DISSERTATION

POPULATION BIOLOGY OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2001

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY STEPHEN J. DINSMORE ENTITLED "THE POPULATION BIOLOGY OF MOUNTAIN PLOVERS IN PHILLIPS COUNTY, MONTANA" BE ACCEPTED AS FULFILLING IN PART THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

POPULATION BIOLOGY OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA

Effective conservation measures for rare or declining species cannot be implemented unless their biology and demography are well understood. The Mountain Plover (*Charadrius montanus*) is a local and declining species breeding on the western Great Plains of North America. Populations are thought to have declined drastically in the last several decades and the species has been proposed to be listed as Threatened. Their breeding biology has been extensively studied, especially in northeastern Colorado, although aspects of their life-history such as their demography have not been studied. During a 6-year study (1995-2000) I investigated their nesting biology, demography, and population trends in southern Phillips County, Montana.

I modeled the daily nest survival of Mountain Plovers as a function of the sex of the incubating adult, daily nest age, year, linear and quadratic time trends, and two weather covariates (maximum daily temperature and daily precipitation). The sample of 432 nests included slightly more male-tended nests (55% of total). Observed (31 May for females and 2 June for males) and expected (27 May for females and 26 May for males) mean nest initiation dates did not differ between nests tended by female and male plovers. I found that daily nest survival was a function of the sex of the incubating adult, daily nest age, a quadratic time trend, and daily precipitation. I found no evidence of yearly differences or an effect of maximum daily temperature on nest survival. Nests tended by male plovers had higher daily survival rates than those tended by females. Daily nest age positively influenced survival with older nests having higher survival, although this effect may have been confounded with individual heterogeneity. Daily precipitation during the nesting season negatively influenced nest survival. Seasonally, the daily survival of Mountain Plover nests was high early in the nesting season, dipped to a low in mid-season, and then gradually rose to a peak at the end of the nesting season. Total nesting success was 0.35 for nests tended by females and 0.49 for nests tended by males.

I used the robust design in program MARK to estimate annual apparent survival (ϕ), conditional capture (p and r) and recapture (c) probabilities, and the annual population size (N) of Mountain Plovers in southern Phillips County, Montana in the presence of temporary emigration. I modeled annual survival rates as a function of two age classes (adults and juveniles), body mass at capture (juveniles only), a radio transmitter effect in 1999, and annual area occupied by prairie dogs within the study area. I modeled year-specific capture probabilities to include a resighting effect (r) for plovers that had been marked in a prior year. The results supported age-specific differences in annual survival that were also a function of juvenile body mass and area occupied by prairie dogs. Body mass had a positive effect on juvenile survival. The area occupied by prairie dogs appeared to have no effect on survival. Estimated annual apparent survival rates were 0.46 to 0.49 for juveniles and 0.68 for adult plovers. Using these estimates, I computed the mean life span of a Mountain Plover at banding as 1.92 years (SE = 0.17; 95% CI was 1.58, 2.26). There was strong evidence for a negative resighting effect on capture probabilities. The size of the adult Mountain Plover population in the study area was estimated at between 95-180 individuals annually. The population size closely tracked annual changes in the area occupied by black-tailed prairie dogs with both prairie dogs and plovers rapidly recovering from an outbreak of sylvatic plague in the mid-1990s.

Finally, I estimated the annual rate of population change (λ) and recruitment rate (f) using the Pradel models. I modeled λ as a constant across years, as a linear time trend, as year-specific, and as a function of the area occupied by prairie dogs. I modeled f only as a function of the area occupied by prairie dogs. The results indicated a strong negative effect of area occupied by prairie dogs on both λ and f. There was also good evidence for a negative time trend on λ; this model had substantial weight ($w_i = 0.31$) compared to models without a time trend. Yearly estimates of λ were >1 in all years except 1999, indicating that the population increased beginning in 1995 and then stabilized in the last year of the study. There was weak evidence for year-specific estimates of λ; the best model with year-specific estimates had a low weight ($w_i = 0.02$), although the pattern of yearly estimates of λ closely matched those estimated with a linear time trend. I found that the population trend of Mountain Plovers closely matched the trend in the area occupied by black-tailed prairie dogs. Black-tailed prairie dogs declined sharply in the mid-1990s in response to an outbreak of sylvatic plague, but their numbers steadily increased since 1996 with subsequent increases in plovers. This suggests that the conservation of Mountain Plovers in this region is closely linked to the available area occupied by prairie dogs. Threats to prairie dogs such as sylvatic plague and recreational shooting pose indirect threats to Mountain Plovers.

