

MATE, SITE, AND TERRITORY FIDELITY IN PIPING PLOVERS

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ABSTRACT.—Breeding-site fidelity, territory retention, and mate fidelity were examined in a color-banded population of monogamous Piping Plovers (*Charadrius melodus*) breeding at five focal sites in southern Manitoba from 1981 to 1986. Frequent nest destruction by predators and storms provided numerous opportunities for birds to change mates and territories during and among breeding seasons. Between years approximately 70% of surviving adults were site faithful. Males did not return significantly more often than females, and both sexes returned regardless of previous reproductive success. Although former mates were present in subsequent years, 30 of 37 birds changed mates. Birds that changed mates from the previous year and whose mates were present in subsequent years had experienced poorer hatching success the previous season than those that retained mates. Birds that retained mates did not improve their reproductive success over the previous year.

After nest destruction during the breeding season, most adults kept mates (34/52 pairs) but changed territories. Birds changed territories significantly more often, and moved significantly farther, following nest destruction by storm than following predation. Birds that retained mates during the breeding season fledged more chicks than those that changed.

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IDENTIFICATION of individual behavioral phenotypes and subpopulation demographic characteristics exposes a vast amount of variation in organisms with even the most rigid social systems (Bekoff 1977, Oring et al. 1983, Mock 1985, Beissinger and Snyder 1987). In birds more than 90% of the species exhibit a primarily monogamous mating system (Lack 1968, Oring 1982). Until recently, monogamy generated little interest, largely because of a belief that exceptional mating systems had more potential for contributing to an understanding of the evolution of avian social systems. Even in monogamous species mate choice and re-pairing occur throughout an individual's lifetime, and present many options for variation in this social system (Ford 1983, Rowley 1983, Wickler and Seibt 1983, Anderson 1985, Mock and Gowaty 1985, Oring and Sayler in press). In this paper we report environmental and social factors that can lead to variability in mate retention, site fidelity, territory retention, and reproductive success in the monogamous Piping Plover (*Charadrius melodus*).

Piping Plovers are biparental, territorial

shorebirds that often breed repeatedly in the same area (Wilcox 1959, Cairns 1982, Wiens 1986, Haig 1987a). Throughout their breeding range Piping Plovers nest in highly ephemeral beach habitat that is regularly washed out or otherwise altered (Haig et al. 1988). Previous studies of monogamous shorebirds indicate that mate retention and site fidelity may produce greater relative reproductive success (e.g. Soikkeli 1970, Hale and Ashcroft 1982, Lessells 1984, Gratto et al. 1985). Therefore, one might predict that Piping Plovers exhibit similar patterns. The dynamic environment they inhabit, however, provides occasions for birds to reassess mates, territories, and breeding sites within and between years.

STUDY AREA AND METHODS

The study was conducted from 1982 to 1985 in Manitoba (Fig. 1). One hundred to 120 Piping Plovers bred annually in Manitoba on 10 sites in the southern portion of the province (Haig 1985, 1987b). We selected study areas from among these sites.

Stony Beach (50°14'N, 98°7'W) is a 2-km stretch of narrow (\bar{x} beach width = 11.5 m), sandy, pebbled beach located 13 km east of Delta Waterfowl and Wetlands Research Station on a beach ridge separating the Delta Marsh from Lake Manitoba. Three to 5 pairs bred there in 1982–1985.

