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BREEDING SITE FIDELITY AND NATAL PHILOPATRY IN THE SEX ROLE-REVERSED RED AND RED-NECKED PHALAROPES

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Abstract.—Return rates of banded Red Phalaropes (*Phalaropus fulicaria*) and Red-necked Phalaropes (*Phalaropus lobatus*) for 6 yr were examined in a multi-year study in western and northern Alaska. Results for Red-necked Phalaropes were also compared to those of Reynolds and Cooke (1988), collected in southern Hudson's Bay, Canada. Inter-site differences in breeding site fidelity were significant for Red-necked Phalaropes, but not Red Phalaropes. Both adult and young Red-necked Phalaropes returned to the previous year's nest site at a greater rate than Red Phalaropes. More male Red-necked Phalarope chicks returned than females. Male and female Red-necked Phalaropes associated with successful nests did not return at a significantly higher rate than unsuccessful nesters. Returning males did not experience a significantly higher hatching success than newly-banded males. The equal return rate of male and female Red-necked Phalaropes is best explained by high ultimate hatching success for both sexes and the comparably high rate of polyandry in the study area. The observed male-biased natal philopatry was consistent with Greenwood's (1980) hypothesis regarding sex-biased dispersal in mate defense mating systems. Species differences in return rates may be related to differences in year-to-year habitat availability associated with latitude.

FIDELIDAD AL ÁREA DE REPRODUCCIÓN Y FILOPATRÍA NATAL EN *PHALAROPUS FULICARIA* Y *P. LOBATUS*

Sinopsis.—A través de 6 años, de un trabajo multianual, que se llevó a cabo en la parte oeste y norte de Alaska, se examinó la tasa de retorno de individuos del falaropo rojo (*Phalaropus fulicaria*) y del falaropo pescuecirojo (*P. lobatus*). Se compararon además los resultados obtenidos para el falaropo pescuecirojo con los informados por Reynolds y Cooke (1988) en la Bahía Hudson, Canada. Las diferencias inter-localidad, en lo que se refiere a fidelidad a las áreas reproductivas, fueron significativas para el falaropo pescuecirojo, pero no para el rojo. Tanto adultos como juveniles del primero, retornaron al área de anidamiento con mayor frecuencia que los falaropos rojos. Además, en el falaropo pescuecirojo, regresaron más machos que hembras a estas áreas. En ambos sexos del falaropo pescuecirojo, no hubo diferencia significativa en el retorno, entre aves altamente exitosas en el anidamiento y otras no exitosas. Entre los machos que retornaron al área de anidamiento, no hubo diferencia significativa entre aquellos que tuvieron un alto grado de eclosionamiento y los que fueron anillados como aves nuevas. La similar tasa de retorno entre hembras y machos del falaropo pescuecirojo, puede explicarse por el alto grado de eclosionamiento para ambos sexos y el alto grado de poliandría que se encontró en el área de estudio. El sesgo observado en la filopatría natal de machos, es consistente con la hipótesis de Greenwood (1980). La diferencia en la tasa de retorno, entre especies, puede estar relacionada a diferencias de año a año en la disponibilidad de hábitat, asociado a la latitud.

Patterns of resource exploitation and social organization, including the mating system, may be used to predict dispersal patterns in birds (Greenwood 1980, Pitelka et al. 1974). Arctic-nesting shorebirds that use predictable and defensible food sources show high return rates (Gratto et al. 1985, Soikkeli 1967). Those species thought to settle opportunistically in the best available habitat should show low breeding site fidelity (Pitelka et al. 1974; F. A. Pitelka, pers. comm.) when favorable sites change annually.

Initial data on Red Phalaropes (*Phalaropus fulicaria*) collected in northern Alaska indicated low breeding site fidelity (Schamel and Tracy 1977), consistent with Pitelka et al.'s hypothesis. These birds feed and nest in low-lying habitats rich in food resources, but which are rendered unavailable some years by delayed snow melt (Mayfield 1978).

