Wilson Bull., 100(4), 1988, pp. 545–553

NEST-SITE TENACITY AND MATE RETENTION OF THE PIPING PLOVER

TERRY P. WIENS AND FRANCESCA J. CUTHBERT[1]

ABSTRACT.—Piping Plovers (*Charadrius melodus*) were studied for three breeding seasons (1982–1984) at Lake of the Woods, Minnesota, to determine the effects of previous breeding success on nest-site tenacity and mate retention. The population consisted of approximately 47 adults that nested at four breeding localities within the study area. Nest-site tenacity was strong; 84% of all breeding birds nested within 200 m of their nest site of the previous year. No significant relationship was found between previous breeding success and nest-site tenacity. Moderate mate retention was observed; of all pairs for which both members returned to the study area the subsequent season, 45% reunited. No significant relationship was found between previous breeding success and mate retention. This study demonstrates the importance of protecting traditional breeding sites used by threatened and endangered populations of Piping Plovers. *Received 3 Nov. 1987, accepted 25 Mar. 1988.*

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). Research has 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 Rowley 1983). Within populations, 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).

The objectives of this research were to determine: (1) extent of nest-site tenacity and mate retention, and (2) the effect of previous breeding success on site and mate fidelity of Piping Plovers (*Charadrius melodus*) nesting in northern Minnesota. We 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.

[1] Dept. Biological Sciences, Univ. of Minnesota–Duluth, Duluth, Minnesota 55812. (Present address FJC: Dept. of Fisheries and Wildlife, Univ. of Minnesota, St. Paul, Minnesota 55108.)

STUDY AREA AND METHODS

This study was conducted along the southern shoreline of the Lake of the Woods (LOTW), Lake of the Woods County, Minnesota. 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, sand barrier island located at the mouth of the Rainy River. The remaining localities are sand spits less than 1 km in length. All nest sites were located on sandy beaches and low dunes formed by extensive wave action and current movement. 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*).

Observations were continuous throughout the plover breeding season, from late April/early May to late July/early August, 1982–1984. 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.

Fieldwork involved observation of plovers to determine reproductive success and the identity and location of individuals. Most observations were made from a boat anchored 5 to 100 m from beaches where plovers were present. In 1982 additional observations were made from a portable land-based blind. Checks to determine nest status and location were conducted on foot. To identify individual plovers, we banded 47 adults and 91 juveniles 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. 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 discontinued if the adults did not return to incubate within 15 minutes. All juvenile plovers were captured by hand.

Nests were checked approximately every other day (except Zippel Bay and Rocky Point) and chicks were monitored until fledging age. Chicks were considered to be fledged if they reached 10 or more days of age (after Cairns 1977, 1982). Pairs were considered to be successful if they raised one or more chicks to fledging.

Some authors have defined nest-site tenacity as the return of birds 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.

Nest-site tenacity was determined by measuring the distance between nests in successive years for each breeding bird. To determine this distance, we marked all nest sites after nesting with permanent stakes to facilitate locating them in subsequent years. Measurements of the distances between nests were made to the nearest meter using a tape measure. For birds moving more than 500 m, the distance between nests was estimated from a map.

In 1983 and 1984 we 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.

TABLE 1
PIPING PLOVER POPULATION SIZE AT FOUR SITES AT 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

To compare the nest-site fidelity of successful breeders to that of unsuccessful individuals, a Mann-Whitney *U*-test was used (Siegel 1956). 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 (14–23%) 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 for any given year. Breeding attempts were limited to four localities within LOTW: Pine and Curry Island (74% of all nests), Morris Point (22%), Rocky Point (3%), and Zippel Bay (1%). These four localities represented most of the suitable nesting habitat present within the Minnesota portion of LOTW.

Nest-site tenacity.—Distances between nests in successive years were not normally distributed with extremes of 0 to over 15,000 m; the median was 41 m (N = 31). Most (84%) of the movements were less than 200 m and occurred within one breeding locality (e.g., Morris Point). Large extremes occurred when birds nested at different localities in successive years.

Comparing nest-site tenacity for birds that bred successfully to those that failed, the median year-to-year movement was 24 m and 297 m, respectively. 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 ($U = 35$, $P = 0.12$ for analysis excluding all birds that reunited [variables not independent]; $U = 48$, $P = 0.10$ for analysis including only one member of each reuniting pair; $U = 61$, $P = 0.08$ for analysis including all members of reuniting pairs). Therefore the hypothesis that nest-site

TABLE 2
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

tenacity is positively influenced by previous breeding success is rejected at the 95% confidence level.