Clandeboye Bay (50°15'N, 98°6'W) is located 2.2 km

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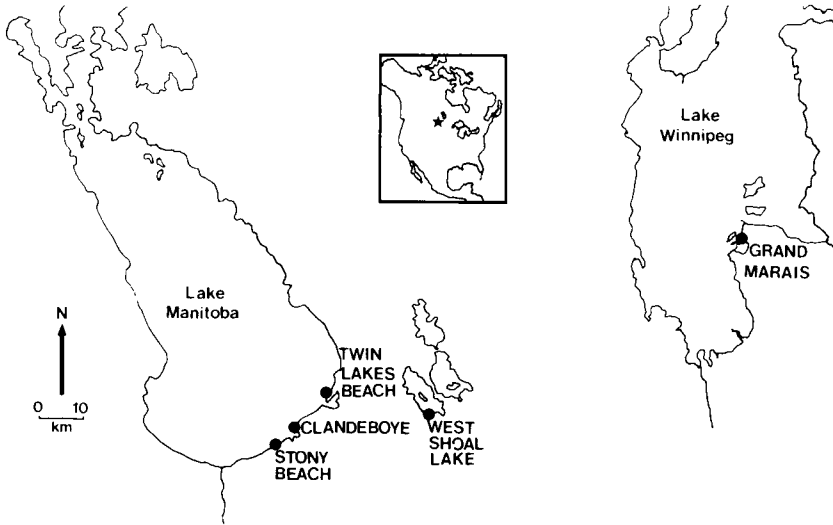


Fig. 1. Piping Plover study areas in southern Manitoba, 1981–1985.

east of Stony Beach and is composed of two sandspits bordering the channel that unites the Delta Marsh with Lake Manitoba. The western sandspit is 95 m long (\bar{x} beach width = 20.7 m) and is bordered by a dense stand of sapling willows (*Salix* spp.). The eastern sandspit is 975 m long (\bar{x} beach width = 46.7 m) and is bordered by dune grasses (*Poa* spp.) and scattered cottonwoods (*Populus* spp.). Five to 8 pairs used the area from 1982 to 1984, and 2 pairs bred there in 1985.

Twin Lakes Beach (50°20'N, 97°53'W), located 13 km northeast of Clandeboye Bay, is a 4-km-long sandspit developed for recreational use by cottage owners. The southern 1 km, used by Piping Plovers, is similar in width and dune structure to Clandeboye Bay (\bar{x} beach width = 20.1 m). Migrating birds used Twin Lakes Beach as a staging area, and 1–2 pairs bred there annually.

West Shoal Lake (50°20'N, 97°36'W) is a shallow, alkali lake located 32 km east of Clandeboye Bay and 70 km west of Grand Marais. Approximately 75% of Piping Plovers in the province used the southern shore during the breeding season and during spring and fall migration. The 5 km of southern shoreline comprises a series of long (1–3 km), sparsely vegetated peninsulas that undergo extreme daily and seasonal variation in the amount of exposed alkali beach.

The Grand Marais (50°30'N, 96°40'W) sites include a 0.75-km-long \times 35-m-wide sandspit separating Lake Winnipeg from Grand Marais Marsh, and the southern 0.5 km of a 1-km-long, narrow (beach width: 10–22 m) island, located approximately 1 km offshore from the sandspit. Two to 3 pairs nested on the spit, and 5–6 pairs nested on the island.

Each study area, by virtue of narrow beach widths, flat terrain, and adjacent large bodies of water, was

vulnerable to extensive flooding when northerly winds were greater than 25 km/h (velocity verified at Delta Waterfowl and Wetlands Research Station weather station). Given almost constant heavy winds in Manitoba, the threat of inundation at all sites was common. Heavy wind, rain, and snow storms in April–June accentuated the phenomenon. Each summer inundation up to the vegetation line occurred at all sites at least twice (and up to four times at certain sites). Severe weather not only affected nest success but reshaped breeding sites.

Breeding birds (50 males, 47 females) at all study sites were captured in mist nets and given individual combinations of color bands. In 1984 and 1985 international flags (Myers et al. 1983) were used as part of the color-band combination. Chicks ($n = 122$) were caught by hand shortly after hatch and color-banded. We obtained life-history patterns for 81 pairs of marked adults and their offspring.

Approximately 2,900 h were spent observing focal birds at Stony Beach (1981–1984), Clandeboye Bay (1981–1984), and West Shoal Lake (1984–1985). Marked birds were observed daily from arrival in mid-April until departure in mid-August. Each day, each observer ($n = 3$ or 4) watched birds 3 times for 2–3-h periods so that all focal pairs were observed at least once. Observation periods were used to identify number and distribution of Piping Plovers present; individual, nest, and chick locations; pair combinations; individual breeding chronologies; nest stage and success; chick stage and success; and various social interactions.

