

## Survival and site fidelity of Piping Plovers on Long Island, New York

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**ABSTRACT.** The threatened Atlantic Coast population of Piping Plovers (*Charadrius melodus*) has not increased in recent years and remains 332 pairs short of the recovery goal of 2000 pairs. Habitat loss to development is a major threat to the population, and there has been interest in restoring nesting and foraging habitat. However, the demographic response of coastal Piping Plovers to either habitat loss or creation has not been documented. We estimated survival rates and site fidelity of a declining Piping Plover population on Long Island, New York, from 2001 to 2005 on a beach subject to human development and recreation. The mean annual adult survival was  $0.703 \pm 0.032$  (SE) and was similar among years. Site fidelity during the period of territory establishment averaged  $0.827 \pm 0.069$  (SE). Given this high site fidelity, ensuring the survival of adults is important for maintaining local populations. Although the 2002–2004 average was high, site fidelity was apparently lower in 2003 than in 2002. This decrease in site fidelity may have been related to several years of habitat loss and increasing predation of nests or chicks, as reported in a partly concurrent long-term study at our site. The species-level effect of local dispersal due to anthropogenic habitat loss depends on the fitness of dispersers, and is currently unknown for Piping Plovers.

### **SINOPSIS. Sobrevivencia y fidelidad a una localidad en Long Island, New York por parte de *Charadrius melodus***

La población de la costa del Atlántico del amenazado *Charadrius melodus* no ha incrementado en números en los últimos años y se mantiene en 332 parejas, número corto de las metas de recobro de 2000 parejas. La pérdida de hábitat a manos del desarrollo se considera una de las amenazas principales. Hay interés en restaurar el hábitat de alimentación y reproducción del ave. Sin embargo, no se ha documentado la respuesta demográfica de la especie a la restauración o pérdida de hábitat. Se hizo un estimado de la tasa de sobrevivencia y fidelidad a una localidad en Long Island, New York, de 2001–2005 en una playa utilizada para la recreación y sujeta a desarrollo. La sobrevivencia promedio anual (similar entre años) fue estimada en  $0.703 \pm 0.032$  (SE). La fidelidad a la localidad durante el periodo del establecimiento de territorios promedió  $0.827 \pm 0.069$  (SE). Dada la alta fidelidad el asegurar la sobrevivencia de los adultos es muy importante para mantener la población de la localidad. Aunque el promedio de sobrevivencia fue alto de 2002–2004, la fidelidad, aparentemente, fue menor en el 2003 que en el 2002. Esta disminución pudiera estar relacionada a varios años de pérdida de hábitat y a un incremento en la depredación de polluelos, ya informado en un estudio a largo alcance. El efecto, a nivel de la especie, de la dispersión local debido a la pérdida de hábitat por efectos antropogénicos, depende de la adaptabilidad de los dispersantes, lo que se desconoce hasta el momento en el ave.

**Key words:** barrier island, *Charadrius melodus*, demography, shorebird, site fidelity, survival

The threatened Atlantic Coast population of Piping Plovers (*Charadrius melodus*) stopped increasing in 2003 after more than doubling in size since being listed as a threatened species in 1986 (USFWS 2004a). The current population is 332 breeding pairs below the recovery goal of 2000 pairs (preliminary estimate; USFWS 2004b). Threats to the population include predation, recreational disturbance, and loss of habitat to coastline development (USFWS 1996). Resource agencies have expressed interest in restoring habitat for the Atlantic Coast Piping Plover

population through beach renourishment and artificial creation of intertidal habitat (USACE 2001). Predicting the effects of local habitat degradation and habitat restoration projects on region-wide recovery requires an understanding of how habitat dynamics affect local reproduction, survival, and dispersal.

