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INFLUENCE OF DROUGHT ON ANNUAL SURVIVAL OF THE MOUNTAIN PLOVER IN MONTANA

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Abstract. I used a robust design to model the influence of age, sex, climate conditions, and chick body mass on the annual survival of the Mountain Plover (*Charadrius montanus*) in north-central Montana from 1995–2006. I found evidence that chick age predicted body mass (i.e., $\log_{10}$ (mass) $= 0.03 * \text{age} + 1.02$) and subsequently modeled juvenile survival as a function of body mass. Juvenile survival was similar for both sexes and was positively influenced by body mass at capture. The predicted annual survival for a juvenile plover from date of hatching (10 g) was 0.06 (95% CI was 0.02, 0.15) and increased with body mass. Annual survival was similar for adults of both sexes and ranged from 0.74 to 0.96 yearly. There was a hint that male survival was higher than that of females, although this effect was weak. Adult survival was affected by a Palmer Modified Drought Index that measured local climate conditions and indicated that annual survival was highest during drought periods. Implications of this study include understanding the processes influencing annual survival in a declining species, providing a basis for long-term population projections, relating demographic processes to climate change, and increasing our knowledge of survival patterns among the Charadriidae.

Key words: Charadrius montanus, *drought, Montana, Mountain Plover, survival.*

La influencia de sequías sobre la supervivencia *Charadrius montanus* en Montana

Resumen. Yo utilicé un diseño robusto para hacer un modelo para evaluar la influencia de edad, sexo, condiciones climatológicas, y masa corporal del pichón sobre la supervivencia de *Charadrius montanus* en la parte norte-central de Montana desde 1995 al 2006. Encontré evidencia de que la edad de los pichones predecía masa corporal ($\log_{10}$ (masa) $= 0.03 * \text{edad} + 1.02$) y posteriormente formule un modelo de supervivencia de juveniles como funcion de masa corporal. La supervivencia de los juveniles fue similar para ambos sexos y estuvo positivamente influenciada por masa corporal en el momento de captura. La predicción de supervivencia anual para un juvenil desde su eclosión (10 g) fue de 0.06 (95% CI 0.02, 0.15) y aumentó con masa corporal. La supervivencia anual fue similar para adultos de ambos sexos y fluctuó entre 0.74 y 0.96 anualmente. Hubo una indicación de que la supervivencia de los machos era mayor que la de las hembras, pero ese efecto no era fuerte. La supervivencia de adultos fue afectada por el índice de sequía modificado de Palmer que mide condiciones climatologicas locales e indico que la supervivencia anual era mas alta durante periodos de sequía. Las implicaciones de este estudio fueron muchas e incluyen el entendimiento del proceso que influencia la supervivencia anual de una especie mermando, proveyendo una base para hacer proyecciones poblacionales a largo plazo, relacionando procesos demográficos a cambios climatológicos, y aumentando nuestro conocimiento sobre patrones de supervivencia entre miembros de Charadriidae.

INTRODUCTION

The Mountain Plover (*Charadrius montanus*) is an endemic and patchily distributed breeding bird of the North American Great Plains that often nests in black-tailed prairie dog (*Cynomys ludovicianus*) colonies (Knowles et al. 1982, Olson-Edge and Edge 1987). The species is of high conservation concern because of perceived long-term declines and threats to its habitat (Dinsmore 2000, U.S. Department of the Interior 2003). Despite this standing, its population biology has received only limited attention (Dinsmore 2001), and the effects of individual attributes (e.g., age and sex) and climate conditions on local survival need further study. Understanding factors that influence survival has important implications for modeling long-term persistence of populations (Burnham et al. 1996) and provides a foundation upon which to ask more detailed questions about a species' ecology.

Mountain Plover annual survival has been studied only in Montana, where estimated annual survival rates were found to be 0.67 for adults and 0.46–0.49 for juveniles (Dinsmore et al. 2003). These juvenile survival rates were from banding to age 1 and did not account for all mortality early in the chick stage (Dinsmore and Knopf 2005). Thus, more robust estimates of juvenile survival (from date of hatching to age 1) are needed. Furthermore, sex-specific survival has not been

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studied in the Mountain Plover, despite the species' diverse mating system that hints that survival may differ between the sexes. The Mountain Plover's unusual rapid-clutch mating system (Graul 1973), coupled with sex-specific differences in nest (Dinsmore et al. 2002) and chick (Dinsmore and Knopf 2005) survival, raise the possibility that annual survival may also differ between the sexes.

Climate conditions may also affect vital rates, including survival, as has been shown in other birds (Franklin et al. 2000). The Mountain Plover nests in semiarid habitats with a bare ground component (Knopf and Miller 1994), short vegetation (Olson and Edge 1985), and regular disturbance (e.g., grazing by prairie dogs or cattle; Knopf and Wunder 2006). The plant community in north-central Montana must regularly contend with drought conditions, which probably leads to adaptations for drought tolerance. In Montana, conditions favorable to the plover appear to be maximized during drought periods—vegetation is shorter and more sparsely distributed (Lambers et al. 1998, Gaspar et al. 2002), and black-tailed prairie dog colonies increase in coverage in response to competition and food needs (Hoogland 1995, U.S. Department of Agriculture 2006) during drought periods. This set of conditions should benefit the plover and may lead to enhanced reproductive success and survival. This also suggests that the plover, like other plains species (Knopf and Samson 1997), may be drought adapted. Ultimately, estimates of annual survival, when combined with information on productivity, dispersal, and abundance will be used to assess long-term population viability of species of conservation concern such as the Mountain Plover (Franklin et al. 2000).

