SOCIAL INTERACTIONS IN FLOCKS OF COURTING WILSON'S PHALAROPES (*PHALAROPUS TRICOLOR*)

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A remarkable diversity of mating systems and related social behavior patterns is found in the sandpiper family Scolopacidae (including the Phalaropodinae, after Jehl, 1968). Mating systems range from territorial monogamy in the Willet (*Cataptrophorus semipalmatus*) (Vogt 1938), possible polygyny in the Pectoral Sandpiper (*Calidris melanotos*) (Pitelka 1959), polyandry in the Northern Phalarope (*Phalaropus lobatus*) (Raner 1972; Hilden and Vuolanto 1972) to lek promiscuity in the Ruff (*Philomachus pugnax*) (Hogan-Warburg 1966). In such species as the Pectoral Sandpiper (Pitelka 1959) and the White-rumped Sandpiper (*Calidris fuscicollis*) (Parmelee et al. 1968), males play the active role in courtship and only females incubate, whereas the reverse is true in the phalaropes (Tinbergen 1935; Höhn 1967; Bengtson 1968). Between these extremes, other species exhibit varying degrees of role-sharing by the sexes. The strategy of pair formation in a given species probably represents a series of adaptations to a set of social and environmental conditions. Holmes and Pitelka (1966) have presented an ecological classification of social systems in calidridine sandpipers based upon the relative conservatism or opportunism in the manner of environmental exploitation. Their classification attempts to explain in particular the adaptiveness of spacing patterns of individuals during pair formation and the resulting monogamous, polygamous, or promiscuous mating system.

In this paper the social phases of early pair formation in Wilson's Phalarope (*Phalaropus tricolor*) are examined in some detail with a view to interpreting the adaptiveness of the social behavior patterns exhibited. No attempt will be made at this stage to explain the reversal of sex roles, for which this species and its congeners are well known (Bent 1927). A later paper will deal with the interactions of the sexes during the subsequent period of avoidance of conspecifics, during which time the pair bond is completed and nesting initiated. This study follows and supplements

earlier investigations into the breeding biology of Wilson's Phalarope, most notably those of Höhn (1967) and Johns (1969). Names of taxa follow the classification of Jehl (1968).

THE STUDY AREA AND METHODS

This study was conducted near Woodworth, Stutsman County, North Dakota, during April, May, and June 1969 and 1970. Woodworth is situated east of the Missouri River near the eastern border of a moraine known as the Coteau du Missouri. The vegetation of the area consists of native and introduced grasses and forbs characteristic of North American mixed-grass prairie. *Poa* spp, are the dominant grasses, especially in areas where grazing is frequent. Most of the region, including the main study site, is either grazed or under cultivation.

Potholes of various sizes are numerous but many are temporary, spring snow melt being a major factor determining the abundance and depths of water areas in any given year. Most potholes are less than 35 ha, but a few larger lakes up to 1000 ha or more are present. Salinities vary greatly. Some potholes contain fresh water with either cattails (*Typha* spp.) or sedges (*Carex* spp.) as the dominant emergent plants; others are highly alkaline with salt-encrusted shorelines and with bulrushes (*Scirpus* spp.) predominating. Many shallow potholes become completely choked by sedges in late May and June. Stewart and Kantrud (1971) have prepared a detailed classification of pothole types in this region of North Dakota.

The local area where most of my observations were made included several shallow, freshwater potholes and one highly alkaline pond about 800 m long and 80 m wide. This pond was the center of activity for most of the phalarope behavior described in this paper.

All observations were made from an automobile or portable blind. Rapid behavioral sequences were documented verbally on tape. Durations of behavioral events were measured with a stopwatch. Phalaropes were captured with horizontal drop-mist-nets slightly modified after the design of Johns (1963). The traps were placed over the water along shorelines and operated manually from a distance of about 100 ft whenever phalaropes waded or swam beneath. Captured birds were banded with aluminum leg bands provided by the U.S. Fish and Wildlife Service and marked for individual recognition with colored leg bands and paint or dye on various parts of the plumage.

RESULTS

COMPOSITION AND GENERAL BEHAVIOR OF SPRING FLOCKS

The asynchrony of the migratory periods of male and female Wilson's Phalaropes has been

[24]

TABLE 1. Daily totals for each sex in spring flocks (1968).

Date	Number	
	Males	Females
30 April	1	9
2 May	0	150
3 May	1	46
6 May	3	37
9 May	8	16
15 May	13	13
17 May	13	19
19 May	27	30

well documented (Bent 1927; Oring and Davis 1966; Höhn 1967; Johns 1969). The female abundance peak precedes that of males during both northward and southward migrations. The records I obtained for spring birds in central North Dakota conform to the usual pattern (Table 1). During spring migration the birds are highly gregarious, often with the birds 1 m or less apart, and both sexes mix freely. Social facilitation is strong during such activities as feeding, bathing, and preening. Although most feeding occurs while the birds are swimming in open water, exceptionally cold weather may necessitate shoreline feeding, in which case small, stationary territories are defended against conspecifics of either sex. Except in these shore-feeding situations, aggressive interactions related to feeding occur only rarely.

