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Author(s): Mark R. Ryan, Brian G. Root, Paul M. Mayer
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Status of Piping Plovers in the Great Plains of North America: A Demographic Simulation Model

MARK R. RYAN
BRIAN G. ROOT
PAUL M. MAYER*

The School of Natural Resources
University of Missouri–Columbia
Columbia, MO 65211, U.S.A.

Abstract: *A stochastic population growth model using empirical demographic data confirmed that the Piping Plover population of the Great Plains of North America is declining by more than 7% annually. Unchecked, this decline would result in extirpation in approximately 80 years. When recent adult (0.66) and immature (0.60) survival rates were held constant, a 31% increase—from 0.86 to 1.13 chicks fledged per pair—was needed to stabilize the population. Annual population increases of 1% and 2% required 1.16 and 1.19 chicks per pair, respectively. Such growth would result in the Great Plains population reaching the level—(2550 pairs)—needed for delisting from the U.S. Endangered Species Act protection in 53 and 30 years, respectively. One- and five-year delays in the initiation of 1% population growth caused 13 and 67 year delays respectively in reaching recovery.*

Estado de los chorlitos (*Charadrius melodus*) en las Grandes Planicies de Norte América: Un modelo demográfico de simulación

Resumen: *Un modelo de crecimiento poblacional estocástico, que usa datos demográficos empíricos confirmó que la población de chorlitos (*Charadrius melodus*) de las Grandes Planicies (América del Norte) está declinando más de un 7% por año. Si esta declinación no es controlada, resultará en extinción en alrededor de 80 años. Cuando las tasas de supervivencia de adultos recientes (0.66) e individuos inmaduros (0.60) fueron mantenidas constantes, se necesitó un 31% de aumento, de 0.86 a 1.13 polluelos volantones por pareja, para estabilizar la población. Crecimientos poblacionales anuales de 1% y 2% requirieron 1.16 y 1.19 polluelos por pareja, respectivamente. Tal crecimiento haría que la población alcance el nivel requerido (2550 parejas) para que sea excluída de la protección, bajo el Acta de Especies en Peligro de los Estados Unidos, dentro de unos 53 y 30 años, respectivamente. Retardos de 1 y 5 años en la iniciación de un crecimiento poblacional del 1% causaría, respectivamente, 13 y 67 años de retardo en la recuperación.*

Introduction

The Great Plains population of Piping Plovers (*Charadrius melodus*) occurs at low densities in patchily distributed habitats in the north-central United States and south-central Canada (Haig et al. 1988). The inaccessibility of much of the breeding habitat makes population monitoring difficult.

Piping Plovers in the Great Plains were listed in 1985 as threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1985) and as endangered in Canada (Haig 1985). Protection was afforded largely based on habitat loss, with no quantification of

* *Current address: Department of Conservation Biology, 318 Church St. SE, University of Minnesota–Twin Cities, Minneapolis, MN 55455, U.S.A.*
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absolute population size or rate of population change available.

Attempts at annual, region-wide counts of breeding Piping Plovers began in 1986 (Haig et al. 1988). In some areas counts probably have been close to complete (R. Lock, Nebraska Game and Parks, personal communication), but elsewhere the counts have been incomplete to an unknown degree. Furthermore, annual changes in water levels have resulted in population shifts on local and regional scales (Mayer 1991). These censusing problems have impeded credible documentation of population change. Counts from 1986–1990, however, were conducted with roughly similar effort, and may provide a gross estimator for population change. Counts during this time interval indicated an approximate decline from 1400 to 1000 breeding pairs (corrected from Haig 1992). In 1991, substantially more effort was expended in the Great Plains than during previous years' counts, resulting in 1486 Piping Plover pairs tallied (Haig & Plissner 1992). Although the most accurate estimate to date, the 1991 data further confound the issue of measuring population change.

Because of limited funding for endangered species conservation the uncertainly about the decline of Piping Plovers, and the lack of information concerning the likelihood of or time frame for recovery may contribute to a low-priority management effort. Therefore, we sought a means independent of population counts to measure changes in the Great Plains Piping Plover population. Using demographic data and simulation processes, we assessed whether or not the Great Plains population of Piping Plovers was stable. We further used the population simulation model to estimate mean reproductive and survival rates necessary to stabilize the population and to increase it to the recovery level identified by Haig et al. (1988). We also present data on the effect on recovery times of delay in initiating high-priority management efforts.