Piping Plovers are adapted to dynamic habitats, nesting and foraging on ocean beaches and intertidal areas, river sandbars, and along wetland margins that vary in size over time and among locations due to weather, tides, and changes in vegetation (Haig and Smith 2004). Thus, they may have a predisposition to disperse in response to range-wide temporal

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and spatial variation in habitat quality leading to the need to select new habitat each year (Gandon and Michalakis 2001). High risk of egg or nestling loss to predation may also induce emigration (Weisser 2001). For Piping Plovers, recreational disturbance may lower reproductive success (Flemming 1988) and may lead to abandonment of breeding sites. If accessible, unoccupied habitat exists, organisms occupying sites that are declining in quality may improve their fitness by dispersing, so regional extinction may be avoided even if local populations decline (Hanski 2001). As habitat becomes rare or inaccessible, however, degradation of occupied breeding sites increases the risk of regional extinction (Hanski 2001). For Piping Plovers breeding in the Great Plains and Prairie Canada, long-distance dispersal between breeding seasons has been documented, and may be due to habitat loss at the original breeding site (Haig et al. 2005). Our objectives were to estimate adult survival and site fidelity of a declining Piping Plover population on Long Island, New York, to determine if survival or site fidelity changed over time as the population declined, and to document dispersal within and among breeding seasons.

## METHODS

**Study area.** We studied Piping Plovers in two villages on Westhampton Island, off the south shore of Long Island, New York. West Hampton Dunes (WHD; 40°46'33"N, 72°42'57"W) was 3 km east of Moriches Inlet, bounded by Moriches Bay on the north and the Atlantic Ocean on the south, and contained approximately 2.8 km of ocean beach and 1.3 km of bay beach. Westhampton Beach (WHB; 40°47'50"N, 72°38'46"W) was adjacent to WHD to the east, and contained 3.2 km of ocean beach. WHB had no bay beach, but contained scattered small bay side sandflats (<1.5 ha total).

In 1992 a winter storm breached Westhampton Island at WHD and increased available nesting habitat for Piping Plovers by destroying houses, clearing dense vegetation, and depositing a sandspit in Moriches Bay. The storm also created large intertidal sandflats in Moriches Bay that served as foraging habitat for migrating Piping Plovers, breeding pairs, and broods. The U.S. Army Corps of Engineers filled the breach

in 1994 and subsequently added sand to the beach via renourishment during the winters of 1996–1997, 2000–2001, and 2004–2005. The number of breeding pairs of Piping Plovers increased after the storm until 2000, then began decreasing in 2001 as nesting habitat was lost to vegetation growth and house construction (Houghton 2005). There was an increase in the number of pairs at WHB in 2002, however, so the total population did not begin to decline until 2003. The population at WHD and WHB in 2001, 2002, 2003, and 2004 included 53, 54, 40, and 28 pairs, respectively (Houghton 2005).

**Marking and resighting.** We captured incubating adult plovers with box-shaped drop traps (Wilcox 1959, Graul 1979) and funnel traps (Paton 1994). We uniquely marked each adult plover with one UV-stable Darvic numbered color band (size 1A; Avinet, Dryden, NY, USA) on each tibiotarsus. No USGS metal bands were used. We captured chicks on hatch day and each chick was banded in the same manner as adults in 2002 and 2003, except that members of a brood received the same combination of colored bands and were distinguishable only by numbers etched on the bands.

We searched for marked birds and nests for an average of 4–6 h/d in all potential Piping Plover habitat from 15 March to 15 August 2002–2004. This period included the spring migration. In 2005, we searched three times per week from 5 April to 24 May. This period included only the latter two-thirds of the spring migration.

**Estimation of survival rate and site fidelity.** We calculated adult survival using records from all birds banded as breeding adults, even if they were observed during migration but did not nest at our sites in years after being marked. For purposes of estimating adult survival and site fidelity, returning banded chicks were added to the sample in the year they began breeding in the study area. We estimated demographic rates using the Barker (1997) model in Program MARK (White and Burnham 1999). The Barker model allows simultaneous estimation of annual survival and site fidelity by incorporating recaptures and resightings between capture events. We designated the year of recapture as year  $i$ , such that  $S_i$  is the probability that an animal alive at capture period  $i - 1$  was alive at period  $i$ ,  $p_i$  is the probability that an

animal at risk of capture at period  $i$  was captured (including by resighting),  $r_i$  is the probability that an animal that died in the interval  $[i - 1, i]$  was found and reported,  $R_i$  is the probability that an animal that survived interval  $[i - 1, i]$  was resighted during that interval,  $R'_i$  is the probability that an animal that died in interval  $[i - 1, i]$  was resighted alive before it died,  $F'_i$  is the probability that an animal available for capture at  $i - 1$  was available for capture at  $i$ , and  $F_i$  is the probability that an animal not available for capture at  $i - 1$  was available for capture at  $i$ , where  $i = 2001-2006$ .

