NEST-SITE TENACITY AND MATE RETENTION IN THE PIPING PLOVER (*Charadrius melodus*)

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ABSTRACT

Piping Plovers (Charadrius melodus) were studied for 3 breeding seasons in Lake of the Woods, Minnesota, to determine: (a) the distribution, philopatry, and breeding success of the local population, and (b) the effect of previous breeding success on nest-site tenacity and mate retention. It was hypothesized that successful breeders would be more likely to return to the same nest-sites and to retain the same mates than individuals that failed to produce offspring the previous year.

The population consisted of approximately 47 adults which nested at 4 breeding localities within the study area. A mean of 1.4 juveniles/breeding pair survived to fledging each year. Both adult and natal philopatry were relatively strong. Sixty-eight percent of adult birds and 21% of second-year birds returned to the study area in consecutive years. Nest-site tenacity was also well developed. The median distance between successive nests for breeding birds was 41 m. No significant relationship was found between previous breeding success and nest-site tenacity. Scarcity of suitable nesting sites in the Lake of the Woods area may explain why individuals returned to the same sites despite experiencing breeding failure the previous year.

Of all pairs for which both members returned to the study area the subsequent season, 45% reunited, indicating moderate mate retention. No significant

relationship was found between previous breeding success and mate retention. Competition for mates or the advantage of reuniting with a familiar and experienced mate may outweigh any advantage gained by separating after breeding failure.

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INTRODUCTION

Interest in the mating systems of higher vertebrates has increased in recent years (e.g. Orians 1969, Emlen and Oring 1977, Greenwood 1980, Oring 1982). Studies have focused not only on overall strategies (e.g. monogamy) but also on specific aspects of reproductive behavior such as nest-site tenacity and mate retention. Numerous studies have demonstrated that the tendency to return to the same breeding site in consecutive years is widespread among temperate-zone birds (see review in Greenwood 1980). The tendency to reunite with the same mate from year to year has been documented to a lesser extent (see review in Rowley 1983). Within a population, the degree of nest-site tenacity and mate retention varies. It has been shown that either or both may be affected by age (Austin 1949, Ryder 1980), sex (Nice 1937, Wilcox 1959, Lenington and Mace 1975, Darley et al. 1977), site stability (McNicholl 1975, Southern 1977), or previous breeding success (Coulson 1966, Nolan 1978, Oring and Lank 1982). This study examined the effects of previous breeding success on nest-site tenacity and mate retention in Piping Plovers (Charadrius melodus) nesting in northern Minnesota.

For most avian species, individual breeding success is significantly influenced by the quality of both

nesting territory and mate. In addition, evolutionary theory predicts that an individual will repeat strategies that are successful and abandon those which are not. Thus, one would predict that successful breeders will be more likely to return to the same nesting sites and retain the same mates than those that fail.

The objectives of this research were to study the distribution, philopatry, and breeding success of a local population of Piping Plovers to determine (a) the extent of nest-site tenacity and mate retention exhibited by members of this population and (b) the effect of previous breeding success on site and mate fidelity. I hypothesized that birds producing offspring in a given year would be more likely to exhibit nest-site tenacity and to retain mates in the next season than birds that failed to breed successfully.

STUDY AREA

This study was conducted along the shoreline of the U.S. portion of Lake of the Woods (LOTW), Lake of the Woods County, Minnesota (Fig. 1). Within the study area, Piping Plovers bred at four specific locations referred to as breeding localities: Pine and Curry Island (48°52'N, 94°45'W), Morris Point (48°51'N, 94°46'W), Zippel Bay (48°53'N, 94°52'W), and Rocky Point (48°58'N, 95°02'W). Pine and Curry Island is a long (7 km), narrow