We also reported a male-bias in returning birds (Schamel and Tracy 1977), consistent with Greenwood's (1980) hypothesis: in mate defense mating systems, as found in sex role-reversed phalaropes (Emlen and Oring 1977), the mate defender (the female in phalaropes) should benefit from greater adult and natal dispersal, through increased access to mates. The limiting sex (the male in phalaropes), meanwhile, should benefit by returning to nest in familiar locations.

In this paper, we compare results from a northern Alaska site (Barrow) with data collected at a more southern Alaska location (Cape Espenberg). At this more southern site, where snow melt preceded arrival of phalaropes, we anticipated higher breeding site fidelity. In addition to nesting Red Phalaropes, the site also supported nesting Red-necked Phalaropes (*Phalaropus lobatus*). As both species are facultatively polyandrous and share similar nesting and foraging characteristics (Hildén and Vuolanto 1972, Reynolds 1987, Schamel and Tracy 1977), we expected similar breeding site fidelity.

STUDY AREAS AND METHODS

We studied Red Phalaropes at Barrow, Alaska (71°17'N, 156°47'W) in 1973–1975. J. P. Myers (pers. comm.) supplied data from 1976. The 100-ha study area was a tundra marsh, interspersed with shallow ponds (Schamel and Tracy 1977). We estimated the number of nesting males in the study area in 1973–1975 as: 13, 15 and 44, respectively.

Red and Red-necked phalaropes were studied at Cape Espenberg, Alaska (66°30'N, 163°30'W) in 1976–1981. The 25-ha study area was a wet tundra marsh (Schamel and Tracy 1987). We estimated the number of nesting males in the study area in 1976–1981 for Red Phalaropes (19, 15, 15, 8, 2 and 2) and Red-necked Phalaropes (24, 22, 39, 60, 57, and 58). Thus, the Red Phalarope population declined and the Red-necked Phalarope population increased.

Nests were examined at 1–3-d intervals until eggs disappeared or hatched. We considered a nest successful if at least one chick hatched. If eggs were pipped on one visit and missing on the next visit, the nest was considered successful, unless the nest bowl was torn.

Adult phalaropes were captured with hoop nets and nest traps (Schamel and Tracy 1977) and banded with a unique combination of three colored bands and one aluminum band (two bands per leg). Chicks were captured by hand at or near nests and banded with one colored band and one aluminum band (one band per leg).

The study areas, and an additional 300 m on each side, were examined each year for banded birds. We noted band combination, breeding status (nesting, paired, single), location and date for each banded bird sighted.

We follow Oring and Lank's (1982) definition of natal philopatry: the return of locally-produced chicks to the study area. Our definition of breeding site fidelity was less restrictive than Oring and Lank's (1982). They reserved this term for local breeders that returned to breed on the study area; we used this term to refer to any local breeder that was resighted on or near the study area in any subsequent year. Oring and Lank's (1982) study area was an entire small island and they had a high probability of identifying all local breeders. In contrast, our study areas were small portions of relatively continuous nesting habitat.

RESULTS

Red Phalaropes.—Both adult male and female Red Phalaropes showed low levels of breeding site fidelity (<20%, Tables 1, 2). Although males at both Barrow and Cape Espenberg returned at apparently higher rates than females (Tables 1 and 2), these differences were not statistically significant ($G = 1.27$, $P > 0.25$, 1 df). The apparently higher rate of site fidelity at Cape Espenberg, compared with Barrow, was not statistically significant ($\chi^2 = 0.43$, $P > 0.50$, 1 df).

Returning adults typically returned in only 1 yr. Only 2 of 12 males returned for more than 1 yr; both returned in two consecutive years (Tables 1, 2). One of three returning females returned in two consecutive years. Of eight returning males whose nest fate (in the initial year of banding) was known, five successfully hatched eggs, two lost clutches to predation and one deserted its nest.

One of 81 banded chicks was resighted at Barrow. It was a yearling male and was recaptured while incubating a clutch of eggs. None of 104 banded chicks was resighted at Cape Espenberg.