Our capture period was the nesting and brood-rearing period (16 April to 15 August), and we considered a marked bird recaptured if it was resighted and we found its nest during that interval. Our inter-capture interval was from 16 August of one year to 15 April of the next, but resightings were likely only during spring migration (15 March to 15 April) when we actively searched for birds.

We considered  $S$  and  $F$  to be apparent survival and site fidelity estimates because some birds may have emigrated without stopping at our sites during migration. The Barker model allowed us to incorporate heterogeneity in resighting rates (Mizroch et al. 2004) between transients and birds that stayed to nest.

No dead birds were found and reported in the inter-capture interval so we fixed  $r$  at 0.0, and all emigration of birds that bred at our site at least once was permanent so  $F'$  was fixed at 0.0. We made several assumptions beyond those typical of a mark-recapture experiment (Larson et al. 2000) and those required by the Barker model (Barker 1997) that allowed us to fix additional parameters. Specifically, we assumed that we had a 100% chance of determining whether marked birds had nested because of the intensity of our surveys, the conspicuous courtship behavior of the plovers, and the openness of the nesting habitat, and we thus fixed  $p = 1.0$ . Because monthly survival rates are unknown for this species, we assumed they were equal among months and fixed  $R'$  (the mortality rate of resighted birds during the period of territory establishment given  $r = 0.0$ ) at  $(1 - 0.74^{(1/12)}) = 0.025$ , where 0.74 is the estimate of annual adult survival in the Atlantic Coast Recovery Plan (USFWS 1996). To examine the sensitivity of survival and site fidelity estimates to this as-

sumption, we also tested models where we fixed  $R'$  at 0.0 (no postresighting mortality during the period of territory establishment) and 0.046 (annual survival = 0.74 and mortality during the period of territory establishment twice as high as in any other month). In models with a year effect in the parameters, we estimated a confounded parameter for 2005 ( $S_{2005} \times R_{2005} \times F_{2005}$ ) because it would have required a sixth capture period to determine whether a bird not observed in 2005 had died or emigrated. Finally, we fixed  $S_{2006}$  and  $R_{2006}$  at 0 because we had no information on resightings between the breeding seasons of 2005 and 2006. We defined a set of eight *a priori* models (Table 1) for apparent survival rate ( $S$ ), resight rate ( $R$ ), and apparent site fidelity ( $F$ ). Using the notation of Lebreton et al. (1992), the candidate models included a year effect ( $t$ ) in  $S$  and  $F$ , and  $R_{2004}$  different than  $R_{2002}$  and  $R_{2003}$  because a change in field crew leaders may have led to a decrease in resighting rate in 2004. Thus, there were potentially nine estimable parameters:  $S_{2002}, S_{2003}, S_{2004}, R_{2002/2003}, R_{2004}, F_{2002}, F_{2003}, F_{2004}$ , and  $S_{2005} \times R_{2005} \times F_{2005}$ .

Although we used the median  $c$ -hat test in MARK to assess goodness-of-fit of the most highly parameterized model and to estimate the over-dispersion parameter ( $\hat{c}$ ), this test may lead to estimates of  $\hat{c}$  that are biased high (G. C. White, unpubl. data) and thus to conservative variance estimates and confidence intervals (Sedinger et al. 2002). We used Program MARK to estimate  $S$ ,  $R$ , and  $F$  for each model, to calculate information-theoretic criteria (i.e., corrected quasi-Akaike's Information Criterion, QAIC<sub>c</sub>), to aid in selecting the most parsimonious model, and to obtain model-averaged estimates and unconditional 95% confidence intervals for  $S$ ,  $R$ , and  $F$  (Burnham and Anderson 2002). Confidence intervals were calculated on logit-transformed estimates, and the endpoints were then back transformed (Lebreton et al. 1992).