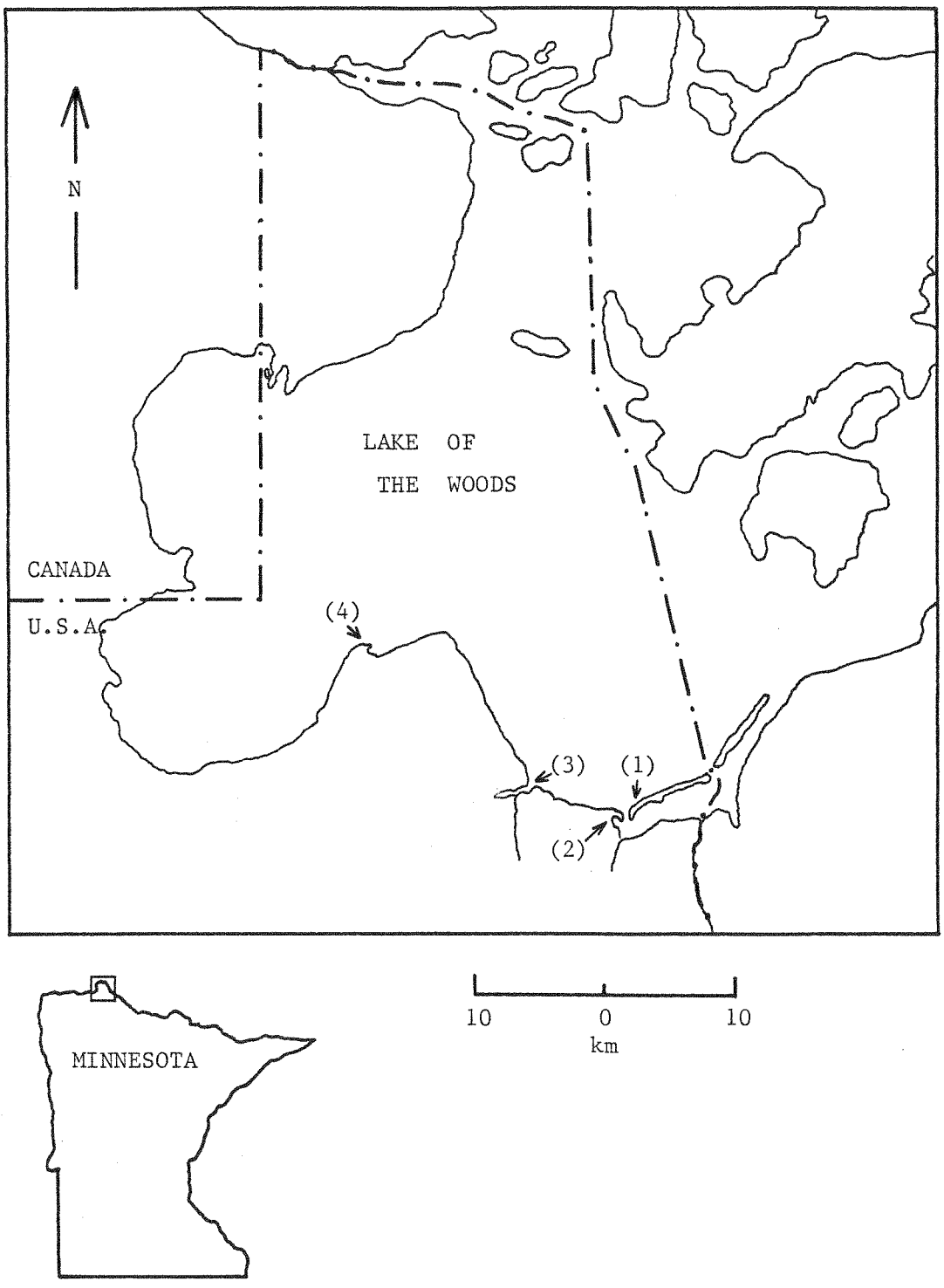

Fig. 1. Map of study area in Lake of the Woods, Minnesota. Breeding localities were (1) Pine and Curry Island, (2) Morris Point, (3) Zippel Bay, and (4) Rocky Point.

sand barrier island located at the mouth of the Rainy River. The Morris Point, Zippel Bay, and Rocky Point localities are sand spits less than 1 km in length. Pine and Curry Island and Morris Point are presently owned by the Minnesota Department of Natural Resources and the Minnesota Chapter of the Nature Conservancy, and have been designated Scientific and Natural Areas. Zippel Bay is part of Zippel Bay State Park, and Rocky Point is State land that is not part of any management unit.

All nest sites were located on sandy beaches and low dunes formed by extensive wave action and current movement. The habitat consisted of open beach and beach community, characterized by relatively sparse vegetation that rarely exceeded 1 m in height. The dominant vegetation was sandbar willow (Salix interior), tail-wormwood (Artemisia caudata), and beach pea (Lathyrus japonicus). Grasses (Poaceae) and sedges (Cyperaceae) were present in moderate densities. Other vegetation included cocklebur (Xanthium sp.), balsam poplar (Populus balsamifera), knotweed (Polygonum sp.), and evening primrose (Oenothera sp.).

