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BREEDING BIOLOGY OF WILSON'S PHALAROPE IN SOUTHCENTRAL SASKATCHEWAN

Mark A. Colwell and Lewis W. Oring[1]

Abstract.—The breeding biology of Wilson's Phalarope (*Phalaropus tricolor*), a sex-role reversed shorebird, was studied from 1982–1987 at Last Mountain Lake National Wildlife Area in southcentral Saskatchewan, Canada. Female mating tactics involved direct competition for mates, rather than competition via territories. Unpaired, competing females ranged more widely than paired or laying females. By contrast, males were more restricted in their movements, particularly during incubation and brooding periods. Modal clutch size was four; and clutches weighed an average of 55% of the body weight of a nonlaying female. Females laid 0–4 clutches in a breeding season. Male reproductive patterns were characterized by nearly exclusive care of eggs and chicks. Weight of incubating males decreased during incubation. Nesting success varied significantly among years, primarily owing to the effects of predation. Approximately 25% of males that lost clutches during the nesting season renested. Among the three species of phalaropes, ecological factors favor higher incidences of polyandry in Wilson's Phalarope, but estimates may be complicated by wide-ranging movements of females during the breeding season. *Received 7 Jan. 1988, accepted 12 May 1988.*

The sex-role reversed, nonterritorial mating system of phalaropes (*Phalaropus* spp.) is unusual among birds (Oring 1982, 1986). Females contest access to mates in "scramble competitions" (Reynolds 1987, Colwell and Oring 1988a), and males perform virtually all parental care. The low incidence of sequential polyandry in all three species (Hildén and Vuolanto 1972, Raner 1972, Schamel and Tracy 1977, Colwell 1986a, Reynolds 1987, Colwell and Oring 1988b) indicates that the ability of females to become polyandrous is limited (Reynolds 1987). Females do not appear to be constrained energetically or by the amount of time available to obtain mates, but rather by the availability of unmated males (Reynolds et al. 1986; Reynolds 1987; Colwell and Oring 1988a, b).

Recent studies have contributed greatly to our understanding of the breeding biology of Red-necked Phalarope (*P. lobatus*; e.g., Hildén and Vuolanto 1972, Reynolds et al. 1986, Reynolds 1987) and Red Phalarope (*P. fulicaria*; e.g., Schamel and Tracy 1977, Mayfield 1979, Schamel and Tracy 1987, Tracy and Schamel 1988). Although published accounts of the reproductive biology of Wilson's Phalarope (*P. tricolor*) are numerous (e.g., Colwell 1986a, b; Colwell and Oring 1988a, b), few studies have spanned more than a breeding season and most have dealt with populations of unmarked individuals. Thus, in many instances, behavioral

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[1] Dept. Biology, Univ. North Dakota, Grand Forks, North Dakota 58202.

interpretation was limited by lack of knowledge of individual reproductive patterns. In this paper, we present data on Wilson's Phalarope breeding biology, emphasizing factors that may contribute to variability in phalarope mating systems in general. We deal only superficially with behavioral aspects of sex-role reversal, because Howe (1975a, b) treated this topic in depth.

METHODS

We studied Wilson's Phalarope from 1982–1987 at Last Mountain Lake National Wildlife Area in southcentral Saskatchewan, Canada (51°10'N, 110°2'W). During 1982 and 1983, phalaropes were observed at East Alkaline Lake, a 40-ha ephemeral wetland and surrounding prairie, separated at its southern third by a road. During the breeding season, cattle grazed around the wetland north of the road in 1982, but not in 1983; otherwise the site was undisturbed. Approximately 45 and 20 males nested at East Alkaline Lake during 1982 and 1983, respectively.

In 1984, phalaropes did not breed at East Alkaline Lake owing to extreme drought conditions (Colwell 1986b). As a result, the study shifted to Lanigan Creek, one of the few remaining areas with sufficient water to support breeding shorebirds; work continued there in 1985–1987. Lanigan Creek was a permanent wetland amid approximately 100 ha of pasture that was heavily grazed by 40 to 65 cattle from late May to autumn in all years. Phalarope numbers at Lanigan Creek were higher than at East Alkaline Lake, totalling approximately 55, 80, 100+, and 100+ nesting males during 1984–1987, respectively. Colwell and Oring (1988a) described the study areas.

Phalaropes were caught with mist nets, walk-in traps, decoy traps, and nest traps, and each bird was banded with a unique combination of three colored leg bands and one metal band. During 1984–1987, phalaropes were marked with a patagial tag (Curtis et al. 1983), and in 1986 and 1987, 28 females were fitted with a 3.5-g radio transmitter (Raim 1978) to investigate reproductive tactics during the breeding season (Colwell and Oring 1988b). Birds were weighed to the nearest g with a 100-g Pesola scale. The length of the flattened wing, tarsus, and culmen (from the tip of the bill to the proximal margin of the nares) were measured with calipers to the nearest 0.1 mm. During 1982–1984, the weight of eggs was measured to the nearest g with a 10-g Pesola scale. Analyses included only those clutches measured immediately after clutch completion, to eliminate error caused by desiccation of eggs over time.