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ACKNOWLEDGMENTS

This study would not have been possible without the support of many people. There are five people that I feel deserve special recognition. First, I thank my parents, James J. and Patricia A. Dinsmore, for instilling me with an early interest in birds and providing me with encouragement throughout my education. My father's advice and insights into all aspects of my education were invaluable. I am sure that both of my parents often wondered if I would ever finish school. Well, I finally did. I thank my advisor, Gary C. White, for his input into nearly all aspects of this study and for being a superb mentor for me. His ability to comprehend and solve complex problems is uncanny – I can only hope that some of it rubbed off on me. I am grateful to Fritz L. Knopf for first introducing me to the "prairie ghost", for his many years of support and involvement with this work, and for being a good friend and mentor. He has certainly taught me to look beyond the fine details to the big picture. Finally, I thank John J. Grensten for his friendship, field assistance, and unwavering support of this study. His knowledge of, and interest in, plovers and prairie dogs spurred many stimulating discussions.

Many organizations provided financial support for this work. I am grateful to the U. S. Department of Defense (Tom Warren, Chris Bandy, and Richard L. Bunn, Fort Carson Military Reservation), the U. S. Fish and Wildlife Service (Bruce D. Rosenlund, Colorado Fish and Wildlife Assistance Office), the Biological Resources Division of the U. S. Geological Survey (Fritz L. Knopf, Midcontinent Ecological Science Center), the U. S. Bureau of Land Management (Rick Hotaling, Phillips Resource Area), the Denver Zoological Foundation (Richard P. Reading), and the Fort Belknap Tribal Community (Jerry Kaiser, U. S. Bureau of Indian Affairs) for financial support. The staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. I appreciate the guidance of my remaining graduate committee members David R. Anderson, Michael F. Antolin, and Kenneth P. Burnham. The following individuals provided assistance with various aspects of this study: Aaron Brees, Corla DeBar, David C. Ely, Tammy Fancher, Tammy Hamer, Lou R. Hanebury, Tim Hanks, Joel G. Jorgensen, Randy Matchett, Ramone McCoy, Chris McQueary, Sara Oyler-McCance, Everett Russell, Tim Vosburgh, and Gene Williams. Jean Grensten deserves special thanks for her friendship and all those great meals. I owe a huge thank you to the Veseths (Fred, Jackie, Dale, and Janet) for providing me with a friendly home

every summer. Finally, I thank Butch Matovitch, Don Robinson, and Jess Robinson for allowing me access to their private lands.

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INTRODUCTION

Measuring and understanding factors that influence populations has always been an important consideration in the management of declining species. The long-term demographic studies of the Northern Spotted Owl (Forsman et al. 1996) provide recent examples of the interplay between population biology and the management of a federally listed species. As human population growth continues, many native communities will become increasingly threatened and there will be an even greater need for managing declining species.

The Mountain Plover (*Charadrius montanus*) is a localized and declining bird of the North American Great Plains. They are classified as an endemic bird of the Great Plains (Mengel 1970), which as a group may have shown the greatest declines of any group of birds (Knopf 1996a). North American populations may have declined by as much as 63% since 1966 (Knopf 1996b), probably because of the removal of prairie dogs and the loss or alteration of wintering habitat (Olson-Edge and Edge 1987, Knopf 1994, Dinsmore 2000). The prairie ecosystem, which is occupied by Mountain Plovers, may be the most endangered ecosystem in North America (Samson and Knopf 1994). At present, it appears that most threats to Mountain Plovers occur on the breeding grounds (Dinsmore 2000), although there are still discussions about possible threats on the wintering grounds. The total population was estimated at 8,000-10,000 birds using information from a variety of informal surveys (Knopf 1996b). These concerns led to a 1997 proposal to federally list the Mountain Plover (Miller and Knopf 1993) and it was proposed as a Threatened species in early 1999 (U. S. Department of the Interior 1999).

Mountain Plovers breed widely in the eastern portions of Colorado, Wyoming and Montana and locally in Mexico, Texas, New Mexico, Oklahoma, Kansas, Nebraska, Utah and Alberta (Knopf 1996b). They have been characterized as a disturbed-prairie or semidesert species rather than a grassland species (Knopf and Miller 1994). They prefer disturbed habitats for nesting, including areas formerly occupied by bison (*Bison bison*) (Knopf 1996b) and prairie dogs (*Cynomys* spp.) (Knowles et al. 1982, Samson and

Knopf 1994, Knopf 1996b) and agricultural fields (Knopf and Rupert 1999). They are a short-distance migrant and winter in a broad area from the Central Valley of California south and east through southern California, southern Arizona, northern Mexico, and southern Texas.