In LOTW, Piping Plover breeding localities are undeveloped and are used only occasionally by humans for recreational purposes. Fishing pressure is especially great in the waters near Pine and Curry Island and Morris

Point (a maximum of 250 boats within 0.5 km of the sites).

Piping Plover nesting was first documented for LOTW in 1932 (Swanson and Carlander 1940). The species was observed to commonly breed on Pine and Curry Island (as many as 15 pairs recorded in one year) from 1932 to 1941 (Swanson and Carlander 1940, Carlander 1941). No records exist from 1941 to 1977, but subsequent observations indicate that the population remained relatively stable during this period. Between 1978 and 1981, the Pine and Curry Island breeding population was estimated to range from 15 to 30 pairs (Anderson 1979, Hirsch 1982). Additional pairs periodically have been recorded at Zippel Bay and Rocky Point (Hirsch 1982).

The present nature of Piping Plover nesting habitat in LOTW is probably much different from that previous to this century. In the early 1900's several dams were constructed at the north end of the lake, raising the water level approximately 9 ft (Lund 1975). Changes in the shoreline included the creation of Pine and Curry Island, which was originally part of the mainland. Water levels have been controlled since completion of the dams, resulting in seasonal variations which are usually 2 to 3 ft in extent.

METHODS

This study was conducted during spring and summer of 1982 through 1984. Observations were continuous throughout the plover breeding season, from late April/early May to late July/early August.

Research was conducted on a daily basis, weather permitting. Most observation time was spent at Pine and Curry Island and Morris Point, where 96% of all LOTW plover nesting occurred. Zippel Bay and Rocky Point were checked approximately once a week and three times a season, respectively. In 1982 and 1983 additional surveys were conducted throughout the Minnesota portion of LOTW to document additional or potential nesting habitat. All breeding localities were accessible by boat. A base camp was established on Pine and Curry Island to facilitate access to all localities.

Most fieldwork involved observing plovers to determine (a) characteristics of plover breeding biology, (b) location of nest sites, (c) number and distribution of plovers present, (d) identity of individual birds, (e) pair combinations, and (f) location and status of nests, eggs and chicks. Most observations were made from a boat anchored 5 to 100 m from the beaches where plovers were present. In 1982 additional observations were made from a portable land-based blind. Use of the boat was preferred

because it caused little or no disturbance to the plovers. Checks to determine nest location and status were conducted on foot. In all cases observation was aided by the use of 7x35 binoculars.

Capture and Color-marking Techniques.--To identify individual plovers, I captured 47 adults and 91 juveniles and banded each with a U.S. Fish and Wildlife Service aluminum leg band and a unique combination of colored plastic leg bands; an additional 15 juveniles received only an aluminum band. Most adults (31) were captured with mist nets placed on open beach and/or near nests. Typically I drove the birds into the nets. The remaining 16 adults were captured on the nest with a wire mesh drop trap (Wilcox 1959). Trapping was restricted to nests a week or more into incubation, and attempts were aborted if the adults did not return to incubate within 15 minutes. All juvenile plovers were captured by hand. Juveniles were not color-banded until they were at least 10 days old.

Sexing Techniques.--Because Piping Plovers are sexually monomorphic, I attempted to sex them by behavioral cues. Males were identified by copulatory position and/or a combination of courtship and territorial behaviors (e.g. scrape digging, courtship display flights, territorial defense displays). Cairns (1977, 1982) describes these behaviors in detail.

Determination of Breeding Success.--Nests were checked approximately every other day (except Zippel Bay and Rocky Point) and chicks were monitored up to fledging age. Chicks were considered to be fledged if they reached 10 or more days of age (after Cairns 1977, 1982). Hatching success was calculated as the percentage of eggs hatched from eggs laid. Breeding success was measured as reproductive success (the average number of chicks fledged per breeding pair) and overall fledging success (the percentage of chicks fledged from eggs laid). Pairs were considered to be successful if they raised one or more chicks to fledging.

Determination of Philopatry and Nest-site Tenacity.--Philopatry has been defined as the return rate of birds to a given study area (Gratto et al. 1985). Adult philopatry specifies the return of birds to the general area of a previous breeding attempt. Natal philopatry specifies the return of second-year birds to the general area of their hatching. For the purposes of this study an individual was considered philopatric if it returned to the U.S. portion of LOTW.

