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ANNUAL SURVIVAL AND POPULATION ESTIMATES OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA

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Abstract. Information about the demography of declining species is especially relevant to their conservation and future recovery. Knowledge of survival rates and population size can be used to assess long-term viability and population trends, both of which are of interest to conservation biologists. We used capture–recapture techniques to study the demography of Mountain Plovers (*Charadrius montanus* Townsend) in southern Phillips County, Montana, USA, in 1995–2000. We used the robust design to estimate annual survival (ϕ), conditional capture (p and r) and recapture (c) probabilities, and the annual population size (N) in the presence of temporary emigration. The results support age-specific differences in annual survival that are a function of juvenile body mass and are correlated with the area occupied by prairie dogs. Body mass had a positive effect on juvenile survival; the slope coefficient for the additive effect of body mass on juvenile survival was 0.77 (95% CI = 0.25, 1.28) on a logit scale. A measure of plover habitat (the area occupied by prairie dogs) appeared to have no effect on survival; the slope coefficient for the additive effect of area occupied by prairie dogs on survival was −0.00004 (95% CI = −0.00003, −0.0001) on a logit scale. Estimated annual apparent survival rates were 0.46–0.49 for juveniles and 0.68 for adult plovers. Using these estimates, the life span of a Mountain Plover was 1.92 ± 0.17 years (mean ± 1 SE) from time of capture as a chick. Resighting rates positively influenced capture probabilities; the slope coefficient for the additive resighting effect was −0.49 (95% CI = −0.86, −0.11) on a logit scale. The size of this adult Mountain Plover population was estimated at 95–180 adults annually. Population size closely tracked annual changes in the area occupied by black-tailed prairie dogs, with both plovers and prairie dogs rapidly recovering from an outbreak of sylvatic plague in the mid-1990s. Given the low annual survival rates and low mean life expectancy of Mountain Plovers, we conclude that sustainable local populations are currently maintained by annual rates of productivity greater than those for other ground-nesting birds.

Key words: *capture–recapture;* Charadrius montanus; *conservation; demography; Montana; Mountain Plover; population size; robust design; survival.*

INTRODUCTION

The conservation of declining species requires a thorough understanding of their life history traits and demography. When baseline biological information is missing, concerns about management and possible recovery may be difficult to address. For federally listed species such as the Northern Spotted Owl (*Strix occidentalis caurina*), studies of demography are especially important because they provide biologists with information about population trends and hint at the effects of various management strategies (Forsman et al. 1996). However, many rare or declining species suffer from a lack of such detailed information. For species like the Mountain Plover (*Charadrius montanus*), knowledge of population numbers and survival rates is extremely important, and combined with information about productivity, is critical to assess long-term viability. Detailed studies of demography are thus vital to understanding the life history of a species and are a necessary component of future recovery efforts.

Demographic parameters such as survival and population size can be estimated from a wide array of capture–recapture studies. Estimation of these parameters has undergone rapid advancement since capture–recapture theory was formalized in the 1960s (Cormack 1964, Jolly 1965, Seber 1965). Two major classes of models have emerged, one dealing with ''open'' populations (Pollock et al. 1990, Lebreton et al. 1992) and the other with ''closed'' populations (Otis et al. 1978, White et al. 1982). A major limitation of these approaches concerns assumptions about emigration and immigration; they are either assumed to be permanent, or are ignored entirely. Biologically, these assumptions

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are unrealistic; emigration and immigration may be important factors influencing population growth rates. Furthermore, temporary emigration may also be an important consideration when estimating parameters such as survival.

Temporary emigration refers to animals that are temporarily unavailable for capture, including those that may have temporarily left the area being sampled (Kendall et al. 1997). Biologically, temporary emigration can explain patterns in which (1) all individuals do not return to the breeding grounds every year, or (2) individuals that inhabit a boundary region of the study area may not be sampled every year. These concerns led to the development of the robust design (Pollock 1982), a model that incorporates features of both open and closed capture–recapture theory and allows temporary emigration to be estimated. The robust design generates less biased estimates of survival and population size in the presence of temporary emigration (Kendall et al. 1997).

The Mountain Plover is an uncommon bird of the western Great Plains that has core breeding areas associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies in eastern Montana, the eastern two-thirds of Wyoming, and eastern Colorado. The species is one of 12 endemic birds of the Great Plains (Mengel 1970), a group that has shown dramatic population declines in recent years (Knopf 1996*a*). Continent-wide, this species has declined by as much as 63% since 1966 (Knopf 1994). Much of this decline is attributed to habitat alterations, especially the removal of prairie dogs (Knopf 1994) and the loss or alteration of wintering habitat (Knopf 1994, Dinsmore 2000). The total population has been estimated at 8000–10 000 birds (Knopf 1996*b*). Concerns over declines led to a 1997 proposal to list the Mountain Plover (Miller and Knopf 1993) under the U.S. Endangered Species Act, and it was subsequently proposed for listing as Threatened in 2002 (U.S. Department of the Interior 2002).

The breeding biology of Mountain Plovers has been well studied, especially in northeastern Colorado (Graul 1975, Miller and Knopf 1993, Knopf and Rupert 1996). There are few studies of this species outside Colorado, mostly local studies of distribution and breeding biology. Other localized studies have looked at diet (Olson 1985, Knopf 1999), mating system (Graul 1973), brood survival (Miller and Knopf 1993), and overwinter survival and habitat use (Knopf and Rupert 1995). The result is that the natural history of Mountain Plovers is reasonably well understood, but there are no published studies on demography or population biology. Annual survival has not been estimated and there have been no rigorous attempts to enumerate the number of breeding adults at a specific breeding site.

In 1995, we initiated a capture–recapture study of Mountain Plovers in southern Phillips County, Montana. Southern Phillips County is thought to contain the largest population of Mountain Plovers in Montana, one of the largest populations in North America (Knopf and Miller 1994), and contains the highest known density of breeding plovers anywhere (Knowles et al. 1982, Olson-Edge and Edge 1987). The main objective of this study was to provide baseline information on the demography of Mountain Plovers. We modeled age-, year-, and time-specific differences in annual apparent survival as a function of available habitat for nesting (area occupied by prairie dogs) and two individual covariates (juvenile body mass and a 1999 transmitter effect), using Huggins robust design (Huggins 1989, 1991, Kendall et al. 1995, 1997). We also estimated annually the number of breeding adult plovers at this isolated breeding area.

Methods

Study area

We studied Mountain Plovers on a 3000 km^2 area in southern Phillips County in north-central Montana (47°40′–47°55′ N, 107°35′–108°30′ W; Fig. 1). The study area is bounded by the Missouri River to the south, the Sun Prairie and Content roads to the east, Beaver Creek to the north, and Highway 191 to the west. Approximately 2250 km^2 of the study area is in public ownership with the Bureau of Land Management (BLM, Malta Field Office) and the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge). This area was a mixed-grass prairie with sagebrush flats bordering the southwestern edge of the Prairie Pothole Region (Knowles et al. 1982, Olson and Edge 1985). Predominant vegetation included big sagebrush (*Artemisia tridentata*), silver sagebrush (*Artemisia cana*), greasewood (*Sarcobatus vermiculatus*), yellow sweetclover (*Melilotus officinalis*), green needlegrass (*Stipa viridula*), and western wheatgrass (*Agropyron smithii*). Active black-tailed prairie dog colonies contained variable amounts of bare ground interspersed with sparse vegetation that included fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polycantha*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*), with fewer grasses generally present on the older colonies. Mean annual precipitation near the center of the study area was 33 cm, most of which fell from May to July (D. Veseth, *personal communication*). Mean elevation was ~930 m.

