DISTRIBUTION AND DISPERSAL IN THE PIPING PLOVER

Susan M. Haig[1] and Lewis W. Oring

*Department of Biology, University of North Dakota, Grand Forks, North Dakota 58202 USA, and
Delta Waterfowl and Wetlands Research Station, Portage la Prairie,
Manitoba R1N 3A1, Canada*

ABSTRACT.—Individually marked Piping Plovers (*Charadrius melodus*) were studied from 1981-1987 in Manitoba and Minnesota relative to dispersal patterns of age and sex classes. Unlike monogamous passerines, males returned to former breeding sites only slightly more often than females. Dispersal distances did not differ between the sexes. Across North America, 24-69% of adults exhibited breeding-site fidelity, a variability equivalent to that among species of migratory shorebirds. Distribution of Piping Plover habitat across the species range accounts for some of this variability: birds used local sites if they were available, rather than disperse long distances. Similar to most migratory shorebirds, few (1.6-23%) Piping Plover chicks returned to natal sites to breed. No difference was found in return patterns between first-year males and females, nor in distances either sex dispersed from natal sites. First-year birds were found in the vicinity of their natal sites when habitat was available. During winter, birds from the Northern Great Plains and Great Lakes were seen primarily in mixed population flocks on the Gulf of Mexico. Piping Plovers from Atlantic coast breeding areas wintered further south on the Atlantic. *Received 27 November 1987, accepted 19 April 1988.*

DELINEATION of dispersal patterns is critical to understanding many aspects of a species' population biology and behavior (Horn 1983, Horn and Rubenstein 1984). Dispersal from a familiar area may be undertaken to avoid close inbreeding or resource competition (Greenwood 1980, Shields 1982, Moore and Ali 1984, Dobson and Jones 1986). Conversely, philopatry may lead to the evolution of cooperative social behavior and adaptation to a local environment (Greenwood 1980, Shields 1982, Waser and Jones 1983). Thus, the adaptive significance of dispersal is problematic: natural selection within a population seemingly mitigates against long distance dispersal, but only dispersers can found new populations (Horn 1983, Swingland 1983, Moore and Ali 1984, Liberg and von Schantz 1985).

Most characterizations of species' dispersal patterns are based on investigations of a single local population during limited periods in the annual cycle. For migratory birds, which spend less than 50% of their annual cycle at breeding sites, it has become increasingly apparent that interactions across seasons must be taken into account to better understand the effects of dispersal on social systems (Keast and Morton 1980;

Morse 1980; Myers 1981, 1983; Rappole et al. 1983; Wilcove and Terborgh 1984). Although the logistics of a project of this scale seem prohibitive, a unique situation exists in populations of the Piping Plover (*Charadrius melodus*). This monogamous, migratory shorebird inhabits isolated sandflats and beaches throughout central and eastern North America (Haig and Oring 1985). The limited nature of the species' distribution and the ease of sighting marked birds on beaches provide an opportunity for following individuals throughout the year. Recent interest in raising Piping Plover populations to former levels spurred development of research in most of the species' major breeding areas, and further increased the chances that marked birds would be resighted. We report Piping Plover dispersal patterns throughout the annual cycle, and suggest that distribution of habitat may explain some of the variability in return patterns exhibited among the sexes, age groups, and different populations of the species.

METHODS

We studied Piping Plovers in southeastern Manitoba from 1981-1986, and in northwestern Minnesota from 1985-1987 (Haig and Oring 1987, 1988a, b). In Manitoba, breeding birds (50 males, 47 females) and their chicks (n = 122) from Lake Manitoba, West Shoal Lake, and Grand Marais on Lake Winnipeg (locations described in Haig and Oring 1988b) were captured in mist nests and given unique combinations of color

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bands. All Piping Plovers banded after 1983 were also given international leg flags (Myers et al. 1983, Haig et al. 1988). Piping Plovers were sexed as described by Haig and Oring (1988b).

