturbed on the nest almost invariably showed a distraction display even when the clutch was not yet complete. The most intense form of it (Figure 3, G) was seen on 4 June 1962, when a male was flushed from four eggs; it ran about 15 yards away from the nest, laid its breast on the ground, and displayed with raised and fanned out tail, while waving its partly extended wings and calling *quaak quaak*. This call is harsher and more querulous than the usual *wa wa* call.

The typical distraction display (Figure 3, H) simply consisted of a fluttering run away from the nest followed by posturing on the ground with outspread tail and wings, accompanied by calls, and never included features which could truly be called injury feigning. The display on the

ground was very soon followed by an "Alarm Flight," the bird flying above the intruder in circles, at times quivering the outer part of the wings as in the pursuit flights. Flying was interrupted by short glides and during these the bird would raise its head slightly and give its *wa wa wa* calls. Distraction displays of females were similar, except that they included false brooding, i.e., sitting down as if on the eggs for a few seconds but at some distance from the nest. In the early stages of incubation the disturbed male was often joined by the female in the Alarm Flight.

Four nests were found in the laying period in 1964; I determined the incubation period for one of them, the others being robbed. In the one nest, two eggs were pipped on the 19th day and all four were hatched 20 days after completion of the clutch. Of two sets of eggs hatched in an incubator, one egg hatched 21 days after the full clutch had been found. Corroborative information is given by the observation made in 1963 that only females collected on 18 and 19 May had shelled eggs in the oviduct and the first young of the season were found, though in another locality, on 12 June. Assuming that the females were mid-way in the laying period when collected, this suggests an incubation of about 22 days. There is no other information on the incubation period of this phalarope. For the Red Phalarope, A. Pedersen, quoted in Salomonsen (1950: 259), gives it as 23–24 days; an observation of it in the Northern Phalarope is 20 days (Brandt, 1943: 399).

(Godfrey [1966] on the authority of D. F. Parmelee gives 20.2 days as the incubation period for Wilson's Phalarope. He also gives new data on the incubation period on the other species of phalaropes.)

A surprisingly large number of nests are robbed, apparently by mammals since in most cases egg shells were found in or near the nest. Of seven clutches of eggs which I was able to follow through the incubation period in 1964, only one set hatched, the other clutches being robbed.

Downy young.—At hatching, the downy young have a whitish egg tooth, raised about one mm above the tip of the beak; it disappears within about 24 hours. In this phalarope I have never observed the female anywhere near the young. In fact, the females leave the nesting areas long before the eggs hatch. The downy young have a simple piping call which may be rendered as a long, drawn-out, disyllabic *peep* or *peeoo*. The male is always in attendance on them and when disturbed with young shows the distraction display and then, calling, flies about over the observer. One male, disturbed from the side of a downy young on 10 July 1964, assumed an extreme posture, standing head and chest down with tail raised in an almost vertical position for a few seconds (Figure 3, I).

Downy young taken to the laboratory were brooded by a captive male which was not their father but did have young of the same age when

captured. The male fluffed out its chest and abdominal feathers, spread his tail, and extended his wings partly but with the terminal portion bent downwards at the wrist joint, and then lowered himself over the young.

For several days after hatching, young were found in the grassy areas in which the nests had been situated and were thus still some distance from the water. One day a male took his young across a road to the nearest large pool in the course of about six hours.

Vocalizations.—The range of the call notes of this species is very limited. The female's usual call, apparently indicating alarm, is a harsh querulous *wa wa wa*, almost always uttered three times as given here. The corresponding call of the male, also uttered three times and most consistently when flying about an intruder near the nest in the Alarm Flight, is slightly deeper in pitch—*woo woo woo*. Pairs feeding together at times utter a more conversational *wook wook*, apparently as a contact call. Also, in the pursuit flights the birds sometimes utter *wook wook* calls. The usual call of males in ground distraction display is *proo proo*, with only two calls being given at a time. When the disturbed male is about to land, presumably near the young, this call changes to the softer *wook wook*, also used in a sequence of two calls only. Adults when uttering a call of any kind noticeably puff out the throat.

Departure of females.—In the Edmonton district, female phalaropes leave the nesting grounds soon after incubation is started. For about a week one may then find small flocks of females only, on the shores of some of the lakes. Thereafter they disappear from the district altogether. They probably do not at first migrate very far, since Bent (1927: 34) says "toward the close of the nesting season the females become very gregarious; as early as June 18, in southern Alberta, we saw them in large flocks."