Each year, the study began prior to the arrival of phalaropes (1983–1986) or initiation of nesting (1982 and 1987) and continued until most or all clutches had hatched. Ad lib observations (Altmann 1974) were conducted regularly during mornings (sunrise: ca 05:00) and evenings (sunset: ca 21:00) mostly from 3-m towers and a field vehicle. During 1986 and 1987, daily movements and behaviors of individuals were recorded on maps of the study site. Nests were located either by watching a pair of birds as they visited nest scrapes during courtship or laying, or by observing males returning to incubate clutches. Occasionally, a clutch was found when an incubating male was flushed from the nest. Most clutches, however, were found during the egg-laying stage (1982, 29% [14/49]; 1983, 72% [18/25]; 1984, 59% [35/59]; 1985, 75% [59/79]; 1986, 84% [52/62]; 1987, 81% [88/108]). Throughout the breeding season, nests were checked regularly, and the fate of clutches (hatched, lost to predators, deserted, crushed by cattle, human-induced loss, or unknown) was recorded. Statistical analyses follow procedures in Siegel (1956) and Sokal and Rohlf (1981).

TABLE 1
MORPHOLOGICAL COMPARISON ($\bar{x}$ ± SD) OF FEMALE AND MALE WILSON'S PHALAROPES

	Female	Male	z
Culmen (mm)	32.8 (1.6) N = 45	29.6 (1.1) N = 139	8.81[a]
Tarsus (mm)	38.5 (1.6) N = 47	36.5 (1.0) N = 140	7.35[a]
Wing (mm)	137.7 (3.2) N = 47	127.1 (2.9) N = 127	9.93[a]
Weight (g)	68.1 (7.1) N = 48	51.8 (4.1) N = 155	10.12[a]
	79.0 (4.9)[b] N = 31		

[a] Mann-Whitney U-test; $P < 0.05$.
[b] Laying females with formed eggs in oviduct.

RESULTS

Sexual dimorphism.—Female Wilson's Phalaropes had brighter plumage and were significantly larger than males in all morphological features (Table 1). Males averaged 92% of the size of females based on tarsus, culmen, and wing measurements, and mass was 76% of that of nonlaying females. Females with at least one egg in their oviduct averaged approximately 11-g heavier than nonlaying females; the average weight of nonlaying females may be biased by the inclusion of "heavy" females of unknown status. One female lost 8 g (74 g − 66 g) in the two days between the laying of her second and fourth egg; she still had not laid the fourth egg when weighed the second time.

Breeding chronology.—Phalaropes arrived at Last Mountain Lake in late April or early May. Female-biased sex ratios early in the season indicate that most females preceded males to breeding areas (Reynolds et al. 1986; Colwell and Oring 1988a, b).

The nesting period (interval between dates of first and last initiated clutch) for the population ranged from 21 days (1983) to 45 days (1982 and 1987) (Fig. 1). There was considerable annual variability in the onset and cessation of nesting resulting in significant differences in the seasonal distribution of clutch initiations (Kolmogorov-Smirnov two sample test, $P < 0.05$), especially in comparison with 1983. The first clutch for the population was initiated between 8 May (1987) and 20 May (1983). In 1983, a spring snowstorm was responsible for delayed onset of nesting,