Observations were made from 10 3-m-high enclosed towers, 2 3-m-high scaffolding platforms, and 3 modified muskrat houses (Nuechterlein 1980). Flagged reinforcing bar rods were staked at 25-m in-

tervals along the beach at Clandeboye Bay, Stony Beach, and West Shoal Lake to verify site fidelity and territory size. Numbered black stakes 15 cm high were used to mark all Piping Plover nests encountered. To reduce disturbance to nesting areas, observers were present on beaches only during banding and to inspect nests that had been destroyed. Eggs in nests were observed from blinds or vegetated areas adjacent to beaches. Nest loss was attributed to storms if the site was washed out and a storm had just taken place. Disappearance of clutches in the absence of a storm was attributed to predation. Unless a specific cause was obvious (e.g. predator tracks to nest during a storm), indeterminate cases were eliminated from analyses.

Surveys of potential Piping Plover habitat and censuses of known Piping Plover breeding sites were carried out in southern Manitoba. During weekly censuses at Stony Beach, Clandeboye Bay, Twin Lakes Beach, and West Shoal Lake, the total number of adults, nests, and chicks was recorded, as well as identification of marked birds and their mates. Weather permitting, weekly censuses of all four sites were carried out simultaneously or within a 24-h period to minimize distortion of overall population estimates. Similar data were collected in censuses conducted every 3 weeks at Grand Marais and annually (1982–1987) at other Piping Plover breeding sites in the province.

Piping Plovers are highly monomorphic, but most breeding adults can be sexed through observation of copulation position and various courtship displays (described by Cairns 1982). During copulation males were observed on females' backs in all but two instances. In these two cases known females mounted males following attempted copulation by their mates. Plumage brightness also distinguished breeding males from breeding females in most cases. Typically, males have brighter and more extensive black breast and forehead bands, and brighter orange bills. Many males had a black mustache in the malar region. Mustaches appeared on some females but were much lighter than those of males. All banded birds were photographed to evaluate and verify sexing from year to year. Only birds that were consistently categorized to the same sex were used in data analyses. We could not sex chicks.

We define "monogamy" as occurring when an individual formed one pair bond at a time during the breeding season. "Perennial monogamy" refers to an individual that maintained a pair bond with the same mate for two or more consecutive years. A "pair bond" is a union between two birds that resulted in the laying of at least one egg. "Mate retention" occurred when the reuniting of a former pair resulted in the laying of at least one egg. An individual exhibited "site fidelity" (or "retention") when it bred in the same area (e.g. Stony Beach, West Shoal Lake, etc.) as the previous year. "Territory fidelity" (or "retention") is more specific and refers to an individual that re-

turned to the specific location (± 25 m) on a breeding site where it bred the previous year.

A nest is considered successful if it produced one chick. Similarly, an individual is successful if it hatched at least one chick per year. Fledging (i.e. observation of sustained flight by the individual chick) at least one chick from a nest was used as a more stringent criterion for nest or individual success in some instances.

Values are reported as means \pm SD.

RESULTS

In each study area Piping Plovers used only certain locations year after year for nesting territories. Pairs initiated pebble-lined nest scrapes 25–100 m apart on multipurpose territories. Females laid 4 eggs per clutch that took 4–8 days ($\bar{x} = 6.2 \pm 1.0$, $n = 10$) to complete. Incubation of clutches by both males and females began after the first egg was laid and continued for 22–31 days ($\bar{x} = 25.7 \pm 2.5$, $n = 9$) past clutch completion. Overall ($n = 73$ nests), 1.1 ± 1.6 chicks hatched per nest. Once chicks hatched, parental care varied: some broods were cared for by both parents, while in others the females deserted the brood within 10 days, leaving males to care for chicks. Fledging rates averaged 0.9 ± 0.9 ($n = 80$) chicks per nest. Adults re-nested up to two times if nest destruction occurred but never raised more than one brood per season. Hence, all adults ($n = 163$ bird years) except one female were monogamous. Parents of first-nest broods spent significantly more days with chicks than parents of chicks that hatched from re-nests (Mann-Whitney $U = 1.5$, $N_1 = 10$, $N_2 = 6$, $P < 0.01$). Hatching and fledging rates did not differ significantly between first nests and re-nests.