AGONISTIC BEHAVIOR

Courtship behavior is common in spring flocks and two lines of evidence indicate that migrants as well as local residents are involved: (1) courting Wilson's Phalaropes are seen in areas where they are not known to breed; and (2) courting groups larger than the local breeding population are seen in some breeding localities. The most conspicuous feature of these groups is aggression among females in the presence of a male. In the context of pair formation, therefore, hostile interactions among females are a regular occurrence.

Instances of female aggressive behavior in spring groups of Wilson's Phalaropes have been described in part by Höhn (1967), Johns (1969), and others. One female selects a male and defends his mobile position against other females which swim to within about 3 m or otherwise indicate attraction to the male. The defending female usually orients herself away from or oblique to the male at a distance of about 1 m or less and, at the approach of another female, adopts a threat posture, with the neck retracted and bill directed forward or

slightly downward. The back and crown feathers are often elevated, giving the bird a ruffled appearance. The form varies only slightly but since the duration is highly variable, it cannot be considered ritualized in its entirety. Höhn (1971) has called this the Head Retraction threat position and I will refer to it as HRT. HRT by itself is often effective in supplanting other females, particularly if the defending female swims toward another while assuming this posture.

If HRT does not succeed in repelling a subordinate female, the defender may lunge toward her without taking flight. Höhn (1967) has termed this posture with the neck extended horizontally the Head-Forward pose. It may occur on land or on water and is accompanied by running or swimming movements. Since it is clearly a threatening action, I prefer to call it Head-Forward Threat (HFT). In terms of the amount of energy expended, HFT must be considered a higher intensity threat than HRT, which precedes it in all cases. Typically, HFT is given only when the subordinate female, after failing to respond to HRT, approaches within about 1 and 1.5 m of the defender. Both HRT and HFT are illustrated by Höhn (1967:225).

Failure of a subordinate female to retreat from HFT usually causes the defender to fly directly toward her. Although Höhn (1967) did not assign a name to this behavior, it comprises part of a ritualized sequence involving both birds and should be considered a high-intensity threat display. I will refer to it as Flying Threat (FT). As soon as the defending female initiates FT, the threatened bird takes flight directly away from her. The pursuer flies after the other several feet, banks abruptly, and alights on the water; the pursued bird immediately banks in the same direction and also alights. Several nearly identical sequences of this sort may occur in rapid succession. Often FT's follow directly from HRT's and some females may perform FT from a distance of up to 7 m.

Occasionally, an intruding female will not react to FT and an overt attack results, in which the defending female lands on the other's back and pecks at the back of the head as described by Johns (1969). The attacked bird often responds with a similar attack and the two may alternate positions for as long as several minutes before one finally supplants the other. More often, however, the bird beneath tolerates the attack for a short period of time, with the neck extended vertically, and then flies away.

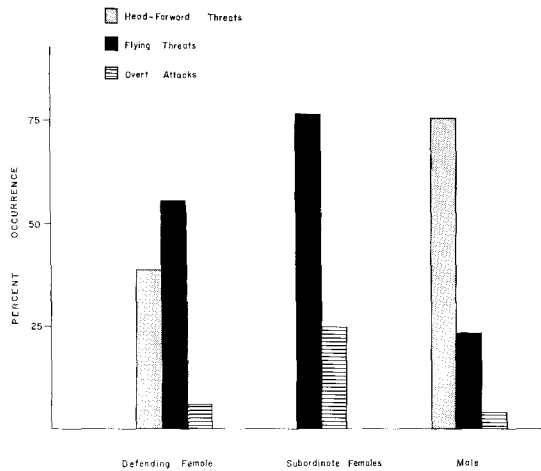Most aggression observed in courting flocks

FIGURE 1. Relative frequencies of Head-Forward Threats, Flying Threats, and Overt Attacks in courting Wilson's Phalaropes.

is among females but males occasionally exhibit aggression toward females (Höhn 1967). The threat and attack postures used by males are identical to those described for females. Aggression by an unpaired male may be elicited by any female that approaches within 2 or 3 ft, especially if she faces him. A female involved in hostile encounters with other females is particularly prone to male attack. A female epigamic display, Chugging, frequently elicits aggression from unpaired males (in 17 of 45 cases observed) but is not a necessary stimulus. Among paired birds, agonistic response to Chugging is less common and the display is often incorporated into a precopulatory sequence. Chugging is described in detail below.

In order to better describe interactions and to clarify roles of males and females, aggressive behavior during active periods of courtship was quantified. Whenever groups of birds were found courting, they were observed as long as possible and the total number of HFT's, FT's, and overt attacks by each participating bird (one male, one defending female, and several subordinate females collectively considered as one) recorded. HRT's were not quantified because they were relatively difficult to observe. Arbitrary "intensity values" (after Recher and Recher 1969) reflecting relative amounts of time and energy expended were assigned to each parameter (HFT = 1, FT = 2, overt attack = 3). Using these values, average scores per aggressive act were calculated for each category of birds. Observations were continued throughout the period of social courtship.