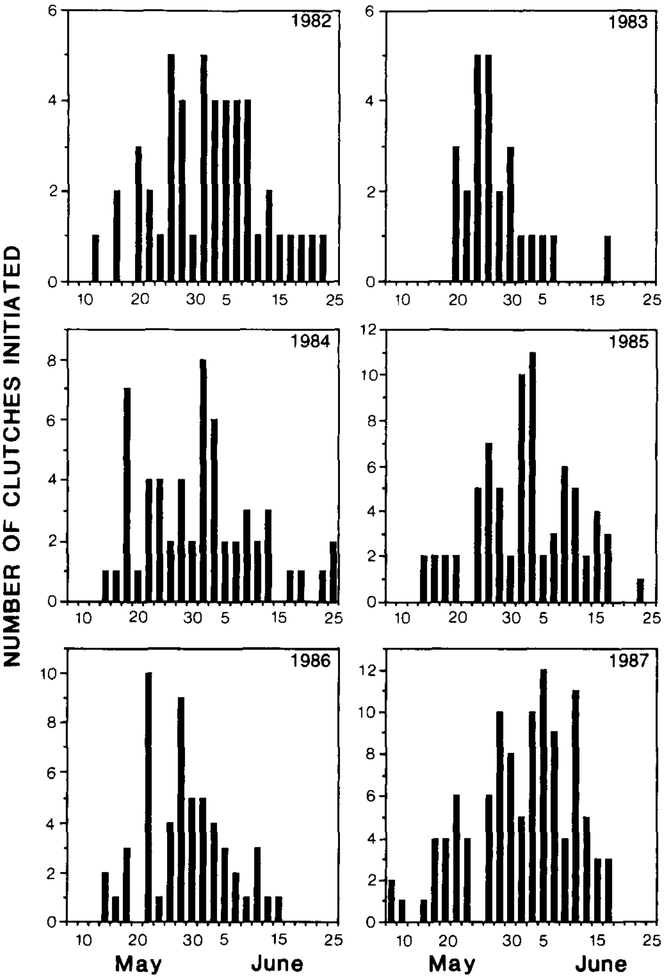

FIG. 1. Seasonal distribution of clutch initiations for 1982–1987.

and drought conditions (Colwell 1986b) truncated late-season nesting. Although drought conditions abbreviated nesting during 1983, this was a local phenomenon. Breeding continued during mid-June at neighboring wetlands with favorable water conditions. On average, 73% of clutch initiations occurred between 22 May and 11 June. Annual duration of the period of hatching varied from 14 (1983) to 38 (1982) days (Fig. 2).

The sexes differed markedly in dates of departure from breeding areas (Fig. 3), which was correlated with differences in the sex roles of males

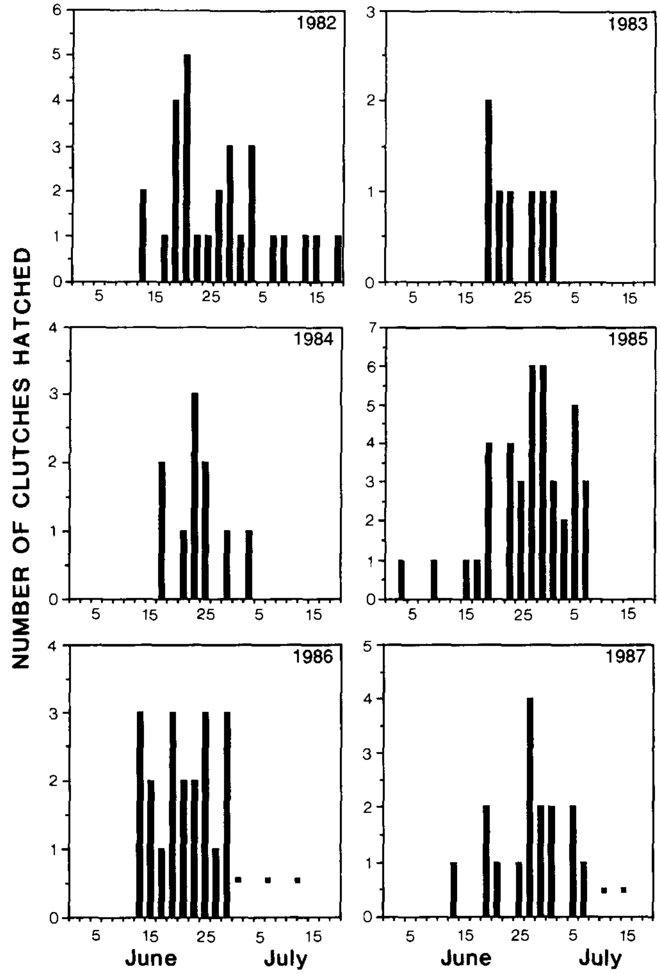

FIG. 2. Seasonal distribution of hatching dates for 1982–1987. Field seasons ended before all clutches had hatched in 1986 and 1987.

and females (see below). Females left nesting areas during mid- to late June. Few females remained when the last clutches were initiated, and females were seldom seen after 1 July. Large saline lakes in southern Saskatchewan supported large numbers of females in early July (W. Harris, pers. comm.). Males that failed to hatch chicks began to leave the study area in mid-June, otherwise care of chicks kept males in the area into July.