We used the logit-link function that restricts parameter estimates to the interval  $[0, 1]$  to fit all models. Model estimation with the logit-link function can result in underestimation of the number of model parameters if any of the estimates are near 1.0 (White and Burnham 1999). Therefore, we manually adjusted the number of model parameters for several models where  $R$  was estimated at or near 1.0.

Table 1. Number of adult Piping Plovers captured and number of resightings at West Hampton Dunes and Westhampton Beach, Long Island, NY, from 2001 to 2005.

| Year | New captures <sup>a</sup> | New recruits <sup>b</sup> | Breeders resighted <sup>c</sup> | Nonbreeders resighted <sup>d</sup> | Nonbreeders missed <sup>e</sup> | Total population <sup>f</sup> |
|------|---------------------------|---------------------------|---------------------------------|------------------------------------|---------------------------------|-------------------------------|
| 2001 | 36                        | 0                         | 0                               | 0                                  | 0                               | 36                            |
| 2002 | 14                        | 0                         | 26                              | 1                                  | 0                               | 41                            |
| 2003 | 16                        | 3                         | 21                              | 10                                 | 0                               | 50                            |
| 2004 | 0                         | 1                         | 24                              | 6                                  | 2                               | 33                            |
| 2005 | 0                         | 1                         | 6                               | 6                                  | —                               | 13                            |

<sup>a</sup>Number of birds trapped on the nest and marked in year  $i$ .

<sup>b</sup>Number of birds marked as chicks prior to year  $i$  that nested at our site for the first time in year  $i$ .

<sup>c</sup>Number of marked birds breeding at our site in year  $i$  that were marked prior to year  $i$  and nested at our site in year  $i - 1$ .

<sup>d</sup>Number of marked birds resighted in year  $i$  that did not breed at our site in year  $i$ , were marked prior to year  $i$ , and bred at the site in at least one year prior to year  $i$ .

<sup>e</sup>Number of marked birds not resighted in year  $i$  but resighted in at least 1 year after year  $i$  that were marked prior to year  $i$ , and bred at the site in at least 1 year prior to year  $i$ .

<sup>f</sup>Total number of marked birds known to be in the population in year  $i$ .

**Juvenile return rate.** Because brood mates were only distinguishable in the hand and we were not able to capture and identify all returning juveniles with certainty, we did not attempt to model survival of hatch-year birds with mark-resighting methods. Instead, we calculated juvenile return rate each year as the proportion of marked fledglings that returned to breed. This measure would be biased low if we considered multiple individuals to be the same individual. Based on territory locations

and natural marks (neck and forehead plumage pigmentation), however, it appeared that only one member of any particular brood returned to breed in our study area.

## RESULTS

**Captures and resightings.** We captured and marked 66 nesting adult Piping Plovers from 2001 to 2005 (Table 1). In addition, 43 banded chicks fledged and 5 of those entered our sample

Table 2. Model-selection criteria for apparent survival rate ( $S$ ), resight rate ( $R$ ), and apparent site fidelity ( $F$ ) of adult Piping Plovers at West Hampton Dunes and Westhampton Beach, Long Island, NY 2001–2005 ( $N = 71$  adults).