The evidence for this early departure of females may be summarized as follows. In 1962, on 9 June there were five females and two males at a breeding slough; on 16 June only one female was left, and on 19 June, none. A nest with a full set of eggs had been found here on 4 June. On 25 June there were no females at another breeding site, but six to eight were found at a slough which seemed to be particularly suitable for feeding. On 5 July, only one female was seen at one of several sloughs visited where about 15 males were encountered.

In 1963, on 12 June at a slough which earlier had held seven females and three males, no females were seen; at two other breeding areas visited that day there were no females. Two other breeding sites visited on 15 June held no females. On 16 June, six females were found at a lake. The number was smaller by 19 June, and none were there on 20 June. On that day a gathering of four females with one or two males, with

which they were not apparently paired, was found at another slough. In 1964 my data are not so helpful on this point, since the area at which I did most of my watching was apparently one in which a small premigratory gathering of females took place also. However, no females were seen 16 June, while on 11 June, at another small lake, a typical female gathering of 18 females with but 1 male was seen. It was noticeable, that while phalaropes of both sexes on the breeding grounds were relatively tame, females encountered in the premigratory gatherings were more shy and therefore more difficult to collect than previously.

The early departure of females from the nest grounds appears to apply to phalaropes in general. Thus, Uspenski *et al.* (1962: 78) stated that in Yakutia, Siberia, Red Phalaropes were first seen on 5 June. The southward migration began in mid-June, reaching a peak on 20 June, while the last female was seen on 10 July. For the Northern Phalarope in Alaska, Gabrielson and Lincoln (1959: 421) stated that females are found on the breeding grounds only very rarely after 20 June.

Maintenance Behavior

Spinning.—I agree with Tinbergen (1935: 16) that spinning in this phalarope, as in the northern species, is not related to courtship but is merely a feeding movement. Wilson's Phalaropes spin less often than other phalarope species; they generally feed by wading or, when swimming, merely make pecking or dabbing motions at the water without rotating. During three seasons of observations, I recorded spinning on one day only, in 1964, when several birds engaged in it. In each case the head was lowered and deflected towards the side on which the observed rotation took place.

There is an apparently innate urge to make this type of movement, for, as first observed in 1963 in one individual and in 1964 in several, it was shown by downy, captive young. The birds were fed on minced beef and beetles in a shallow Petri dish approximately 1 cm deep. Before starting to pick up food, the bird would walk into the food dish and then trip about in such a way as to rotate its body around and around while remaining in the same spot. In a bird afloat this would clearly have been true spinning. It would do this "Spin Walking" for about half a minute before actually starting to feed. The movement is thus undoubtedly innate. Dr. E. W. Pfeiffer, of Montana State University, tells me that he has also seen adult captive phalaropes perform such Spin Walking. Whatever may be the purpose of spinning, it was clearly unnecessary in the conditions of laboratory feeding, for food was abundant and easily visible. Spin Walking seems therefore to be an instance of a vacuum activity.

One young bird which I saw Spin Walking almost invariably turned

to the right in its rotations; this suggests the possibility that, in spinning, individual phalaropes might tend to rotate mostly in one direction. As a species, Wilson's Phalaropes certainly rotate in either direction while spinning. In 1964 I paid special attention to possible instances where an individual phalarope changed the direction of its spin. Such a reversal was seen only twice; thus the question of marked individual preferences in spin direction must be considered open.

(See also the observations on spin direction in Red Phalaropes by Cooch [1965].)

The speed of spinning movements, in the few cases I have been able to time, was 46 to 58 complete revolutions per minute, during which 60 dabs per minute were made at the water with the beak. In Northern Phalaropes I have watched spinning I had the impression that the frequency of pecks at the water surface was much higher than in Wilson's Phalaropes.