From 1982–1986, distribution of the 100–120 Piping Plovers breeding in Manitoba and identification of marked birds were determined through province-wide censuses and surveys (Haig 1985, 1987a). Weekly censuses were carried out at 3 sites on Lake Manitoba: Stony Beach, Twin Lakes Beach, and Clandeboye Bay, from 1982–1985; and at West Shoal Lake from 1984–1985. Grand Marais was censused every 3 weeks from 1983–1985, and twice in 1986. Lake Manitoba, West Shoal Lake, and Lake Winnipeg sites were censused at least once in 1987 by the Manitoba Department of Natural Resources (W. Koonz pers. comm.). The number of adults, nests, and chicks was recorded, as well as identification of marked birds and their mates.

In Minnesota, Piping Plovers primarily bred at 4 sites on the southwestern barrier islands of Lake of the Woods (Wiens 1986). Research begun in 1982 (Wiens 1986) was continued by the authors from 1985–1987 (Haig and Oring 1987). From 1982–1986, 53 adults and 110 chicks were individually marked with color bands and, after 1984, with international flags. In 1985–1987, 31–42 adults and their chicks were censused approximately every 3 weeks during the breeding season. Censuses in Minnesota used methodology similar to that in Manitoba.

The presence of researchers at major Piping Plover breeding sites in the surrounding area enhanced monitoring marked birds that dispersed to Michigan (Pike 1985), Wisconsin (S. Matteson pers. comm.), Ontario (L. Heyems pers. comm.), central North Dakota (Prindiville 1986, Mayer and Ryan 1986), or Nebraska (Nebraska Game and Parks Commission 1978–1987). In addition, marked birds were recorded during censuses at major breeding sites in Saskatchewan in 1984 and 1985 (Harris et al. 1984, Haig unpubl. data); in South Dakota in 1986 (Schwalbach et al. 1986); and in Montana during 1986–1987 (Montana Piping Plover Recovery Committee 1986, A. Dood pers. comm.). Atlantic coast sites were heavily censused during the past 5 years (Dyer et al. 1987). Dispersal data from Piping Plovers on Long Island, New York (Wilcox 1959), are presented for comparison between inland and Atlantic birds.

We determined Piping Plover distribution (Fig. 1) by direct censuses, and coordination of surveys and censuses carried out in North America between 1982 and 1987 (Haig 1985, 1986, 1987b; Haig and Oring 1985; Dyer et al. 1987; Haig et al. 1988). In 1982, we established an information clearinghouse at Delta Waterfowl and Wetlands Research Station that requested sightings of marked Piping Plovers, census data, and distribution information from over 700 government agencies, museums, universities, biologists, and conservation groups, throughout the Americas and the Caribbean. Although data collected during
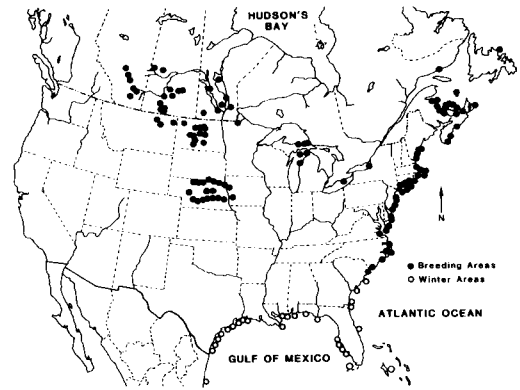

Fig. 1.　Distribution of Piping Plover breeding and winter areas as of 1987.

surveys and censuses varied among researchers, we included only the following in further analyses: identification of sites that Piping Plovers used throughout the year, adult population sizes, and identification of marked birds. Currently, most major breeding sites are censused at least annually (Dyer et al. 1987, Haig et al. 1988). Major Gulf of Mexico sites and a few Atlantic coast winter sites are frequently censused from August–April (Johnson 1987, T. Amos pers. comm., T. Eubanks pers. comm., J. Nicholls pers. comm., J. Toups pers. comm.).

We define *breeding dispersal* as movement of breeding adults between breeding seasons, whereas *breeding-site fidelity* is the return of a breeding bird to its former breeding site (e.g. Stony Beach, Grand Marais) in successive years. *Natal dispersal* is dispersal of young prior to first breeding, *natal philopatry* occurs when a first-year bird returns to its hatch site to breed. *Winter dispersal* is the movement of adults and fledglings from breeding/hatch sites to winter sites.