Survival of young precocial birds is difficult to estimate, mainly because the young leave the nest within hours of hatching, are mobile, and are not easily monitored during this stage of life. With advances in techniques for accurately aging bird nests (Mabee et al. 2006), it is possible to predict date of hatching and then use radio-telemetry or other means to monitor the young. Another option is to mark a sample of birds during the chick or postfledging periods to estimate juvenile survival to age 1 (i.e., the start of the next breeding season). Still other studies measure chick survival by alternate means (e.g., radio-telemetry; Dinsmore and Knopf 2005) and attempt to merge estimates of chick and juvenile survival to arrive at a meaningful estimate of survival from date of hatching to age 1.

Herein, I assess the importance of age, sex, chick mass, and local climate (i.e., drought) conditions on the annual survival of the Mountain Plover in north-central Montana from 1995–2006. This includes a reanalysis of annual age-specific survival with an additional six years of data and expands on earlier survival estimates (Dinsmore et al. 2003) by addressing annual variation in survival and the influence of sex and drought.

METHODS

STUDY AREA

I studied Mountain Plovers within a 3000-km^2 area in southern Phillips County in north-central Montana (Dinsmore et al. 2003) and worked exclusively on active black-tailed prairie dog colonies preferred by the plover (Olson and Edge 1985, Dinsmore 2001). This mixed-grass prairie region 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 and includes lands managed by the Bureau of Land Management (BLM, Malta Field Office) and the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge). Active black-tailed prairie dog colonies in this area were comprised of bare ground interspersed with sparse vegetation dominated by fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polycantha*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), and Sandberg bluegrass (*Poa secunda*).

DATA COLLECTION

I studied Mountain Plovers in Phillips County from 1995–2006. Fieldwork began on 20 May each year and ended in late July or early August when nesting activity ceased. As previously reported (Dinsmore et al. 2003), the sampling followed a robust design (Kendall et al. 1995, 1997) with three secondary sampling periods (20 May–10 June, 11–30 June, and 1–20 July) nested within a breeding season (the primary sampling period). All prairie dog colonies within the study area were surveyed during each secondary sampling period, and resightings of color-banded plovers were recorded. This sampling scheme implies that the population was closed during the nesting season (20 May–20 July), which is corroborated by color banding data showing that plovers were largely sedentary during this period (SJD, pers. obs.), high survival of adults here during the 1999 nesting season (Dinsmore and Knopf 2005), and high breeding season survival of the Mountain Plover in Colorado (Miller and Knopf 1993).

Adult plovers were captured with a walk-in trap placed over their nests; juveniles were caught with a hand-held net during the chick stage. At capture, each plover was aged as juvenile (hatching year) or adult (after hatching year), weighed (to the nearest gram), fitted with a unique series of four colored leg bands and an aluminum size 3A U.S. Geological Survey numbered leg band for future identification, and had a feather sample taken for sex determination (AvianBiotech International, Tallahassee, FL). Color band combinations were derived from seven possible colors (red, orange, yellow, dark blue, green, black, and white), and some combinations were avoided to minimize possible reading errors. I used UV stable Darvic leg bands (A. C. Hughes, London, United Kingdom) to reduce color fading. Banding and resighting data for each secondary sampling period were summarized in an encounter

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history for each plover with a total of 36 encounter occasions during the study.

STATISTICAL ANALYSES

POPULATION MODELING

Estimation of vital rates such as annual survival has undergone rapid development in the last decade, with a proliferation of detailed models in software packages such as program MARK (White and Burnham 1999, Cooch and White 2006). One such model is the robust design (Pollock 1982), which incorporates aspects of open and closed capture-recapture theory to estimate survival in the presence of temporary emigration (Kendall et al. 1995, 1997). Temporary emigration can occur when some animals 1) do not return to the study area every year or 2) utilize areas within the study area that are not subject to sampling (e.g., individuals on the study area boundary may move in and out of the study area between years). In both scenarios, the bias in survival estimates introduced by temporary emigration can be reduced by using a robust design (Pollock 1982).

I modeled apparent annual survival (ϕ_i), temporary emigration (γ_i'', γ_i'), and conditional capture (p_{ij}) and recapture (c_{ij}) probabilities in program MARK (White and Burnham 1999). I defined 24 groups (2 age classes $*$ 12 years) for my analyses and included sex (male, female, and unknown) and body mass (mass) as individual covariates. I used Huggins's robust design (Huggins 1989, 1991) for all analyses because this approach can incorporate individual covariates on capture and recapture probabilities and removes estimates of abundance (not of interest in this paper) from the model's likelihood function.