Red-necked Phalaropes.—Adult Red-necked Phalaropes showed strong breeding site fidelity and no sex bias in return rate (Table 3). When all banded adults were considered, 50% ($n = 120$) of the males and 51% ($n = 89$) of the females returned. Our banding program was designed to capture primarily locally settled birds (those that were paired or were attempting to form pairs). Considering known nesting birds only, 56% ($n = 99$) of the males and 61% ($n = 41$) of the females returned (Table 3). There was no significant difference between male and female return rates ($\chi^2 = 0.43$, $P > 0.50$, 1 df).

There was a strong tendency for individuals to return for multiple years (Table 3). Although only 51% of males ($n = 99$) and 51% of females ($n = 41$) were resighted the year after banding, of these returning birds 79% of the males ($n = 44$) and 67% of the females ($n = 21$) were resighted again the following year (1976–1979). The return rate remained high in all subsequent years. Nearly half the males who nested in 1976 were resighted in 1981 (Table 3). There was no overall sex bias in return rates any year subsequent to banding ($\chi^2 = 1.85$, $P > 0.25$, 2 df).

There was no significant difference in return rates of males that hatched

TABLE 1. Adult breeding site fidelity of Red Phalaropes at Barrow, Alaska.

Banding Year	Sex	*n*	Number returning in 1974	1975	1976	Total[a]
1973	Male	9	1	1[b]	0	1
	Female	5	0	0	0	0
1974	Male	13	—	1	0	1
	Female	8	—	0	0	0
1975	Male	44	—	—	4	4
	Female	17	—	—	1	1
Total	Male	66	—	—	—	6 (9.1%)
	Female	30	—	—	—	1 (3.3%)

[a] Total number of individuals that returned.
[b] Also returned previous year.

young and those that did not ($\chi^2_c = 1.54$, $P > 0.10$, 1 df, $n = 83$ nests). Returning adult males experienced the same rate of hatching success (71%, $n = 56$ nests) as unbanded and newly-banded males (72%, $n = 77$ nests) ($\chi^2 = 0.001$, $P = 0.975$, 1 df). Returning males also experienced the same ultimate hatching success (fate of the last known nesting attempt) (91%, $n = 44$ nests) as newly-banded males (82%, $n = 62$ nests) ($\chi^2 = 1.55$, $P > 0.10$, 1 df). Note that ultimate hatching success was very high compared to other reports of nest fate (Hildén and Vuolanto 1972, Reynolds 1987). Females experienced high ultimate hatching success in their year of banding (88%, $n = 34$ females). The hatching success of females that returned (95% success, $n = 19$) was not significantly higher ($G = 1.79$, $P > 0.10$, 1 df) than those who did not return (80% success, $n = 15$).

Not all females who produced multiple clutches showed an equal ten-

TABLE 2. Adult breeding site fidelity of Red Phalaropes at Cape Espenberg, Alaska.

Banding year	Sex	*n*	Number returning in 1977	1978	1979	1980	1981	Total[a]
1976	Male	20	3	1[b]	0	0	0	3
	Female	9	1	0	0	0	0	1
1977	Male	13	—	0	1	0	0	1
	Female	5	—	1	1[b]	0	0	1
1978	Male	2	—	—	1	0	0	1
	Female	5	—	—	0	0	0	0
1979	Male	3	—	—	—	1	0	1
	Female	1	—	—	—	0	0	0
Total	Male	38	—	—	—	—	—	6 (16%)
	Female	20	—	—	—	—	—	2 (10%)

[a] Total number of individuals that returned.
[b] Also returned previous year.

TABLE 3. Adult breeding site fidelity of Red-necked Phalaropes at Cape Espenberg, Alaska.

Banding year	Sex	n	Number and (%) returning in					Total[a]
			1977	1978	1979	1980	1981	
1976	Male	24	11 (46%)	11 (46%)	12 (50%)	8 (33%)	5 (21%)	14 (58%)
	Female	1	0	0	0	0	0	0
1977	Male	12	—	6 (50%)	5 (42%)	3 (25%)	3 (25%)	7 (58%)
	Female	6	—	4 (66%)	3 (50%)	2 (34%)	2 (34%)	4 (67%)
1978	Male	24	—	—	10 (42%)	9 (38%)	8 (33%)	12 (50%)
	Female	11	—	—	9 (82%)	6 (55%)	6 (55%)	9 (82%)
1979	Male	28	—	—	—	17 (61%)	13 (46%)	17 (61%)
	Female	22	—	—	—	8 (36%)	8 (36%)	12 (54%)
1980	Male	11	—	—	—	—	6 (54%)	6 (54%)
	Female	1	—	—	—	—	0	0
Total	Male	99	—	—	—	—	—	56 (56%)
	Female	41	—	—	—	—	—	25 (61%)