| Model                                      | Number of parameters | QAIC <sub>c</sub> <sup>a</sup> | $\Delta$ QAIC <sub>c</sub> <sup>b</sup> | QAIC <sub>c</sub> weights <sup>c</sup> | Model likelihood <sup>d</sup> | Q deviance <sup>e</sup> |
|--|----------------------|--------------------------------|---|--|-------------------------------|-------------------------|
| {S(t) <sup>f</sup> R(·) <sup>g</sup> F(t)} | 8                    | 197.425                        | 0.000                                   | 0.323                                  | 1.000                         | 36.420                  |
| {S(t)R(·)F(·)}                             | 6                    | 198.117                        | 0.692                                   | 0.229                                  | 0.707                         | 41.371                  |
| {S(·)R(2004) <sup>h</sup> F(t)}            | 7                    | 198.387                        | 0.963                                   | 0.200                                  | 0.618                         | 39.521                  |
| {S(t)R(2004)F(t)}                          | 9                    | 199.037                        | 1.612                                   | 0.144                                  | 0.447                         | 35.874                  |
| {S(·)R(·)F(t)}                             | 6                    | 201.471                        | 4.046                                   | 0.043                                  | 0.132                         | 44.725                  |
| {S(·)R(·)F(·)}                             | 3                    | 202.262                        | 4.837                                   | 0.029                                  | 0.089                         | 51.772                  |
| {S(·)R(2004)F(·)}                          | 5                    | 203.283                        | 5.858                                   | 0.017                                  | 0.054                         | 48.640                  |
| {S(t)R(2004)F(·)}                          | 7                    | 203.558                        | 6.134                                   | 0.015                                  | 0.047                         | 44.692                  |

<sup>a</sup>Corrected Quasi-Akaike's Information Criterion, where estimated  $\hat{c} = 1.67$ .

<sup>b</sup>Difference between the QAIC<sub>c</sub> of a particular model and that of the best model.

<sup>c</sup>Likelihood of a particular model/ $\sum$  Likelihood of all models.

<sup>d</sup> $e^{(-0.5 \times \Delta \text{QAIC}_c)}$ .

<sup>e</sup>Deviance corrected for estimated  $\hat{c}$ .

<sup>f</sup>(t) = Parameter value varies by time (i.e., year).

<sup>g</sup>(·) = Parameter value constant across time.

<sup>h</sup>(2004) = Parameter value different in 2004 than in 2002 and 2003.

of breeding adults in a subsequent year (Table 1). We observed no partial band losses.

**Adult survival, site fidelity, and resighting rate.** Five of eight models had a likelihood  $>0.125$  (Table 2), indicating some support (Burnham and Anderson 2002). When a large subset of models have support, inferences should be made on model-averaged parameter estimates and unconditional confidence intervals that take into account model selection uncertainty as well as sampling error (Burnham and Anderson 2002). Therefore, we based inferences on model-averaged estimates and unconditional confidence intervals on  $S$ ,  $R$ , and  $F$ . Assuming that  $R' = 0.025$ , the mean ( $\pm$ SE) survival, site fidelity, and resighting rates for 2002–2004 were  $0.70 \pm 0.03$ ,  $0.83 \pm 0.07$ , and  $0.97 \pm 0.01$ , respectively. There was no difference in survival or resighting rate among years based on overlap of confidence intervals (Table 3). Site fidelity may have been lower in 2003 and 2004 than in 2002 because the 95% confidence intervals on the 2003 and 2004 estimates did not contain the 2002 estimate (Table 3) when  $R'$  was fixed at 0.025. However, the confidence interval on

the 2002 estimate contained the 2003 and 2004 estimates (Table 3), so evidence for a difference among years was not conclusive. Mean survival, resighting rate, and site fidelity varied by  $<5\%$  when we used different assumptions about  $R'$  (Table 3). When we fixed  $R'$  at 0.000 or 0.046, there was still evidence for a difference in site fidelity between 2002 and 2003, but not between 2002 and 2004 (Table 3).

**Observed dispersal.** In 2001 one female moved approximately 1.3 km from WHB to another nest site on the ocean side of WHD after abandoning her initial nest. Her original mate was never resighted after the abandonment. A second female moved from WHB to another nest site on the ocean beach just outside our study area east of WHB (approximately 1.5 km) after losing her nest to a predator. A female that nested successfully on the bay side in 2001 nested on the ocean side of WHD in 2002, and another female that nested successfully on the ocean side of WHD in 2001 nested on the bay side in 2002. During the 2002 breeding season, one pair moved from the bay side of WHD to the ocean side (approximately 1 km)

Table 3. Model-averaged estimates and unconditional confidence intervals on apparent survival rate ( $S$ ), resighting rate ( $R$ ), and apparent site fidelity ( $F$ ) of adult Piping Plovers, West Hampton Dunes and Westhampton Beach, Long Island, NY 2001–2005 ( $N = 71$  adults).