The results are presented in table 2 and figure 1. Since observations were made only on actively courting birds, the totals do not reflect accurately the amount of aggression per unit time. However, the relative totals, expressed as a percentage of the total for all birds, provide a measure of the distribution of aggressive activity among the participants. The high value for defending females (78.1%) indicates that these females do not act only in response to aggression by subordinate females. They evidently must direct frequent threats toward any nearby female in order to establish and maintain a dominant position. If any stimuli other than proximity alone (except possibly orientation toward the male) are necessary to elicit threat from a defending female, it is not apparent. Perhaps vocalizations or subtle posture changes play a role. The need for relatively high aggressive levels in defending females is probably related in part to the mobile and social nature of the courting process, which inevitably leads to encounters with strange females.

The very low percentage of total aggression attributable to subordinate females (4.4%) does not necessarily imply a correspondingly low aggressive tendency. More likely it reflects the inhibiting effect of threats by the female in the dominant position. Although they were not quantified, even HRT's by the defending female often cause a nearby subordinate to withdraw. Only rarely will a subordinate female spontaneously threaten a dominant one. Most threats by the former are retaliatory.

Males are intermediately aggressive between defending and subordinate females, accounting for 17.5% of the total aggression

TABLE 2. Aggressive behavior during social courtship (observation time = 429 min).

	Total no. of aggressive acts	% of total for all birds	Total intensity score[a]	Mean intensity per aggressive act
Defending Female	304	78.1	511	1.68
Subordinate Females	17	4.4	38	2.24
Males	68	17.5	87	1.28
Totals	389	100.0	636	1.63

[a] Scores were assigned to behavior patterns as follows: Head-Forward Threat = 1, Flying Threat = 2, Overt Attack = 3. (See text for explanation and fig. 1 for breakdown of aggressive acts.)

quantified from courting groups. This relatively low figure, when compared with the 78.1% for defending females, may be attributable in part to the lower levels of testosterone in males than in females (Höhn and Cheng 1967). The relationship between testosterone levels and aggressiveness has long been realized (Collias 1950). But, since males of this species are the objects of competition among females instead of being the competitors themselves, one should naturally expect relatively fewer agonistic encounters involving males during the period of courtship.

The role of a bird in a courting party determines not only the frequency with which aggression is expressed but also the types of threat utilized. This is illustrated by figure 1 and the "average intensity" scores in table 2. The occurrence of overt attacks is relatively low for all birds. The greatest differences between defending females, subordinate females, and males are found in the frequencies of HFT's. No HFT's were recorded for subordinate females, whereas they occurred with a frequency of 38% in defending females and 75% in males. It is largely this disparity that accounts for the differences in average intensity scores.

Differential usage of HFT's by different birds probably represents differences in threat effectiveness rather than in aggressive motivation. Each bird seems to maximize threatening efficiency by using the simplest threat which can supplant the target bird. A defending female can frequently supplant another with a simple HFT. This has the further advantage allowing her to remain close to the male. Subordinate females, however, are probably unable to supplant with HFT's. For these females higher-intensity threats or attacks, though used sparingly, have a greater likelihood of supplanting the defender and also bring them closer to the male. Males rarely need to resort to FT's or overt attacks since they are dominant in such situations and easily supplant any females with HFT's.

THE ROLE OF VOCAL COMMUNICATION

Vocal behavior is not as conspicuous in this species as in more territorial shorebirds which perform aerial displays. The tendency for Wilson's Phalaropes to be gregarious during early pair formation minimizes the need for loud, complex vocal signals, but vocalizations geared toward short-range communication play an important role. In this paper I will only attempt to describe briefly some of the calls associated with this stage of the breeding cycle and suggest possible functions.
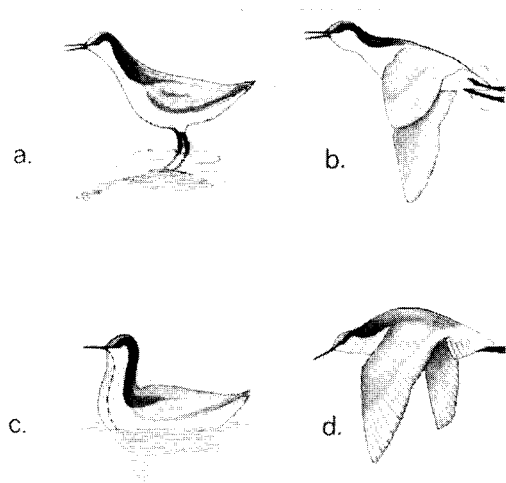

FIGURE 2. Displays of courting female Wilson's Phalaropes. a. *Wa* vocalization, standing. b. *Wa* vocalization in flight. c. Chug (broken line indicates normal neck position). d. Loon Flight.

The most frequently heard call is a short, nasal *Ernt*, the basic call from which most other phalarope calls appear to be derived. *Ernts* are used by both sexes and often seem to function as contact signals in a wide variety of contexts. During social courtship, however, they are given primarily by females and the rate of delivery increases in direct proportion to the intensity of aggressive behavior. Certain vocalizations and motor patterns of males can also stimulate females to produce a burst of *Ernt* calls (see below). Because several females are usually involved in these situations, I have not been able to determine whether defending females or subordinate females give most of the calls. It is also not clear whether they are given in a definable pattern by individuals. Until a more specific function can be attributed to this call in a courtship situation, I prefer to apply the general term, Contact *Ernt*, to it in all situations.