The Population Model

We constructed a stochastic population growth model to predict changes in the Piping Plover population in the Great Plains. Parameters incorporated in the model included reproductive rate (chicks fledged per pair) and survival rates for adults (on year old or more) and immatures (from fledging to one year old).

Input Parameters

We used the mean annual survival rate for adult Piping Plovers calculated by Root et al. (1992). No other survival rate data for Piping Plovers have been published.

No information is available on survival rates for immature piping plovers because of low return rates to natal areas (Wilcox 1959; Root et al. 1992). However, first-year survival rates of Snowy Plovers (*C. alexandrinus*; Page et al. 1983) and Ringed Plovers (*C. hiaticula*; Pienkowski 1984) ranged from 71% to 87% that of adults. Because the immature survival rate for Piping Plovers was unknown, we used values corresponding to 70%, 80%, 90%, and 100% of the adult survival rate in our model (Table 1). Although highly unlikely, an immature survival rate equal to that of adults provides a conservative test of population stability.

We compiled reproductive rate data for Piping Plovers from studies conducted between 1980 and 1990 throughout the Great Plains. We calculated a mean reproductive rate for 32 site-years, from six U.S. states and three Canadian provinces, representing the range of breeding habitats (alkaline lakes, fresh-water lakes, rivers) in the Great Plains (Table 1).

Model Assumptions and Processes

Estimates of survival and reproductive rates were obtained from individuals and pairs, respectively. To make these data comparable and because no sex-specific survival data are available (Root et al. 1992), we modeled only the female portion of the population. Piping Plovers are monogamous breeders from age one (Haig 1992), and few nonbreeding adults have been observed in the Great Plains (Haig & Oring 1988). Therefore, we assumed that the number of adult females was directly proportional to the total number of breeding adult plovers in the population.

Piping Plovers typically lay four-egg clutches, but five-egg clutches occur rarely (Haig 1992). We based reproductive rates on a maximum clutch size of 5, with an equal sex ratio of fledged chicks. Thus, the maximum number of female chicks fledged per adult female was 2.5.

Table 1. Means of Great Plains Piping Plover reproductive rate, adult survival rate, and four levels of immature survival rate used in population simulations, with projected extirpation times.

Reproductive rate ($\bar{x} \pm SE$)[a]	*Adult survival* ($\bar{x} \pm SE$)[b]	*Immature survival* ($\bar{x} \pm SE$)[c]	*Years to extirpation (min–max)*[d]
0.86 ± 0.09	0.66 ± 0.06	0.46 ± 0.06	44 (25–54)
		0.53 ± 0.06	56 (28–77)
		0.60 ± 0.06	81 (29–105)
		0.66 ± 0.06	120 (36–148)

[a] *n = 32; sources: Haig, personal communication; L. Weber, personal communication; Wiens & Cuthbert 1984; Whyte 1985; Wiens 1986; Haig 1987; Haig & Oring 1987; Prindiville-Gaines & Ryan 1988; Schwalbach 1988; Mayer 1990, 1991.*
[b] *Source: Root et al. 1992.*
[c] *Mean values = 70%, 80%, 90%, and 100% of adult survival; see text for additional explanation.*
[d] *Value is the first year the mean population size = 0, based on simulations with 500 replications/year; minimum is first year one of the 500 replications = 0; maximum is first year all 500 replications = 0.*

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As the basis for the population growth model, we used the deterministic equation

$$AF_{t+1} = (AF_t \times CF_t \times S_i) + (AF_t \times S_a),$$

where AF_{t+1} = number of adult females at the beginning of year t + 1; AF_t = number of adult females at the beginning of year t; CF_t = number of female chicks fledged per adult female in year t; S_i = survival rate of immature females from fledging to age 1; and S_a = annual survival rate of adult females.