Frequent nest destruction by storms and predators during the breeding season created a situation where focal breeding adults had multiple nests and mates (Table 1); even so, many birds in the population did not attain a mate or initiate a nest. Among all adults a significant number did not reproduce successfully in any given year ($\chi^2 = 10.9$, 1 df, $P < 0.005$). The Lake Manitoba and West Shoal Lake sites differed in population size and reproductive success (Table 2), but the overall pattern was similar: less than half of the breeding pairs were successful each year.

Of 72 nests monitored from laying of the first egg through destruction or fledging, 63.8% were subsequently destroyed. Low nest success (in all cases of nest loss, the complete clutch was

TABLE 1. Annual individual reproductive effort of Piping Plovers breeding in southern Manitoba, 1982-1985.

	<i>n</i>	Mean	Range	SD
No. of mates	71	1.3	0-2	0.5
No. of nests	80	1.6	0-3	0.6
Eggs laid/female	78	6.2	0-12	2.3
Chicks hatched	92	1.7	0-4	1.7
Chicks fledged	94	0.9	0-4	1.4

destroyed) was attributed to storms (23.8%), predation (40%) by skunks (*Mephitis mephitis*) and red fox (*Vulpes vulpes*), or human interference. First nests were destroyed 72% of the time, whereas only 43.3% of renests were destroyed.

Sixty-eight percent (44/65) of breeding adults returned to their previous breeding sites the next year. Eighteen birds that did not return to previous breeding sites the next year were seen at different breeding sites in Manitoba or returned to their old breeding sites two or more years later (dispersal patterns were discussed further by Haig 1987a). Therefore, 71% (44/62) of birds known to survive returned to their former breeding sites.

There was no significant difference in return patterns among males and females, nor was the likelihood of return influenced by previous reproductive success (Table 3). Birds that returned did not significantly improve their reproductive success. Where subsequent reproductive success was monitored, 50% (22/44) were as successful (had chicks hatch again) or improved their success (did not hatch chicks the first year,

TABLE 2. Population reproductive success of Piping Plovers at Lake Manitoba and West Shoal Lake, Manitoba, 1982-1985.

	West Shoal Lake	Lake Manitoba	Total
Years	1984-1985	1982-1985	1982-1985
Birds	61	37	98
Pairs	33	20	53
Nests	45	27	72
Chicks fledged per:			
Breeding pair	1.5	0.3	1.0
Pair with brood	3.1	1.3	2.7
Percentage pairs fledging chicks	48.5	20.0	37.7

TABLE 3. Breeding-site fidelity of Piping Plovers in southern Manitoba by previous year's reproductive success. Sample sizes (in parentheses) are the number of individuals monitored.

Previous success	Percentage return		
	Males	Females	Overall
Chicks hatched	73.3 (15)	54.5 (11)	65.4 (26)
Nests failed	76.5 (17)	57.1 (14)	67.7 (31)

hatched chicks the second year), and 50% (22/44) were unsuccessful again or did worse (hatched chicks the first year, failed the following year).

Piping Plovers that returned to a site varied in mate or territory fidelity, or both (Table 4). Males stayed on territories more often than did females, but more than 70% of both males and females paired with new mates. Where success was known among birds that changed mates, only 40% (10/25) of birds had been successful in hatching chicks the previous year. On the other hand, 4 of 7 perennially monogamous pairs were successful the previous year. Among perennially monogamous pairs, 1 pair improved its success the following year, 4 pairs hatched chicks again, and 2 pairs failed.

Closer examination of pair-bond dissolution indicated that 30 of 37 of the returning birds' mates were present on the study area the following spring, and reuniting was theoretically possible. When both members of the pair were present the following spring, however, 20 of 30 pairs did not reunite. Birds that subsequently changed mates, but whose mates were present, had poorer hatching success (hatch vs. no hatch)

TABLE 4. Interyear mate fidelity and territory retention of Piping Plovers breeding in southern Manitoba, 1982-1985. Sample sizes (in parentheses) are the number of individuals monitored. Asterisks indicate significant differences between males and females (χ^2 , $P < 0.01$).