RESULTS

Breeding dispersal.—Piping Plover population studies demonstrate a high degree of variability in site fidelity among study sites (Table 1). In 5 of 8 studies, over 50% of adults returned to former breeding sites. In most studies, breeding-site fidelity of males and females was not reported, but in Manitoba, returns of males and females did not differ significantly ($\chi^2 = 2.23$, 1 df, NS; Haig and Oring 1988b). Most marked breeding birds seen in subsequent years (Fig. 2) returned to former breeding sites in Minnesota and New York. Manitoba breeding birds, however, returned to the general area (i.e. southern Manitoba), but frequently changed breeding sites.

TABLE 1. Breeding-site fidelity and natal philopatry in Piping Plovers.

Study location	Nesting adults banded	n return (%)	Fledged chicks banded	n return (%)	Focal sites	Years of study	Source
Southern Manitoba	65	44 (67.7)	90	5 (5.5)[a] 11 (12.2)[b]	5	4	This study
Cape Cod, Massachusetts	16	11 (68.9)	28	0 (0.0)[a] 12 (42.9)[b]	12	3	MacIvor et al. 1987
Waugoshance Pt., Michigan	16	9 (56.3)	35	1 (2.9)[a] 8 (2.9)[b]	1–10	11	Pike 1985, pers. comm.
Lake of the Woods, Minnesota	47	32 (68.0)	70	15 (21.0)	4	3	Wiens 1986
Long Island, New York	1,173	288 (24.6)	979	34 (3.4)[a] 47 (4.8)[b]	3	20	Wilcox 1959
Chain of Lakes, North Dakota	111	32 (55.2)	123	7 (6.0)	7	2	Mayer & Ryan 1986
Cadden Beach, Nova Scotia	19	7 (36.8)	39–57	1 (1.6–2.6)	1	2	Cairns 1982
Big Quill Lake, Saskatchewan	14	6 (42.0)	12	1 (8.3)	1	2	Whyte (1985)
Total	1,461	429 (29.4)	1,376–1,394	64 (4.7)[a] 102 (7.3–7.4)[b]			

[a] Return to natal site.
[b] Return to local area (including natal site). In all cases, except Whyte 1984, local sites were surveyed in addition to focal sites.

Dispersal distances of Piping Plovers that chose new breeding sites varied considerably from former sites (Table 2). In New York, only 3 adults that returned to Long Island did not settle on former sites. These birds bred 9–26 km from previous nests (Wilcox 1959). Piping Plovers in Manitoba frequently moved between Lake Manitoba and West Shoal Lake during the breeding season (Haig and Oring 1988b) as well as between years. Only 1 adult moved from these areas to Grand Marais. Manitoba birds were never seen in Minnesota. However, adults from Lake of the Woods, Minnesota, moved into Manitoba in 1984, 1985, 1986, and 1987 ($n = 4$). Current data are limited, but do not indicate a significant sex bias in distances dispersed. In New York, 2 females dispersed 25.9 and 18.3 km from previous nest sites, while 1 male bred 9.1 km from its former nest (Wilcox 1959). In Manitoba, resighted males that were not site-faithful dispersed further than females, although the difference was not significant ($\bar{x} = 35$ km, SD = 14.5, $n = 8$ for males vs. $\bar{x} = 26$ km, SD = 9.8, $n = 10$ for females) (Mann-Whitney $U' = 29$, NS).