[a] Total number of individuals that returned. Some birds did not return until two or more years after banding.

dency to return. Considering newly-banded females only, those that were polyandrous returned at a greater rate than those who produced replacement clutches for original mates ($G = 7.8$, $P = 0.05$, 3 df). Females with previous experience in the area did not exhibit this relationship ($G = 1.6$, $P > 0.50$, 3 df).

Assuming a 50:50 sex ratio at banding, 17% ($n = 161.5$) of banded male chicks and 2% ($n = 161.5$) of banded female chicks returned (Table 4). This difference is significant ($\chi^2 = 16.5$, $P < 0.001$, 1 df). Returning cohorts ranged from 5 to 30% of banded chicks for males and 0–6% for females (Table 4). Locally-produced yearling males showed strong breeding site fidelity; 77% of those who nested ($n = 13$) returned the subsequent year. This figure is not significantly different from the overall return rate of males in the year subsequent to banding ($\chi^2 = 1.02$, $P > 0.25$, 1 df). In contrast, none of four yearling females was resighted in subsequent years. Two yearling females were seen only briefly in the study area; neither was paired. The other two were paired and probably nested in or near the study area.

DISCUSSION

As availability of nesting habitat is apparently less dependable further north (Mayfield 1978), we anticipated a latitudinal difference in return rates between Barrow and Cape Espenberg as predicted by the model of Pitelka et al. (1974). Greater site fidelity has been noted in more southerly populations of Pied Flycatchers (*Ficedula hypoleuca*) (von Haartman 1949, Nyholm 1986) and Temminck's Stints (*Calidris temminckii*) (Hildén 1979). Although we found a similar trend in Red Phalaropes, the difference was not statistically significant. It is possible that actual latitudinal differences do exist, but they are small and difficult to detect with a small sample

TABLE 4. Natal philopatry in Red-necked Phalaropes at Cape Espenberg, Alaska.

Hatch year	Sex	n^a	Number sighted in 1977	1978	1979	1980	1981	Total[b]
1976	Male	37.5	4	3	1	2	2	6 (16%)
	Female	37.5	0	0	0	0	0	0 (0%)
1977	Male	37	—	2	0	0	0	2 (6%)
	Female	37	—	0	0	0	0	0 (0%)
1978	Male	34	—	—	9	8	5	10 (30%)
	Female	34	—	—	2	0	0	2 (6%)
1979	Male	53	—	—	—	10	7	10 (19%)
	Female	53	—	—	—	2	0	2 (4%)
Total	Male	161.5	—	—	—	—	—	28 (17%)
	Female	161.5	—	—	—	—	—	4 (2%)

[a] A 50:50 sex ratio is assumed. The number of either-sex chicks banded in any year is determined by: total number of chicks banded/2.

[b] Total number of individuals that returned. Some birds did not return until two or more years after banding.

size. In contrast, breeding site fidelity was significantly greater in Red-necked Phalaropes at Cape Espenberg (51%) than at LaPerouse Bay, in southern Hudson's Bay (34%, Reynolds and Cooke 1988) ($\chi^2 = 8.54$, $P < 0.005$, 1 df). Although LaPerouse Bay (58°24′N) is located further south than Cape Espenberg (66°30′N), arrival of summer there is more delayed; Red-necked Phalarope nesting dates were typically 7–8 d later than at Cape Espenberg (Reynolds 1987; Schamel and Tracy, unpubl. data).