The purpose of spinning movements has been interpreted as being to stir up edible objects from the bottom of shallow waters or to cause prey, e.g., mosquito larvae, to start swimming movements (Tinbergen, 1935: 15). However, phalaropes have been observed spinning at sea (Witherby *et al.*, 1943: 214) when neither of these factors could be operative. I think a general purpose it may serve is to cause potentially edible objects to move, whether passibely or actively, and thus to become more noticeable. Certainly, disturbed water has an attraction for phalaropes. Bent (1927: 23), citing R. C. Ross, describes how Northern Phalaropes congregated, till they were actually about his feet, around the warden of a gun club who was pulling up water weeds, and how they stayed with him, feeding from the water surface, until he stopped working. Williams (1953) has described a gathering of about 400 Wilson's Phalaropes around feeding American Avocets (*Recurvirostra americana*).

I have never seen Wilson's Phalaropes pursuing insects on the wing though I have seen birds on foot or swimming snap at what was obviously flying prey.

Preening, bathing, and sleeping.—When preening, phalaropes turn the head over the back and touch the area of the oil gland with the bill. The feathers of the rump are fluffed up while the gland area is being touched with the beak; the bill is then rubbed over the breast and shoulder feathers. When head scratching, the head is tilted towards the side being scratched and the foot used was brought up around the bend of the carpal joint of the wing, on all occasions on which I observed this action. This "direct" head scratching (to use the terminology of Simmons, 1964) is of interest since Larson (1957: 96) regards the phalaropes as having been derived from the avocets, while in the method of head

scratching Wilson's Phalaropes resemble other shore birds rather than avocets, stilts, and oyster-catchers.

Bathing is typically performed by standing in shallow water and repeatedly dipping the head, neck, and breast under water; during this the body feathers are fluffed up and the wings are partly extended at the sides of the body. A variant of this procedure which was presumably directed specifically at washing the wing was seen in a female on 4 June 1964. This bird tilted her body so that one wing was uppermost and then after each dip performed vibratory wing movements resembling shivering. She then tilted in the opposite direction so as to bring the other wing uppermost and repeated the process; throughout the tail was fanned.

Like other shore birds, phalaropes occasionally sleep in full daylight, either when standing or afloat. E. W. Pfeiffer has told me that in keeping phalaropes in captivity he found it essential to provide heat by keeping an electric light bulb on in the cages at all times. This made me curious as to whether these birds had some special way of keeping warm at night. On 19 June, I succeeded in finding a female phalarope after dark; it noticed the light of my flashlight before I spotted it, but I found a hummock of mud above the shallow water near the bird and think it probably had been sleeping on this. This does not suggest the use of particularly sheltered sleeping places. Possibly captive birds need extra heat because they feed less continuously than they do in the wild.

COMMENTS

Polyandry in phalaropes.—The suggestion of polyandry in Wilson's Phalaropes seems to have originated with W. L. Dawson (cited in Bent, 1927: 29–30). It was based on observations showing an excess of males over females during incubation. However, this merely reflects the fact that most females have left the nesting area by this time.

Several observations speak against polyandry in phalaropes. First, the early departure of females from the nesting areas hardly gives them time to lay more than one set of eggs. In 1963 and 1964, I noted the number of enlarged ovarian follicles of 46 females; in no case were more than three or four follicles with a diameter of 5 mm or greater found. I did not record the number of collapsed follicles, but the observation indicates the production of only one clutch per bird.

Armstrong (1964) stated that "in most polyandrous species males are believed to outnumber the females." However, in Wilson's Phalaropes, at hatching, the sex ratio is apparently close to 50:50, for in a sample of 22 downy young I found 13 males and 9 females. In the breeding population, before the departure of females, the latter are present in excess (see also

TABLE 3
NUMBER OF MALE AND FEMALE WILSON'S PHALAROPES SEEN BETWEEN SPRING ARRIVAL AND 31 MAY[1]

Year	*Males*	*Females*
1962	16	24
1963	19	22
1964	54	73
Totals	89	119
Percentages	42.3	57.7

[1] Numbers for two areas in which females predominated throughout the period in question, and which are referred to in the text, are excluded from this table.

Bent, 1927: 29). I observed one breeding area where seven females and only three males spent the 1963 breeding season; at another there were seven females and four males in 1964. No breeding site at which males exceeded females was found. Table 3 shows the number of birds of the two sexes observed in three seasons up to 31 May, when incubation was about to begin. This tabulation excludes the occasional flocks of birds probably still on migration in which there was a great preponderance of females, as well as observations at the two areas referred to above which showed an excess of females.