Natal dispersal.—Piping Plovers frequently bred the first year after hatch (Haig and Oring 1988b), and only a few ($n = 6$) remained in wintering areas for the entire year (S. Haig unpubl. data, T. Eubanks pers. comm.). Few Piping Plover chicks from any study area returned to natal sites to breed (Table 1). Many non-philopatric chicks settled in areas surrounding their natal sites in Manitoba, New York, and Minnesota. There was no sex bias among philopatric birds in New York (16 males vs. 18 females returned; Wilcox 1959) and Manitoba (2 males vs. 2 females vs. 1 unknown-sex bird returned). Further, there was no significant sex bias in distances dispersed by birds hatched in Manitoba or New York (Table 3). On average, females resighted in New York dispersed 12.8 km (SD = 24.5, $n = 25$) from natal sites, while males were found approximately 8.6 km (SD = 16, $n = 21$) from natal sites. In Manitoba, all returning first-year birds bred at West Shoal Lake after hatching at a site on Lake Winnipeg or Lake Manitoba (Table 3). Similarly, Long Island birds converged on Shinnecock (Wilcox 1959). Resighted first-year birds that did not return to Lake of the Woods moved north to Manitoba, settling at West Shoal Lake and Grand Marais on Lake Winnipeg.

All non-philopatric Lake-of-the-Woods chicks dispersed over 200 km from hatch sites (Fig. 2). In Manitoba and New York, more birds bred at
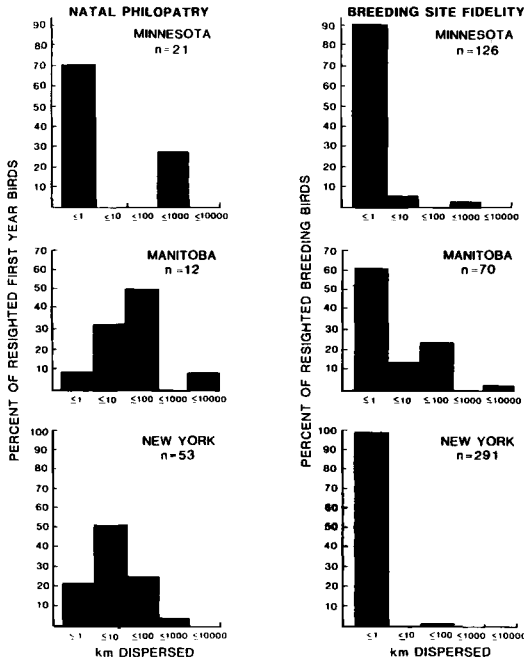
Fig. 2. Comparison of distances dispersed from natal sites in Piping Plover chicks resighted their second year (left column) and distances adults dispersed between breeding sites in successive years (right column). Distance intervals (km) on bars are: 0–1.0, 1.1–10.0, 10.1–100.0, 100.1–1,000.0, 1,000.1–10,000.0. Sources: this study, Wilcox 1959, Wiens 1986.

a site 1.1–10 km from their natal site than returned to natal sites. Furthermore, 50.9% ($n = 12$) of Manitoba chicks and 24.5% ($n = 53$) of New York chicks observed the next year were found 10.1–100 km from natal sites. The greatest distance dispersed (approximately 1,500 km) was by a male that hatched at West Shoal Lake in 1985 and was captured in a mist net the following August at Long Point, Lake Erie.

Winter dispersal.—Ninety-one winter sightings of Piping Plovers banded during the breeding season indicate that inland breeding birds wintered primarily on the Gulf of Mexico. Birds that bred along the Atlantic coast wintered further south along the Atlantic (Fig. 3). A few birds from Manitoba, North Dakota, and Michigan were sighted along the Atlantic coast, but there was only 1 sighting of an Atlantic breeding bird wintering on the Gulf. Marked birds from inland breeding areas wintered throughout the Gulf, and did not demonstrate significant geographic differentiation by breeding site location: Piping Plovers from North Dakota, Minnesota, Michigan, and Manitoba occurred in both Florida and Texas.