Less frequently heard is the *Wa* call of females (after Höhn 1967). This is a relatively loud, hollow-sounding call given singly or several times in succession. It is normally used to communicate over distances longer than 15 ft. Often a female uses it in flight before landing in a group of courting birds. Its occasional use prior to copulation in paired birds suggests that its function may be epigamic, but I have not observed any overt male response to it during early pair formation. The postures adopted as the *Wa* call is given are distinctive and are illustrated in figure 2 a and b.

A third important vocalization, used frequently by defending females, is the *Purr*, a

low-frequency, guttural call audible only at very close range. The *Purr* is probably identical to the *pittera pittera* call described by Johns (1969). It is given in the HRT posture, often immediately following a FT to another female. The fact that the *Purr* is also used between members of a pair after a bond is formed suggests that it may function as a means of inhibiting male aggression, either when the female is actively threatening other birds or when she is in violation of the individual distance requirement of a male.

The *Chug* is used by females and directed toward males at close range. It is visually and vocally distinct and there appears to be no male homologue. When performing this display, the female swims within several feet of the male, expands the neck feathers, and extends the neck vertically with the bill directed forward (fig. 2c). A low-amplitude, frog-like vocalization, quite unlike any other call of the repertoire, is repeated several times. She may face the male or swim parallel to or ahead of him. The form of the display suggests homology with the imposing posture of Red Phalaropes (*Phalaropus fulicarius*) and Northern Phalaropes (Höhn 1971). *Chugs* are often performed in the absence of other females but may also be given by individuals in groups. The aggressive reaction of males to *Chugs* during social courtship has already been mentioned. Since this display may also occur in precopulatory situations, it seems to be related directly to the formation of the pair bond.

The only prominent male vocalization during this stage of pair formation is a rapid series of *Ernt* calls given in the HRT posture. The male swims away from the defending female as the call is given and sometimes takes flight, initiating an aerial chase (see below). This call, termed the Courtship *Ernt* because of the context in which it occurs, seems to induce females to give Contact *Ernts* and also provokes inter-female aggression. During active agonistic sequences, the tempo of the individual notes of the Courtship *Ernt* increases noticeably and the total duration of the call may be prolonged. The Courtship *Ernt* and behavior patterns accompanying it are the only suggestions of an incitive male role in aquatic social courtship.

AERIAL CHASES

Aerial activities also play an important pair-formation role. As soon as males arrive in the spring, short flights consisting of a male being pursued by several females take place. Later in the season, longer flights of several minutes reaching altitudes of 500 ft or more occur commonly. These flights are usually associated temporally with aquatic social courtship and involve many of the same vocalizations and displays. Although I was unable to mark many birds participating in aerial chases, marked birds known to be paired were almost never observed to take part. This evidence suggests that most participants in aerial chases are unpaired and the activity is related to pair formation.

Höhn (1967) noted that aerial chases in Wilson's Phalarope are nearly always initiated by males taking flight. My observations support this. Only 5 of over 300 chases that I observed were initiated by females and each of these was the second, third, or fourth in a series of short chases, the first of which was initiated by the male. The active role of the male extends beyond the initiation of a chase, however. After a flight has begun, males often swoop down over swimming females, causing them to fly up and join the chase. Although no quantitative data were collected on this behavior, its frequency was great enough to indicate that swoops are directed at females rather than occurring near females by chance alone. The result is a larger group of courting females and presumably a corresponding increase in competition among them.

A further indication that the male's role in aerial chases is that of a leader rather than the object of a pursuit is the tendency to hover occasionally in one spot, with wing-beats above the horizontal and legs dangling. Hovering usually takes place less than 20 ft above the ground or water and normally lasts less than 5 sec. Females hover around a hovering male and often one swoops at another from above, sometimes making bill contact on the nape region of the bird beneath. These aggressive interactions might result at times in the defending female being supplanted, although I have been unable to document any such case. Hovering males almost always give Courtship *Ernts*, the same call which provokes inter-female aggression on the water.

One other behavior pattern of males in aerial chases is a fluttering of wings below the horizontal through a very narrow arc. This mainly occurs shortly before landing. Fluttering was first described by Höhn (1967), who suggested a homology with Rattling (Tinbergen 1935) in Northern Phalaropes, a precopulatory display in which rapid fluttering of the wings produces easily audible noise. In Rattling, however, the wing-beats are above the horizontal. The function of fluttering is not clear.

Two displays are given by females during aerial chases. One is the *Wa* call given with

TABLE 3. Duration of aerial chases.