| $R'^a$             | Year <sup>b</sup> | Survival |       |             | Resighting rate |       |             | Site fidelity |       |             |
|--------------------|-------------------|----------|-------|-------------|-----------------|-------|-------------|---------------|-------|-------------|
|                    |                   | $S$      | SE    | 95% CI      | $R$             | SE    | 95% CI      | $F$           | SE    | 95% CI      |
| 0.025 <sup>c</sup> | 2002              | 0.714    | 0.091 | 0.551–0.856 | 0.984           | 0.022 | 0.807–0.999 | 0.945         | 0.082 | 0.443–0.997 |
|                    | 2003              | 0.751    | 0.095 | 0.527–0.891 | 0.984           | 0.022 | 0.807–0.999 | 0.707         | 0.117 | 0.443–0.880 |
|                    | 2004              | 0.643    | 0.087 | 0.462–0.791 | 0.948           | 0.051 | 0.660–0.994 | 0.830         | 0.084 | 0.601–0.940 |
|                    | Mean              | 0.703    | 0.032 | 0.637–0.762 | 0.972           | 0.012 | 0.936–0.988 | 0.827         | 0.069 | 0.650–0.925 |
| 0.000 <sup>d</sup> | 2002              | 0.731    | 0.092 | 0.521–0.871 | 0.984           | 0.022 | 0.797–0.999 | 0.904         | 0.094 | 0.532–0.987 |
|                    | 2003              | 0.753    | 0.091 | 0.539–0.888 | 0.984           | 0.022 | 0.797–0.999 | 0.702         | 0.116 | 0.443–0.874 |
|                    | 2004              | 0.651    | 0.087 | 0.468–0.798 | 0.946           | 0.060 | 0.635–0.994 | 0.812         | 0.084 | 0.595–0.927 |
|                    | Mean              | 0.712    | 0.031 | 0.648–0.769 | 0.971           | 0.013 | 0.931–0.988 | 0.806         | 0.058 | 0.668–0.896 |
| 0.046 <sup>e</sup> | 2002              | 0.721    | 0.119 | 0.447–0.892 | 0.984           | 0.022 | 0.813–0.999 | 0.947         | 0.078 | 0.464–0.997 |
|                    | 2003              | 0.738    | 0.098 | 0.512–0.884 | 0.984           | 0.021 | 0.813–0.999 | 0.721         | 0.119 | 0.447–0.892 |
|                    | 2004              | 0.638    | 0.087 | 0.457–0.787 | 0.950           | 0.053 | 0.677–0.994 | 0.844         | 0.084 | 0.607–0.950 |
|                    | Mean              | 0.699    | 0.031 | 0.635–0.756 | 0.973           | 0.011 | 0.941–0.988 | 0.837         | 0.065 | 0.669–0.929 |

<sup>a</sup> $R' =$  The probability that a bird sighted between 15 March and 15 April died later in that interval without being reported dead. Because we fixed  $r$  (the probability of a bird being found dead and reported) at 0.0,  $R'$  equals the mortality rate of resighted birds in the territory establishment period (15 March to 15 April).

<sup>b</sup>Year of resighting.

<sup>c</sup>Assumes an annual survival rate of 0.74 (USFWS 1996) and constant monthly survival rates.

<sup>d</sup>Assumes no mortality of resighted birds in the territory establishment period.

<sup>e</sup>Assumes an annual survival rate of 0.74 and that mortality during the territory establishment period is twice as high as in other months.

after losing their nest to a fox (*Vulpes vulpes*). Between the 2002 and 2003 breeding seasons, one pair, one male, and two females moved from the bay side to the ocean side after failing to breed successfully the previous year. One female that nested successfully in 2002 moved in the opposite direction and, in 2003, this female lost a nest to an unidentified predator and then re-nested on the ocean side at WHB, approximately 1 km away, with the same male.

**Juvenile return rate.** The rates at which juveniles returned to breed were  $0.11 \pm 0.06$  (SE;  $N = 28$ ) and  $0.13 \pm 0.09$  (SE;  $N = 15$ ) in 2003 and 2004, respectively.