For each simulation of persistence time, 500 replicate model calculations were made for each year, and the mean of those replicates was used to represent the annual population size. The model simulated stochastic processes by randomly selecting new values for S_a, S_i, and *CF* for every iteration within each year, based on beta probability distributions (Hastings & Peacock 1975). Probability distributions were governed by the sample means and variances of the three input parameters. We assumed that the variance of S_i was equal to that of S_a. Comparison of mean persistence time under this assumption with that of simulations using a variance of S_i twice that of adults yielded no difference ($t = 0.35$, $p = 0.75$, $n = 10$), but the standard deviation nearly doubled. Tests of the model's sensitivity to changes in input parameter values are reported in the Appendix.

We attempted to simulate realistically past and future changes for the Great Plains population. We used 1500 adult females as the initial population size for all simulations (Table 1). This value was slightly higher than the 1986 and 1991 population estimates (Haig et al. 1988; Haig & Plissner 1992) to account for any breeding pairs uncounted (likely in Saskatchewan and North Dakota). Model simulations based on recent demographics were compared to the count data from 1986–1990.

Model Results

Recent Status

All simulations representing recent demographics indicated that the Great Plains Piping Plover population is undergoing a substantial decline (Table 1). Extirpation of the population occurred at 44, 56, 81, and 120 years after the beginning of the simulations, depending on the immature survival rate used (equaling 70%, 80%, 90%, or 100% of adult survival, respectively). For the four immature survival rates, the annual population decline was 13.7%, 10.0%, 7.6%, and 4.7%, respectively. Annual declines in the 1986–1990 Piping Plover count data averaged 7.5% (corrected from Haig 1992). Based on this small data set (n = 5 years), the immature survival rate of 0.60, used in conjunction with the empirically-derived adult survival and reproductive rates (Table 1), best reflected trends in the count data (Fig. 1). Because of this concordance, we used the immature survival rate of 0.60 in further simulations. Repeatability of model output was high; 10 replicate simulations yielded a mean extirpation time of 79.1 (SE = 0.71) years.

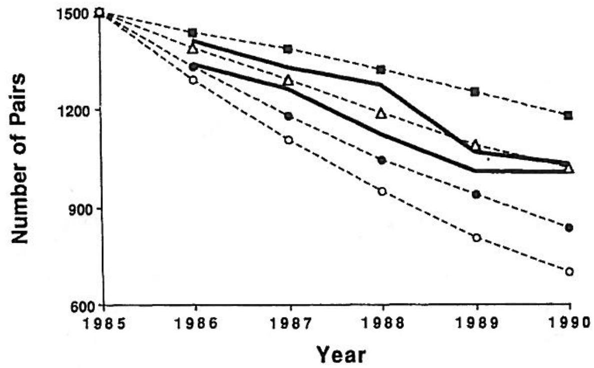

Figure 1. Comparison of count data and simulated population size of the Great Plains Piping Plover. Solid lines represent count data (corrected from Haig 1992); upper line = maximum estimate, lower line = minimum estimate. Population simulations are represented by open circles = [immature survival = 0.7 (adult survival)]; closed circles = [immature survival = 0.8 (adult survival)]; open triangles = [immature survival = 0.9 (adult survival)]; closed squares = [immature survival = adult survival]. See Table 1 for survival and reproductive rate data.

Population Stabilization

Based on our simulations, substantial increases in reproductive success or survival will be necessary to stabilize the Great Plains Piping Plover population (Table 2). Holding adult and immature survival rates constant, a mean annual reproductive rate of 1.13 chicks fledged per breeding pair was required to stabilize the population. Although substantial, such an increase may be feasible. On a limited scale, protecting nests from predators

Table 2. Reproductive and survival rates necessary for stabilization and growth of the Great Plains Piping Plover population, with reproductive rate or survival rates alternately held constant (dashes within columns).

Population status	*Chicks fledged per pair (% increase)*	*Adult survival (% increase)*	*Immature survival (% increase)*
Recent[a]	0.86	0.66	0.60
Stable	1.13 (31.4)	—	—
Stable	—	0.72 (8.7)	0.65 (8.7)
1% Growth	1.16 (34.8)	—	—
1% Growth	—	0.73 (9.6)	0.66 (9.7)
2% Growth	1.19 (38.4)	—	—
2% Growth	—	0.74 (10.7)	0.67 (10.9)

[a] *Recent population decline = 7.6%; see Table 1 for sources.*

raised fledging rates to 1.18 (Mayer & Ryan 1991) and more than 2.0 (Powell 1991) chicks per breeding pair.