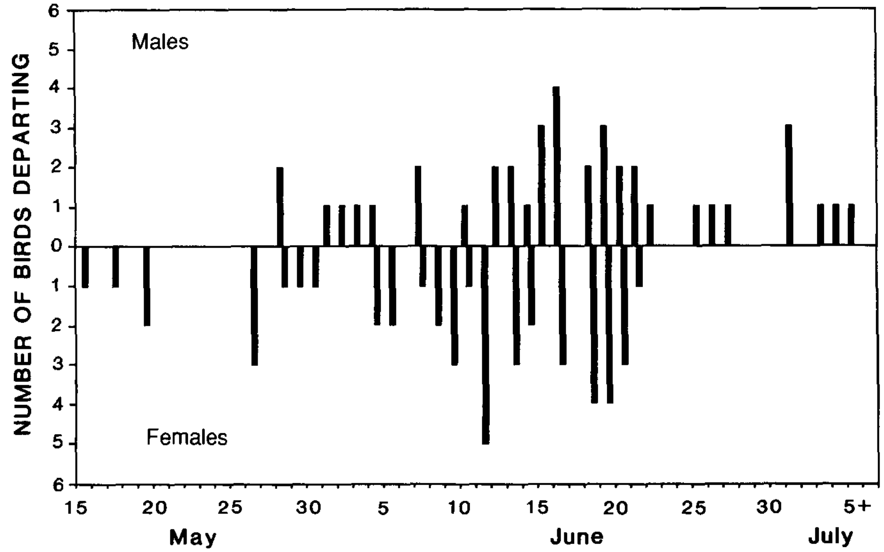

FIG. 3. Departure dates of male and female Wilson's Phalaropes based on dates of last observation of marked individuals during 1986 and 1987. Departure dates of brooding males (N = 41) extend beyond 5 July.

Mating system and space use.—Mate acquisition was mediated directly in scramble competition among females; neither sex was territorial. Both sexes of phalaropes frequently fed together in tight flocks with no apparent aggression related to food resources (primarily *Daphnia* spp., and dipteran larvae and adults). Aggression was observed regularly, but it was always related to competition for mates (Colwell and Oring 1988a).

Typically, females assumed the active role in courtship and competition for mates (Colwell and Oring 1988a). On several occasions, however, intrasexual competition among males occurred briefly when local sex ratios were male-biased. Aerial chases of males by females marked the early stages of competition for mates. Throughout the breeding season, however, unpaired females pursued males about the wetland (Colwell and Oring, in press). Male breeding status was significantly associated with the tendency for females to pursue them ($G = 19.9$, df = 2, $P < 0.001$). On nearly all occasions (28/29) when males departed an area and females followed, males were either unpaired (N = 8) or on incubation recess (N = 20). Either sex was equally likely to follow the other among pairs (N = 37). During courtship, females remained close to prospective mates, and defended them by posturing toward contesting females or fighting (see Höhn 1969, Howe 1975a, Colwell and Oring 1988a).

Once paired, females led males on circling flights (Howe 1975b) about upland areas. Nest scraping behavior usually followed flights. Pairs that nested in close proximity to the wetland walked into the vegetation to scrape. In 1982 and 1983, nests around the wetland were hyperdispersed. At the time of clutch initiation for each nest, the average distance to the nearest active conspecific nest deviated significantly from the expected mean distance based on a random dispersion (nearest neighbor technique: 1982, $\bar{x} = 57$ m, $z = 3.07$, $P < 0.05$; 1983, $\bar{x} = 105$ m, $z = 4.02$, $P < 0.05$).

Most females (75%, N = 36) laid eggs between 05:00 and 11:00. Males accompanied mates on 34% (18/53) of occasions when females were observed laying. During 1986 and 1987, 30% (7/23) of females that were captured while they were laying were caught simultaneously with their mates. When their mate was laying an egg, an accompanying male remained alert within several m of the nest.

The interval between laying of successive eggs in a clutch averaged approximately 26 h (range: 24–27 h, N = 5). Occasionally, females skipped a day during laying, especially if they were disturbed early in the nesting season. Ninety-one percent of clutches (N = 158) that were followed from laying of first to last egg were completed in four days, and 9% required more than four days. Inclement weather occasionally interrupted normal laying patterns with the subsequent desertion of an incomplete clutch. Human disturbance sometimes had a similar effect on laying patterns. During 1986, a female that was captured as she laid her second egg skipped three days before laying two additional eggs. Her mate subsequently deserted this clutch and the pair renested.

During the six years of the study, we observed four instances of sequential polyandry (Colwell 1986a, Colwell and Oring 1988b). Females that had completed a clutch occasionally paired with second mates but left the study area shortly thereafter (Colwell 1986a, Colwell and Oring 1988b). Most females obtained at least one mate; a small proportion may not have bred.

Males and females differed in their use of space during various reproductive stages (Fig. 4). During prelaying and laying stages, both sexes (males: N = 16; females: N = 28) exhibited localized movements at foraging sites near nests. Unpaired, competing females ranged widely owing to intrasexual competition and mate-locating tactics. Groups of females frequently pursued individual males for more than 1 km during aerial chases related to mate acquisition. Competing females frequently traversed the wetland, vocalizing to other phalaropes, and engaging in chases of males (Colwell and Oring, in press).