Nest-site tenacity has been defined as the tendency for each individual to return to the same "breeding site" year after year (Austin 1949). Nest-site tenacity is commonly considered to be much more specific than philopatry, focusing on the tendency to return to a

precise location within the study area. Some authors have defined nest-site tenacity as the degree to which birds return to their former territories (Lenington and Mace 1975, Darley et al. 1977, Holland et al. 1982, Petrinovich and Patterson 1982). Others consider nest-site tenacity to be the tendency of birds to return to a specific nest location (MacDonald 1977, Howe 1982, Fiedler and Grewe 1983, Morse and Kress 1984, Shields 1984, Gratto et al. 1985). The latter interpretation is used in this study, with nest-site being defined as the precise location of a nest within a breeding locality.

Philopatry was calculated as the percentage of all banded birds present in one season that returned to the study area the next season. Nest-site tenacity was determined by measuring the distance between successive nests for each breeding bird. To determine this distance, I marked all nest-sites with permanent stakes to facilitate locating them in subsequent years. Measurements of the distances between nests were made to the nearest m using a tape measure. For birds moving more than 500 m, the distance between nests was estimated from a map.

Determination of Mate Fidelity.--In 1983 and 1984 I classified each breeding pair from the previous year into one of four categories: reunite (both birds remate with each other), separate (both birds present but at least

one mating with a different bird), discontinue (one bird absent and the other mating with a different bird), and status unknown. Only pairs that reunited or separated were considered in determining mate fidelity.

Analysis.--I used a x^2 test of independence (Freedman et al. 1978) to compare adult philopatry to natal philopatry. To compare the nest-site fidelity of males to that of females and of successful breeders to that of failures, a Mann-Whitney U test was used (Siegel 1956). Birds that reunited were not considered in the analysis of nest-site fidelity. Comparisons of mate changes based on reproductive success were made using Fisher's exact test of independence (Sachs 1982). For all analyses data from more than one year were combined. As a result some individuals may have been represented more than once in a sample.

RESULTS

Population Size and Distribution

The LOTW Piping Plover population had a mean size of 47 adults per year, with little variation (Table 1). Breeding adults represented 68% to 94% of the total population. Breeding attempts were limited to four localities within LOTW: Pine and Curry Island, Morris Point, Zippel Bay, and Rocky Point (Fig. 1). These four

TABLE 1. Local population size for Piping Plovers in Lake of the Woods.

	Year		
	1982	1983	1984
Breeding Adults			
Pine and Curry Island	24	32	36
Morris Point	4	6	8
Zippel Bay	0	2	0
Rocky point	2	2	0
Non-breeding Adults	14	7	3
Total	44	49	47

localities represented most of the suitable nesting habitat present within the Minnesota portion of LOTW.

Of all nesting attempts, 74% were on Pine and Curry Island, 22% on Morris Point, 3% on Rocky Point, and 1% at Zippel Bay. The greatest concentration of nesting (58% of all nests) occurred on Pine and Curry Island within 500 m of the southwest end (Fig. 2).

Breeding Success

Reproductive data for each season are presented in Table 2. Combining all three years, the average number of juveniles fledged per breeding pair was 1.4. Overall fledging success was 31%. Variation in breeding success from year to year resulted primarily from variation in hatching success, which ranged from 19% to 75%. In contrast, survival from hatching to fledging was consistently high (68-69%).

Philopatry

Banding return records are summarized in Table 3. Adult birds returned to the study area in consecutive seasons with greater frequency than second-year birds. Combining all years, 68% (n=80) of the adults returned, whereas 21% (n=70) of the second-year birds returned, a highly significant difference (x^2=34, $p<0.001$).

There was no difference between return rates of adult males and adult females. Seventy-five percent