## DISCUSSION

Our mean annual adult survival estimate (0.70) was similar to that for Piping Plovers in Maryland in the late 1980s (0.71; Loegering 1992), Massachusetts in the late 1980s (0.74; USFWS 1996), and the Great Plains during a 10-yr study in the 1980s and 1990s (0.74; Larson et al. 2000). Piping Plovers from different breeding populations mix on their wintering grounds (Haig et al. 2005). Because plovers at widely separated breeding sites likely face different types and intensities of threats to survival (e.g., predators and weather), the apparent similarity in survival in different breeding populations suggests that mortality during the nonbreeding period may be more important in determining annual survival than mortality on the breeding grounds. Although multi-year studies at different locations have revealed similar average survival estimates, Larson et al. (2000) found that annual survival fluctuated among years (range 0.3–1.0). Thus, additional studies of survival at different times of the year and at different locations are needed before conclusions about the relative importance of mortality in breeding and wintering areas can be drawn. Understanding period-specific survival rates and sources of mortality would help managers determine if improving the survival rates of adult Piping Plovers is possible.

The above survival estimates for Piping Plovers were close to those for Snowy Plovers (*C. alexandrinus*) in Utah (mean 0.68, range 0.58–0.88, Paton 1994), Semipalmated Plovers (*C. semipalmatus*) in Canada (0.71, Nol and Blanken 1999), and Mountain Plovers (*C. montanus*) in Montana (0.69 in each of 5 years,

Dinsmore et al. 2003). These four congeners have similar life history and ecological traits (e.g., small, rather invariant clutch sizes, similar prey items and foraging behaviors, and, with the exception of Semipalmated Plovers that migrate medium to long distances, short-distance migration). Average annual survival of Piping Plovers might thus have evolved with other physiological, behavioral, or life history traits (Stearns 1977) shared with their congeners. If so, management for improved long-term average survival may not be possible. Populations where survival is consistently lower than reported elsewhere, however, might represent opportunities for improvement if the timing and sources of mortality can be identified.

Mean site fidelity in our study (0.83) was higher than reported for eight species of shorebirds in the family Scolopacidae (range = 0.38–0.73; Oring and Lank 1982). In a study conducted from 1937 to 1958 that included our sites and others in New York (Wilcox 1959), site fidelity of 291 known surviving Piping Plovers was 0.99. At Lake-of-the-Woods, Minnesota, 84% of Piping Plovers that returned to breed in successive years nested within 200 m of their previous year's nest site (Wiens and Cuthbert 1988), indicating high nest-site tenacity. Site fidelity for 62 Piping Plovers known to have survived between breeding seasons in Manitoba, however, was 0.72 (Haig and Oring 1988). Thus, our estimate of site fidelity was near the midpoint of the range reported in previous studies. Investigators in previous studies, however, did not statistically account for resighting rates, potentially inflating their estimates if more birds survived and emigrated than were observed to do so. Given the high site fidelity of Piping Plovers, factors that decrease local adult survival could lead to local population declines if immigration rates are low.

The high site fidelity of coastal Piping Plovers suggests that patches of coastal breeding habitat have remained suitable over long enough periods to select for site faithfulness, despite the typical perception of such habitats as dynamic (USFWS 1996). In Manitoba, where site fidelity was lower than in the coastal studies, habitat quality during the settlement and breeding periods varied within and among seasons due to the effect of weather on water levels near nesting beaches (Haig and Oring 1988). Thus, Piping Plovers tend to be site faithful, but may disperse

when habitat quality is poor or declining. In the Great Plains, census data indicated a potentially large movement of breeding pairs from Prairie Canada, where the availability of suitable habitat may be declining, to the Missouri River (Haig et al. 2005). On a smaller scale, the quality of breeding habitat for Ringed Plovers (*Charadrius hiaticula*) nesting in agricultural fields in Scotland varied with field status (old fallow fields were too vegetated to be used; Jackson 1994). Dispersal rates of experienced breeders depended on the number of years since plowing, and dispersal was always to higher-quality nesting sites (Jackson 1994). The possible change in Piping Plover site fidelity we observed between 2002 and 2003 might thus be related to a change in habitat quality at our site, as measured by reproductive success and quantity of nesting area, although demographic stochasticity may have also played a role.