Males on incubation recess were regularly observed foraging at the same

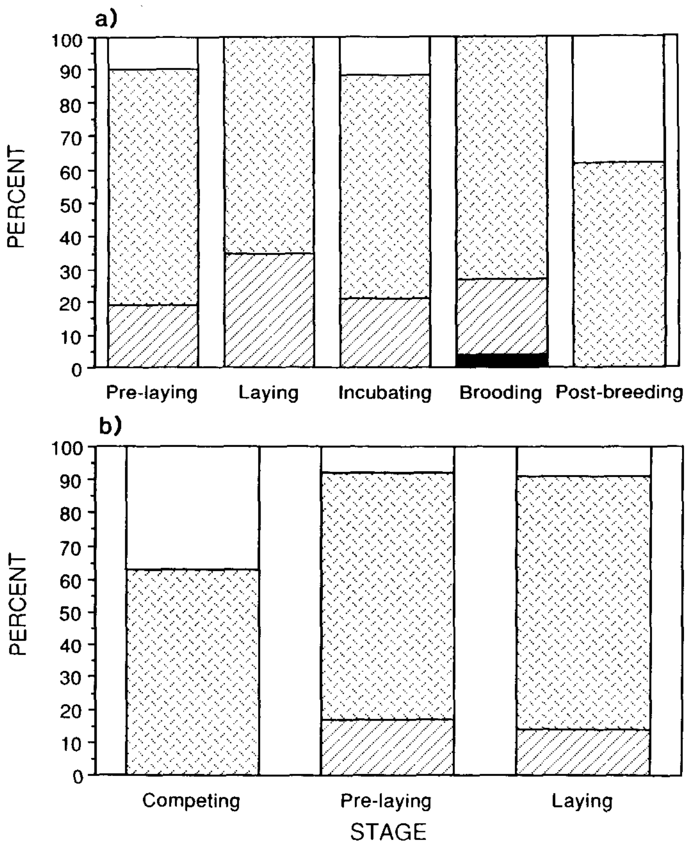

FIG. 4. Space use by male (A) and female (B) Wilson's Phalaropes during the reproductive cycle. Individuals were assigned to a distance class based on the largest observed movement during a reproductive stage. Distances were estimated on a logarithmic scale, where ■ = 0–10 m, ▨ = 10–100 m, ▩ = 100–1000 m, and □ = greater than 1 km.

site, suggesting advantages of site familiarity despite a nonterritorial mating system. Although most males foraged at wet meadow sites closest to their nests, some males repeatedly moved >1 km to forage at a given site. Brooding males sometimes moved chicks >1 km during the first days after hatch, but, in general, daily movements of brooding males were restricted to a small area of wet meadow. Males usually moved chicks away from nests to the nearest area of dense, wet vegetation. Brooding males foraged with their chicks and seldom left broods unattended. In 1983, wetland desiccation forced males that hatched chicks in mid-June to move them over 1 km of upland to the nearest wetland.

TABLE 2
REPRODUCTIVE OUTPUT OF PHALAROPES BREEDING AT EAST ALKALINE LAKE (1982–1983) AND LANIGAN CREEK (1984–1987)

Year	Banded males	Total clutches	Total eggs	Average clutch size	% Males successful	% Clutches successful[a]	$\bar{x}$ Chicks hatched	% Eggs hatched	Total chicks
1982	37	49	189	3.9 (0.2)	62.2	56.0	3.5 (0.9)	49.7	94
1983	21	25	95	3.8 (0.4)	28.6	28.0	3.1 (1.1)	23.2	22
1984	38	60	216	3.7 (0.6)	31.6	18.3	3.2 (1.0)	16.2	35
1985	78	82	310	3.9 (0.4)	50.0	43.2	3.4 (0.7)	43.9	136
1986	49	62	227	3.9 (0.4)	42.9	33.9	2.9 (1.0)	27.3	62
1987	75	108	382	3.5 (0.8)	21.3	16.7	2.9 (1.1)	12.0	46

[a] Clutch success was significantly different among years ($G = 40.1$, df = 5, $P < 0.001$). A clutch was successful if it hatched at least one chick. The proportion of males that were successful in hatching chicks is conservative in that it includes males of unknown reproductive fate. Average (±SD) chicks hatched deals only with successful clutches.

Clutch size, nesting success, and renesting.—Clutch size averaged 3.8 eggs (Table 2); modal clutch size was four. Although three-egg clutches were recorded on occasion, partial predation or disturbance during laying probably resulted in these seemingly smaller clutches. For instance, on two occasions in 1987 we witnessed partial clutch loss during laying, resulting in a smaller clutch size. We observed three five-egg clutches and one seven-egg clutch. The latter resulted when two females laid eggs in the same nest (Colwell 1986b). On one occasion, a four-egg clutch lost an egg eight days into incubation and gained an egg three days later; we did not know the identity of the female that laid the single egg during incubation. At hatch, clutch size averaged 3.7 eggs. Most successful clutches produced four chicks, but one male hatched five (Table 3).