DISCUSSION

Natal dispersal.—Recent consideration of the costs and benefits of juvenile dispersal contrasts possible negative genetic effects with somatic

TABLE 2. Dispersal of breeding Piping Plovers between years.[a]

State or province	Breeding site 1	Breeding site 2	Sex[b] M	Sex[b] F	Sex[b] U	Km dispersed
Manitoba	Clandeboye Bay, Lake Manitoba	Stony Beach, Lake Manitoba		1		3
	Clandeboye Bay, Lake Manitoba	West Shoal Lake	3	3		32
	Stony Beach, Lake Manitoba	Twin Lakes Beach, Lake Manitoba		1		15
	S. West Shoal Lake	N. West Shoal Lake			8	8
	West Shoal Lake	Clandeboye Bay, Lake Manitoba	2	3		32
	West Shoal Lake	Grand Marais, Lake Winnipeg	1			70
	West Shoal Lake	Twin Lakes Beach, Lake Winnipeg	2	2		25
Massachusetts	Plymouth Beach	Sandy Neck		1		37
Minnesota	Lake of the Woods	Clandeboye Bay, Lake Manitoba	1			314
	Lake of the Woods	Long Point, Lake Winnipeg	1			546
	Lake of the Woods	West Shoal Lake	1	1		273
New York	Moriches	Shinnecock		1		18
	Shinnecock	Moriches		1		25
	Shinnecock	Mecox	1			14
Ontario	Long Point, Lake Erie	Waugoshance Pt., Lake Michigan			1	595

[a] Sources: this study (Manitoba, Minnesota), Wilcox 1959 (New York), MacIvor et al. 1987 (Massachusetts), Pike 1985 (Michigan).

[b] Values represent the number of males, females, and unknown-sex birds that moved from one breeding site to another in successive years.

TABLE 3. Dispersal of Piping Plovers from natal sites to breeding sites.[a]

Hatch site	Breeding site	Sex[b]			Km dispersed
		M	F	U	
Manitoba					
Grand Marais, Lake Winnipeg	West Shoal Lake	1	1	—	70
Stony Beach, Lake Manitoba	West Shoal Lake	—	1	1	35
Twin Lakes Beach, Lake Manitoba	West Shoal Lake	1	—	1	25
West Shoal Lake	West Shoal Lake	2	2	1	5
West Shoal Lake	Long Point, Lake Erie	1	—	—	1,500
Massachusetts					
Harding Beach	Monomoy	—	—	1	22
Michigan					
Waugoshance Pt., Lake Michigan	Cathead Bay, Lake Michigan	—	—	1	74
Waugoshance Pt., Lake Michigan	Grand Marais, Lake Superior	—	—	6	112
Minnesota					
Lake of the Woods	West Shoal Lake	—	2	—	273
Lake of the Wood	Grand Marais, Lake Winnipeg	1	2	1	222
New York					
Atlantic Beach	Shinnecock	—	1	—	101
Mecox	Shinnecock	2	2	—	9
Moriches	Shinnecock	2	3	—	25
Oak Beach	Shinnecock	—	1	—	62
Tobay Beach	Moriches	1	—	—	66
Penn Yan	Long Point, Lake Erie	—	—	1	240

[a] Sources: This study (Manitoba, Minnesota), MacIvor et al. 1985 (Massachusetts), Pike 1985 (Michigan), Wilcox 1959 (New York).
[b] Values represent numbers of males, females and unknown-sex first-year adults that dispersed from their natal site to a non-natal site to breed.

factors such as intense competition for resources (Greenwood 1980, Pusey 1987). Although extreme cases of inbreeding or outbreeding may have detrimental effects on individuals and populations (Ralls and Ballou 1983), in many cases dispersal patterns can be explained in terms of somatic rather than genetic factors (Shields 1982, Moore and Ali 1984, Dobson and Jones 1986).

Among monogamous avian species with resource-defense mating systems, males generally exhibit greater natal philopatry and breeding-site fidelity, whereas females show a greater tendency to disperse (Greenwood 1980). Because males must acquire a territory in order to attain a mate, Greenwood (1980) predicted that higher return rates among males to natal sites and successive breeding sites facilitated territory acquisition through familiarity with the area and its residents. Females have more freedom to choose the best or most resources, and may find better opportunities at non-natal sites. An alternative hypothesis predicts male-biased philopatry because parents prohibit female offspring from returning to natal sites to parasitize their nests (Liberg and von Schantz 1985). Contrary to either hypothesis, male and fe-

male Piping Plover chicks returned to Manitoba and New York in equal numbers. Comparative charadriid data are limited to Mountain Plovers (Charadrius montanus) where 1 female was philopatric, and 1 male returned to breed within 10 km of its hatch site (Graul 1973). Similarly, monogamous scolopacids did not exhibit a sex bias in natal philopatry (Oring and Lank 1984). With the low incidence of natal philopatry in shorebirds (Tables 1 and 4; Oring and Lank 1982, 1984), further discussion of sex biases is not warranted.