For Northern Phalaropes, Tinbergen (1935: 27) dismissed the evidence for polyandry as being scanty and contradictory; no new evidence supporting its occurrence in this species seems to have been published since then. Brandt (1943: 397) recorded a greater number of ovarian follicles in Red Phalaropes than he found in other shore birds, but this observation is contradicted by Uspenski *et al.* (1962: 78) who stated that the ovaries of all females of this species they dissected indicated that only four eggs had been laid in the preceding breeding season. The extensive unpublished observations of F. Pitelka (pers. comm.) on this species also do not suggest polyandry.

Thus, there is no real evidence indicating polyandry in any of the phalaropes.

Territoriality.—A female Northern Phalarope observed by Tinbergen (1935: 4) had well developed territorial behavior manifested by special "ceremonial flights" over an area which was used both for feeding and later for nesting and by attacks on other females which entered this territory. I have made one observation which I interpreted as showing territorial behavior in females of this species (Höhn, 1958: 98) but in a seven-week period of observations on many pairs of this species in 1965, I saw no further evidence of such. Possibly territorialism in this species occurs only where there are but few suitable feeding areas in a

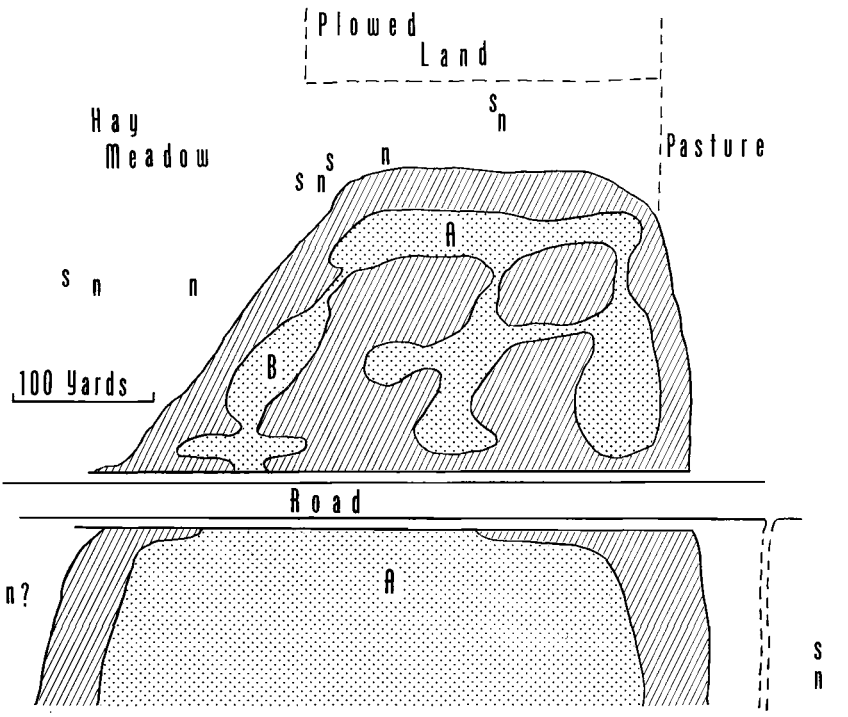

Figure 4. Location of nests (n), nest scrapes (s), and feeding areas at one locality, North Cawes Lake, in 1964. A and B, major and minor collective feeding areas, respectively.

given locality. F. Pitelka (pers. comm.) states that he has not found the Red Phalarope to be territorial.

(Pitelka, however, points out that there are, as in Wilson's Phalarope, elements of behavior which promote scatter of the population but no occupation and defense of an area.)

Wilson's Phalaropes make no special flights over the areas where the nests are eventually placed. At the time of nest selection the birds visit the nesting areas in pairs, rather unobtrusively. The aggressive behavior between females evidently takes place in the area about the male, which moves with him, and not in a specific locality which is defended by the female. The feeding areas are used by the birds of a colony collectively, with much wandering about, so it is evident that no one pair is attached to a particular part of the feeding grounds. Once pairs are formed, aggressive actions between females become less prominent and groups of birds were very often seen peacefully feeding or preening within a few feet

of one another. Thus, there is definitely no division of the feeding areas into territories. The nesting grounds on the grassland are visited by the females for only a relatively short period and, except on the island which held five nests, the nests were too far apart for the birds to manifest aggressive actions if they claim but a small area around the nest. The defense of a small area around nests is not excluded, but I saw no evidence of such. As shown on the map of one colony (Figure 4), there is often a belt of territory between the collective feeding ground and the nesting zone, in which phalaropes do not land.