Total clutch weight (four-egg clutches only) averaged 38 g, approximately 55% of the average weight of a nonlaying female. Total clutch weight was positively correlated with initiation date in 1984, but not in 1982 or 1983 (Kendall's correlation: 1982, $t = -0.17$, N = 9, $P > 0.05$; 1983, $t = -0.06$, N = 15, $P > 0.05$; 1984, $t = 0.41$, N = 15, $P < 0.05$).

Nesting success varied among years (Table 2). Significantly more clutches hatched during 1982 and 1985; success was especially low in 1984 and 1987. In all years, however, the breeding success of individual males was slightly higher than nesting success owing to renesting (see below). Predators took 12–60% of clutches annually (Table 3). Predation (59%), desertion (21%), and cattle (10%) accounted for the greatest proportion of nest loss. During 1987, 10% of clutches lost one or more eggs during incubation, but the male continued to incubate. We observed three American Crows (*Corvus brachyrhynchos*) and one Ring-billed Gull (*Larus*

TABLE 3

FATE OF WILSON'S PHALAROPE CLUTCHES EXPRESSED AS PERCENT OF TOTAL CLUTCHES

Year	Total clutches	Number of chicks at hatch				Unknown	Depredated	Cattle	Abandoned[a]	Human	Infertile
		4	3	2	1						
1982	49	34.7	8.2	8.2	4.1	4.1	12.2	10.2	16.3	2.0	0.0
1983	25	16.0	0.0	12.0	0.0	0.0	60.0	0.0[b]	12.0	0.0	0.0
1984	60	8.3	6.6	1.7	1.7	0.0	60.0	5.0	15.0	0.0	1.7
1985	82	25.0[c]	19.5	3.7	0.0	4.9	20.7	17.1	7.3	1.2	0.0
1986	62	11.3	16.1	1.6	4.8	9.7	46.8	0.0	9.7	0.0	0.0
1987	108	5.5	4.6	1.9	2.8	6.5	50.0	2.8	23.2	2.8	0.0
Average		16.3	9.2	4.9	2.2	4.2	41.6	7.0	13.9	1.0	0.3

[a] Abandonment was often caused by partial clutch loss to predators.

[b] Cattle were not present on the study site this field season.

[c] Includes one clutch that hatched five chicks.

delawarensis) as they consumed phalarope eggs. During 1984, a striped skunk (*Mephitis mephitis*) denned under an observation tower and probably was responsible for the loss of some clutches (one direct observation) and one incubating male. Unknown predators killed four males as they incubated, about 1% of marked males (N = 275).

Daily risk of clutch loss (Table 4) varied within and among years. Overall, clutches experienced less risk of failure in 1985, and were especially vulnerable in 1984. Average weekly risk was greatest early in the season. Males often renested following clutch loss (Table 5). On average, 27% (range: 23–36%) of marked males that lost a clutch before the end of the nesting season (prior to 24 June) obtained a replacement clutch on the study site. The average interclutch interval (period between clutch failure and occurrence of the first egg of the renest) was six days (N = 21). Four males nested three times in a season. In 1985, a male obtained three clutches in 19 days; the identity of the laying female(s) was unknown. In 1986, a male nested three times in approximately 21 days, each time with a different female. In 1987, two males nested three times in 25 and 34 days, respectively, each changing mates once between attempts.

Renesting intervals did not differ for males renesting with the same mate and a new mate (Mann-Whitney *U*-test, $P > 0.05$). However, polyandrous females (N = 4) laid second clutches after significantly longer intervals than females laying replacement clutches for their initial mate (N = 5) (Mann-Whitney *U*-test, $P < 0.05$). In 1987, two females laid at least 11 eggs, one in three nests (clutch sizes: 4, 4, and 3) and the other in four attempts (clutch sizes: 3, 3, 3, and 3). Small clutch sizes (<4) resulted from clutch loss to predators or desertion during laying. The