The significance of low return rates found among many avian species (Baker 1978, Shields 1982) is difficult to interpret without mortality data, and without knowledge of the social and environmental factors that influence behavior during all phases of the annual cycle. For example, competition among Spotted Sandpiper (Actitis macularia) chicks during their natal year may play a primary role in determining the rate of dispersal or philopatry the following year (Oring in press). Global competition for space also may result in dispersal even if dispersing individuals have little chance of success in a new, less crowded location (Hamilton and May 1977).
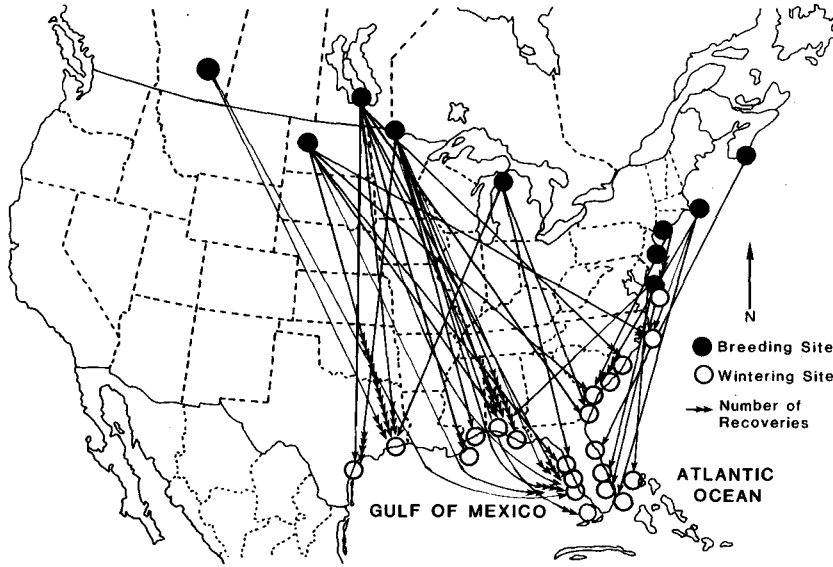
Fig. 3. Dispersal of Piping Plovers from breeding sites to wintering sites, based on 91 sightings of marked birds.

Breeding dispersal.—Breeding dispersal patterns among monogamous charadriid and scolopacid species are similar to Piping Plovers in that the majority of adults are site-faithful, and return rates between the sexes are not significantly different (Tables 1 and 4; Oring and Lank 1982, 1984; Haig and Oring 1988b). However, variability in return patterns among charadriid and scolopacid *species* are equivalent to the variability exhibited among *local populations* of Piping Plovers. These results reflect differences among local populations of Piping Plovers and the nature of particular studies. They also illustrate that classifying species' trends

TABLE 4. Breeding-site fidelity and natal philopatry in the Charadriidae.

Species[a]	Adults banded	n return	% return M	% return F	% return Total	Chicks banded	n return (%)	Years/ study	Source
Golden Plover (*Pluvialis apricaria*)	112	87	78	77	77.7	41	26 (63.4)	6	Parr 1980
Mountain Plover[b] (*Charadrius montanus*)	8	5	—	—	62.5	229	2 (0.9)	4	Graul 1973
Snowy/Kentish Plover (*C. alexandrinus*)[c]	410	243	—	—	59.3	1,220	68 (5.5)	9	Rittinghaus 1956
	129	91	77	66	70.5	—	—	5	Warriner et al. 1986
Common Ringed Plover (*C. hiaticula*)	—	—	—	—	—	—	(4.4)	4	Laven 1940
	40	36	100	79	90.0	42	24 (57.1)	4	Pienkowski 1984
Killdeer (*C. vociferus*)	31	13	63	20	41.9	48	0 (0.0)	4	Lenington & Mace 1975
White-fronted Plover[d] (*C. marginatus*)	18	18	100	100	100	—	—	4	Summers & Hockey 1980
Spur-winged Plover[d] (*Lobivanellus lobatus*)	119	119	100	100	100	70	14 (20.0)	5	Barlow 1972
	—	—	—	—	—	14	12 (85.7)	3	Thomas 1969