Pattern	Males (%)	Females (%)	Overall (%)
Changed mate	73.1 (26)	78.6 (14)	75.0 (40)
Changed territory	41.0 (39) *	85.7 (14)	52.8 (53)
Changed mate			
Changed territory	26.3 (19) *	100.0 (11)	53.3 (30)
Kept territory	73.7	0.0	46.7
Kept mate			
Changed territory	42.9 (7)	33.3 (3)	40.0 (10)
Kept territory	57.1	66.7	60.0

TABLE 5. Comparison of previous hatching success among Piping Plovers that retained territories in southern Manitoba with those that changed territories. Sample sizes (in parentheses) are the number of individuals monitored.

Pattern	Percentage that hatched chicks in previous year ^a		
	Males	Females	Combined
Kept territory	28.6 (14)	100.0 (2)	37.5 (16)
Changed territory	44.4 (9)	33.3 (12)	38.1 (21)

^a Differences within sexes were not significant ($P \leq 0.05$).

the previous season than those that retained mates, although the difference was not significant ($\chi^2 = 3.23$, 1 df, $P < 0.075$). Three pairs that remained together failed in their first nesting attempts the following year. All three pairs terminated their pair bonds before reneating. Therefore, previous success did not affect site fidelity, but birds that were not successful tended not to retain mates.

When changing mates, 8 of 13 males paired with females that were present on the study site the year before. The other 5 males paired with unbanded females that may have been present in the area the previous year but were not present on any of the focal sites. Seventy-one percent of females (5/7) paired with males present the year before.

Territory retention, and distances moved by birds that changed territories, varied with success. Males that changed territories had better reproductive success the previous year than those that retained territories (Table 5). The two females that returned to the same territory had been successful the previous breeding season and also kept the same mate. Previously successful males and females that changed territories moved 1-2 territories away. Birds that changed territories following nest failure traveled significantly farther than those that changed territories following a successful year (Mann-Whitney $U = 36$, $N_1 = 17$, $N_2 = 9$, $P < 0.05$). Seventy-eight percent (7/9) of males and 50% (4/8) of females that changed territories following previous nest failure actually changed breeding sites.

Territory- and mate-retention options available to returning birds were available to reneating birds within years as well. Following nest destruction 50 of 96 adults reneated on one of the study areas, 39 of 96 were not seen again on any study area for the remainder of the sea-

TABLE 6. Intra-year mate and territory fidelity of Piping Plovers breeding in southern Manitoba, 1982-1985.^a Sample sizes (in parentheses) are number of individuals monitored.

Pattern	Males (%)	Females (%)	Overall (%)
Changed territory	63.6 (22)	70.8 (24)	64.7 (46)
Changed mate	40.7 (27)	28.0 (25)	34.6 (52)
Changed mate			
Changed territory	62.5 (8)	100 (19)	88.9 (27)
Kept territory	37.5	0.0	11.1
Kept mate			
Changed territory	62.5 (16)	62.5 (16)	62.5 (32)
Kept territory	37.5	37.5	37.5

^a Data represent birds that reneated following nest failure.

son, and 7 of 96 remained in the area but did not reneate. Following nest destruction more adults changed territories than remained on previous territories ($\chi^2 = 5.6$, 1 df, $P < 0.05$), but most did not switch mates ($\chi^2 = 4.8$, 1 df, $P < 0.05$) (Tables 6 and 7). If the second nest was destroyed, most birds deserted their territories ($\chi^2 = 14.4$, 1 df, $P < 0.005$), and most did not reneate ($\chi^2 = 6.8$, 1 df, $P < 0.01$). Birds reneating for a second time did not change mates ($\chi^2 = 19$, 1 df, $P < 0.005$).