I used an approach similar to that taken in an earlier analysis (Dinsmore et al. 2003) when modeling demographic parameters, which followed the suggestions of Pollock et al. (1990) and Burnham and Anderson (2002). I developed a list of a priori factors I believed would influence one or more of the parameters. From these factors, I used a hierarchical modeling approach to arrive at a set of models for inference, which were ranked by second order Akaike's Information Criterion (AIC_c) values (Akaike 1973, Burnham and Anderson 2002). The process I used began by assuming juvenile survival was a function of mass and year, adult survival was constant across years, and that the two parameters associated with temporary emigration were constant across years (but different from each other). I chose this set of factors because they were all included in the best model from an earlier analysis of the first six years of these data (Dinsmore et al. 2003). To this model structure, I next incorporated specific effects of interest on capture and recapture probabilities (see below). To all competitive models ($\Delta AIC_c \leq 2$) from this step, I then added the effects of age, sex, drought severity, and annual variation in apparent survival and temporary emigration parameters (see below) to arrive at the full model set for inference. I also included a fully parameterized global model, which resulted in a set of 29 models for inference. In general, I report model-averaged parameter estimates ($\pm$ SE), except where I chose to use a single model to make inferences about a particular effect.

Annual apparent survival (ϕ_i). Here, apparent survival refers to the period between any two successive breeding seasons (primary sampling periods). I used models with two age classes to estimate apparent annual survival, and I allowed survival to vary annually for each age class. In an earlier analysis (Dinsmore et al. 2003), we ignored annual variation in adult survival. However, in this study, with 12 years of data, I chose to evaluate possible annual variation in adult survival by including a model with year effects and two additional models (linear and quadratic trends across all years) that also allowed for annual variation, but with a forced pattern across years. I did not consider more complex patterns in annual survival (e.g., a cubic trend across years) due to the risk of overfitting.

I modeled juvenile survival as a function of body mass at capture. Mountain Plover chicks (here defined as dependent young that fledge at 33–35 days) are difficult to accurately age in the field, although body mass is correlated with age. Using a sample of known-age chicks with body mass data spanning the chick stage (ages 1–35 days), I regressed log-transformed body mass on age and performed an analysis of variance ($\alpha = 0.05$) to determine the strength of the relationship between these variables. I used a $\log_{10}$ transformation of body mass because of concerns about a nonlinear relationship between mass and age (Miller and Knopf 1993, Ruthrauff and McCaffery 2005). Because I did not know the date of hatching of all chicks I handled during the study, I was unable to model a direct age effect on juvenile survival; body mass thus served as a surrogate for age, and this relationship was established using a smaller sample of known-age chicks. For survival analyses in program MARK, I hypothesized that there would be a strong positive relationship between body mass and juvenile survival if mass were positively correlated with age. Based on earlier results (Dinsmore et al. 2003), I assumed the relationship between juvenile mass and annual survival was constant across years.

I also investigated the effect of local climate conditions on the annual survival of juvenile and adult Mountain Plovers. The species' breeding range spans drought-prone regions of western North America, and its general habitat requirements seem to favor areas with reduced vegetation, bare ground, and increased disturbance by grazers, all of which may be enhanced during drought conditions. The potential link between drought and survival requires justification. Drought probably influences plovers' habitat use with local or possibly regional distributional shifts between wet and dry years. Thus, separating survival from site occupancy is critical. With the use of the robust design, temporary movements in response to weather are handled, and resighting data and conditional capture

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probability estimates from a previous study of these birds (Dinsmore et al. 2003) indicate high site fidelity in Montana. Thus, estimates of apparent survival from this study can be interpreted as having removed much of the possible bias due to site occupancy.

A further concern is the link between drought and plover survival. Survival of Mountain Plover nests is in part weather related (Dinsmore et al. 2002), while chick and adult survival are thought to result from predation (Knopf and Wunder 2006). There is little information on mortality of adult plovers, and none from migration. Both breeding (Miller and Knopf 1993) and overwinter (Knopf and Rupert 1995) survival are high, suggesting that most mortality occurs during migration or in the pre- and postbreeding periods. If the species is drought adapted, there may be fitness benefits (e.g., higher annual survival) incurred during periods of drought as a result of reduced predation, especially on adults.

Drought conditions can be measured in many ways, but I chose to use the widely accepted Palmer Drought Severity Index (PDSI; Palmer 1965) and a recent modification to this index (PMDI; Heddinghause and Sabol 1991) as indicators of drought conditions. Both are measures of dryness (drought) based on temperature and precipitation data, and for both, a value less than zero indicates drought. The Palmer indices have limitations although they are intended for use in semiarid regions like Montana and are considered the best indicators of drought available (Heim 2002). Using data from Montana's north-central region (Climate Division 3; Western Regional Climate Center 2007), I incorporated values of each index as year effects. I chose to use mean values across a 12-month period as a primary predictor because impacts to survival of plovers, if present, would be affected by a suite of factors (e.g., predator abundance, food resources, and habitat for nesting) that were best represented by a drought index that spanned the annual cycle. Some factors (e.g., habitat for nesting) may be less influenced by the complete annual cycle, although I believe the use of data from a 12-month period is sensible because climate impacts often accumulate over longer periods. I calculated this 12-month period in two ways: 1) as the average across the calendar year (Jan–Dec) that preceded the survival interval of interest (e.g., I used the 1995 mean drought indices to predict survival from 1995 to 1996; PDSI and PMDI), and 2) as the average across the year preceding the period of the survival interval of interest (e.g., I used the mean from June 1994 to May 1995 to predict survival from 1995 to 1996; PDSI2 and PMDI2).