	Time period	No. of chases	Mean duration (sec)	S.D.
A.	29 Apr.–8 May	23	14.4[a]	16.5
B.	9 May–18 May	19	38.7	34.0
C.	19 May–28 May	50	28.4	25.9
D.	29 May–7 June	17	26.7	19.3
	Totals	109[b]	27.0	24.3

[a] Significantly shorter than means from periods B, C, or D ($P < 0.01$).
[b] For 18 of these, the times recorded are minimum times. For 22 of the 23 chases from period A, the times recorded are exact.

the wings set below the horizontal and the head elevated (fig. 2b). This display is usually given by females approaching a chasing party from a distance but may also be given by a female very close to the male. Its function is presumably the same as its function in aquatic social courtship and has already been mentioned. The other display, which often immediately follows a bout of *Wa's*, is the Loon Flight, in which a female flies ahead of the male and adopts a hunchbacked posture with the head below the horizontal (fig. 2d). Although I have not heard any vocalizations associated with this posture, the Loon Flight may be an aerial form of the Chug display, particularly since *Wa's* and *Chugs* are sometimes given in direct succession in the precopulatory displays of paired birds. If the *Chug* call is not given during the Loon Flight, it is the only vocalization used by females in aquatic courtship which is not repeated at some point in the aerial chase. Both Contact *Ernts* and *Purrs* are often heard but it has not been possible to determine the identity of individual birds making these sounds.

Early in the season most aerial chases begin and end on the open-water portions of large or small ponds. The termination point usually differs from the starting point. The chase is immediately followed by a burst of inter-female aggression as the defending female attempts to re-establish her position of dominance. The male often continues giving Courtship *Ernts* and turns away from the defending female in the HRT posture. Male hostility is common following a chase (recorded in 28% of the chases for which subsequent behavior was observed, N = 40).

Most chases terminate in small, shallow sloughs instead of on open water once emergent vegetation begins to appear. After landing, the male swims or runs quickly away from the females, leading them into the dense vegetation. All the females attempt to follow, at the same time directing threats and attacks at
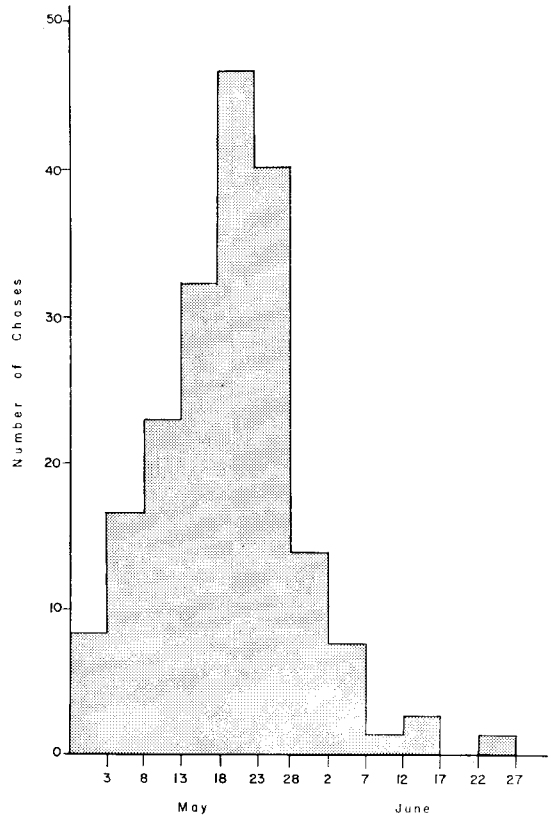

FIGURE 3. Seasonal distribution of aerial chase frequency (total observations for one season).

one another. After 20% of the chases I observed, the male swam to shore and ran into the grass, performing intention movements of precopulatory displays and nest-site selection (Howe 1972). The end of an aerial chase such as the one described above seems to be a critical part of pair formation, a stage transitional between aquatic courtship and terrestrial nest-searching behavior.

Duration of aerial chases. From 29 April to 7 June 1970, the duration of every aerial chase observed was recorded. The results are presented in table 3. For the first 10-day period after arrival of the birds in spring, chases were significantly shorter than those occurring in any of the following periods ($P < 0.01$). There were no significant differences in chase duration between any of the final three observation periods. The increase in the first week of May roughly coincides with the log phase of testicular growth of birds collected by Höhn in Alberta (Höhn 1967), suggesting a possible causative relationship. Some implications of chase duration for the pair-formation process are discussed below.

Seasonal distribution of aerial chases. My observations suggest that there was a gradual

increase in aerial-chase frequency during the first part of May, reaching a peak between 19 and 23 May and tapering off thereafter until late June, when the last females deserted the breeding grounds (fig. 3). Interpretation of this distribution is complicated by the variation in actual number of birds present on any given day, due to the presence of migrants and to short-term changes in local distribution. Despite these variables, however, the early peak (6–11 days before the mean date of clutch initiation, N = 19 clutches) indicates that most participants in aerial chases are incompletely paired birds. This supports the conclusion drawn above from observations of marked birds. If most chases occurred during the egg-laying period or near the beginning of incubation, as suggested by Höhn (1967), the shape of the curve would likely be unaffected by migrants and the peak would span the last few days of May.

DISCUSSION

FUNCTION OF AERIAL CHASES

Aerial chases in which a female is followed by several males are common components of courtship in a wide variety of bird species. Often they are viewed as attempts by females to escape from sexually aggressive males (e.g., Summers-Smith 1963:59). Evidence from some species, however, suggests a more active female role. Smith (1968) indicated that courtship chases in Pintails (*Anas acuta*) are always begun by females and Armstrong (1955) described what appeared to be active provocation of male chase behavior by females in the Winter Wren (*Troglodytes troglodytes*). Parmelee (1970) reported female initiative in Sanderling (*Calidris alba*) aerial chases. In this paper I have shown that in Wilson's Phalarope, a species in which females chase males, chases are initiated by the male, who plays an active role in determining their course, duration, and the number of females participating.