We selected this study area in part because previous studies of Mountain Plovers had established a strong link between nesting plovers and active black-tailed prairie dog colonies in Phillips County (Knowles et al. 1982, Knowles and Knowles 1984). Specific testing of this plover–prairie dog relationship is beyond the scope of this paper; hereafter, we assume that this relationship exists in Phillips County. Thus, we studied Mountain Plovers exclusively on, or adjacent to, active black-

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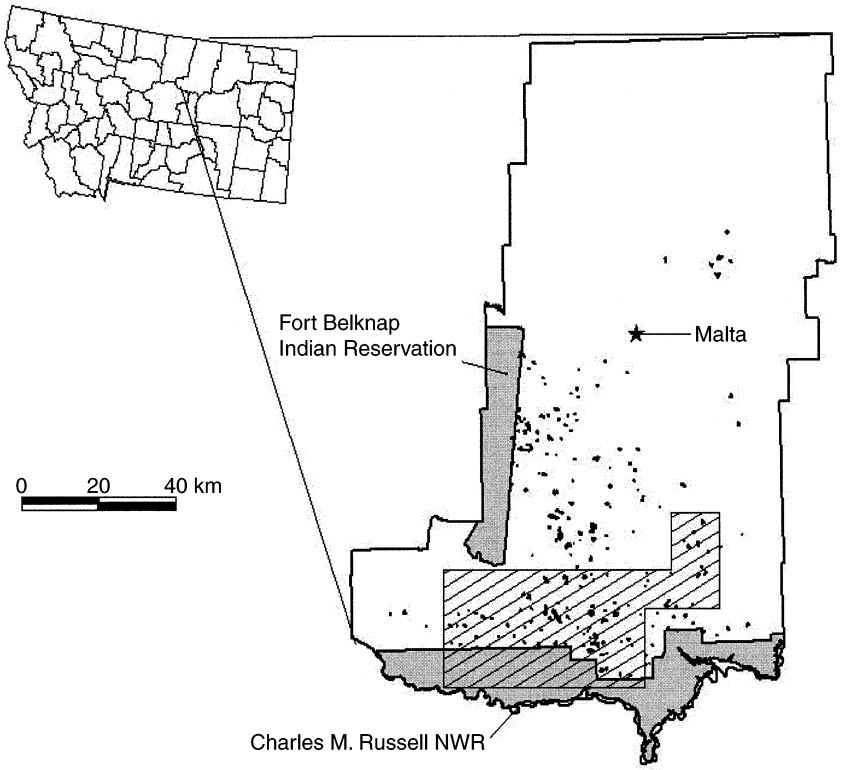

FIG. 1. Map of Phillips County, Montana, USA, showing the year 2000 distribution of black-tailed prairie dog colonies (in black), Charles M. Russell National Wildlife Refuge, and Fort Belknap Indian Reservation. The hatched region represents the study area.

tailed prairie dog colonies in this region. Mountain Plovers did not occupy all active prairie dog colonies in this region; they were generally most common in the southern part of the county and avoided prairie dog colonies that lacked eroded soil or had unsuitable vegetative characteristics (see Olson and Edge 1985). Inactive prairie dog colonies, mostly the result of plague outbreaks, often became unsuitable for plovers, sometimes within a few weeks of the outbreak.

The area occupied by prairie dogs generally increased in southern Phillips County during the course of the study (Fig. 2). On the annual census, BLM staff used a portable global positioning unit (Trimble ProXR, Trimble, Sunnyvale, California, USA) to delineate the boundaries of active prairie dog colonies. In four years (1995, 1996, 1997, and 1999) a sample of one-third of all known active colonies was censused; a complete census of all known active colonies was done in 1998 and 2000. The area occupied by prairie dogs was calculated in a spatial database (ArcInfo GIS 3.2 [ESRI 2000]), and annual measures of the area occupied by prairie dogs were based on the percentage change in the sample of one-third of the colonies (except in 1998 and 2000). For example, if the 1997 survey showed a 16% increase in the sample, then the estimate of total area occupied by prairie dogs for 1997 was obtained by multiplying all 1996 colony areas by 1.16. On the first complete census in 1988, prairie dogs occupied 8675 ha in southern Phillips County, but this total dropped markedly by the time the study began in 1995. It is important to note that the area occupied by prairie dogs represented only an index of plover habitat. A measure of the area of a prairie dog colony does not account for factors such as prairie dog density, vegetative differences, or differences in topography such as slope and elevation, all of which may be important to plovers (Knopf 1996*b*). Inactive prairie dog colonies were not included in this total because they were essentially unsuitable for plovers. Annual fluctuations in the area occupied by prairie dogs were largely caused

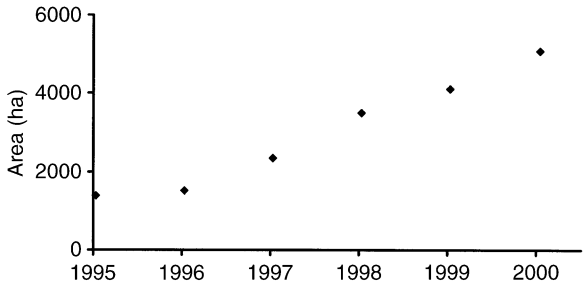

FIG. 2. Area occupied by black-tailed prairie dogs, calculated from annual Bureau of Land Management surveys in southern Phillips County, Montana, 1995–2000.

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by sylvatic plague, an epizootic (Barnes 1993), although recreational shooting may have had a negative impact on some of the smaller prairie dog colonies (Vosburgh and Irby 1998). The last known plague outbreak occurred in the early 1990s, and infected colonies recovered rapidly after 1996.

The area where we studied Mountain Plovers was isolated from other areas occupied by plovers. The nearest plovers were along the Milk River in northwestern Phillips County 32 km to the north, at Fort Belknap Indian Reservation in Blaine County 40 km to the northwest, and in southern Valley County 40 km to the northeast. The boundaries of the study area were the same each year, although the number and distribution of prairie dog colonies within that area changed annually. Thus, the study area was clearly defined and distinct from other areas occupied by plovers.

Capture and marking

We studied Mountain Plovers during six breeding seasons (1995–2000). Each year, fieldwork began on 20 May and extended through 20 July. We systematically searched all known active prairie dog colonies within the study area at least three times each year for plovers. On these searches, we slowly drove a vehicle across each colony and periodically stopped to scan for plovers. Individual adult plovers were watched from a distance until they returned to a nest. Once a nest was located, the adult was trapped immediately with a walk-in wire mesh trap placed over the nest, and then was banded with a unique combination of four colored leg bands and an aluminum size 3A U.S. Geological Survey numbered leg band. Color band combinations were derived from six possible colors (red, orange, yellow, dark blue, green, and white), which were chosen to minimize possible reading errors. We used UV stable Darvac leg bands (A. C. Hughes, London, UK) to reduce color fading. All birds were weighed to the nearest gram with a spring scale prior to release. Beginning in 1996, we collected a feather sample from every plover for determining sex by DNA analyses. In 1999, 40 plovers (28 adults and 12 fledglings) were fitted with transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) to estimate chick and fledgling survival. Transmitters weighed 3.0 g (adults) and 1.4 g (fledglings) and were glued to the mantle feathers of the bird using an epoxy (Titan Corporation, Lynnwood, Washington, USA). Most transmitters were carried by the bird for <30 days, and all transmitters were lost when the birds molted prior to their fall migration. All plovers were released within 15 minutes of capture. Capture techniques did not result in any immediate mortality. Juvenile plovers were typically banded as flightless chicks ($\geq$10 days old). In July of most years, small numbers of plovers of mixed ages were captured and banded at night. The birds were located at roosts with a spotlight, approached on foot, and netted.