The large difference in breeding site fidelity between Red and Red-necked phalaropes was a surprise, about which we can only speculate. As the mating systems of these two species are essentially the same, differences in habitat use might explain site fidelity differences. Red Phalaropes are the more northern species, with breeding grounds from western Alaska (60°N) to northern Canada (80°N) (Mayfield 1979). Red-necked Phalaropes breed from 58°N to 71°N (Cramp and Simmons 1983). Red Phalaropes may be adapted for exploiting an environment where food resources and nesting habitat are frequently rendered unavailable in any given location by late snow melt or early summer snow storms (Mayfield 1978). For example, harsh weather caused major delays or precluded nesting in 2 of 7 yr in northern Canada (Mayfield 1978) and 1 of 3 yr at Barrow (Schamel and Tracy 1987). The more southerly-nesting Red-necked Phalarope, in contrast, may exploit a more predictable environment where food resources generally fluctuate less and late snow melt may occasionally delay, but not preclude, nesting. In contrast to the above northern sites, weather-related nesting delays were noted in only 1 of 5 yr at LaPerouse Bay, Manitoba, Canada (Reynolds 1987) and 1 of 6 yr at Cape Espenberg (Tracy and Schamel, unpubl. data).

Our data on natal philopatry, showing male-biased natal philopatry, support Greenwood's (1980) predictions concerning a mate defense mating system. It is unlikely, however, that this pattern was related either to avoidance of inbreeding or to avoidance of competition for mates (between yearling females and their mothers), as suggested by Greenwood (1980). The suggestion that yearling females may be more likely than older birds to form pair bonds on migration seems more plausible (Colwell et al. 1989, Reynolds and Cooke 1988). All other studies of phalaropes have also found male-biased natal philopatry (Colwell et al. 1989, Hildén and Vuolanto 1972, Reynolds and Cooke 1988).

Although the average return rates of male and female Red-necked Phalaropes were the same, females appeared to show greater variability than males (Table 3). Our data suggest that females gauge the desirability of returning to a nesting area by the number of different mates obtained, not the number of clutches produced. The 1978 adult female banding cohort showed the highest female return rate the year after banding (82%). In 1978, females experienced the highest rate of polyandry (21% of the females, half of whom were banded in 1978) and the lowest nest predation rate (14%) (Schamel and Tracy, unpubl. data). In contrast to 1978, only 36% of females in the 1979 banding cohort returned in 1980 (Table 3). In 1979, 11% of females were polyandrous (including only one female banded in 1979) and 35% of all clutches were lost to predators (Schamel and Tracy, unpubl. data). Even though many lost clutches were replaced in 1979, 19% of the females departed the study area with no active or hatched clutches (compared to 0% for 1978). In fact, the production of a second clutch of eggs, in the form of a replacement clutch, actually appeared to lessen the likelihood of returning. All females that were polyandrous in the year of capture, however, returned in subsequent years.

A correlation between hatching success and breeding site fidelity has been demonstrated for passerines (Darley et al. 1977, Harvey et al. 1979) and numerous shorebirds (Gratto et al. 1985, Oring and Lank 1982, Redmond and Jenni 1982), including Red-necked Phalaropes (Reynolds and Cooke 1988). We were surprised, therefore, to find no such correlation in our study. In addition, experienced males did not have significantly greater hatching success than inexperienced males, a phenomenon also noted in Spotted Sandpipers (*Actitis macularia*) (Oring et al. 1983). This probably is due to the very high ultimate hatching success (>80%) experienced by Red-necked Phalaropes in our study area.

The observed pattern of a lower percentage of birds returning between year X (the banding year) and year X + 1 than between year X + 1 and X + 2 (Table 3) is common in shorebirds (Heldt 1966, Hildén 1979, Oring and Lank 1982, Soikkeli 1967, Thompson and Hale 1989). The initial large percentage of non-returners has been explained in terms of the dispersal of unsuccessful breeders (Oring and Lank 1982, Thompson and Hale 1989) and/or first-time breeders (Soikkeli 1967). These explanations do not hold for our population of Red-necked Phalaropes, because we found no relationship between nesting success and breeding site fidelity, and yearling males exhibited strong breeding site fidelity.

We are intrigued by Hildén's (1979) suggestion that "missing" birds were vagrants, who shifted breeding grounds regularly. Such a strategy would complement the latitudinal flexibility in breeding site fidelity discussed earlier. Unfortunately, neither Hildén (1979) nor we have data to test this hypothesis.

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