Crook (1962) felt that aerial chases in Ploceid weavers promote maturation of the neuroendocrine mechanism controlling sexual tendencies, particularly in females. Others studying aerial chases have come to similar conclusions (Tinbergen 1939; Summers-Smith 1963). Phillips and van Tienhoven (1962) showed that Pintail females collected from aerial chases arising from spring flocks had only partially developed ovaries; therefore they concluded that these flights are probably associated with pair formation. No data were available to show that ovary size increased through the period of aerial chasing, although

the weights of ovaries collected at later stages lead to the conclusion that some ovarian development undoubtedly took place during that time. I have shown in this paper that the period of increase of aerial-chase duration which I determined for a North Dakota population of Wilson's Phalarope coincides with the log phase of testicular growth in an Alberta population sampled by Höhn (1967) in a different year. Although the evidence is circumstantial, it suggests that the aerial chasing periods for both female Pintails and male Wilson's Phalaropes correlate with part of the period of gonadal recrudescence. I cannot, however, determine at this stage whether the relationship is a causal one. It is also possible that aerial chases are stimulating to the pursuing birds as well. The overall similarities of Pintail and phalarope chases, despite sex-role differences, raise questions about the hormonal control of chase behavior.

Regardless of the causal basis or proximal effects, aerial chases appear to be adaptive as a mechanism of ensuring that the sexual cycles of the members of forming pairs are closely synchronized. Often females are seen to drop out of chases and return to the point of origin. Since long chases usually terminate away from the starting point, a single male and female are often all that remain of the original group. Because all evidence indicates that aerial-chase participants are nearly always unpaired, I believe that females which abandon chases are unpaired birds with low sexual motivation. The female persisting longest in the chase is probably more sexually mature and might therefore be a more efficient mate for the male to select.

The possibility that long flights serve as a mechanism for spacing pairs must also be considered. This potential function of aerial chases has been most intensively studied in the Anatidae. Smith (1968) drew a functional distinction between the courtship chases of Pintails (see above) and chases initiated by paired males during the pre-egg-laying and egg-laying stages. The latter type of chase appears to be an attempt on the part of a paired male to drive away strange pairs flying overhead, the net result being a dispersion of pairs. This interpretation has been made for a wide variety of waterfowl (Hochbaum 1944; Sowls 1955; Dzubin 1955; McKinney 1965).

The evidence for a spacing function in Wilson's Phalarope, however, is weak. Chases involving paired phalaropes rarely occur. Four marked, paired females were observed carefully prior to and during the egg-laying period and none was ever seen to join chases, even

when chases passed directly overhead. Several times, however, paired males initiated chases with strange females. But in each case the chase was very short and circular and did not result in females being led away from the nest area. If aerial chases by Wilson's Phalarope function in part as a spacing mechanism, it is most likely a passive process in that the male flies until only he and one female remain and then both land in an area where no conspecifics are present. There is some evidence for male territorial defense unrelated to aerial chases, but this occurs later during the period of nest-building (Howe 1972).

ADAPTIVENESS OF SOCIAL PAIRING

The early stages of pair formation in Wilson's Phalarope involve intense social competition in mixed-sex flocks on the water and in aerial sexual chases. Competition for potential mates takes place among females, which are larger, more colorful, and much more aggressive than males. Males, however, play an active role by initiating and determining the course and duration of aerial chases. Males also make use of vocal signals which stimulate agonistic interactions among females. The display repertoire of the species is small and the vocalizations are geared toward short-range communication. Territorial behavior at this stage of pairing is restricted to defense by a female of a small area surrounding a mobile male; the elaborate aerial displays characteristic of most shorebird species which maintain pairing territories are absent. All of these factors in combination constitute a strategy of pair formation which makes Wilson's Phalarope, and possibly the Northern and Red Phalaropes, unique among the Scolopacidae. Even discounting the reversal of sex roles, which is more highly developed in the phalaropes than in any other scolopacid, the pattern of establishing a pair bond through aggressive interaction and sexual display in tight social aggregations is a significant departure from the usual pattern of advertisement within territories established and defended by one sex.

The few other scolopacids which have social pairing systems exhibit certain basic differences from the phalaropes. The true lek species such as the Ruff (Hogan-Warburg 1966) and the Great Snipe (*Gallinago media*) (Ferdinand 1966) differ in that the display grounds and individual territories within them are static and no prolonged pair bond develops as a result of interactions of the sexes. Wilson's Phalaropes form a bond which continues through the egg-laying period (Höhn 1967; Howe 1972). The Buff-breasted Sandpiper

(*Tryngites subruficollis*) exhibits a form of lek behavior in which the territories are larger than those of the above species and the location of the lek itself may vary (Parmelee et al. 1967). This species is apparently promiscuous (R. T. Holmes, pers. comm.). Another calidridine, the Pectoral Sandpiper, may not establish pair bonds and the male territories are apparently relatively static and probably too large to be considered part of a lek system (Pitelka 1959). The Ruddy Turnstone (*Arenaria interpres*) under certain circumstances may perform apparent courtship behavior in nonterritorial, social aggregations with males displaying before females (Parmelee and MacDonald 1960). Except for the reversal of sex roles, this feature superficially resembles the social and mobile pattern of Wilson's Phalarope more than the pairing behavior of any of the scolopacids. Of the species mentioned above, the Pectoral Sandpiper (Pitelka 1959) and the Ruddy Turnstone (Bergman 1946) perform aerial chases (males pursuing a female) at some point during the breeding cycle.

