

## NEW WORLD SECTION



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## RETURN RATES OF PRAIRIE SHOREBIRDS: SEX AND SPECIES DIFFERENCES

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We studied return rates of five shorebird species (Killdeer *Charadrius vociferus*, American Avocet *Recurvirostra americana*, Willet *Catoptrophorus semipalmatus*, Marbled Godwit *Limosa fedoa* and Wilson's Phalarope *Phalaropus tricolor*) banded as adults and chicks at Last Mountain Lake National Wildlife Area, Saskatchewan, Canada from 1982 to 1987. Adult and natal returns were male-biased for Wilson's Phalarope. Most birds returned only in the year subsequent to banding and individuals remained for highly variable amounts of time. Interspecific differences in return rates are correlated with a species' mating system but also may be influenced by habitat requirements and mortality away from breeding areas. Current hypotheses regarding sex-biased philopatry are discussed.

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Patterns of avian dispersal parallel interspecific variation in mating system (Greenwood 1980). Male-biased philopatry is typical of most bird species (e.g. many passerines), in which territorial males compete for resources necessary for mate acquisition. In non-territorial species (e.g. many waterfowl) where males defend females directly and females invest heavily in parental care, sex-biased patterns of philopatry are reversed; females are more site-faithful than males. Patterns of philopatry vary considerably, however, even among closely related taxa (Greenwood 1980).

Sex-biased patterns of philopatry have been attributed to a number of causes, including 1) intrasexual competition for resources or mates (Dobson 1982, Moore & Ali 1984), 2) inbreeding avoidance (Greenwood 1980), 3) avoidance of cuckoldry and misdirected parental care (Liberg & von Shantz 1985) or some combination of multiple factors (Dobson & Jones 1985). Comparative data from closely related species can offer valuable insights into the evolution of philopatric behavior, especially when species are studied in sympatry. The comparative approach has limitations, however, because data derived from closely related species may not be independent (Clutton-Brock & Harvey 1984).

Shorebirds (suborder Charadrii) are a well studied group with regard to philopatry (see references in Oring & Lank 1984 and Haig & Oring 1988). Here, we present data on natal and adult return rates for five shorebird species that breed sympatrically in the prairie region of North America. Species and sex differences are discussed in terms of a species' mating system, breeding habitat and demography.

## METHODS

We studied shorebirds at Last Mountain Lake National Wildlife Area in southcentral Saskatchewan (52° 10'N, 110° 02'W) between 1982 and 1987. The shorebird community and principle study area are described in detail elsewhere (Colwell & Oring 1988a, 1988b, 1988c). Briefly, we conducted research during 1982-1983 at East Alkaline Lake, a 40 ha site comprised of an ephemeral wetland amid grazed grassland. East Alkaline Lake was dry in 1984 owing to severe drought. As a result, we studied shorebirds from 1984 to 1987 at Lanigan Creek, a 100 ha site embracing a heavily-grazed pasture and wetland. Compared to East Alkaline Lake, water levels at Lanigan Creek were less subject to effects of drought due to regulation by a man-made dam.

We captured birds using mist nets, nest traps, decoy traps, and walk-in funnel traps and we banded each adult with a unique combination of three colored plastic leg bands and a metal band. In addition, most individuals captured during 1984-1987 were marked with colored nylon patagial tags (Curtis et al. 1983). The tags did not affect return rates (Colwell et al. 1988). During 1986, 19 females were fitted with 3.5 g radio transmitters (Raim 1978), which remained on birds 6-21 days. In addition, blood was sampled from the brachial vein of Wilson's Phalaropes during 1984-1987. Return rates were not influenced by blood sampling techniques (Colwell et al. 1988). Chicks were banded shortly after hatching with a brood-specific combination of one color and one metal band.

We collected data on shorebird nesting ecology, including dates of arrival, clutch initiation and hatch and fate of nesting attempts (hatched

at least one chick, or clutch failed owing to predators, abandonment, trampling by cattle, or human error). The return of individuals was monitored during daily observation periods. We also surveyed surrounding wetlands for marked birds, especially during drought years. Birds were considered to be philopatric if they were seen at least once during the breeding season.

Data were summarized by species and sex and philopatric individuals were tallied only once, regardless of how many years the individual returned. Individuals banded as chicks that returned in multiple years were not included in analyses of adult philopatry. These criteria maintained independence of observations for statistical analyses. Statistical procedures follow Sokal & Rohlf (1981). All tests are nonparametric.

## RESULTS

### Adult return rates

Adult philopatry differed among species (Table 1). Overall, Wilson's Phalarope returned significantly less often than Killdeer, American Avocet, Willet and Marbled Godwit ( $G=37.1$ ,  $df=4$ ,  $P=0.0001$ ). In 1983, one Willet not considered philopatric was observed at a wetland 5 km away from East Alkaline Lake.