I included two post hoc tests to strengthen the case for a drought effect on Mountain Plover annual survival. The first test explored the temporal nature of the drought effect by concentrating only on the nesting season. The second test explored the drought effect spatially, and I hypothesized that if Mountain Plover annual survival and drought were linked, drought data from other regions would not explain plover survival in north-central Montana. The tests were: 1) the PMID2 covariate modified to include only the three-month period (May–July) that encompassed the breeding season preceding the survival interval of interest (e.g., I used the mean from May 1995 to July 1995 to predict survival from 1995 to 1996), and 2) the 12-month PMDI2 covariate described above calculated for other areas with substantial numbers of breeding Mountain Plovers (Climate Divisions 1 and 4 in Colorado, 4 in Montana, 1 in Nebraska, 2 in New Mexico, and 4 and 10 in Wyoming; Western Regional Climate Center 2007).. For the latter test, I added the modified PMDI2 covariate for each region singly to the best model and did not average drought indices across climate divisions. For each test, I compared the new model(s) to the best model with a drought effect in my original analysis to see if model performance was improved.

Temporary emigration (γ_i'', γ_i'). Temporary emigration is defined by two parameters: 1) the probability (γ_i'') that an animal is a temporary emigrant in primary sampling period i, given that it was alive and available for sampling in primary sampling period $i-1$, and 2) the probability (γ_i') that an animal that was a temporary emigrant in primary sampling period $i-1$ remains a temporary emigrant in primary sampling period i. Typically, plovers in my study area remained faithful to a prairie dog colony both within and between years (SJD, pers. obs.) although it was possible for an individual to temporarily "emigrate" by occupying smaller, unsurveyed colonies within the study area, or colonies lying just outside the study area. In each case, I considered such movement temporary because the bird could become available for sampling in a subsequent year. I modeled parameters associated with temporary emigration with age effects only, sex effects only, and a random emigration model where $\gamma_i'' = \gamma_i'$ (Kendall et al. 1997).

Conditional capture (p_{ij}) and recapture probabilities (c_{ij}). With a robust design, the probability of first capture (p_{ij}) and recapture (c_{ij}) are estimated for each secondary sampling period, except that there is no probability of recapture for the first secondary sampling period within each primary sampling period. I modeled capture and recapture probabilities carefully because initial captures within a year occurred by two different methods (Dinsmore et al. 2003). New adult plovers were initially captured on nests; recaptures occurred by live resightings. Because intuitively, these recapture probabilities seemed different (the probability of a live resighting should be higher), I built models to account for this difference. To do this, I altered the parameter index matrix (PIM) structure in MARK (Cooch and White 2006) so that I could fit models where p for the initial capture of an adult differed from p for a resighting of a previously marked adult at the same time. I also modified the PIMs to model the initial resighting of a previous year's juvenile differently than other adults resighted at the same time. I hypothesized that second-year birds might be more difficult to resight because they might be more mobile as they searched for their first breeding sites.

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As with any long-term study, the effects of breeding phenology, courtship activity, observer experience and effort, habitat conditions, and other factors provided a justification for including temporal variation in capture and recapture probabilities. To do this, I considered four scenarios. I began by forcing all capture and recapture probabilities equal within secondary sampling periods, resulting in 36 estimates of capture and recapture probability (p_{i1}, $p_{i2} = c_{i2}$, and $p_{i3} = c_{i3}$ for each of the 12 years). I then added an effect that constrained 1) initial adult capture probability, 2) initial capture probability of a juvenile from the previous year, or 3) an additive model that included the effects in the two former factors. As a result, these parameters were estimated for each secondary sampling period within year for a maximum of 102 estimates of p and 68 estimates of c.

MODEL FIT

The robust design has no standard goodness-of-fit test (Cooch and White 2006), unlike live recapture studies that use program RELEASE (Burnham et al. 1987) or closed capture studies that use program CAPTURE (Otis et al. 1978, White et al. 1982). I therefore relied on untested assumptions of this approach (Pollock 1982, Kendall et al. 1995, 1997), rather than collapsing the robust design data into an ad hoc goodness-of-fit test in program RELEASE (pooled result of tests 2 and 3 in RELEASE; Dinsmore et al. 2003).