The formation of pairs through group interaction in Wilson's Phalarope probably results from certain selective advantages conferred upon individuals which form flocks. All species of phalaropes are highly social during migration and winter, and to a lesser extent during the nesting season. Moynihan (1962) postulated that one function of feeding in flocks is that flock members benefit from food organisms flushed by other members. Observations of Wilson's Phalarope by Siegfried and Batt (1972) suggest that larger flocks may facilitate food procurement, presumably because larger quantities of prey items are stirred up to within reach of the birds. Further observations by Siegfried and Batt (1972) and also Williams (1953) suggest that similar enhancement of feeding may be derived from commensal association with other aquatic species, specifically the Northern Shoveler (*Anas clypeata*) and American Avocet (*Recurvirostra americana*), respectively. If this advantage of flock-feeding persists into the first part of May when much of early pair formation takes place, it could constitute a strong selective pressure for a group-oriented pairing system.

It is also possible that Wilson's Phalaropes favor larger bodies of alkaline water, which support a more abundant invertebrate fauna than small bodies of fresh water. Censuses of breeding birds in North Dakota by Robert E. Stewart (pers. comm.) indicate a positive correlation between the distribution of phalaropes and the distribution of alkaline sloughs. My own local observations suggest a similar

relationship: areas near alkaline sloughs harbor larger breeding populations of phalaropes and the slough serves as the primary feeding place. While this relationship may effect a clumped distribution of phalaropes, however, it does not by itself account for a need for maintaining tight groupings.

By exploiting an exposed feeding niche with little potential for concealment, Wilson's Phalaropes risk direct exposure to avian predation. Particularly in spring, when alternate plumage is worn, birds on the open water can be highly conspicuous. Lone birds must be especially vulnerable. Selection should favor the evolution of a social tendency as a defense against the potential hazard of predation under these conditions. Although I have not witnessed encounters between Wilson's Phalaropes and avian predators, I have seen a flock of Northern Phalaropes respond to a flying Marsh Hawk (*Circus cyaneus*) by circling it rapidly and erratically as a highly compact unit in a single plane. From a distance this flock at times banked in such a way as to reflect sudden flashes of sunlight, giving it the appearance of a miniature flying saucer. Such a highly coordinated response suggests that there has been strong selective pressure for a social reaction to avian predators. While this mobbing reaction may be only a consequence of a flocking tendency, its effectiveness over individual anti-predator responses may have been a significant force in the evolution of phalarope sociality.

Thus flocking, both as an adaptation for increasing feeding efficiency and as a predation-inhibiting mechanism, provides a social substrate from which social pair formation can evolve. Though proof for these adaptations is wanting, both seem plausible for a species feeding on surface and subsurface invertebrates in an exposed, aquatic environment. Other functions of flocking, such as facilitation of mate attraction (Collias and Collias 1969), are also possible for Wilson's Phalarope but supporting evidence is not available.

SUMMARY

The social behavior patterns of early pair formation in Wilson's Phalarope are examined. Courtship is initiated within groups of birds swimming in open-water situations during spring migration. Three main features distinguish courting groups from feeding groups: aggression among females in the presence of a male; female sexual display to a male; and aerial chases in which females pursue a male. Aggressive displays are described and quantified for males, defending females, and subordinate females. The differences among them in total aggression and relative use of different aggressive displays are interpreted in terms of motivation levels and dominance relationships. A female display given to males at close range, Chugging, is described. Chugging is the only display given exclusively by females. Aerial chase behavior is described in detail. Behavioral data from marked birds and from a frequency distribution of aerial chases through the period of courtship indicate that predominantly unpaired birds participate. The chases probably serve to ensure synchronization of the sexual cycles of potential pair members and do not have a significant effect on the spacing of pairs. Vocalizations used in all social courtship activities are described briefly. Possible selective pressures leading to the evolution of a social pairing system are discussed.

ACKNOWLEDGMENTS

LITERATURE CITED

ARMSTRONG, E. A. 1955. The wren. Collins, London. 312 p.

BENGTSON, S. 1968. Breeding behaviour of the Grey Phalarope in west Spitsbergen. Var Fågelvärld 27:1–13.

BENT, A. C. 1927. Life histories of North American shorebirds, Vol. 1. U.S. Natl. Mus. Bull. 142:1–420.

BERGMAN, G. 1946. Der Steinwälzer, *Arenaria i. interpres* (L.), in seiner Beziehung zur Umwelt. Acta Zool. Fennica 47:1–151.