Mate retention.—Combining data from 1982 and 1983, a total of 36 pairs was present (Table 2). For 11 pairs (31%) both male and female were present the next season. Five (45%) of those 11 reunited. Two pairs nested 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. Five (63%) of 8 successful pairs reunited the next season, whereas none of 3 pairs that failed reunited (Table 3). The results suggest a tendency for previous breeding success to influence mate retention. However, there was no significant difference in mate retention between the two groups ($P = 0.12$).

DISCUSSION

Nest-site tenacity.—Although the criteria for comparing nest-site tenacity are not well defined in the literature we conclude that Piping Plover site tenacity was strong during this study. The results of this study are consistent with those obtained from similar studies of plovers and related species. Nest-site tenacity has been reported in other populations of Piping Plovers (Wilcox 1959, Cairns 1982), and in Mountain Plovers (*C. montanus,* Graul 1973), Killdeers (*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). Nest-site tenacity is hypothesized to be adaptive because familiarity with a site facilitates food exploitation, territorial defense, and predator avoidance. Superimposed on these benefits is the fact that Piping Plover nesting habitat is limited in LOTW; very few localities possess the relatively narrow ecological requirements that Piping Plovers appear to prefer. Therefore, plovers that choose to breed in LOTW have very limited nest-site choices.

TABLE 3
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

Data from our 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 from many other studies of philopatric birds. Breeding success was found to increase nest-site tenacity in 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).

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.—The degree of mate retention by Piping Plovers observed in this study was not extensive. Wilcox (1959) also reported mate retention in less than half the birds he retrapped during his 20-year study of Piping Plovers on the east coast.

Results of our 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 in Western Sandpipers (*Calidris mauri,* Holmes 1971), 72% in Dunlins (*C. alpina,* Soikkeli 1967), 81% in Semipalmated Sandpipers (Gratto et al. 1985), 95% in Willets (*Catoptrophorus semipalmatus*) (Howe 1982), and 100% in 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. There is no evidence, however, to indicate that Piping Plover longevity is low relative to other shorebirds.

It is possible that mate fidelity of Piping Plovers is related to site stability. 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. During years of higher than average water levels significant plover habitat is submerged or periodically inundated by storm driven waves. 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. Cuthbert (1985) presents evidence that the degree of mate fidelity in Caspian Terns (*Sterna caspia*) may be positively correlated with site stability. The relatively weak mate fidelity observed in Piping Plovers at LOTW may be related to the lack of long-term site stability at this location. For example, following several years of very high water levels a plover banded during our study was sighted in a subsequent season in southern Manitoba (R. Johnston, pers. comm.).

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. In addition, 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.

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. It is also possible that competition for mates is very intense at LOTW. Although there was no direct evidence for this (e.g., 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. Rowley (1983) argued that nest-site tenacity may function to reunite pairs that are split during the non-breeding season. Jehl (1973) believed 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. Because they show strong nest-site tenacity and a lower frequency of mate retention, Piping Plovers at LOTW fit this pattern.

Conservation implications.—In 1986 the Piping Plover was listed as threatened and endangered under the provisions of the federal 1973 Endangered Species Act; LOTW plovers are considered part of the threatened northern Great Plains population. One of the reasons for the decline of this species appears to be loss of breeding habitat to shoreline development or river channel modification for commercial or recreational purposes (Sidle 1985). Our study found that a significant portion of the breeding population returned in consecutive years to nest at limited localities in northern Minnesota. These results demonstrate the importance of preserving important traditional plover breeding sites and, if necessary, managing these sites to minimize impacts of naturally occurring ecological processes (e.g., predators, fluctuating water levels) that may cause individuals to move to other breeding localities.

ACKNOWLEDGMENTS

We thank the Nongame Wildlife Program of the Minnesota Department of Natural Resources and the Minnesota Chapter of the Nature Conservancy for funding this project. Logistical support was provided by the Baudette Regional Headquarters of the Minnesota Department of Natural Resources and the University of Minnesota-Duluth Biology Department. L. Pfannmuller of the Minnesota Nongame Wildlife Program was instrumental in initiating this project and was very supportive from start to finish. We are very grateful to T. Martin and R. Fox for providing extensive field assistance. The cooperation of D. Braaten and the Morris Point resort is greatly appreciated. D. Christian and R. Green provided valuable advice throughout the study. P. Bergstrom, M. Ryan, C. Griffin, and L. MacIvor reviewed the manuscript and provided suggestions for its improvement. This manuscript was prepared while Cuthbert was supported by a grant from the Minnesota Agricultural Experiment Station (publication 15375).