MODEL-BASED PREDICTIONS

I was interested in using the modeling results to predict the survival of a juvenile plover from date of hatching to age 1. I decided a priori to make predictions from the best model that included a juvenile mass effect on survival, but only if that model was competitive (i.e., $\Delta\text{AIC}_c \leq 2$; Burnham and Anderson 2002). With this model, I used values of the continuous body mass covariate to predict a survival response (Shaffer and Thompson 2007). At hatching, Mountain Plover chicks weigh approximately 10 g, and they fledge at >70 g (Miller and Knopf 1993; SJD, pers. obs.). Because I had body mass data from chicks of all ages up to 35 days, I chose to predict juvenile survival in 5 g intervals from 10 to 85 g to bracket the interval from date of hatching to date of fledging and encompass the range of fledging masses observed in this and other studies. This approach 1) predicts the probability of chick survival from date of hatching to age 1 ($\hat{\phi}_H$; mass of 10 g), and 2) illustrates how predicted juvenile annual survival changes with age (using body mass as a surrogate for age).

I computed a 95% confidence interval for these survival estimates (e.g., $\hat{\phi}_H$) as follows. If $X\beta$ is a column vector of explanatory values used to predict survival (logit $\hat{\phi}_H = \alpha + X\beta$), and V is the variance-covariance matrix of those values (also on the logit scale), then

$$SE(\hat{\phi}_H) = \sqrt{[X\beta]' * [V] * [X\beta]}.$$

TABLE 1. Numbers of Mountain Plovers (*Charadrius montanus*) by age and sex banded in Phillips County, Montana, 1995–2006.

	Juvenile			Adult			
Year	Male	Female	Unknown	Male	Female	Unknown	Total
1995	3	9	57	16	14	36	135
1996	6	4	4	28	14	3	59
1997	8	7	7	34	21	11	88
1998	24	12	11	43	26	6	122
1999	19	20	1	33	33	0	106
2000	30	24	10	30	26	3	123
2001	2	5	22	11	12	0	52
2002	8	9	2	22	18	0	59
2003	32	41	12	41	61	1	188
2004	16	27	2	49	26	1	121
2005	34	38	1	37	34	1	145
2006	21	24	93	35	24	0	197
Total	203	220	222	379	309	62	1395

I constructed a standard 95% confidence interval on the logit scale ($\hat{\phi}_H \pm 1.96 * SE(\hat{\phi}_H)$) and then back-transformed the lower and upper 95% bounds (CI_L and CI_U) on the logit scale using the formulas

$$\text{lower 95\% confidence limit} = \frac{1}{(1 + EXP(-(CI_L)))}$$

and

$$\text{upper 95\% confidence limit} = \frac{1}{(1 + EXP(-(CI_U)))}$$

to construct a confidence interval around the predicted survival estimate. This method resulted in asymmetrical confidence intervals around predicted survival probabilities because of the back-transformation.

RESULTS

CAPTURES AND RESIGHTINGS

I uniquely color banded 1395 Mountain Plovers during the 12-year study (Table 1). All age and sex combinations were well represented, although the adult sex ratio favored males. Juvenile numbers varied annually, mainly as a result of yearly differences in productivity. The high proportion (up to 83%) of unknown-sex juveniles in some years illustrates the difficulty in sexing chicks when I was able to collect only 1–2 small feathers per individual. From this sample, I generated 2654 live resightings of banded birds to estimate annual survival.

MODEL SELECTION RESULTS

Annual survival of Mountain Plovers varied by age; juvenile survival was influenced by body mass at capture, while adult survival showed evidence of annual variation, a sex effect, and a drought effect (Table 2). For juvenile plovers, the

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TABLE 2. Model selection results for the annual survival of Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, 1995–2006. Models are ranked by Akaike's Information Criterion (AIC_c), where K is the number of parameters, ΔAIC_c is the difference in AIC_c from the top model, and w_i is the model weight. Factors included in the models are apparent survival (ϕ); temporary emigration (γ'', the probability that an animal is a temporary emigrant in primary sampling period, given that it was alive and available for sampling in the previous sampling period, and γ', the probability that an animal that was a temporary emigrant in previous remains a temporary emigrant in the current sampling period); capture (p) and recapture (c) probabilities, which included the effects of two age classes (i.e., adults [Ad] and juveniles [Juv]), differences between males and females (sex); $\log_{10}$ body mass (logmass) on juvenile survival; temporal variation that included year effects (year); linear (T) and quadratic (TT) trends across years; and the influence of a modified Palmer Drought Severity Index (PMDI2). In all models, p and c were equal and varied by secondary sampling period, except that the initial capture probability of the previous year's juvenile was allowed to differ from all others by a constant. Only the global model and models with ΔAIC_c values < 5 are shown.

Model[a]	K	Deviance	ΔAIC_c	w_i
ϕ_{Juv}(logmass) ϕ_{Ad}(TT + PMDI2) $\gamma''_{(age)}$ $\gamma'_{(age)}$	49	137 113.57	0.00	0.38
ϕ_{Juv}(logmass) ϕ_{Ad}(TT + PMDI2 + sex) $\gamma''_{(age)}$ $\gamma'_{(age)}$	50	137 112.61	1.09	0.22
ϕ_{Juv}(logmass + PMDI2) ϕ_{Ad}(TT + PMDI2) $\gamma''_{(age)}$ $\gamma'_{(age)}$	50	137 112.90	1.38	0.19
ϕ_{Juv}(logmass) ϕ_{Ad}(year) $\gamma''_{(age)}$ $\gamma'_{(age)}$	56	137 103.53	4.33	0.04
ϕ_{Juv}(logmass) ϕ_{Ad}(TT) $\gamma''_{(age)}$ $\gamma'_{(age)}$	48	137 120.14	4.50	0.04
ϕ_{Juv}(logmass) ϕ_{Ad}(TT+3 mo. PMDI2) $\gamma''_{(age)}$ $\gamma'_{(age)}$	49	137 118.11	4.54	0.04
Global model	198	136 872.91	76.59	0.00