Territory retention and mate switching were uncommon among reneating birds but warrant more thorough examination. First, there was no relationship between birds changing mates and the number of days of laying or incubating they had invested in first clutches (Mann-Whitney U , not significant). Furthermore, the source of nest destruction did not significantly affect mate-switching tendencies. After nest destruction by a storm, 8 of 26 changed mates; 5 of 14 birds whose nests had been depredated changed mates. Seven of 9 Lake Manitoba birds reneated with individuals not present on the study area

TABLE 7. Intra-year pair-bond retention following destruction of Piping Plover nests in southern Manitoba, 1982-1985.^a

Year	Pair bond		n
	Dissolved (%)	Persisted (%)	
1982	58.3	41.7	12
1983	33.3	66.7	6
1984	42.9	57.1	14
1985	15.0	85.0	20
1982-1985	34.6	65.4	52

^a Data represent pairs in which at least one member of pair reneated on a study site in Manitoba.

before nest destruction. All West Shoal Lake birds paired with birds that were present before nest failure.

The number of days invested in the previous clutch did not affect the likelihood of territory retention. Rather, the likelihood of changing territories was related to the source of nest destruction. Piping Plovers changed territories significantly more often following nest destruction by a storm than following nest predation ($\chi^2 = 6.67$, 1 df, $P < 0.05$). Birds whose nests had been destroyed by a storm changed territories significantly more often than not (22/27 changed; $\chi^2 = 10.7$, 1 df, $P < 0.005$), while only 11 of 32 pairs whose nests had been depredated changed territories. Furthermore, birds that re-nested following storms moved significantly farther from their first nest sites than did birds whose nests had been depredated ($z = 3.74$, $P < 0.01$). There was no difference in reproductive success among birds that changed territories compared with birds that stayed on territories following predation (5/9 pairs that stayed hatched chicks vs. 4/6 pairs that changed territories) or storm destruction (10/21 pairs that stayed hatched chicks vs. 3/6 pairs that changed territories) of first nests.

Five pairs that switched mates took approximately 13 ± 6.4 days to initiate a new clutch; 11 pairs that remained together took 8.3 ± 1.5 days. Hatching success in second nests where birds retained mates ($n = 26$) was 42.3%, slightly higher than success for birds that changed mates (35.7% nests produced hatchlings, $n = 16$). Birds that retained mates were significantly more successful in fledging chicks than birds that chose new mates ($\chi^2 = 11.6$, 1 df, $P < 0.005$).

DISCUSSION

Piping Plovers, like other charadriids (reviewed by Oring and Lank 1982, Haig 1987a), tend to return to breeding sites in subsequent years. Familiarity with an area may facilitate acquisition of food, territories, and mates and may enhance territory defense and predator avoidance (Shields 1982, 1984; Moore and Ali 1984; Dobson and Jones 1986). Although there are potential benefits to site fidelity, lack of other breeding-site options may also influence return patterns. When local population densities are high, a bird may be more successful if it returns to a familiar area than if it moves elsewhere (Weatherhead and Boak 1986). In Man-

itoba, Piping Plover site fidelity may be intensified because of a lack of suitable, stable habitat. Censuses and distribution information (Haig 1985, 1987b; Haig and Oring 1985) indicate there is a vast amount of undisturbed beach habitat in the region, yet over 90% of the Piping Plovers in Manitoba were found on our study sites (Haig 1987b). The nearest population, in northern Minnesota, is suffering from a decline in habitat quality, and the number of breeding sites there is decreasing (Wiens 1986, Haig and Oring 1987). Many nonbreeding birds were present at West Shoal Lake, further suggesting there was a lack of suitable nest sites at other locations.

Many birds are less likely to return to an area after poor breeding success the previous year (e.g. Martin 1974, Darley et al. 1977, Brooke 1978, Harvey et al. 1979, Oring and Lank 1982, Oring et al. 1983, Blockstein 1986, Weatherhead and Boak 1986). Piping Plovers returned regardless of their previous success at sites in Manitoba and Minnesota (Wiens 1986). This indicates a lack of suitable alternatives, or reflects the species' preference for breeding in ephemeral sites where annual nest destruction is common. Because experience in an area can improve an individual's lifetime reproductive success, it is not surprising that returning birds in Manitoba had higher reproductive success than the overall population for any given year. The increasing age of adults also leads to greater reproductive success, but we could not make detailed comparisons among age classes.