When the reproductive rate was held constant at the recent level, adult and immature survival rates had to be increased by 8.7% to stabilize the population (Table 2). The recent estimate for survival of adult Piping Plovers (0.66) is lower (by ≥11%) than that reported for congeneric species (Root et al. 1992), suggesting that such an increase may be feasible. However, almost nothing is known about the causes of mortality of adult Piping Plovers. Conservation efforts to increase survival, therefore, seem unlikely at this time.

Estimates of Population Recovery Time

The U.S. recovery plan for Great Plains Piping Plovers established a goal of 2550 pairs (including Canada) for removal of the species from Endangered Species Act protection (Haig et al. 1988). Simulated population growth of 1% and 2% annually, beginning immediately (initial population = 1500 pairs), resulted in recovery levels being attained in 51 (95% C.I. = 37–61) and 30 (95% C.I. = 26–34) years, respectively. Under current survival conditions, reproductive output had to be increased to 1.16 and 1.19 chicks per pair to achieve 1% and 2% annual population growth, respectively (Table 2).

Assuming a continued population decline of 7.6% annually, delays in the initiation of intensive, rangewide management actions (such as nest protection and habitat enhancement) to increase the population had increasingly costly effects on recovery time. A one-year delay resulted in a 13-year lag in reaching the recovery level. A five-year delay more than doubled the recovery time (Table 3).

Conclusion

All available evidence points to a substantial decline in the Great Plains Piping Plover population, even under the most favorable demographic conditions. The most realistic projections indicate extirpation in about 80 years. The population decline may be buffered by locally-operating density-dependent reproduction (Mayer 1991), but continuing degradation of habitat at both breeding and wintering areas is likely to accelerate the extirpation rate.

Our simulation results suggest that recovery of the Great Plains Piping Plover population is feasible, but that it will require more aggressive implementation of the recovery plan (Haig et al. 1988). Our simulations suggest that recovery could be hastened by even a small increase in survival, but more data are needed on causes of Piping Plover mortality before management strategies can be designed. Protection of nests and chicks (see Mayer & Ryan 1991), enhancement of nesting beach habitats (Prindiville-Gaines & Ryan 1988), and better management of river levels to protect nesting islands (Mayer 1990; U.S. Fish and Wildlife Service 1990) throughout the breeding range could substantially increase reproductive rates. Delays in implementation of intensive management will substantially lengthen recovery times, increasing cost and the risk of extirpation.

Table 3. The effect of population growth rate and management delays on Piping Plover population growth to recovery levels.

Management initiation year	*Projected population size*[a]	*Population growth rate*	*Years to recovery (95% confidence limit)*
Immediate	1500	2%	30 (26–34)
Immediate	1500	1%	51 (37–61)
Delay 1 year	1386	1%	64 (47–94)
Delay 5 years	1010	1%	118 (88–144)

[a] *Based on simulations under recent demographic conditions (with immature survival = 0.60), see Table 1 for data.*

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Appendix

Model sensitivity analysis: the effect of varying input parameter values on piping plover persistence times (years).

Parameter changes	*Input parameters*[a] S_a	S_t	*CF*	*Persistence (min–max)*	*± % Change*[b]
Recent	0.66	0.60	0.86	81 (29–105)	
Survival					
−5%	0.63	0.57	——	50 (25–68)	−38
−10%	0.60	0.54	——	36 (21–45)	−56
+5%	0.70	0.63	——	225 (41–273)	+178
+10%	0.73	0.66	——	∞	
Reproduction					
−5%	——	——	0.82	64 (30–85)	−21
−10%	——	——	0.77	58 (27–77)	−28
+5%	——	——	0.90	97 (35–131)	+20
+10%	——	——	0.95	114 (37–168)	+41

[a] *S_a = annual survival rate of adult females; S_t = survival rate of immature females from fledging to age one; CF = number of female chicks fledged per adult female; dashes (——) indicate input parameters equal to recent values.*
[b] *From persistence time = 81 years.*