Sex-biased philopatry was evident for Wilson's Phalarope, in which males returned significantly more often than females (Table 1). Return rates were not sex-biased for the other four species, but sample sizes were small.

Male Wilson's Phalaropes that hatched at least one chick (23/108) exhibited significantly

Table 2. Interspecific comparison of philopatry presented as the number of individuals of both sexes returning in subsequent years. Data include individuals banded as adults and chicks.

Species		n	years present since banding			
			1	2	3	4
Killdeer	males	3	3			
	unknown	2	1	1		
American Avocet	males	2	2			
	males	4	3		1	
Willet	females	2	2			
	males	4	3		1	
Marbled Godwit	females	4	3		1	
	males	4	3		1	
Wilson's Phalarope	males	55	48	4	3	
	females	8	7	1		

higher return rates ( $G=5.1$ ,  $df=1$ ,  $P=0.02$ ) than failed breeders (8/84). There was no relationship between hatching success and return rate for the other four species (Fisher's Exact Probability Test; all comparisons  $P>0.05$ ).

The number of years that philopatric individuals returned to a site was similar among species (Table 2). Most birds were seen only in the year following banding. However, a small proportion of individuals of each species returned in multiple years. A pair of Marbled Godwits returned to East Alkaline Lake and nested on the same territory in three of four years, being absent only in the year the site was dry (1984). This pair was observed at a nearby wetland however, during 1984. Inter-year (1982-1983) distance between nests of this godwit pair was 40 m.

During the drought year of 1984, East Alkaline Lake provided unsuitable habitat for breeding shorebirds (Colwell 1986, Colwell & Oring, unpubl. data). Despite a lack of water, a single banded Willet, four Marbled Godwits and three Wilson's Phalaropes were observed at the nearest wetland (approximately 1 km away) that held water. In 1985, when East Alkaline Lake again held ample water, we observed two marked godwits and five phalaropes. The godwits were the same pair that returned in four successive years, whereas none of the phalaropes had been observed since 1982 or 1983.

Returning individuals varied considerably in length of stay at study sites (Table 1). Individuals of territorial species were seen more often throughout a breeding season, whereas non-territorial phalaropes, especially females, often were seen only once.

### Natal philopatry

Return rates for chicks were low (Table 1). Male Wilson's Phalaropes returned significantly more often than females (Table 1). One Willet chick banded at East Alkaline Lake was observed at Lanigan Creek in three successive years, a distance of approximately 5 km.

## DISCUSSION

### Interspecific differences

Overall, adult return rates for five species of prairie shorebirds were similar to levels of philopatry reported elsewhere for these species or other closely related waders (Oring & Lank 1982, 1984, 1986, Gratto et al. 1985, Colwell et al. 1988, Haig & Oring 1988, Oring 1988, Thompson et al. 1988). Moreover, interspecific differences were apparent despite small sample sizes for all species but Wilson's Phalarope.

Table 1. Interspecific comparison of adult and natal return rates and length of stay. Natal philopatry was calculated as the proportion of males and females resighted, assuming an equal sex ratio among young at hatch. Average length of stay ( $\pm$  SD) was calculated as the interval between first and last date of observation.

	% Adults returned (n)				p*	% Chicks* returned				p*	Tenure at site <sup>b</sup>		
	Males	Females	Unknown	n		Males	Females	Unknown	n		mean ( $\pm$ SD)	n	range
Killdeer	40 (5)	0 (3)	100 (2)	0.1	10	0	0	20	0.5	68 $\pm$ 45	5	1- 90+	
American Avocet	5 (2)	50 (2)	0	1.0	0	0	0	13	1.0	3 $\pm$ 2	2	1- 4	
Willet	100 (3)	100 (2)	0	1.0	0	0	11	9	0.5	34 $\pm$ 22	4	1- 90+	
Marbled Godwit	80 (5)	60 (5)	0	0.5	0	11	0	19	0.5	36 $\pm$ 40	4	1- 90+	
Wilson's Phalarope	19 (189)	5 (87)	0	0.0001	12	3	0	314	0.001	25 $\pm$ 23	20	1- 60+	
										12 $\pm$ 13	7	1- 37	

\* Sex of chicks was determined by morphology, plumage and behaviour.

<sup>b</sup> Maximum values for length of stay were estimated for individuals with unfledged young prior to the end of research.

\* Probability associated with Fisher's Exact Test (for small n) or G-Test.

Oring & Lank (1984) observed that interspecific differences in philopatry among shorebirds were correlated with social systems. They noted that strongly philopatric species were characterized by monogamy, biparental care and joint defense of breeding territories. By contrast, species typified by non-territorial mating systems and uniparental care returned much less often.