Endocrine basis of breeding plumages and sexual behavior.—It is well known that in all three species of phalaropes the breeding plumage of the female is more highly colored than that of the male. Also, in Wilson's Phalaropes, females are more aggressive than males and apparently are solely responsible for pair formation although the initiative for copulation may come from either sex. Further, in the only phalarope in which territorial behavior has been reported, the Northern, only the female shows it. Finally, in all species of phalaropes only the males incubate and only they develop brood patches.

Recently Johns (1964) has demonstrated that testosterone, but not estradiol or prolactin, could induce the growth of brilliant new nuptial feathers in Wilson's or Northern phalaropes of either sex, grown in replacement of plucked feathers of the winter or juvenal plumage. Also Höhn and Cheng (1967) found that phalarope ovaries contain an unusually high amount of testosterone (in two out of four samples exceeding the amount found in the testes of male phalaropes) relative to the amount of estradiol. A relatively high secretion of male sex hormone from the ovary therefore seems to be responsible for the more aggressive behavior and brighter plumage of the female in these birds.

Further, Johns and Pfeiffer (1963) showed that brood patches can be induced out of season in Wilson's and Northern phalaropes of either sex by injections of testosterone plus prolactin, but not by estradiol and prolactin. Since analyses show that female phalaropes are not deficient in testosterone production (Höhn and Cheng, 1967), the natural formation of the brood patch in males only requires explanation. This seems to be found in evidence that male phalaropes secrete prolactin (Höhn and Cheng, 1965: 198), while females produce much less of this hormone than the males, or none at all (see also Nicoll *et al.*, 1967).

A possible evolution of the present state of affairs may therefore be envisaged along the following lines. The birds may originally have had a similar, androgen-dependent, breeding plumage in both sexes and, as is the case with some shore birds, both sexes may have incubated. A heredi-

tary deficiency of prolactin secretion appeared in females. Thereafter only males developed brood patches and only they incubated. It is a widespread phenomenon that in sexually dimorphic birds the dull-colored sex is the one that incubates, presumably because of the special exposure of the incubating bird to predators. Selection would thereafter favor dull plumaged males, i.e., those which at the time of the formation of the nuptial plumage were relatively poor androgen secretors. In females, on the other hand, once they had ceased to incubate there was no restraint on androgen production which eventually came to exceed that of males, with the resulting, brighter breeding plumage and greater (androgen-induced) aggressiveness now characteristic of the females of this family.

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SUMMARY

Wilson's Phalaropes were observed in the Edmonton district of Alberta during the breeding seasons of 1962–64. Spring arrival is in early to mid-May. Both sexes are represented in the first sightings of the year but at first females outnumber males.

Pair formation seems to result from a female threatening or attacking other females which approach the male to which she has attached herself. Females defend the vicinity of the male but not a specific area; no evidence of territorial behavior was found. Attacks by females on mounted skins of females occurred. Pursuit flights, in which a male is followed by several females, take place about the time males begin to incubate.

Precopulatory and copulatory behavior are described. Females take part in, or may even be solely responsible for, making the nest scrapes. There is some circumstantial evidence that nest building is done by the males. Extra scrapes were found near several nests. Eggs were laid at 24- or 48-hour intervals. Clutches of only three eggs were found in 3 of 15 nests. The incubation period was 20 days for one nest of four eggs; one incubator-hatched egg required 21 days to hatch. Of seven nests observed in one season, young hatched in only one; the other clutches were robbed, apparently by mammalian predators. The distraction displays of males and females are described.

Females leave the nesting grounds in early June, apparently as soon as the males begin to incubate. The supposed polyandry of this species is dismissed since it is based only on circumstantial evidence which is open

to other interpretations. Evidence is presented that adult females outnumber males in this species.

The testicular, ovarian, and oviduct weight cycles were studied and recent experimental work on the endocrine basis of phalarope nuptial plumages and aggressive behavior of females is summarized.

Walking in circles, or "spin walking," an action which in deep water would manifest itself as spinning, was observed in downy young; this indicates that this action is innate. The number of revolutions and number of pecking movements per minute while spinning were recorded.

Weights and measurements for approximately 100 male and 50 female Wilson's Phalaropes are summarized.

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