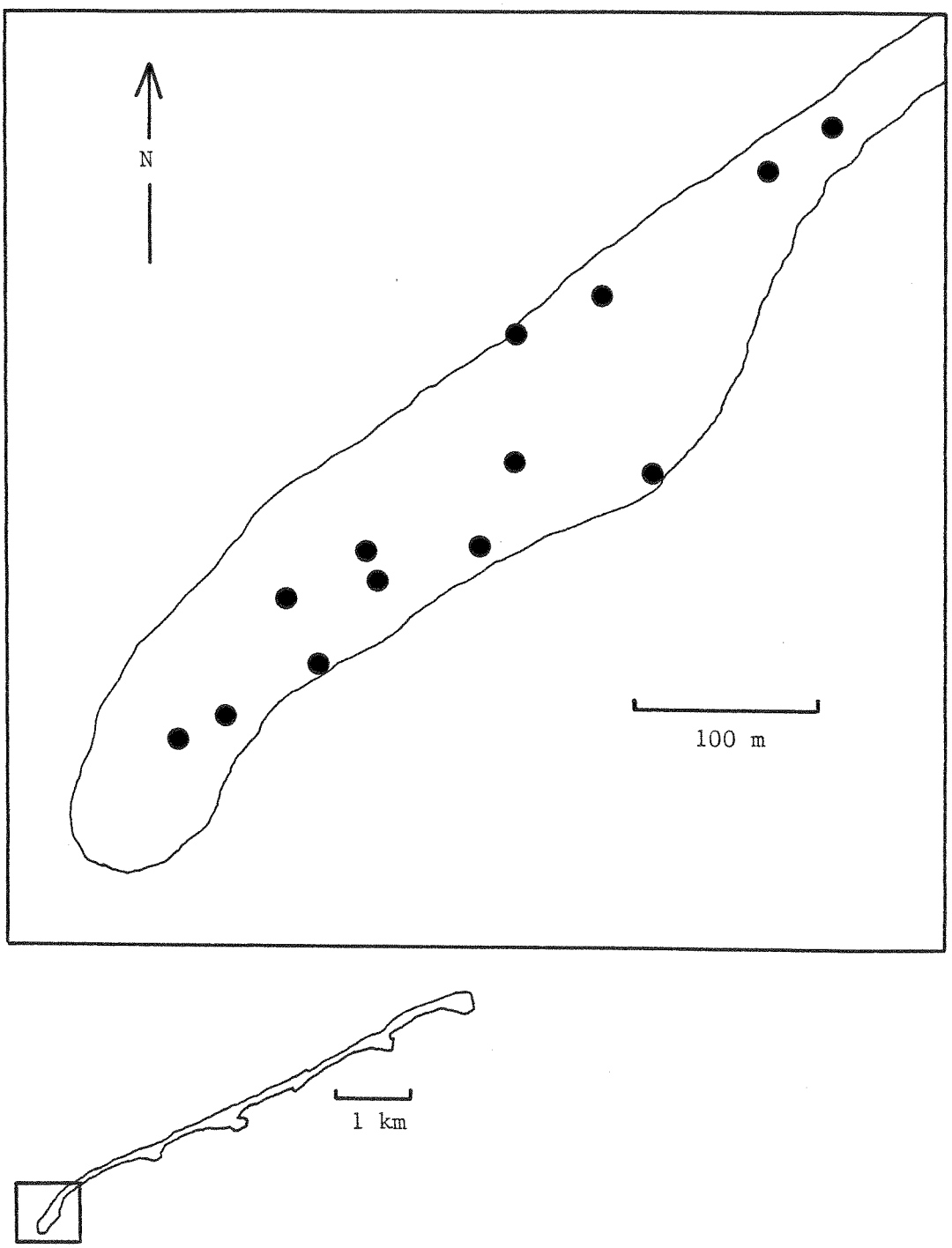

Fig. 2. Map of the southwest end of Pine and Curry Island showing spatial relationship of nest-sites (1983).

TABLE 2. Breeding success for Piping Plovers in Lake of the Woods.

	Year		
	1982	1983	1984
Eggs laid	86	85	99
Eggs hatched	38	64	19
Hatching success	44%	75%	19%
Young hatched	38	64	19
Young fledged	26	44	13
Reproductive success (Fledglings/breeding pair)	1.7	2.1	0.6
Overall fledging success	30%	52%	13%

TABLE 3. Returns of banded Piping Plovers to Lake of the Woods.

	Birds banded as adults		Birds banded as juveniles	
	1982	1983	1982	1983
Originally banded	37	8	26	44
Observed in 1983	26	-	9	-
Observed in 1984	16	7	5	6

(n=28) of the males and 63% (n=24) of the females returned in consecutive seasons (x^2=1.11, p=0.30).

Reproductive success in one season had no apparent effect on the return rate in the next season. Sixty-six percent (n=47) of the birds that succeeded returned, while 76% (n=17) of those that failed returned (x^2=0.45, p=0.50).

Nest-site Tenacity

The distances between successive nests for breeding birds were not normally distributed with extremes of 0 to over 15000 m; the median was 41 m (n=31). Most (84%) of the movements were less than 200 m and occurred within the confines of one breeding locality (e.g. Morris Point). The large extremes occurred when birds nested at different localities in successive years.