TABLE 4

SEASONAL CHANGES IN THE DAILY RISK[a] (N) OF CLUTCH LOSS FOR WILSON'S PHALAROPE DURING 1983–1987

Week	Year					Average
	1983	1984	1985	1986	1987	
2	—	—	0 (1)	0 (1)	0 (19)	0
	—	—	0 (1)	0 (1)	0 (19)	0
3	0 (5)	21 (29)	0 (38)	15 (20)	10 (63)	9
	0 (5)	7 (29)	0 (38)	15 (20)	3 (63)	5
4	8 (53)	6 (70)	1 (102)	3 (99)	8 (102)	5
	4 (53)	4 (70)	1 (102)	2 (99)	6 (102)	3
5	9 (88)	5 (121)	4 (208)	2 (229)	7 (210)	5
	9 (88)	4 (121)	2 (208)	3 (264)	4 (210)	4
6	3 (66)	2 (193)	2 (302)	3 (264)	4 (296)	3
	3 (66)	2 (193)	0 (302)	3 (264)	3 (296)	2
7	3 (60)	8 (153)	3 (341)	4 (211)	6 (343)	5
	3 (60)	7 (153)	1 (341)	3 (211)	4 (343)	4
8	0 (39)	9 (86)	2 (312)	4 (120)	6 (230)	4
	0 (39)	9 (86)	0 (312)	3 (120)	3 (230)	3
9	6 (17)	6 (16)	1 (206)	6 (35)	—	5
	6 (17)	0 (16)	1 (206)	3 (35)	—	3
10	—	0 (2)	9 (59)	—	—	5
	—	0 (2)	7 (59)	—	—	4
Average	4	10	3	5	6	
	4	4	1	4	3	

[a] Daily risk was calculated by dividing the total number of clutches lost each week by the number of nest-days that week (×100). The two weekly entries represent calculations based on all nest failures and those lost to predators, respectively. Week 1 = 1–7 May, etc.

minimum interclutch interval (3 days) for these interrupted attempts indicates that subsequent clutches were probably not an extension of laying of the destroyed clutch.

Parental care.—In nearly all cases, males were solely responsible for care of eggs and chicks. Exceptions involved females that continued to associate with their incubating mates, circled the nest site when a human observer approached, or defended the nest site (when male was absent) from other females (Colwell and Oring 1988b). Banded females did not tend chicks, and most were absent at the time their clutches hatched. During 1986, one female was within 100 m of her hatching chicks, but she failed to aid her mate in mobbing when an observer approached the nest. Most females deserted males immediately following clutch completion, especially if surplus males were available (Colwell and Oring 1988b).

TABLE 5

ANNUAL COMPARISON OF RENESTING BY WILSON'S PHALAROPES

	Year					
	1982	1983	1984	1985	1986	1987
Nesting period (days)	45	21	42	42	38	45
% Males renesting[a] (N failed)	25 (8)	23 (13)	24 (21)	30 (20)	36 (14)	24 (45)
Average male interclutch interval (N)	7 (2)	5 (1)	2 (1)	4 (4)	2 (4)	8 (9)
Average female interclutch interval (N)[b]	——	——	——	10 (1)	2 (2)	5 (9)

[a] Includes only clutch failures of marked males.

[b] Includes second clutches of polyandrous females (1985, N = 1; 1987, N = 3).

However, some females continued to defend their mates when the males were on incubation recess (Colwell 1986a, Colwell and Oring 1988b). Females were never observed incubating eggs or mobbing predators (other than humans) in defense of broods. In defense of clutches and broods, males mobbed potential predators such as mink (*Mustela vison*), Franklin's ground squirrel (*Spermophilus franklini*), and Richardson's ground squirrel (*S. richardsoni*).

Incubation (interval between laying of the fourth egg and hatch) averaged 23 days (range: 18–27 days) and was inversely correlated with date of clutch initiation (1982–1987 combined, $r = -0.47$, N = 39, $P < 0.01$); clutches that were initiated at the end of the season required approximately five days less incubation than early clutches. During 1984, one male incubated a clutch of addled eggs for 34 days before he was collected as part of the endocrinology study.

Weight of males (N = 73) decreased significantly during the breeding season. Overall, 78% of males lost an average of 0.5 g per day, 14% maintained weight, and 8% gained an average of 0.3 g per day. One male lost 12 g in 25 days. Although there was no relationship between the weight of a male and date of capture (Kendall's correlation: 1982–1987 combined, $t = -0.174$, N = 66, $P > 0.05$), repeated captures of individuals revealed that weight declined steadily during the breeding season, especially in incubating birds. Male weight dropped significantly from early (first five days) to late (more than 17 days) incubation (paired *t*-test: $t = 6.3$, df = 27, $P < 0.0001$), representing a loss of approximately 6% of male body weight. The few males for which we have weights during late incubation and early brooding continued to show a significant decline in weight (paired *t*-test: $t = 8.9$, df = 4, $P < 0.003$). We noted nothing unusual about the reproductive histories of males that gained weight.

DISCUSSION

Polyandry in phalaropes.—Phalaropes are unusual among birds in exhibiting extreme sex-role reversal (Oring 1982, 1986; Erckmann 1983). Variable mating tactics (Colwell and Oring 1988b) and correlations between seasonal changes in mate availability and intensity of intrasexual competition in Wilson's Phalarope (Colwell and Oring 1988a) indicate that female phalaropes may experience strong sexual selection.

Despite evidence of intense intrasexual competition among females (Colwell and Oring 1988a) and the opportunity for sexual selection, the incidence of polyandry in all three species of phalaropes appears to be low (Hildén and Vuolanto 1972, Raner 1972, Schamel and Tracy 1977, Colwell 1986a, Reynolds 1987, Colwell and Oring 1988b). Differences in the incidence of polyandry and renesting among phalarope populations may be related to any number of proximate factors, including: (1) duration of breeding season, (2) breeding synchrony of males and females, and (3) levels of clutch failure (Emlen and Oring 1977).