[a] AIC_c of the top model was 137 212.80.

log-transformed mass effect was strong and positive (from best model: $\hat{\beta}_{LogMass} = 3.45$, 95% CI was 1.65, 5.24 on a logit scale), and adding a drought effect did not improve model fit. There was no evidence of a sex effect on juvenile survival. I found strong evidence for annual variation in adult survival (Table 2). The best model included a quadratic trend in adult survival across years and an additive effect of PMDI ($\hat{\beta}_{PMDI2} = -0.38$, 95% CI was -0.74, -0.02 on a logit scale). Evidence for a sex effect on adult survival was weak. Adding a sex effect to the best model resulted in a drop of 1.09 AIC_c units and only hinted that male plovers had higher survival than females ($\hat{\beta}_{Male} = 0.11$, 95% CI was -0.10, 0.31 on a logit scale).

Parameters associated with temporary emigration included age effects only; models with sex effects or random emigration were not supported by the data. Age effects were weak with overlapping confidence intervals. Model-averaged parameter estimates were $\gamma''_{Juvenile} = 0.40 \pm 0.11$, $\gamma''_{Adult} = 0.43 \pm 0.02$, $\gamma'_{Juvenile} = 0.90 \pm 0.11$, and $\gamma'_{Adult} = 0.91 \pm 0.03$. Capture and recapture probabilities varied by secondary sampling period within year. The initial capture probability of the previous year's juveniles was lower than that of adults (from best model: $\hat{\beta}_{Juv} = -0.83$, 95% CI was –1.48, –0.10 on a logit scale), and this effect appeared in the top 11 models. Capture and recapture probabilities were relatively high, with means of $\hat{p} = 0.49$ (range 0.14–0.81) and $\hat{c} = 0.54$ (range 0.27–0.81) across all secondary sampling periods.

ANNUAL SURVIVAL

Among chicks, the relationship between chick age and $\log_{10}$ body mass was significant ($F_{1,182} = 2489$, $P < 0.01$, $R^2 =$ 0.93; Fig. 1). The predicted annual survival for a plover chick from date of hatching was 0.06 ± 0.03 (95% CI was 0.02, 0.15); older chicks had substantially higher predicted annual survival (Fig. 2). Adult annual survival varied yearly from a low of 0.74 in 2001 to a high of 0.96 in 2005 (Fig. 3), although the 95% confidence intervals were overlapping for all years. The predicted response in adult survival from the best model ($\hat{\phi}_{Ad} = 6.59 - 1.74 * T + 0.13 * TT - 0.38 * PMDI2$, where T denotes the linear term and TT the quadratic term that forced the curvilinear relationship in survival across years) seemed to be enhanced during drought conditions, although the confidence intervals on these estimates also overlapped (Fig. 4). The pattern in adult survival also generally followed the calculated PMDI2 values (Fig. 4). None of the post hoc tests for the drought effect on adult annual survival improved model performance (all $\Delta AIC_c > 4.50$).

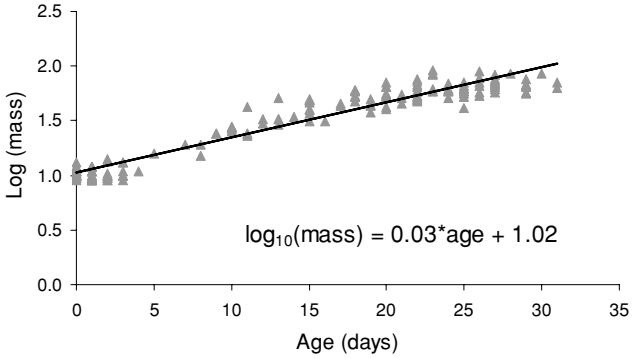

FIGURE 1. Log_{10} body mass (g) increased with age (days) in juvenile Mountain Plovers (*Charadrius montanus*; $n = 183$) in Phillips County, Montana, 1995–2006. The equation explaining their relationship is shown on the figure.

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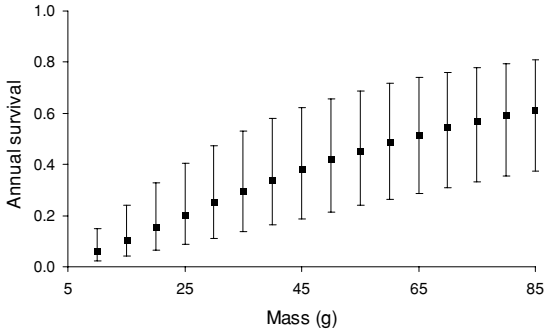

FIGURE 2. Predicted annual survival (95% CI) as a function of $\log_{10}$ body mass (g) at capture for juvenile Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, 1995–2006. Survival is predicted from date of hatching (10 g) to a representative mass at fledging (85 g).