Males demonstrated greater site fidelity than females. The median year to year movement was 24 m (n=7) for males and 160 m (n=9) for females, a significant difference (U=14, p<0.05). However, if the outliers (movements between breeding localities) are removed from consideration, the median year to year movement was 24 m (n=7) for males and 86 m (n=6) for females, not significantly different (U=14, p=0.18).

Comparing nest-site tenacity for birds that bred successfully to those that failed, 92% (n=13) of the

successful birds moved less than 200 m whereas 50% (n=8) of the failing birds moved more than 500 m. The median year to year movement was 24 m for successful birds and 297 m for birds that failed. These results suggest a correlation between nest-site tenacity and previous breeding success. However, there was no significant difference in nest-site tenacity between birds that succeeded and those that failed (U=35, p=0.12). Therefore the hypothesis that nest-site tenacity is positively influenced by previous breeding success is rejected at the 95% confidence level.

Mate Retention

Combining data from 1982 and 1983, 36 pairs were present. The fates of these pairs are summarized in Table 4. For 11 pairs (31%) both male and female were present the next season. Five (45%) of those 11 reunited. Two pairs remained together for all three years, accounting for 4 of the 5 pairs reuniting per year.

The effect of previous breeding success on mate retention was inconclusive. The data are presented in Table 5. Five (63%) of 8 successful pairs reunited the next season, whereas none of 3 failing pairs reunited. The results suggest a tendency for previous breeding success to influence mate retention. However, there was no significant difference in mate retention between the

TABLE 4. Fates of breeding Piping Plover pairs in consecutive seasons in Lake of the Woods.

Year	No. of pairs	Fate of pairs in subsequent season			
		Reunite	Separate	Discontinue	Status unknown
1982	15	3	3	7	2
1983	21	2	3	9	7
Total	36	5	6	16	9

TABLE 5. Relationship between mate retention and previous reproductive success in Lake of the Woods Piping Plovers.

Reproductive success in original season	Number of pairs	Fate of pairs in subsequent season			
		Reunite	Separate	Discontinue	Status Unknown
Succeeded	27	5	3	12	7
Failed	9	0	3	4	2

two groups ($p=0.12$). Therefore the hypothesis that birds producing offspring are more likely to reunite the following season than birds that fail is rejected at the 95% confidence level.

DISCUSSION

Results of this study indicate that the LOTW Piping Plover population consisted of a small but relatively stable number of individuals that nested at a few well-defined localities within the study area. The average yearly reproductive rate of 1.4 juveniles produced per breeding pair was comparable to rates of 1.5, 1.7, and 1.3-2.1 determined for east coast Piping Plovers (Cairns 1977, Flemming 1984, Tull 1984). The strong philopatry of adults (almost 70% returning in consecutive years) was typical of migrant species that defend breeding territories. Also typical was the low natal return rate (21% in consecutive years) relative to the adult return rate. Juvenile birds characteristically disperse to a greater extent and have higher mortality than adults. However, natal philopatry at LOTW was high relative to the return rates found for second-year birds in the following studies: 5% in east coast Piping Plovers (Wilcox 1959), 4% in Ringed Plovers (Charadrius hiaticula, Laven 1940), and 6% in Snowy Plovers (C. alexandrinus, Rittinghaus 1956). It is not clear why

relatively high natal philopatry was observed in this study. One possibility is a regional shortage of suitable nesting habitat to which young birds might disperse. There is some indirect evidence which suggests such a shortage may exist. Piping Plovers require open, undisturbed sandy beaches, sandbars, or alkaline flats for nesting (Cairns 1977, Johnsgard 1981, Haig 1983). Such habitat requirements are specialized and may not be easily found. In addition, breeding records for Piping Plovers have always been scarce and usually very localized for areas adjacent to LOTW such as Minnesota (Green and Janssen 1975), North Dakota (Stewart 1975), and Ontario (Bell, 1978). If, indeed, suitable nesting habitat is limited, many second-year birds may be better off returning to their natal area for their first breeding attempt.