Social factors may contribute to the site fidelity of Piping Plovers in southern Manitoba. In some instances Piping Plovers nest as single pairs (e.g. Twin Lakes Beach), but in many instances (e.g. Chain of Lakes, North Dakota; Big Quill Lake, Saskatchewan) they nest in large concentrations (Harris et al. 1984, Prindiville 1986). A tendency to nest in loose aggregations eliminates the use of smaller, seemingly viable sites simply because of a lack of appropriate social stimuli.

While most adult Piping Plovers exhibit breeding-site fidelity, the ephemeral nature of their nesting habitat prevents some individuals from returning to previous territories or nest sites. Changes in the microhabitat and social structure at breeding sites also lead to changing territories if suitable areas of higher quality are available elsewhere. Song Sparrows (*Melospiza melodia*; Weatherhead and Boak 1986), Eurasian Sparrowhawks (*Accipiter nisus*; Newton and

Marquiss 1982), and Black-billed Magpies (*Pica pica*; Baeyens 1981) changed and, consequently, upgraded territory quality when conditions in their present territories deteriorated.

Greenwood (1980, 1983) predicted sex-biased site fidelity among monogamous territorial birds when resources are defended by one sex to attract members of the opposite sex. Selection is hypothesized to favor site fidelity in the former and dispersal in the latter. Data for Piping Plovers generally support this hypothesis, although the difference between the sexes is not statistically significant. Generally, monogamous sandpipers (Oring and Lank 1982, Gratto et al. 1985) and plovers (Haig 1987a) lack any statistical difference in return patterns between the sexes, although males usually return more often than females. Female Piping Plovers are not constrained by territory acquisition, and the benefit of pairing with a familiar individual provides one explanation for return rates close to males. Longer-term studies of Piping Plovers may reveal sex biases in survivorship that will better explain these patterns. Wilcox (1959) found that only 13% of female Piping Plovers lived past 5 years of age, compared with 28% of males. It is problematic, however, as to whether the females he monitored had dispersed to other sites or died.

Birds can enhance their lifetime reproductive success by finding and retaining a mate in a stable environment (e.g. Brown 1966, Nelson 1966, Conroy 1972, Mills 1973, Brooke 1978, Ollason and Dunnet 1978, Newton and Marquiss 1982, Coulson and Thomas 1983, Rowley 1983, Cuthbert 1985). For migratory birds, finding a previous mate is encumbered by fluctuations in arrival times, variation in site fidelity and site stability, and differential mortality rates between the sexes (Soikkeli 1967, Holmes 1971, Coulson and Thomas 1983, Rowley 1983, Eliason 1986). Most shorebird species are limited by these factors, but many reunite with former mates if both are present (Soikkeli 1967, Hale and Ashcroft 1982, Oring and Lank 1982, Gratto et al. 1985, Warriner et al. 1986).

Many long-term studies have outlined the potential benefits of mate retention, but few have examined the effect of previous reproductive success on perennial mate retention (Rohwer 1983, Rowley 1983). In southern Manitoba, where a few pairs contribute most of the new individuals to the population and nest destruction is common, there is no predictable pattern

for success. Therefore, either mate retention does not matter, or the factors involved are so diverse and variable that differences are not measurable. Males can benefit by returning to the same territory, but if environmental or social conditions change, they may be more successful if they change territories. Females also respond to variable conditions but are not restricted by acquiring territories. Each year they must reassess their choice of territory and mate.

Nest destruction and renesting are common events during the breeding season for Piping Plovers in Manitoba. For some birds remaining on the same territory with the same mate allows rapid renesting. Subsequent reproductive success is improved because they are familiar with their surroundings and mates and need not invest time in acquiring new mates and territories (Soikkeli 1970, Harvey et al. 1979, Parker 1981). Many species, including Piping Plovers, are less likely to reuse a nest site or territory after a poor breeding experience early in the season (Greig-Smith 1982). Changing territories may facilitate finding a better mate, decrease the chance of repeated predation, avoid resource depletion on the first site, or improve territory quality. Piping Plovers frequently change territories after their nests have been destroyed by a storm. Indeed, the territory and surrounding area may be so altered that it is no longer suitable for nesting. Furthermore, there is the chance of repeated washout.