Surveys for marked plovers

Active prairie dog colonies were searched at least three times each year, once or more in each of three secondary sampling periods (20 May–10 June, 11–30 June, and 1–20 July). In this study, live recaptures occurred by resighting marked plovers. For each plover that we encountered on surveys, we recorded the age (adult or juvenile) and the exact sequence of color bands, if the bird was marked. Because Mountain Plovers were generally not wary, they were easy to approach; virtually all band combinations were read successfully.

The robust design model

To model demographic parameters such as apparent survival, we used the robust design model (Pollock 1982, Kendall et al. 1995, 1997, Schwarz and Stobo 1997). A limitation of the traditional Jolly-Seber approach is that it estimates parameters associated with the general population (N_i^0) in the study area and not with the subset of the population that is exposed to sampling (N_i). Consideration of this sampling issue was necessary because some plovers may have nested at sites not exposed to our sampling efforts in some years, making them temporary emigrants. Their possible status as temporary emigrants, with a conditional capture probability of 0, could have introduced heterogeneity into estimates of capture probability. This relationship is clarified by the formula

$$E(N_i) = (1 - \gamma_i)N_i^0$$

where γ_i is the probability that an individual is not exposed to capture in period i and is thus a temporary emigrant (see Kendall et al. 1997:564). Furthermore, the relationship between the probability of temporary emigration (γ_i) and the capture probabilities of animals that are exposed to sampling (p_i^*) and those of all individuals in the population (p_i^0) is

$$p_i^0 = (1 - \gamma_i)p_i^*.$$

The probability of temporary emigration is then estimated (see Kendall et al. 1997:566) as

$$\hat{\gamma}_i = 1 - \frac{\hat{p}_i^0}{\hat{p}_i^*}.$$

The robust design incorporates features of both the open and closed capture–recapture models (Pollock 1982). The general design includes i primary sampling periods, each with l_i secondary sampling periods. The number of secondary sampling periods in each primary sampling period need not be equal. Closure (no births, deaths, immigration, or emigration) is assumed during the secondary sampling periods within each primary sampling period. The population is ''open'' to births, deaths, emigration, and immigration in the time interval between primary sampling periods (20 July–20 May in this study). Information from secondary sam-

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pling periods is used to estimate conditional capture (p_{ij}) and recapture (c_{ij}) probabilities and population size (N_i). A pooled capture probability (p_i^*) is then calculated for each primary sampling period as follows:

$$p_i^* = 1 - \prod_{j=1}^{l_i} (1 - p_{ij})$$

which is simply the probability that an animal is captured in at least one of the l_i secondary sampling periods in primary sampling period *i*. The pooled capture probabilities are used to estimate annual apparent survival and temporary emigration. It is important here to distinguish between true survival and apparent survival (the product of true survival and fidelity). Temporary emigration is defined by two parameters, γ_i'' and γ_i'. Here, γ_i'' is the probability that an animal is a temporary emigrant in period *i*, given that it was alive and available for sampling in primary sampling period $i - 1$. This contrasts with γ_i' which is the probability that an animal that was a temporary emigrant in primary sampling period $i - 1$ remains a temporary emigrant in primary sampling period *i*. This design allows the estimation of annual apparent survival ($\phi_1, \ldots, \phi_{k-1}$) and population size ($N_1, \ldots, N_k$) in the presence of temporary emigration. By estimating capture probabilities separately for each secondary sampling period, this approach is effectively robust to heterogeneity and trap response in capture probability (Pollock et al. 1990). The advantages of the robust design are many and include the ability to estimate temporary emigration, population size, and apparent survival simultaneously with a single study.

The assumptions of this approach were summarized by Kendall et al. (1995) and are similar to the assumptions for other capture–recapture models. The assumptions include:

1) independent fates of animals with respect to survival and capture probabilities;
2) closure during secondary sampling periods within each primary sampling period (no births, deaths, emigration, or immigration);
3) conditional survival probabilities are the same for all animals in the population;
4) all marks are unique and are not lost or misread;
5) capture and marking do not affect survival rates; and
6) marked individuals are representative of the population being sampled.

Population modeling

We modeled the apparent survival (ϕ_i), temporary emigration (γ_i'', γ_i'), and conditional capture (p_{ij}) and recapture (c_{ij}) probabilities of Mountain Plovers in southern Phillips County using the robust design model in program MARK (White and Burnham 1999). Parameter estimates in MARK are maximum likelihood estimates with 95% confidence intervals based on a logit or log transformation. To use individual covariates on capture and recapture probabilities and remove the estimates of population size from the likelihood, we used Huggins' estimator (Huggins 1989, 1991). With this approach, we estimated annual apparent survival rates for five years (1995–1999) and the adult population size for six years (1995–2000).

We defined three secondary sampling periods (20 May–10 June, 11–30 June, and 1–20 July) within each year. We assumed closure for adults during the breeding season (20 May–20 July), an assumption that was supported by the high survival of a sample of transmittered birds in 1999 and from the results of a similar study in Colorado (Miller and Knopf 1993). Resightings of marked birds indicated that most adult plovers were sedentary within this period, with few movements farther than 10 km from nest sites; therefore, emigration within secondary sampling periods was assumed to be negligible. Resightings were then summarized in encounter history format with 12 groups (two age classes in each of six years) and two individual covariates (body mass at capture and a 1999 transmitter effect) for each bird.

Our general approach to modeling demographic parameters followed Pollock et al. (1990), Lebreton et al. (1992), and Burnham and Anderson (1998). We first developed a list of a priori factors that we believed would influence one or more of these parameters. Using these factors, we defined a set of 18 candidate models. The model set included a fully parameterized global model and 18 additional models supported by biological hypotheses. We will outline the justification for the factors affecting these parameters.

Annual survival (ϕ_i).—We used models with only two age classes to estimate annual survival. Mountain Plovers breed at age 1 (S. J. Dinsmore, *personal observation*), so models with any additional age classes seemed unnecessary. We considered models that allowed juvenile survival to vary annually, but we modeled adult survival primarily as constant across years. We hypothesized that adults were less susceptible to annual variation in survival because of past experience. As a post hoc test for time variation in adult survival, we took the best model, added year effects on adult survival, and then compared the results to the model without year effects. Juveniles, however, were expected to be more susceptible to annual variation in survival. We also assessed time variation in the survival of both age classes by including two models that forced an additive linear trend on the logit scale on survival, one for each age class.