Our data supplement observations of Oring & Lank (1984) linking philopatry to a species' social system. Return rates for Willet, Marbled Godwit and Killdeer, all species with territorial mating systems and biparental care, were much higher than Wilson's Phalarope, which has a non-territorial, sex-role reversed mating system with uniparental care. Philopatry of American Avocet, which may or may not nest colonially, was similar to territorial species. A correlation between philopatry and mating system suggests that high return rates of territorial species are associated with advantages of site familiarity in competition for breeding sites (Greenwood 1980; see below). By this reasoning, non-territorial species return less often because breeding opportunities are not limited by intraspecific competition for resources. In addition, site familiarity confers less of a breeding advantage compared with territorial species, especially for the sex experiencing stronger intrasexual competition.

Although the association between philopatry and mating system appears strong, return rates may differ among species for proximate reasons. For instance, interspecific differences in breeding habitat requirements may influence philopatry, especially at ephemeral wetlands. Such wetlands hold resources that change dramatically on a seasonal or annual basis (Colwell 1986, Colwell unpubl. data); and the suitability of these sites for breeding may vary among species. Since choice of breeding site can be cued by differences in aquatic habitat (e.g. Greenberg 1988), species with specialized habitat needs may shift breeding sites more readily than species with less rigid habitat requirements.

At Last Mountain Lake, breeding shorebirds exhibited considerable interspecific variation in use of wetland microhabitats (Colwell & Oring 1988b, Colwell unpubl. data). In particular, American Avocet and Wilson's Phalarope were highly aquatic, whereas Killdeer, Willett, and Marbled Godwit were more terrestrial. These differences in use of aquatic habitat appear to be correlated with return rates at ephemeral wetlands. One American Avocet returned to East Alkaline Lake early in the 1983 breeding season but failed to nest there, presumably because water levels were low.

Breeding habitat was more ephemeral at East Alkaline Lake than Lanigan Creek, yet return rates of Wilson's Phalarope did not differ between sites (Colwell et al. 1988). This comparison, however, only considered years when East Alkaline Lake held water and ignores the obvious lack of philopatry during the drought year of 1984, when returning birds homed to the nearest available wetland. The return of individuals to East Alkaline Lake in 1985 suggests that development of philopatric behavior may be set by experiences operating early in the life of individuals (Oring & Lank 1984). In addition, habitat characteristics prevailing at the time of return may strongly influence site fidelity.

Interspecific differences in philopatry may arise via other demographic factors associated

with the annual cycle of species. All of the species included in this study are migratory, so that dispersal to wintering grounds occurs annually (Oring & Lank 1984). Differential patterns of mortality for species that inhabit geographically distinct wintering areas and, therefore, that differ in timing, distance and route of migration may contribute to apparent differences in philopatry. Additionally, differences in mortality and longevity among shorebird species are correlated with size (Boyd 1962); large species have lower mortality and greater longevity than small taxa. Average mass of species in this study ranged from 52 ± 4 g (n=155) for male Wilson's Phalaropes to 353 ± 45 g (n=9; both sexes combined) for Marbled Godwits.

#### Sex differences

The lack of sex difference in adult and natal philopatry for Killdeer, American Avocet, Willet and Marbled Godwit does not support the mating system hypothesis as described by Greenwood (1980). Small sample sizes for all but Wilson's Phalarope may account for the lack of fit. Additional factors, such as age and breeding experience may influence levels of philopatry (Oring & Lank 1984, 1986) and, thus, may mask any sex differences. For instance, long term monogamy in Long-billed Curlews *Numenius americanus* may account for equal adult return rates of males and females (Redmond & Jenni 1982). We resighted one godwit pair and two willet pairs together in subsequent years indicating long term mating relationships. Additionally, successful breeders usually return significantly more often than failed breeders (e.g. Redmond & Jenni 1982, Oring & Lank 1982, 1984, 1986, Gratto et al. 1985). In this study, nesting success was correlated with higher return rates for male Wilson's Phalaropes.

Only Wilson's Phalaropes exhibited significant male-biased adult and natal philopatry, an observation that is consonant with predictions of the mating system hypothesis (Greenwood 1980). In non-territorial, sex-role reversed phalaropes, the mating system hypothesis predicts that males should be more philopatric than females. This occurs because males contribute virtually all parental care and, therefore, benefit more from site familiarity. Female phalaropes generally are present for shorter periods (Table 3) and range more widely than males (Colwell & Oring 1988b). Phalarope philopatry, however, is not consistently male-biased (Colwell et al. 1988). There is no sex bias in adult philopatry for either Red Phalarope *P. fulicaria* or Red-necked Phalarope *P. lobatus*; in addition to Wilson's Phalarope, only Red-necked Phalarope exhibits male-biased natal philopatry.

Philopatry can have a profound impact on the evolution of social behavior (Redmond & Jenni 1982, Shields 1983). Inbreeding and other demographic conditions necessary for the evolution of cooperative behavior are however, very restrictive, requiring high site fidelity and longevity. These criteria likely operate less strongly in many migratory species that breed at ephemeral wetlands. Thus, it is unlikely that kin-selected behaviors are related to the social behavior of many prairie-breeding shorebirds.

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