Asynchronous arrival of males over a long breeding season favors polyandry by enhancing opportunities for acquiring multiple mates and producing multiple clutches (Emlen and Oring 1977, Erckmann 1983, Reynolds 1987). The opportunity for obtaining multiple mates is constrained by the interaction between the length of breeding season and period required to complete a nesting attempt. Because female Wilson's Phalaropes require 7–10 days to complete a nesting attempt (Colwell and Oring 1988b), or approximately one sixth of the nesting period, considerable time remains for many early-nesting females to pursue additional mates.

Nesting periods vary considerably among the three phalarope species. The duration of nesting for Wilson's Phalarope is nearly twice that reported for most populations of Red and Red-necked phalaropes (see Erckmann 1983), providing more time for second nesting attempts and replacement clutches. Multiple renesting, observed in Wilson's Phalarope, has not been recorded for either Red or Red-necked phalaropes.

Frequent clutch failure may provide additional breeding opportunities for females by reintroducing males into the breeding population, but it also may result in renesting by a pair, depending on the timing of clutch loss with respect to pairbond and clutch completion (Oring et al. 1983, Colwell and Oring 1988b). Levels of clutch failure vary greatly among phalarope species, ranging from 0–100% losses (Table 2, see Erckmann 1983, Reynolds 1987).

The incidence of polyandry may also be constrained by factors influencing competitive abilities of females. Reynolds (1987) argued that the ability of female Red-necked Phalaropes to obtain multiple mates was not energetically constrained by egg production. Similarly, female Wilson's Phalaropes do not appear to be energetically limited by egg laying, but are capable of rapid, multiple clutch production.

Overall, the relationship between proximate and ultimate factors affecting levels of polyandry in phalarope species remains poorly understood. Estimates of incidence of polyandry may be complicated by a number of factors related to the species' unusual mating system. In particular, the lack of territoriality and wide-ranging movements of individuals, particularly females, affects arrival and departure dates and tenure at a given site. Many females that complete a clutch early in the breeding season depart the study area and presumably compete for second mates (Colwell 1986a). On several occasions, females have paired with second mates on the study site, and disappeared shortly thereafter (Colwell and Oring 1988b). Similarly, females that arrive late may have nested elsewhere. In short, estimates of the incidence of polyandry in phalaropes may be premature. Ideally, estimates require an isolated population with very restricted movement of individuals. To date, only the study by Hildén and Vuolanto (1972) of an insular population of Red-necked Phalaropes in Finland meets these standards, and even there arrival patterns of females may influence estimates of polyandry.

Male reproductive patterns. —In contrast to variable female mating patterns (Colwell and Oring 1988b), reproductive tactics of smaller, dull-plumaged male phalaropes are less diverse, characterized by exclusive care of eggs and chicks. Males, however, occasionally compete for mates when local sex ratios are male-biased (Colwell and Oring 1988a, Tracy and Schamel 1988), indicating plasticity to some behavioral aspects of sex-role reversal.

Uniparental care by male phalaropes may impose costs in terms of increased predation and energetic stress during incubation. Comparative details are not available for incubation-related predation in Red or Red-necked phalaropes. Weight loss by incubating males, however, is not typical of all phalarope species. Erckmann (1981) reported that, based on repeated captures of individuals, male Red and Red-necked phalaropes at Wales, Alaska, did not lose weight during incubation. Additional weight change estimates (Erckmann 1981, Schamel and Tracy 1987), based on regression of bird weight vs number of days into incubation, indicate that incubating males in some populations of Arctic breeding phalaropes do lose weight. Such conclusions, however, may be premature because a similar relationship may obtain owing to a correlation between bird weight and clutch initiation date.

Interspecific differences in weight loss may be related to variability in resources available to incubating males at Arctic and temperate latitudes.

A thorough understanding of the energetic costs of male incubation, however, requires a rigorous experimental approach.

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KIRTLAND'S WARBLER SYMPOSIUM

The Huron-Manistee National Forests are co-sponsoring a nationwide symposium on the endangered Kirtland's Warbler February 9–11, 1989, in Lansing, Michigan. The symposium, entitled, "Kirtland's Warbler at the crossroads—extinction or survival" is designed to provide information to wildlife biologists, researchers, special interest groups, and the public. For additional information telephone 1-800-999-7677 or 1-616-779-8715 and ask for Kenneth R. Ennis. Written inquiries can be made to Mr. Ennis, USDA—Forest Service, Huron-Manistee National Forests, 421 South Mitchell Street, Cadillac, MI 49601.