Nest-site Tenacity

Although the criteria for comparing nest-site tenacity are not well defined in the literature, it is reasonable to conclude that Piping Plover site tenacity was strong in this study. Eighty-four percent of all breeding birds nested within 200 m of their nest of the previous year; the median distance between nests in consecutive years was 41 m. Austin (1949) considered any trait expressed by more than 50% of a population to be of

"major importance". The results of this study are consistent with those of similar studies of plovers and related species. Nest-site tenacity has been found to varying degrees for Piping Plovers (Wilcox 1959, Cairns 1982), Mountain Plovers (Charadrius montanus, Graul 1973), Killdeer (C. vociferus, Lenington and Mace 1975), Spotted Sandpipers (Actitis macularia, Oring and Lank 1982), Common Sandpipers (A. hypoleucos, Holland et al. 1982), and Stilt Sandpipers (Micropalama himantopus, Jehl 1973).

Traditionally, nest-site tenacity is considered adaptive because familiarity with a site facilitates food exploitation, territorial defense, and predator avoidance. More specifically, Piping Plovers at LOTW may benefit from knowledge concerning high water levels and the local habits of egg predators such as gulls and corvids. High water and egg predation were the predominant causes of nest failure at LOTW (Wiens and Cuthbert 1984). Yet despite the advantages gained by returning to the same nest-site, not all plovers did so. The nest-site tenacity observed in this study was strong but not extremely so. Howe (1982) in a study of Willets (Catoptrophorus semipalmatus) found that all marked pairs returned to the same territories each year. The lack of such extreme nest-site tenacity in plovers may reflect a lack of long-term stability in the nesting habitat. The

nesting habitat at LOTW can be considered to be of intermediate stability; it is altered to some extent each year by beach erosion, sand deposition, and changes in vegetation. McNicholl (1975) suggested that nest-site tenacity is directly correlated to site stability for colonial nesting larids; the gradual change in LOTW habitat may prevent plovers from becoming extremely site specific.

It is not suprising that male nest-site tenacity was significantly greater than female tenacity. This is the case for many territorial bird species (e.g. Darley et al. 1977, Hilden 1979, Greenwood 1980, Gratto et al. 1985). The sex bias in nest-site tenacity may be related to the fact that male Piping Plovers are primarily responsible for territorial establishment and defense. It has been argued by Greenwood (1980) that when resources are defended by one sex to attract members of the other sex, selection will favor site tenacity in the former and greater dispersal in the latter.

Data from this study do not provide statistically significant support for the hypothesis that nest-site tenacity is influenced by previous breeding success. Lack of a significant relationship between previous breeding success and nest-site tenacity has also been observed in studies of Semipalmated Sandpipers (Calidris pusilla, Gratto et al. 1985) and Savannah Sparrows (Passerculus

sandwichensis, Bedard and LaPointe 1984). Yet these results contrast with those of many other studies of philopatric birds. Breeding success was found to have a positive influence on nest-site tenacity for Yellow-eyed Penguins (Megadyptes antipodes, Richdale 1957), Gray Catbirds (Dumetella carolinensis, Darley et al 1977), Northern Fulmars (Fulmarus glacialis, MacDonald 1977), Prairie Warblers (Dendroica discolor, Nolan 1978), Bank Swallows (Riparia riparia, Freer 1979), Great Tits (Parus major, Harvey et al. 1979), and Spotted Sandpipers (Oring and Lank 1982). Newton and Marquiss (1976) found that female Eurasian Sparrowhawks (Accipiter nisus) demonstrate greater site tenacity following breeding success, but males do not.

It is possible that breeding success may have little effect on nest-site tenacity if suitable nesting habitat is limited, as it appears to be in LOTW. Competition for territories may be intense, and as a result any individual that has established a territory may be better off retaining it despite failure in the previous season.

Mate Retention

Mate retention by Piping Plovers was observed in this study but was not extensive. Of all pairs for which both members returned in consecutive seasons, 5 (45%) of 11 reunited. These results are similar to those reported

by Wilcox (1959) in his 20-year study of Piping Plovers on the east coast. Although his data are not specific, he states that "out of the 1,173 adults trapped, 288 were retrapped, but only 39 pairs remained mated from one year to another", implying that mate retention was limited.

Results of this study indicate that Piping Plovers may retain mates less frequently than other shorebirds with similar mating systems. Studies have shown that of all breeding pairs for which both members returned in consecutive seasons, 62% reunited for Western Sandpipers (Calidris mauri, Holmes 1971), 72% for Dunlins (C. alpina, Soikkeli 1967), 81% for Semipalmated Sandpipers (Gratto et al. 1985), 95% for Willets (Howe 1982), and 100% for Stilt Sandpipers (Jehl 1973). If Piping Plovers retain mates less frequently than shorebirds in general, the explanation for this difference is not immediately apparent. Rowley (1983) has argued that the extent of mate retention found in monogamous, migrant species depends largely on longevity; a greater survival rate leading to greater mate fidelity. Yet there is no evidence to indicate that Piping Plover longevity is low relative to other shorebirds. The philopatry of plovers (in effect an index of survival) is approximately the same if not greater than that of Dunlins (Soikkeli 1967), Semipalmated Sandpipers (Gratto et al. 1985), Willets (Howe 1982), and Stilt Sandpipers (Jehl 1973).