We modeled juvenile survival as a function of body mass at capture. We hypothesized that there would be a positive linear relationship between body mass and juvenile survival because mass was positively correlated with age. Because we did not know the hatch date of all chicks, we were unable to model an age effect

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on juvenile survival. We allowed juvenile mass effects to be both constant across years and to have separate year effects. In 1999, we also considered the possible effects of a transmitter on the survival of a sample of plovers of both ages. We considered models that allowed the effect of the transmitter to vary between the two age classes, and then constrained the transmitter effect to be constant across both age classes.

Finally, we considered the effect of annual area occupied by prairie dogs on the survival of Mountain Plovers. The influence of specific habitat characteristics (such as amount of habitat) on life history attributes such as survival has been demonstrated in other studies (see Franklin et al. 2000). For Mountain Plovers, other studies found an apparent relationship between plovers and prairie dogs in Montana (Knowles et al. 1982, Olsen-Edge and Edge 1987). If, as suggested by Knopf (1996*b*), plovers evolved in a prairie dog ecosystem, then it is reasonable to hypothesize that the amount of optimal nesting habitat (active prairie dog colonies) might be related to survival because the amount of habitat could influence predation rates, which subsequently influence survival. We hypothesized that the area occupied by prairie dogs represented available plover habitat in the study area, and then surmised that survival would be positively correlated with the amount (area) of this habitat. We modeled this as a single additive effect on the survival of plovers of both ages.

Temporary emigration (γ_i'', γ_i').—Mountain Plovers were strongly associated with active black-tailed prairie dog colonies in southern Phillips County, and we hypothesized that they might move between colonies both within and between years. Although we made an attempt to survey all active prairie dog colonies in the study area, we undoubtedly missed a few small (<5 ha) colonies each year. There also were large complexes of prairie dog colonies in the surrounding counties, and it was possible that small numbers of plovers might emigrate there temporarily before returning to the study area in a subsequent year. Therefore, temporary emigration of Mountain Plovers seemed plausible in southern Phillips County. Because these emigration parameters are often difficult to estimate, we constrained our considerations to only six simple models for γ_i'' and γ_i'. We modeled the effects of age (adults and juveniles) on each parameter, and then simplified each model to one with no age effects. We also considered a model where we set γ_i'' and γ_i' equal to evaluate a hypothesis of random emigration, and then we further constrained both gammas to be equal to zero.

Conditional capture (p_{ij}), resighting (r_{ij}), and recapture probabilities (c_{ij}).—To deal with problems of identifiability, estimates of conditional capture and recapture probability must be constrained (e.g., set equal or allowed to differ by some constant) in the robust design model (Pollock 1982). We modeled the conditional capture and recapture probabilities of Mountain Plovers to account for differences in initial yearly capture and a resighting effect. In the standard robust design approach, the probability of first capture (p_{ij}) and of recapture (c_{ij}) are estimated for each primary sampling period. That approach was not applicable to this study, however, because the probability of first capture within a primary sampling period occurred by both physical capture (new birds) and resighting (previously marked birds). Therefore, we split the probability of first capture into the probability of physical capture (p_{ij}) and the probability of first capture by resighting (r_{ij}).

We hypothesized that physical capture occurred with lower probability than resighting because the bird had to be seen and captured, rather than just seen. With this reasoning, we considered models that forced the relationship $p = r + C$ where C was some negative constant. We call this relationship a resighting effect. We also hypothesized that the probability of recapture in a given year (c) was equal to the probability of first capture by resighting (r), or that $r = c$. All recaptures were by resightings, and we saw no reason why they should differ from the initial resighting of a previously marked plover. We also considered a model where all capture and recapture probabilities were equal, but lacked a resighting effect (e.g., $p = r = c$). In each of these models, we allowed all three parameters (p, r, and c) to vary by secondary sampling period and year (full time variation), resulting in a maximum of 18 estimates of p, 15 estimates of r, and 12 estimates of c. We reasoned that time variation was present in each of these parameters because both breeding phenology and courtship activity changed across each primary sampling period and would affect our ability to capture and resight plovers. When we began modeling, we immediately encountered identifiability problems with the 1995 data. Initial capture probabilities in 1995 were extremely low and we were forced to use models in which all of the p's were constant for this year.

Goodness of fit

We used a goodness-of-fit test to assess the overall fit of our data to the robust design model. There are no standard goodness-of-fit tests for the robust design model. However, one measure of goodness of fit is to collapse the encounter histories into a Cormack-Jolly-Seber format and then use program RELEASE (Burnham et al. 1987). Program RELEASE cannot directly handle age structure, so this approach may result in a conservative measure of goodness of fit. This test also does not account for temporary emigration; however, temporary emigration was low and this did not substantially affect the goodness of fit. We followed this procedure to assess goodness of fit.

We computed the ratio of differences in log likelihood values as an approximate measure of the proportion of deviance explained by the best model (Skalski et al. 1993). We calculated this quantity as

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$$\text{proportion of deviance} = \frac{\log L(\text{best}) - \log L(.)}{\log L(\text{global}) - \log L(.)}$$

using log likelihoods from the best model, the global model, and the simplest (.) model. Here, the (.) model had three parameters (ϕ, γ, and p) and the global model had full age and year variation in ϕ, full age and year variation in γ'' and γ', and full variation by session within year for p, r, and c (120 parameters).

Model selection and parameter estimation

Model selection followed the methodology of Burnham and Anderson (1998). We ranked the set of R candidate models using AIC_c (Burnham and Anderson 1998), which was defined as

$$AIC_c = -2 \log L + 2K\left(\frac{n}{n - K - 1}\right)$$

where log L was the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates, K was the number of estimable parameters, and n was the sample size. The second term in the equation was a correction for small sample size. Here, the sample size was the total number of releases (new releases plus resightings). We did not correct for extra binomial variation in these data; there is currently no standard method of estimating the extra binomial variation in the robust design model.

Once AIC_c values were computed for each model, we ranked the R models relative to the model with the lowest AIC_c value. Comparisons between models were made using ΔAIC_c values, where for each model i

$$\Delta AIC_{c_i} = AIC_{c_i} - AIC_{c_{min}}.$$

The ΔAIC_c values compared the relative distances between the best approximating model ($AIC_{c_{min}}$) and each competing model (AIC_{c_i}). Generally, models with ΔAIC_c values ≤ 2 have strong support, whereas those with ΔAIC_c values >10 have little support (Burnham and Anderson 1998). Normalized Akaike weights (w_i) were also computed for each of the R models as

$$w_i = \frac{e^{-\{\Delta AIC_{c_i}/2\}}}{\sum_{r=1}^{R} e^{-\{\Delta AIC_{c_r}/2\}}}.$$

These normalized weights provided another means of directly evaluating the strength of evidence for each model and were useful for computing parameter estimates that reflected model selection uncertainty (Burnham and Anderson 1998). Instead of using parameter estimates from a single ''best'' model, we model averaged (Burnham and Anderson 1998) parameter estimates across all 19 models. This procedure weighted the individual parameter estimates according to their Akaike weights; parameter estimates from models with higher weights received stronger support than those from models with little or no weight. For models that incorporated an individual covariate on survival (mass or transmitter), we computed the survival using the mean estimate of the covariate(s). When building models, we used two link functions in MARK. Models incorporating an individual covariate used a logit link function; all other models used a sine link function. Formulae for the two link functions were

$$\text{logit}(\hat{\phi}_i) = \ln\left(\frac{\hat{\phi}_i}{1 - \hat{\phi}_i}\right) = \hat{\beta}_0 + \hat{\beta}_1(X)$$

$$\sin(\hat{\phi}_i) = \hat{\beta}_0 + \hat{\beta}_1(X)$$

where X represents some variable of interest such as the mass of a juvenile plover at capture. We used back transformation to generate real parameter estimates.