DISCUSSION

The Mountain Plover is a species of high conservation concern (Brown et al. 2001), and estimates of vital rates are critical to future conservation efforts. This study revises earlier estimates of annual survival (Dinsmore et al. 2003), provides a more robust estimate of juvenile survival, including an understanding of survival from date of hatching, and offers insight into the effects of sex and climate conditions on adult annual survival. These estimates are important for the future conservation of the species but should be interpreted carefully.

JUVENILE SURVIVAL

The predicted annual survival of a Mountain Plover from date of hatching was 0.06 in this study. However, heavier (and thus older) chicks had greater predicted annual survival, peaking at 0.62 for an 85 g individual. The striking increase in juvenile survival with increasing chick body mass may balance a high loss of chicks early in the brood-rearing period. A chick that survives to age 11–13 days (about 30 g) more than triples its probability of first year survival. Studies of the Snowy Plover (*C. alexandrinus*; Warriner et al. 1986, Colwell et al. 2005), Piping Plover (*C. melodus*; Powell 1992, Loegering and Fraser 1995), and Killdeer (*C. vociferous*; Powell 1992) have all noted high mortality (>50%) of chicks within the first 10 days of life. Patterns of age-related survival in Mountain Plover chicks have revealed that most mortality occurs soon after hatching and that survival increases with chick age (Graul 1975, Knopf and Rupert 1996). Although the probability of survival from date of hatching to age 1 is small, it is important to remember that this is an estimate of apparent survival, and any permanent emigration will bias this estimate low. Juvenile Mountain Plovers regularly emigrate to surrounding areas to breed (Dinsmore 2001), so true first-year survival probably exceeds 0.06.

My approach provides a single estimate of survival from date of hatching to age 1, albeit with important assumptions. I made no attempt to age Mountain Plover chicks when I banded them. Instead, I relied on the relationship between known age and body mass in a relatively large ($n = 183$) sample of chicks to predict "age" in all chicks using body mass as a surrogate. Based on the strength of this relationship, I believe this is a reasonable assumption. I also assumed this relationship was nonlinear, which was strongly supported in other studies (Miller and Knopf 1993, Ruthrauff and McCaffery 2005). My

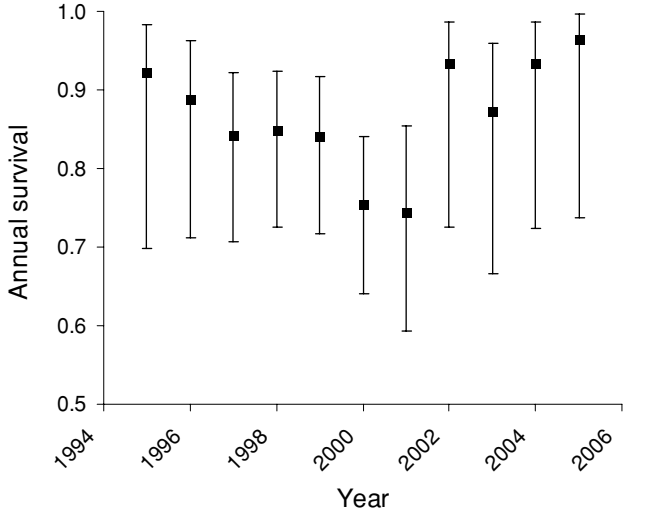

FIGURE 3. Model-averaged estimates of annual survival (95% CI) of adult Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, 1995–2006.

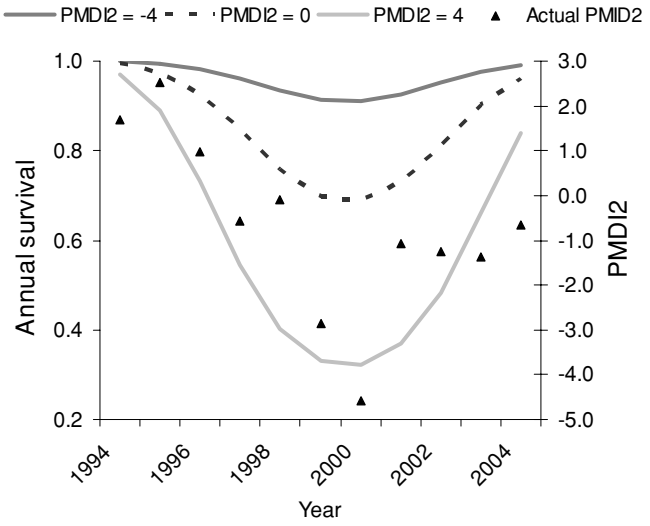

FIGURE 4. Predicted annual survival rates of adult Mountain Plovers in response to the modified Palmer Drought Severity Index (PMDI2) in Montana, 1995–2006. I modeled PMID2 from 4 (extremely wet) to –4 (extremely dry), with 0 representing "normal" conditions (Palmer 1965). A second axis plots the actual values of PMDI2 that were calculated for each year of the study.