Following nest depredation Piping Plovers usually remain on their territories and place the next nests within 30 m of the previous nests. If nest predators are patchily distributed, dispersal before renesting can decrease the chance of future nest depredation. If predators are universally distributed, it does not pay to disperse (Rohwer 1983). Because Piping Plover territories in Manitoba tend to be clumped, moving to a new territory on the current site should not decrease the chances of future predation. Furthermore, the time involved in dispersal following predation may not be compensated for by any benefit from a reduction in the probability of predation on the new nest (Wunderle 1984). Reproductive success for Piping Plovers was not improved for birds that changed territories following predation, and the benefit in moving seems small.

Generally, if new territories are unavailable, dispersal may not result in improved reproductive success (Weatherhead and Boak 1986).

In Manitoba, territories or mates, or both, become available when nests are simultaneously destroyed or through habitat alteration. Early-summer storms usually destroy many nests synchronously, providing opportunities to obtain new mates or territories. New nesting territories also are created throughout the season by evaporation of Manitoba lakes.

Resource depletion on territories has been proposed as a factor influencing intrayear dispersal patterns (Nice 1937, Greig-Smith 1982). We did not measure food abundance, but territories that were deserted (and not completely washed out) following first-nest destruction were inhabited immediately by a new pair that usually stayed for the remainder of the breeding season. Resource depletion therefore was not critical. Because Piping Plovers forage both on and off their territories, the importance of food abundance and quality on the territory is lessened.

Finally, intrayear mate switching was not common in Piping Plovers, but we observed it more frequently than has been reported for other single-brooded monogamous species (reviewed by Rohwer 1983). Even among non-monogamous avian species, the phenomenon is rarely reported and is usually the result of nest failure (Rohwer 1983). A relatively high occurrence among Piping Plovers in Manitoba may stem from easy access to new mates after frequent nest destruction. Intrayear mate switching may be reported more frequently when monogamy is examined on a finer scale.

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100 Years Ago in The Auk



From "Notes and News" (1888, *Auk* 5: 223):

"The subject of the voluntary interlocking of the primaries in soaring birds (see *Jan. Auk*, pp. 126, 127) came up again for discussion at the meeting of the New York Academy of Sciences, held Jan. 9 last, and formed the special topic of the evening. The discussion was opened by a paper by Mr. J. A. Allen, entitled 'On the Flight of Birds, with special reference to recent alleged discoveries in the Mechanism of the Wing,' in which he answered certain criticisms made at the previous meeting of the Academy, reflecting on the motives and animus of the ornithologists, and then took up the structure of birds in relation to flight, describing at some length the bones and muscles involved, and the arrangement and structure of the feathers. The alleged 'new muscles' were shown to have been well known for over a century, and by means of a freshly-killed *Buteo borealis* it was demonstrated that the tips of the primaries, when the wing is fully extended, as in soaring, do not even touch each other, but are separated by a considerable

space, and that consequently overlapping at the tip, or 'interlocking,' is simply impossible. It was shown that the wing must be partly closed before the tips of the primaries can be brought near enough to overlap, and that if they should overlap—which they can do only in the partly closed state of the wing—they would fail entirely to aid in relieving muscular strain in keeping the wing distended. In short, it was shown that the 'interlocking' claimed was not only an impossibility, but was wholly unnecessary as a provision for relieving muscular tension in flight. Yet the advocate of the new discovery refused to be convinced, and stated that if any one expected him to 'back down' they would find themselves 'mistaken in their man,' or words emphatically to this effect. Those interested in the original paper and in the discussion which followed it will find the subject quite fully reported in the Academy's 'Transactions' (Vol. VII, giving reports of the meetings for November and December, 1887, and January, 1888)."