Using the Akaike weight and estimate of apparent annual survival from each of the R models, we computed a model-averaged estimate of apparent annual survival as

$$\bar{\hat{\phi}}_i = \sum_{r=1}^{R} w_i(\hat{\phi}_i)$$

with sampling variance

$$\widehat{\text{var}}(\bar{\hat{\phi}}_i) = \left[\sum_{r=1}^{R} w_i \sqrt{\widehat{\text{var}}(\hat{\phi}_i \mid M_i) + (\hat{\phi}_i - \bar{\hat{\phi}}_i)^2}\right]^2$$

where M_i was the ith model in the candidate set (Burnham and Anderson 1998). The 95% confidence interval for model-averaged estimates of apparent annual survival was

$$95\%\text{CI}_L = \bar{\hat{\phi}}_i - 1.96[\widehat{\text{SE}}(\bar{\hat{\phi}}_i)]$$

$$95\%\text{CI}_U = \bar{\hat{\phi}}_i + 1.96[\widehat{\text{SE}}(\bar{\hat{\phi}}_i)]$$

where

$$\widehat{\text{SE}}(\bar{\hat{\phi}}_i) = \sqrt{\widehat{\text{var}}(\bar{\hat{\phi}}_i)}.$$

We computed model averaged estimates of γ'' and γ' in a similar manner.

Estimating mean life span

Using age-specific estimates of annual survival, we computed the mean life span (MLS) of Mountain Plovers at capture using a formula from Brownie et al. (1985:211) as

$$\text{MLS} = \left\{\frac{1}{-\ln(\hat{\phi}_J)} + \frac{\hat{\phi}_J}{-\ln(\hat{\phi}_A)} + \frac{\hat{\phi}_J}{\ln(\hat{\phi}_J)}\right\}$$

where ϕ_J is juvenile survival and ϕ_A is adult survival. We used estimates of ϕ_J and ϕ_A from the best model; age-specific survival estimates differed very little among the top models, so we believed that this procedure provided a reasonable estimate of the mean life span of Mountain Plovers from the time of capture. We computed the variance of mean life span (MLS) using the delta method (Seber 1982) as

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$$\widehat{\text{var}}(\text{MLS}) = \left\{\frac{\partial(\text{MLS})}{\partial(\phi_J)}\right\}^2 \text{var}(\phi_J) + \left\{\frac{\partial(\text{MLS})}{\partial(\phi_A)}\right\}^2 \text{var}(\phi_A) + 2\left\{\frac{\partial(\text{MLS})}{\partial(\phi_J)} \times \frac{\partial(\text{MLS})}{\partial(\phi_A)}\right\}\text{cov}(\phi_J, \phi_A)$$

where

$$\frac{\partial(\text{MLS})}{\partial(\phi_J)} = \left\{\frac{1}{\phi_J \times \ln(\phi_J)^2} - \frac{1}{\ln(\phi_A)} + \frac{1}{\ln(\phi_J)} - \frac{1}{\ln(\phi_J)^2}\right\} \frac{\partial(\text{MLS})}{\partial(\phi_A)} = \frac{\phi_J}{\phi_A \times \ln(\phi_A)^2}.$$

Estimating population size

We estimated the annual size of the breeding population (number of adult plovers) using the Huggins robust design in program MARK. We modeled adults as a single group, with seven individual covariates per bird. Each bird had one covariate for a resighting effect in each year (six covariates) and a covariate for the 1999 transmitter effect. The resighting effect took on a value of 1 until the bird was available to be resighted in the year following initial capture, after which the resighting effect was 0. With this model structure, we used MARK to generate estimates of annual population size and the appropriate standard errors.

RESULTS

During the six-year study, we individually color banded 633 Mountain Plovers (377 adults and 256 juveniles; Table 1). The total number of releases (newly marked plovers plus resightings of previously marked plovers) was 1735. Low numbers of juveniles banded in 1996, 1997, and 1999 were due to poor reproduction in those years. Samples of adult plovers were similar among years. Juvenile body mass varied greatly (61.50 ± 17.38 g, mean ± 1 SD; range 20–110 g) and generally increased with the age of the chick. Band loss during the study was minimal. Only nine of 620 birds (1.5%) lost one or more color bands; five of these birds were later recaptured, identified using the USFWS band number, and were rebanded and released. The others were not identifiable.

Model selection results

The pooled results from Tests 2 and 3 in program RELEASE showed that there was a good fit to the reduced Cormack-Jolly-Seber model ($\chi^2_9 = 8.03$, $P = 0.53$). The proportion of deviance explained by the best model was 93% of variation. The data were best explained by a model with two age classes and a juvenile mass effect on survival, a single estimate for each measure of temporary emigration, and equal capture, resighting, and recapture probabilities with a resighting effect (Table 2). At least six additional models could be considered as competing models (ΔAIC_c values ≤ 2). All of these models had age and juvenile mass effects on survival and equal capture, resighting, and recapture probabilities with a resighting effect.

TABLE 1. Summary of banding data for Mountain Plovers (*Charadrius montanus*) in southern Phillips County, Montana, USA, from 1995 to 2000.

Year	Juvenile	Adult	Total
1995	69	66	135
1996	14	45	59
1997	22	66	88
1998	47	75	122
1999	40	66	106
2000	64	59	123

Body mass was an important predictor of juvenile survival (in the best model, $\hat{\beta}_{\text{mass}} = 0.77$; 95% CI = 0.25, 1.28 on a logit scale). There was a positive relationship between juvenile body mass and survival in all models that contained a juvenile body mass effect. The second best model had a nonsignificant additive effect on a logit scale of area occupied by prairie dogs on survival ($\hat{\beta}_{\text{prairie dog}} = -0.00004$; 95% CI = −0.00003, 0.0001). A common additive transmitter effect on all birds ($\Delta\text{AIC}_c = 1.79$) had better support than a model in which the transmitter effect varied by age ($\Delta\text{AIC}_c = 3.83$); the transmitter effects were nonsignificant in both models. There was little support for time variation in survival. The fourth and fifth best models had nonsignificant linear trends on adult and juvenile survival, respectively. When year effects in survival were added to the best model, the resulting models performed poorly for both juveniles ($\Delta\text{AIC}_c = 2.60$) and adults ($\Delta\text{AIC}_c = 6.75$).

Temporary emigration was important in this study. Evidence for age effects in γ'' and γ' were weak; models with no age effects received better support than an identical model with the age effects removed. We found weak support for models where γ'' and γ' were equal ($\Delta\text{AIC}_c = 2.28$) and no support of a model where they were both set to zero (no emigration; $\Delta\text{AIC}_c = 76.72$).

We found strong evidence for a resighting effect. The resighting effect was always negative (in best model, $\hat{\beta}_{\text{resighting}} = -0.49$; 95% CI = −0.86, −0.11 on a logit scale), indicating that the probability of physical capture (p) was substantially lower than the resighting probability (r). When the resighting effect was removed from the best model, the resulting model performed poorly ($\Delta\text{AIC}_c = 5.35$) and had little weight.