The movements of individual birds in our study suggest that emigration was related to habitat quality. From the middle of the breeding season in 2002 until the beginning of the breeding season in 2003, six marked individuals moved their territories from the bay side nesting area at WHD to the ocean side at WHD and all had experienced reproductive failure on the bay side in 2002. Concurrently, the total number of pairs on the bay side declined from seven to two. Of the 10 marked birds that were seen alive in early 2003 but did not nest, seven had nested on the ocean side at WHD in the previous year and five successfully fledged chicks. The number of ocean side pairs decreased from 27 to 25 in 2003. Poor reproductive success on the bay side was part of a long-term trend. In a partly concurrent, 12-year study (1993–2004) in our study area, Houghton (2005) found that chick survival on the bay side decreased from 61% in 1999 to 0% in 2002, whereas the decrease was from 91% to 69% on the ocean side. The decrease in chick survival coincided with a loss of nesting habitat on the bay side. Available habitat decreased from 28 ha to 17 ha between 2000 and 2001 and to 5.6 ha in 2002, then remained about the same thereafter (Houghton 2005). On the ocean side, habitat area remained nearly stationary at 25–27 ha during the same period (Houghton 2005). Thus, it appears that a decline in habitat quantity and quality on the bay side at WHD prompted within-site movements, and that in-

creased competition for space on the ocean side led to displacement of some individuals in 2003.

A second possible explanation for the decreased site fidelity in 2003 may be demographic stochasticity. The population at WHB in 2002 reached a record high of 20 pairs, far above the 12-year average of 11 pairs in that part of the study area. This may have been due in part to good reproductive success for plovers at WHB in 2001 that was the second highest recorded in 12 years (1.67 fledglings/pair Houghton 2005). In 2003 the number of pairs at WHB decreased to 13, possibly representing a readjustment of the population to the local carrying capacity. Available habitat area at WHB remained relatively constant at 26–30 ha from 2000 to 2003. Two of the 10 emigrating birds in 2003 came from WHB.

The increase in site fidelity in 2004 did not appear to be related to an improvement in habitat conditions. In fact, 2003 was the second-worst year recorded for reproductive success (0.55 fledglings/pair, Houghton 2005), and the total area of nesting habitat in the study area decreased by 6% in 2004. It is more likely that site fidelity increased because the population had already adjusted in the previous year to a lower carrying capacity at WHD and typical carrying capacity at WHB.

In the 12-yr study reproductive output averaged  $1.01 \pm 0.17$  (SE) chicks fledged/pair from 2001 to 2004 (Houghton 2005). This is below the replacement rate of 1.24 calculated for Atlantic Coast plovers, assuming apparent survival of 0.74 for adults and 0.48 for second-year birds (USFWS 1996). Given the lower return rates for adults and juveniles at our local breeding site than for the regional population modeled by the USFWS (1996), our replacement rate would likely be higher than 1.24. Thus, the population in our study area was prone to decline in the absence of immigrants. One year with moderately low adult site fidelity, such as 2003, could, therefore, have led to the precipitous decline we observed that year. Several demographic variables likely contributed to the continued population decline in 2004, despite slightly increased adult site fidelity. Reproductive success in 2003 was low throughout the study area (Houghton 2005). Furthermore, given the continued decrease in habitat area in 2004 and the low quality of remaining habitat on the

bay side of WHD, it was unlikely that new immigrants would have been attracted to the site.

The rate at which dispersing Piping Plovers find and reproduce successfully at new sites is unknown. Although Piping Plovers may be adapted to dynamic habitats, coastal stabilization and development by humans may have affected the rate at which new habitat forms (Dolan et al. 1973) and becomes available for dispersers. If dispersing plovers fail to find alternative breeding habitat, then population-level recovery will be hindered by local habitat degradation.

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