LITERATURE CITED

AUSTIN, O. L. 1949. Site tenacity, a behavior trait of the Common Tern (*Sterna hirundo* Linn.). Bird-Banding 20:1–39.

BEDARD, J. AND G. LAPOINTE. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. Wilson Bull. 96:196–205.

CAIRNS, W. E. 1977. Breeding biology and behavior of the Piping Plover (*Charadrius melodus*) in southern Nova Scotia. M.S. thesis, Dalhousie Univ., Halifax, Nova Scotia.

———. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bull. 94:531–545.

COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. J. An. Ecol. 35:269–279.

CUTHBERT, F. J. 1985. Mate retention in Caspian Terns. Condor 87:74–78.

DARLEY, J. A., D. M. SCOTT, AND N. K. TAYLOR. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. Bird-Banding 48:145–151.

EMLEN, S. T. AND L. W. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

FIEDLER, C. AND A. GREWE. 1983. Mate and nest-site fidelity among Tree Swallows in central Minnesota. J. Minn. Acad. Sci. 49:22–26.

FREER, V. M. 1979. Factors affecting site tenacity in New York Bank Swallows. Bird-Banding 50:349–357.

GRATTO, C. L., R. I. G. MORRISON, AND F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102:16–24.

GRAUL, W. D. 1973. Adaptive aspects of the Mountain Plover social system. Living Bird 12:69–94.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. An. Behav. 28:1140–1162.

HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). J. An. Ecol. 48:305–313.

HOLLAND, P. K., J. E. ROBSON, AND D. W. YALDEN. 1982. The breeding biology of the Common Sandpiper *Actitis hypoleucos* in the Peak District. Bird Study 29:99–110.

HOLMES, R. T. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7:191–208.

HOWE, M. A. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). Auk 99:88–102.

JEHL, J. R., JR. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. 85:115–147.

LENINGTON, S. AND T. MACE. 1975. Mate fidelity and nesting site tenacity in the Killdeer. Auk 92:149–151.

MACDONALD, M. A. 1977. Adult mortality and fidelity to mate and nest-site in a group of marked Fulmars. Bird Study 24:165–168.

MCNICHOLL, M. K. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92:98–104.

MORSE, D. H. AND S. W. KRESS. 1984. The effect of burrow loss on mate choice in the Leach's Storm-Petrel. Auk 101:158–160.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. Trans. Linnaean Soc. New York 4:1–247.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. No. 26.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

ORING, L. W. 1982. Avian mating systems. Pp. 1–92 *in* Avian biology, Vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, New York, New York.

——— AND D. B. LANK. 1982. Sexual selection, arrival times, philopatry, and site fidelity in the polyandrous Spotted Sandpiper. Behav. Ecol. Sociobiol. 10:185–191.

PETRINOVICH, L. AND T. L. PATTERSON. 1982. The White-crowned Sparrow: stability, recruitment, and population structure in the Nuttall subspecies (1975–1980). Auk 99: 1–14.

RICHDALE, L. E. 1957. A population study of penguins. Clarendon Press, Oxford, England.

ROWLEY, I. 1983. Re-mating in birds. Pp. 331–359 *in* Mate choice (P. Bateson, ed.). Cambridge Univ. Press, London, England.

RYDER, J. P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. Pp. 153–168 *in* Behavior of marine animals. Vol. 4 (J. Burger, B. L. Olla, and H. E. Winn, eds.). Plenum Press, New York, New York.

SACHS, L. 1982. Applied statistics. Springer-Verlag, New York, New York.

SHIELDS, W. M. 1984. Factors affecting nest and nest fidelity in Adirondack Barn Swallows (*Hirundo rustica*). Auk 101:780–789.

SIDLE, J. 1985. Determination of endangered and threatened status for the Piping Plover. Fed. Reg. 50:50720–50734.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, New York.

SOIKKELI, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4:158–198.

SOUTHERN, W. E. 1977. Colony selection and colony site tenacity in Ring-billed Gulls at a stable colony. Auk 94:469–478.

WILCOX, L. 1959. A twenty year banding study of the Piping Plover. Auk 76:129–152.