Parameter estimates

The model-averaged estimates of the annual survival of Mountain Plovers were 0.46–0.49 for juveniles and 0.68 for adults (Fig. 3). Juvenile Mountain Plovers appeared to have lower survival than adult plovers, although the 95% confidence intervals for both age classes overlapped slightly during each year of the study.

The model-averaged estimate of the probability of emigrating (γ''_i) was 0.24 (1 SE = 0.06; 95% CI = 0.14, 0.37) for juveniles and 0.22 (1 SE = 0.04; 95% CI =

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TABLE 2. Summary of model selection results for Mountain Plovers in southern Phillips County, Montana, 1995–2000, with models ranked by ascending ΔAIC_c.

Model	Deviance†	*K*‡	AIC_c§	ΔAIC_c	w_i‖
$\phi_{age,\ juv\ +\ mass}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4090.40	24	4139.10	0.00	0.19
$\phi_{age,\ juv\ +\ mass,\ all\ +\ prairie\ dog\ area}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4089.25	25	4140.01	0.90	0.12
$\phi_{age,\ juv\ +\ mass}\ \gamma''_{age}\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4089.27	25	4140.03	0.92	0.12
$\phi_{age,\ juv\ +\ mass,\ adult\ +\ T}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4089.69	25	4140.45	1.35	0.10
$\phi_{age,\ juv\ +\ T\ +\ mass}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4089.96	25	4140.72	1.62	0.09
$\phi_{age,\ juv\ +\ mass,\ transmitter}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4090.14	25	4140.90	1.79	0.08
$\phi_{age,\ juv\ +\ mass}\ \gamma''(.)\ \gamma'_{age}\ p_t = r_{t+C} = c_t$	4090.29	25	4141.05	1.94	0.07
$\phi_{age,\ juv\ +\ mass}\ \gamma''(.) = \gamma'(.)\ p_t = r_{t+C} = c_t$	4094.74	23	4141.38	2.28	0.06
$\phi_{age,\ juv\ \times\ year\ +\ common\ mass}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4084.76	28	4141.71	2.60	0.05
$\phi_{age,\ juv\ +\ mass}\ \gamma''_{age}\ \gamma'_{age}\ p_t = r_{t+C} = c_t$	4089.24	26	4142.06	2.95	0.04
$\phi_{age,\ juv\ +\ mass,\ transmitter\ \times\ age}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4090.11	26	4142.93	3.83	0.03
$\phi_{age,\ juv\ \times\ year}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4088.20	27	4143.09	3.98	0.03
$\phi_{age,\ juv\ +\ mass}\ \gamma''(.)\ \gamma'(.)\ p_t = r_t = c_t$	4097.81	23	4144.45	5.35	0.01
$\phi_{age,\ juv\ +\ mass,\ adult\ \times\ year}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4088.91	28	4145.86	6.75	0.01
$\phi_{age}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4099.85	23	4146.50	7.40	0.00
$\phi_{age,\ juv\ +\ mass\ separate}\ \gamma''(.)\ \gamma'(.)\ p_t = r_{t+C} = c_t$	4084.12	33	4149.36	10.25	0.00
$\phi_{age,\ juv\ +\ mass}\ \gamma''(.) = \gamma'(.) = 0\ p_t = r_{t+C} = c_t$	4171.24	22	4215.83	76.72	0.00
Global model	3998.35	120	4256.33	117.23	0.00
$\phi(.)\ \gamma''(.) = \gamma'(.)\ p(.) = r(.) = c(.)$	5343.93	3	5349.94	1210.84	0.00

Notes: Apparent survival (ϕ), temporary emigration (γ'' and γ'), and capture (p, r) and recapture (c) probabilities included the effects of two age classes (adults and juveniles), transmitter attachment in 1999 (transmitter), additive effect of body mass on juvenile survival (juv + mass), area occupied by prairie dogs each year (prairie dog), time (year), a linear trend (T), and a resighting effect ($p = r + C$).

† Deviance is computed as $-2[\log_e(L(\hat{\theta})) - 2\log_e(L_s(\hat{\theta}))]$ where $\hat{\theta}$ represents a maximum-likelihood estimate whose log-likelihood is evaluated for the model in question $[L(\hat{\theta})]$ and for the saturated model $[L_s(\hat{\theta})]$ (see *Methods*).

‡ The number of parameters.

§ Akaike's Information Criteria.

‖ Akaike's model weight.

0.15, 0.31) for adults. The probability of remaining a temporary emigrant, given that a plover had previously emigrated (γ_i'), was 0.46 (1 SE = 0.18; 95% CI = 0.18, 0.78) for juveniles and 0.47 (1 SE = 0.17; 95% CI = 0.19, 0.77) for adults. Thus, the probability of emigration for Mountain Plovers was moderate, although a relatively high proportion of temporary emigrants eventually returned to the study area.

Capture, resighting, and recapture probabilities were generally quite high for Mountain Plovers, except in 1995. Physical capture probability in 1995 was extremely low (0.17), but it was much higher in all other years (range 0.37–0.74). Resighting and recapture probabilities were also quite high (range 0.49–0.81), except for slightly lower recapture probabilities in 1995 (0.57 and 0.24).

The mean life span at capture of a Mountain Plover in southern Phillips County was 1.92 years (1 SE = 0.19; 95% CI = 1.55, 2.29). This estimate was calculated using $\phi_J = 0.4759$ (1 SE = 0.0745) and $\phi_A = 0.6775$ (1 SE = 0.0327).

Population size

Estimates of the number of breeding adult Mountain Plovers in the study area ranged from 95 to 180 individuals annually (Fig. 4). Estimates from 1995 were imprecise and of little use. Beginning in 1996, the es-

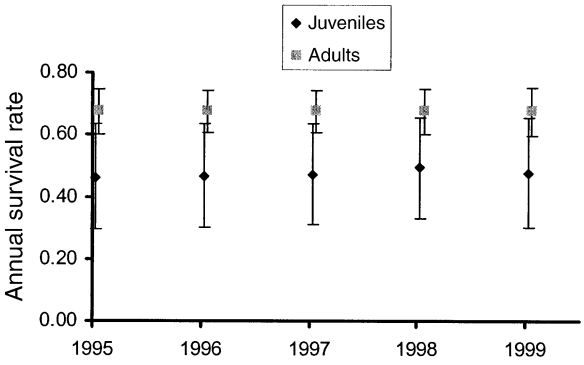

FIG. 3. Annual age-specific apparent survival rates and 95% confidence intervals for Mountain Plovers in southern Phillips County, Montana, 1995–1999.

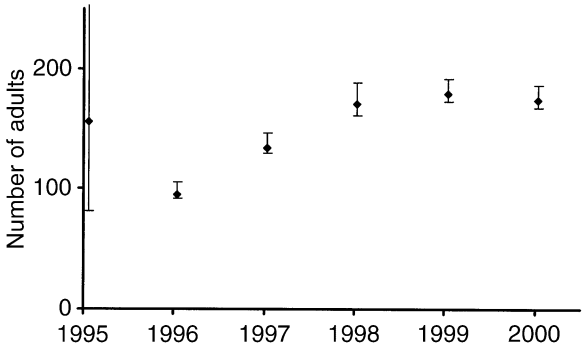

FIG. 4. Number of breeding adult Mountain Plovers (mean and 95% CI) in southern Phillips County, Montana, 1995–2000. The upper confidence limit for 1995 was 579 birds and was omitted so that the scale of the graph would be readable.