It is possible that the mate fidelity of Piping Plovers is related to site stability. Cuthbert (1985) presents evidence that the degree of mate fidelity in colonial seabirds may be positively correlated with site stability. As previously mentioned, nesting habitat in LOTW changed to some extent from year to year. In contrast, shorebirds such as Dunlins, Semipalmated Sandpipers, Stilt Sandpipers, and Western Sandpipers nest in the arctic tundra where changes in habitat from year to year are comparatively slight. The relatively weak mate fidelity observed in Piping Plovers may be related to the lack of long-term site stability at LOTW.

Data from this study do not provide statistically significant support for the hypothesis that mate retention is influenced by previous breeding success. Few other shorebird species have been studied to determine if any relationship exists between breeding success and mate retention. What little is known supports the conclusions of this study. Howe (1982) found that breeding failure did not diminish the strong mate fidelity of Willets. Studies of Stilt Sandpipers (Jehl 1973) and Semipalmated Sandpipers (Gratto et al. 1985) revealed no significant difference in previous breeding success between individuals that reunited and those that separated.

Much of the evidence for a relationship between previous breeding success and mate retention has been

found in seabirds. Many studies have shown that individuals are more likely to separate following breeding failure than following breeding success (Mills 1973, Brooke 1978, Ollason and Dunnet 1978, Boersma et al. 1980, Coulson and Thomas 1983). However, not all seabirds demonstrate this tendency. Studies of Flightless Cormorants (Nannopterum harrisi, Harris 1979) and Caspian Terns (Sterna caspia, Cuthbert 1985) have shown no significant relationship between previous breeding success and mate retention.

There may be no relationship between previous breeding success and mate retention in Piping Plovers if selection favors reuniting despite breeding failure in the previous year. It has been argued by Rowley (1983) that there are distinct advantages to reuniting with the same mate; established pairs may obtain better breeding sites, pair members will be familiar with each other, and there is certainty that both individuals will have at least some experience. It is possible that these factors are more important for LOTW plovers than previous breeding success. There may be a better chance of succeeding in subsequent years with the same partner (despite failing in the past) than there is with a new, "unknown" mate. It is also possible that competition for mates is very intense at LOTW. Although there was no direct evidence for this (such as a skewed sex ratio),

the small size of the population limits the number of choices available to an individual. The importance of obtaining a mate may outweigh any tendency to avoid a particular individual following breeding failure.

It is difficult to separate the effects of mate retention from nest-site tenacity in a study such as this. Is mate retention a result of recognition and choice of an individual, or is it a result of nest-site tenacity? Rowley (1983) argued that nest-site tenacity may function as a means to reunite pairs which are split during the non-breeding season. Jehl (1973) felt that for older pairs of Stilt Sandpipers, mate retention appeared to be largely a consequence of territorial fidelity. Morse and Kress (1984) artificially removed nest-sites within a colony of Leach's Storm Petrels (Oceanodroma leucorhoa) to assess the roles of mate fidelity and site tenacity in retaining mates. Their results indicated mate retention was strongly site-dependent. Thus, it appears that for at least some territorial species nest-site tenacity is of primary importance and mate retention may be a secondary benefit of returning to the same nest territory used the previous year. Piping Plovers fit this pattern, having strong nest-site tenacity and a lower frequency of mate retention.

This study does not provide statistically significant evidence for a relationship between previous

breeding success and nest-site tenacity or mate retention. However, the results were marginally non-significant ($p=0.12$ in both cases) despite extremely small sample sizes. Definite trends suggested that previous breeding success positively influenced both nest-site tenacity and mate retention. A larger sample size might have revealed those trends to be significant at the 5% level. For example, if the sample size were doubled (with proportionately the same results) there would be a statistically significant difference between birds that succeeded and those that failed for both nest-site tenacity ($p=0.04$, $n=42$) and mate retention ($p=0.01$, $n=22$). Continued sampling of the LOTW population may reveal that previous breeding success does play a role in the choice of nest-site and mate.

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