[a] Species are monogamous and migratory unless otherwise specified.
[b] Species has rapid multi-clutch breeding system and is migratory.
[c] Population is partially non-migratory and partially sequentially polyandrous.
[d] Species is monogamous and non-migratory.

based on limited numbers of populations or geographic areas within species' ranges is unsatisfactory.

Habitat distribution and availability provide at least a partial explanation for variability in dispersal patterns among Piping Plover populations. During the first half of this century, Piping Plovers and their breeding sites were abundant and were distributed almost continuously along the east coast of North America (Bent 1929, Haig 1986). Beach habitat along the Atlantic coast was fairly homogeneous, compared with inland Piping Plover areas. Low breeding-site fidelity in New York may have occurred due to equivalent options in many locations, and lessened the importance of site fidelity.

Conversely, Piping Plovers at Lake of the Woods have few available nest sites and no nearby alternate breeding options. The total number of Piping Plovers (less than 200 birds) and viable breeding sites in the Great Lakes, Lake of the Woods, and interlake region of Manitoba is low (Haig et al. 1988). This leaves few possibilities for birds to move to other populations within the region. Piping Plovers that are not site-faithful at Lake of the Woods must disperse great distances to adjacent populations. Thus, over 90% ($n = 26$) of birds breeding at Lake of the Woods in 1987 were site-faithful adults or philopatric chicks (Haig and Oring 1987).

Piping Plovers in Manitoba represent an intermediate situation. Contrary to Lake of the Woods, there are a number of local sites to which they may disperse. Unlike New York Piping Plovers, birds that leave the interlake region must disperse great distances before reaching another breeding area. Therefore, site fidelity is similar to that at Lake of the Woods, but many birds that are not site-faithful return to the region. Other factors contributing to dispersal in Manitoba birds are discussed in Haig and Oring (1988b).

Dispersal can be hazardous for any bird, but Piping Plovers face a great risk that a new breeding site will be less satisfactory than a former site. Throughout their range, nesting and winter sites are ephemeral and subject to frequent destruction or reconfiguration (Haig 1985; Haig and Oring 1985, 1988b; Dyer et al. 1987). Inland Piping Plovers, dispersing a great distance from former sites, may face habitat and

population densities that are quite different from those at previous sites. Beach habitat appears similar on the Great Lakes, Lake of the Woods, and southern Manitoba; but saline potholes in North Dakota, expansive alkali sloughs in Saskatchewan, and river sandbars in South Dakota and Nebraska could present prohibitive social or environmental obstacles to newcomers. Therefore, birds that have bred in an area where they, or their neighbors, have had a degree of reproductive success may find it advantageous to return rather than chance failure at an unknown site. Conversely, when sites prove to be nonproductive, Piping Plovers may improve their reproductive success by moving to a new location.

Winter dispersal.—Pair bonds are presumably formed on breeding grounds; and natal and breeding dispersal are responsible for the interpopulation genetic mixing that appears to occur. Little genetic differentiation has occurred between local or regional Piping Plover populations (Haig and Oring 1988b). Furthermore, allele frequencies in local populations conformed to Hardy-Weinberg predictions for equilibrium. Hence, regular gene flow occurs, but the mechanism remains unclear. Few Piping Plovers are seen during spring migration and it appears that, once birds leave winter areas, most do not stop until they are near breeding sites (Haig 1986, Haig et al. 1988). If Piping Plovers form pair bonds before or during spring migration, the extent of population mixing documented on winter sites may significantly affect the genetic structure of breeding populations.

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