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TABLE 3. Estimates of annual survival rates for shorebirds derived from capture–recapture studies.

Species	Adult	Juvenile	Reference
Family Burhinidae			
Stone-curlew	0.83	0.61	Green et al. (1997)
Family Charadriidae			
Snowy Plover	0.69	0.39	Paton (1994)
Piping Plover	0.66		Root et al. (1992)
Mountain Plover	0.68	0.46–0.49	this study
Family Scolopacidae			
Willet	0.85		Howe (1982)
Bristle-thighed Curlew	0.85		Marks and Redmond (1996)
Long-billed Curlew	0.85		Redmond and Jenni (1986)
Bar-tailed Godwit	0.88		Evans and Pienkowski (1984)
Sanderling	0.83		Evans and Pienkowski (1984)
Semipalmated Sandpiper	0.70		Gratto et al. (1985)
Semipalmated Sandpiper		0.09	Sandercock and Gratto-Trevor (1997)
Semipalmated Sandpiper	0.53–0.73 (males)		Sandercock and Gratto-Trevor (1997)
Semipalmated Sandpiper	0.43–0.71 (females)		Sandercock and Gratto-Trevor (1997)
Temminck's Stint	0.81		Hilden (1978)

timates showed a general increase in plover numbers through 1998, when the population stabilized at ~175 individuals.

DISCUSSION

Annual survival rates

This study provides the first estimates of the age-specific annual survival of Mountain Plovers. It should be noted that these are estimates of apparent survival (Pollock 1982), which is the product of true survival and site fidelity. Fidelity of adult plovers to southern Phillips County appeared to be high, with many individuals returning to nest on the same prairie dog colony in subsequent years. Permanent emigration can introduce a negative bias into estimates of true survival, thereby biasing apparent survival. As stated earlier, we found no evidence of permanent emigration for adult Mountain Plovers. No adult Mountain Plovers banded in the study area were found breeding elsewhere, including other states such as Colorado or Wyoming, where similar studies were ongoing. Similarly, no Mountain Plovers banded elsewhere were ever recovered in southern Phillips County. Thus, apparent survival estimates for adult plovers were probably close to true survival rates.

For juvenile Mountain Plovers, the interpretation of survival estimates was not as straightforward. Some juvenile plovers permanently emigrated from the study area. Surveys of Fort Belknap Indian Reservation, 40 km to the northwest, located two plovers (out of a total of 284 examined for bands) banded as juveniles in the study area. Similar surveys of prairie dog colonies along the Milk River southwest of Malta located three more plovers (out of a total of 84 examined for bands) that were banded as juveniles in the study area. Undoubtedly, small numbers of juvenile Mountain Plovers banded in southern Philips County subsequently bred in other areas.

A second source of bias in the estimates of juvenile survival was that not all juvenile plovers were banded immediately after hatching. Most were banded at ≥10 days of age, and some young birds were not banded until just prior to fledging, at 33–35 days of age. Mountain Plovers exhibit severe brood reduction during the first 1–2 weeks after hatching (S. J. Dinsmore, *personal observation*), so many young plovers died before they could be banded. In this study, juvenile survival measured the probability of surviving from ~2–3 weeks of age until age 1 year. Thus, this banding technique introduced a positive bias into estimates of juvenile annual survival. Exactly how these sources of bias jointly affected juvenile survival is unclear; they may have balanced each other, or the resulting bias could have been positive.

Adult Mountain Plovers had an estimated annual survival rate of 0.68. The low adult annual survival was surprising, in contrast with higher rates for several shorebird species (Table 3). Typically, these are based on return rates from short-term studies, although some are more detailed capture–recapture studies of shorebirds in the recent literature (e.g., Paton 1994). Annual survival estimates from capture–recapture studies were generally high for members of the Burhinidae and Scolopacidae, but were lower for members of Charadriidae. Poor adult survival of Mountain Plovers probably favors birds with annual increased reproductive output. Mountain Plovers have evolved a rapid multi-clutch mating system (Graul 1973) in which each member of a pair independently incubates a separate nest and cares for the brood. This strategy results in almost a doubling of annual reproductive output for each pair relative to most other shorebirds (6 vs. 3 or 4 eggs), although this output may be even greater if suspected sequential polyandry is occurring (S. J. Dinsmore, *personal observation*). Their uniparental care strategy is probably more costly than most other breeding strategies in

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shorebirds, although the benefits may include increased production. The additional reproductive costs incurred by female Mountain Plovers are great, especially the costs of egg-laying (Sæther et al. 1986). Male plovers incur similar increased reproductive costs that include increased investment in incubation and parental care (see Oring 1982).

Mountain Plovers may suffer the highest mortality during migration. The low annual survival rate of adult plovers (0.68) contrasted with high survival during two portions of their annual cycle: the breeding season in Colorado (survival rate of 1.0 with no losses between mid-May and late July; Miller and Knopf 1993) and the winter in central California (survival rate of 0.95 for the period 1 November–15 March; Knopf and Rupert 1995). High mortality would not be surprising, given the presumed high costs of migration, even for a mid-distance migrant like the Mountain Plover. Piping Plovers (*Charadrius melodus*) were recently shown to have similar low annual survival (Table 3) and high overwinter survival (no losses between mid-August and late April; Drake et al. 2001).

A comparison between juvenile survival rates of Mountain Plovers and other shorebirds is difficult because few estimates of juvenile survival for other species are available. Among the Charadriidae, Paton (1994) estimated the juvenile survival of Snowy Plovers (*Charadrius alexandrinus*) at 0.39, which is similar to the estimate for Mountain Plovers. We found no other estimates of juvenile survival among the Charadriidae.

We estimated the mean life span of Mountain Plovers as 1.92 years. This low estimate is not surprising, given that the longevity record is 8 years (S. J. Dinsmore, *personal observation*), which is lower than most other shorebirds including the Snowy Plover (15 years; Page et al. 1995) and Piping Plover (11 years; Haig 1992).

All previous estimates of annual survival in shorebird species were derived using open-population models (see Table 3); none has used the robust design to estimate survival in the presence of temporary emigration. Although many of these studies noted potential biases with permanent emigration, few commented on possible problems with temporary emigration. Temporary emigration may be a widespread problem for studies of shorebirds. Many shorebirds do not reach breeding age in their first year, and subadult age classes may effectively represent temporary emigrants. Also, possible gaps in study area coverage (for example, we may have missed a few newly formed prairie dog colonies each year) may result in temporary emigrants. Clearly, the ability to estimate survival in the presence of temporary emigration may represent a substantial improvement over estimates obtained using the open models, and is certainly an improvement over estimates of minimal survival obtained from return rates. This, in turn, will result in more realistic survival estimates for use in conservation planning.

Band loss during this study was minimal, with only nine plovers (1.5% of the total number banded) losing one or more color bands. Band loss in other studies is seldom reported, although Root et al. (1992) noted a 6% band loss in a capture–recapture study of Piping Plovers. Band loss by Mountain Plovers did not appear to negatively bias survival estimates.