COLLIAS, N. E. 1950. Hormones and behavior with special reference to birds and the mechanisms of hormone action, p. 277–329. *In* E. S. Gordon [ed.], A symposium on steroid hormones. Univ. of Wisconsin Press, Madison.

COLLIAS, N. E., AND E. C. COLLIAS. 1969. Size of breeding colony related to attraction of mates in a tropical passerine bird. Ecology 50:481–488.

CROOK, J. H. 1962. The adaptive significance of pair formation types in weaver birds. Symp. Zool. Soc. Lond. 8:57–70.

DZUBIN, A. 1955. Some evidences of home range in waterfowl. Trans. 20th N. Amer. Wildl. Conf., p. 278–298.

FERDINAND, L. 1966. Display of the Great Snipe (*Gallinago media* Latham). Dansk Ornithol. Foren. Tids. 60:14–34.

HILDEN, O. AND S. VUOLANTO. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. Ornis Fenn. 49:57–85.

HOCHBAUM, H. A. 1944. The Canvasback on a prairie marsh. Amer. Wildl. Inst., Washington, D.C. 207 p.

HOGAN-WARBURG, A. J. 1966. Social behavior of the Ruff, *Philomachus pugnax* (L.). Ardea 54: 109–229.

HÖHN, E. O. 1967. Observations on the breeding biology of Wilson's Phalarope (*Steganopus tricolor*) in central Alberta. Auk 84:220–244.

HÖHN, E. O. 1971. Observations on the breeding behaviour of Grey and Red-necked Phalaropes. Ibis 113:335–348.

HÖHN, E. O., AND S. C. CHENG. 1967. Gonadal hormones in Wilson's Phalarope (*Steganopus tricolor*) and certain other birds in relation to plumage and sex behaviour. Gen. Comp. Endocrinol. 8:1–11.

HOLMES, R. T., AND F. A. PITELKA. 1966. Ecology and evolution of sandpiper (*Calidritinae*) social systems. Proc. Int. Ornithol. Congr. XIV (abstract), p. 70.

HOWE, M. A. 1972. Pair bond formation and maintenance in Wilson's Phalarope, *Phalaropus tricolor*. Unpubl. Ph.D. thesis. 169 p.

JEHL, J. R., JR. 1968. Relationships in the Charadrii (shorebirds): a taxonomic study based on color patterns of the downy young. San Diego Soc. Nat. Hist. Memoir 3:1–54.

JOHNS, J. E. 1963. A new method of capture utilizing the mist net. Bird-Banding 34:209–213.

JOHNS, J. E. 1969. Field studies of Wilson's Phalarope. Auk 86:660–670.

MCKINNEY, F. 1965. Spacing and chasing in breeding ducks. Wildfowl Trust 16th Ann. Rept., p. 92–106.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll. 143(7):1–140.

ORING, L. W., AND W. M. DAVIS. 1966. Shorebird migration at Norman, Oklahoma: 1961–1963. Wilson Bull. 78:166–174.

PARMELEE, D. F. 1970. Breeding behavior of the Sanderling in the Canadian high Arctic. Living Bird 9:97–146.

PARMELEE, D. F., AND S. D. MACDONALD. 1960. The birds of west-central Ellesmere Island and adjacent areas. Natl. Mus. Canada Bull. 169:1–103.

PARMELEE, D. F., H. A. STEPHENS, AND R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. Natl. Mus. Canada Bull. 222:1–229.

PARMELEE, D. F., D. W. GREINER, AND W. D. GRAUL. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the Central Canadian Arctic. Wilson Bull. 80:5–29.

PITELKA, F. A. 1959. Numbers, breeding schedule and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

PHILLIPS, R. E., AND A. VAN TIENHOVEN. 1962. Some physiological correlates of Pintail reproductive behavior. Condor 64:291–299.

RANER, L. 1972. Förekommer polyandri hos smalnäbbad simsnäppa (*Phalaropus lobatus*) och svartsnäppa (*Tringa erythropus*)? Fauna och Flora. no. 3:135–138.

RECHER, H. F., AND J. A. RECHER. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. Wilson Bull. 81:140–154.

SIEGFRIED, W. R., AND B. D. J. BATT. 1972. Wilson's Phalaropes forming feeding association with Shovelers. Auk 89:667–668.

SMITH, R. I. 1968. The social aspects of reproductive behavior in the Pintail. Auk 85:381–396.

SOWLS, L. K. 1955. Prairie ducks. Wildl. Management Inst., Washington, D.C. 193 p.

STEWART, R. E., AND H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Bur. Spt. Fish & Wildl. Res. Publ. 92, p. 1–57.

SUMMERS-SMITH, D. 1963. The House Sparrow. Collins, London. 269 p.

TINBERGEN, N. 1935. Field observations of east Greenland birds. I. The behaviour of the Red-necked Phalarope (*Phalaropus lobatus* L.) in spring. Ardea 24:1–42.

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. Trans. Linnaean Soc. New York 5:1–94.

VOGT, W. 1938. Preliminary notes on the behavior and ecology of the eastern Willet. Proc. Linnaean Soc. New York 49:8–42.

WILLIAMS, G. C. 1953. Wilson's Phalaropes as commensals. Condor 55:158.