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approach might have been biased if the sample of known-age chicks were skewed toward heavy or light individuals. However, my sample included chicks of all ages (mean = 14 ± 10 days SD) and was representative of the prefledging period. Known-age chicks were sampled throughout a 12-year study; my approach also assumes that the relationship between age and body mass is not year-dependent.

ADULT SURVIVAL

Survival of adult Mountain Plovers showed considerable annual variation. This variation was explained by the combination of a quadratic trend across years and the effect of local drought conditions. The quadratic trend alone (fifth best model) had survival decreasing through 2000 and then increasing to peak in 2005. This quadratic pattern was better supported than models with no annual variation, a linear pattern in survival across years, or a model with full year effects. This may have been confounded with the drought effect, although it might also have resulted from other environmental factors or an unknown cause. The PMDI effect was additive on the quadratic trend and altered the pattern slightly so that the low year was 2001. Although I did not find strong evidence for a drought effect on juvenile survival, it is important to note that a model a model of juvenile survival with PMDI2 was competitive ($\Delta AIC_c = 1.38$). In this model, the parameter for the drought effect was negative (same direction as with adults), but was estimated poorly with a confidence interval that overlapped zero. This hints that juvenile survival may also have been affected by drought, although I cannot state this with much confidence.

My finding that annual survival of adult Mountain Plovers is correlated with drought conditions prompts further questions on this topic. An earlier examination of survival found little evidence that it was directly related to habitat (i.e., acreage of black-tailed prairie dogs; Dinsmore et al. 2003), prompting me to examine climate conditions (e.g., drought) that influence habitat. For a mobile bird such as the plover, linking a survival response to habitat is challenging, because it experiences a range of habitat and climatic conditions throughout the annual cycle. In the Great Plains, weather patterns are variable with alternating wet and dry periods and local annual variation in precipitation (Ojima et al. 2002, Western Regional Climate Center 2007). This cyclical weather pattern suggests that, if the plover is indeed a drought-adapted species, it may experience a series of "normal" breeding seasons punctuated by infrequent years with high reproductive success and survival. Here, reproductive success is a combination of nest success and juvenile survival. I found no evidence for annual variation in juvenile survival in this study but have found substantial variation in annual nest survival in this region (SJD, pers. obs.).

How, then, might local drought conditions in Montana affect survival throughout the annual cycle? The plover spends half of its annual cycle (April–September) in Montana. During this time it breeds, gathers in post-breeding flocks, and probably gains fat reserves for fall migration. During the nesting season (late May–mid-July), survival of adults is high (Dinsmore and Knopf 2005). However, survival has not been measured during the prenesting and postbreeding periods, which jointly account for almost one third of the annual cycle. My results suggest that drought may 1) negatively influence body condition through a diminished food supply, which might affect local survival or survival during fall migration, or 2) change predation risk to adult plovers during the prenesting and postbreeding periods with a resultant change in annual survival. Future work should attempt to better untangle why annual survival appears linked to drought in the Mountain Plover.

ANNUAL SURVIVAL IN SHOREBIRDS

The estimates of annual survival reported here are substantially higher than those found in an earlier analysis of the first six years of these data (Dinsmore et al. 2003) and in studies of other Charadriidae (see below). The reasons for the increase in survival are unknown, but it is likely that the six-year study was simply too short to incorporate older (> six years old) individuals and temporary emigrants into estimates of annual survival. At the time of the earlier study, Mountain Plovers were thought to be short-lived, and we assumed that the six-year period would provide reasonable estimates of annual survival. However, if the earlier study failed to account for older individuals, the resulting estimates of annual survival would have been biased low. It should be noted the present study has since revised the longevity record for the Mountain Plover to more than 10 years (SJD, pers. obs.), and individuals that are 5–7 years old were frequently encountered. This suggests that the Mountain Plover is a longer-lived bird than previously thought.

I found only weak evidence for a sex effect on annual survival in the Mountain Plover, with males appearing to have slightly higher survival than females. It is possible that a survival difference plays a role in the unusual rapid multiclutch mating system of the species, where adults of both sexes tend separate nests during the breeding season (Graul 1973). Graul (1976) suggested that this was an infrequent response to variable food supply, but more recent work (Dinsmore et al. 2002) suggests that it occurs with greater frequency. In this system, the roles of each sex differ from those of most birds. For example, males have a greater role in courtship and territory defense (Graul 1973), whereas females are responsible for egg production. Males tend to exhibit greater nesting success than females (Dinsmore et al. 2002), but females have greater brood success (Dinsmore and Knopf 2005).

The results of this study have important implications for 1) understanding the population biology of Mountain Plovers, 2) providing information about an important demographic component for modeling the plover's long-term viability, and

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3) adding to our broad understanding of shorebird ecology. The estimates of annual survival reported here are much greater than previously thought and are greater than those for other members of the Charadriidae. Furthermore, understanding survival patterns as they relate to age, sex, and chick body mass further teases apart the biological mechanisms that ultimately influence population growth patterns. The finding that adult annual survival in the Mountain Plover was related to local climate patterns hints that the species may be drought adapted and suggests that global climate change predictions for the Great Plains as a warmer and drier environment (Ojima et al. 2002) may ultimately benefit the plover.

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