Confounded effects in estimates of survival

We found that body mass at capture was a good predictor of juvenile Mountain Plover survival. However, body mass is positively correlated with age, so these two effects are confounded. Because we did not know the age of every juvenile plover that we banded, we were unable to use this as a covariate in our models. Instead, we used body mass, which we suspected was highly correlated with age. Because of this confounding of age and body mass, the significance of our findings is less clear. Although body mass appears to be a good predictor of juvenile Mountain Plover survival, the causal factor may be age and not body mass. Another possible confounding effect with chick survival is time of season; in many birds, early-hatched chicks survive better than those that hatch later.

Population estimates

The annual estimate of the number of breeding adult Mountain Plovers in the study area varied from 95 (in 1996) to 180 (in 1999) birds. Estimates of population size in 1995 were imprecise compared to estimates in all other years. This lack of precision in 1995 can be explained in two ways. This was the first year of the study and the proportion of the population that was marked was smaller than in subsequent years. More importantly, capture probabilities in 1995 were extremely low ($p = 0.17$), resulting in a lower pooled capture probability (p^*) and imprecise estimates of population size. Low capture probabilities were probably the result of observer inexperience and our lack of familiarity with the study area in 1995.

The relatively low estimate of the number of breeding Mountain Plovers was unexpected because previous ad hoc estimates had placed the number at ~400–500 individuals. Our estimates of population size appear to be accurate because capture probabilities were high, and the pooled capture probability for a given year (p^*) was extremely high, often >0.90. High capture probabilities meant that few marked plovers were missed on surveys and that the resulting population estimates were close to the number of marked animals known to be alive. Coverage of prairie dog colonies within the study area approached 100% and included all colonies that were most likely to be occupied by plovers (Olson-Edge and Edge 1987). The combination of good coverage and high capture probabilities supports the accuracy of the population estimates, given the assumption that few plovers nest off prairie dog colonies. Few plovers and only seven nests were seen

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off prairie dog colonies in southern Phillips County during this study. If there is an unsampled segment of the Mountain Plover population, it is small compared to the numbers found on prairie dog colonies.

The magnitude of the annual population changes merits discussion. The greatest increase was from 1996 to 1997 (95 to 134 birds). For such a small population of birds, a 41% increase in one year is noteworthy. Production in 1996 was low, with below-average apparent nesting success (53%), and only 14 juvenile plovers were banded. Therefore, it is unlikely that the increase from 1996 could be explained solely by local reproduction. Our most optimistic estimates of breeding success, based largely on the demographic parameters discussed previously, suggest that fledging and recruitment rates would have to be several times greater than those we observed in this study to account for the observed population growth, based on only local reproduction.

A more likely explanation is that the increase in available plover habitat (e.g., the area occupied by prairie dogs) attracted plovers from areas that we did not survey. The source of these immigrants is unknown, but the most likely locales are Fort Belknap Indian Reservation in Blaine County (40 km northwest of the study area) and in southern Valley County (40 km northeast of the study area). Since 1998, the size of this population has leveled off, despite the continued increase in area occupied by prairie dogs. This hints that local recruitment could not keep pace with increases in prairie dogs, possibly as a result of (1) inadequate local production, (2) off-site mortality during migration or on the wintering grounds, (3) reduced opportunity for immigration at this northern breeding locale, or (4) some combination of these or other unknown factors.

Population estimates of Mountain Plovers in southern Phillips County appeared to closely track changes in the amount of area occupied by prairie dogs. Black-tailed prairie dogs were beginning to recover from a major outbreak of sylvatic plague in 1995. In 1988, prior to the plague outbreak, the area occupied by prairie dogs in the study area had reached 8675 ha, but this total was reduced to 1371 ha in 1995 (Fig. 2). The area occupied by prairie dogs was lowest in 1995–1996 and has since steadily risen in a nearly linear fashion at an average of 30% per year (J. Grensten, *personal communication*). Population estimates of Mountain Plovers followed this same general pattern; the numbers were extremely low in 1996 and have steadily risen since then, until they stabilized in 1998–2000.

When the survival of Mountain Plovers was modeled as a function of area occupied by prairie dogs, the result was a model with good support ($\Delta AIC_c = 0.90$, $w_i = 0.12$), but with a nonsignificant coefficient for this effect. This suggests that a measure of area (hectares of land occupied by prairie dogs) may not be the best means of assessing Mountain Plover habitat. Area measures do not account for the variability in prairie dog density on those colonies. Prairie dog density affects the plant community, which in turn may determine the suitability of the colony for plovers (see Olson and Edge 1985). Area measures also do not account for possible differences in topography such as slope and elevation, both of which may influence occupancy of a particular colony by plovers (S. J. Dinsmore, *personal observation*).

We did not formally explore the plover–prairie dog relationship (Knowles et al. 1982, Olson and Edge 1985) in this study, but did find evidence to further support the claim that these species are strongly associated. Our high capture probabilities (0.90) suggest that plovers are conspicuous, readily sampled members of the local avifauna, that they occupy a specific habitat type (active prairie dog colonies), and that there is little or no movement of individuals into the study area from nearby areas. These observations strongly suggest that most plovers in this region inhabit prairie dog colonies.

Conservation of Mountain Plovers in Phillips County, Montana

Mountain Plovers are one of a number of Great Plains bird species that are thought to be declining throughout their range. Causes for their decline are poorly understood any may include the loss of breeding habitat, the loss or alteration of wintering habitat, high mortality during migration, and possibly other factors such as weather and predation (Dinsmore 2000). The recent move to list the Mountain Plover as a federally Threatened species may thus be indicative of threats to the Great Plains ecosystem as a whole.

Our demographic study of Mountain Plovers has several important conservation implications. Our estimates of age-specific annual survival, estimates of temporary emigration, and mean life expectancy are the first for this species. The relatively low adult annual survival, high site fidelity, and short life expectancy of these plovers will be important for future conservation planning and possible recovery efforts. This information, coupled with a detailed study of their nest survival (Dinsmore et al. 2002), provides insight into this species' population biology at a specific, but important, breeding site.

Mountain Plover numbers seemed to closely track changes in black-tailed prairie dog distribution in southern Phillips County. Plover numbers were reduced to year following outbreaks of sylvatic plague, but rapidly recovered soon thereafter. Although large areas of seemingly suitable plover habitat are available nearby (e.g., Fort Belknap Indian Reservation), adult Mountain Plovers appear to be faithful to breeding sites in southern Phillips County and may be reluctant to move long distances. Adult plovers were not known to disperse from the study area, even though other plovers occupied surrounding areas and the distances involved (<50 km) would not seem to be a barrier. The affinity

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of plovers to southern Phillips County was supported by low rates of emigration, high rates of return for the few emigrants, and the almost complete lack of emigrants being detected in surrounding areas. This suggests that southern Phillips County may provide optimal Mountain Plover habitat that is occupied to the fullest extent, and immigrants from surrounding areas rapidly fill this suitable habitat as it becomes available. If the plover–prairie dog relationship is indeed strong, Mountain Plovers in Montana and elsewhere should benefit from recent initiatives to conserve black-tailed prairie dogs through the use of state management plans (see Knowles 1999) and possible listing under the U.S. Endangered Species Act (Gober 1999).

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