The mating system of Mountain Plovers is not fully understood. The sexes are monomorphic but can be readily distinguished by molecular sexing techniques. Most Mountain Plovers breed at age one (Graul 1973). The mating system has been described as rapid multiple-clutch where females lay two clutches, the first incubated by the male and the second by the female, with a single adult plover tending each nest (Graul 1973). Graul (1976) speculated this was a response to variable food resources, with some females laying more than two clutches in good years. Graul (1973) also documented one instance where a female bred with more than one male; this was the first indication of sequential polyandry.

Northeastern Colorado, and especially Weld County, has long been considered the center of the Mountain Plover breeding range (Graul and Webster 1976). However, other areas of Colorado (South Park and southeastern Colorado) may currently have greater numbers of breeding Mountain Plovers (Kingery 1998). In Weld County, the species' breeding biology has been extensively studied (Graul 1975, Miller and Knopf 1993, Knopf and Rupert 1996). In this region, plovers prefer to nest in areas heavily grazed by cattle (Graul and Webster 1976) although there is some use of fallow crop fields (Knopf and Rupert 1999) and prairie-dog colonies. Plovers arrive in mid- to late March (Graul 1975, Knopf and Rupert 1996), begin nesting in late April, with the peak hatching period in early to mid-June. Clutch size is normally 3 eggs, although it can range from 1-6 eggs (Knopf 1996b, Dinsmore and Knopf 1999).

The apparent nest success of Mountain Plovers has varied: 65% for 80 nests and 48% for 21 nests (Graul 1975), 45% for 20 nests (McCaffery et al. 1984), 50% for 14 nests (Miller and Knopf 1993), and 26% for 34 nests and 37% for 54 nests (Knopf and Rupert 1995). Little work has been done on the post-hatching survival of Mountain Plovers. Knopf and Rupert (1996) reported a fledging rate of 0.26 chicks per nesting attempt on the Pawnee National Grassland. After accounting for post-fledging predation, 0.17 (Knopf and Rupert 1996) to 0.70 (Miller and Knopf 1993) chicks per nesting attempt left the breeding grounds.

The population biology of Mountain Plovers has not been previously studied. There are no estimates of age-specific annual survival for this species. The survival of adult plovers during the breeding season (14 May to 28 July) was 100% in northeastern Colorado (Miller and Knopf 1993). The over-winter (1 November to 15 March) survival rate of adult plovers in California was 0.95 (Knopf and Rupert 1995). Knopf (1996b) reported a maximum life span of 6 years and 7 days, but one male in Montana has subsequently reached an age of 8 years and 1 month (pers. obs.).

There is less information on Mountain Plovers in Montana. Southern Phillips County is thought to contain the largest population of Mountain Plovers in Montana, and one of the largest populations in North America (Knopf and Miller 1994). Mountain Plovers selectively nest on black-tailed prairie dog (*Cynomys ludovicianus*) colonies in southern Phillips County (Knowles et al. 1982, Knowles and Knowles 1984, Olson and Edge 1985), although limited nesting can occur off prairie-dog colonies (pers. obs.). Mountain Plovers do not use agricultural fields in Montana (Shackford et al. 1999, pers. obs.). In other parts of Montana, nesting occurs on areas heavily grazed by sheep (Knowles and Knowles 1993) and on lands once mined for bentonite (Knowles and Knowles 2000). Suitable shortgrass habitat for Mountain Plovers is more limited in Montana than elsewhere in the breeding range. Olson (1984) surveyed a variety of potential plover habitats in southern Phillips County and reported that 98% of all plover sightings were on prairie-dog colonies. Mountain Plovers in Montana select mid-sized prairie-dog colonies between 6 and 50 ha in size (Olson-Edge and Edge 1987).

The nesting phenology in Montana is slightly later than in the southern part of the breeding range. In southern Phillips County, Mountain Plovers arrive the first week of April, nesting begins during the first week of May, and the peak hatching period is in mid- to late June (pers. obs.). Mountain Plovers selected nest sites on prairie-dog colonies that were in patches with greater vegetation cover and lower vegetation height than at randomly selected sites within those colonies (Olson and Edge 1985). Erosion pavement cover (a bare ground component) was greater at randomly-selected sites than at nest sites (Olson and Edge 1985), suggesting that bare ground may not be a critical nest-site characteristic of prairie-dog colonies.

There were no previous estimates of the size of the Mountain Plover population in southern Phillips County. Knowles et al. (1982) estimated a density of 0.20 plovers/km^2 within a portion of Charles M.

Russell National Wildlife Refuge and Olson-Edge and Edge (1987) estimated a density of 0.28 plovers/km^2 in the same area. These figures do not include prairie-dog colonies on Bureau of Land Management lands where most plovers now occur. Graul and Webster (1976) predicted a density of 8 plovers/km^2 for Montana, a figure that is too high for even the best habitat in southern Phillips County.

In Montana, there is compelling evidence that Mountain Plovers are dependent on active prairie-dog colonies for nesting (Dinsmore 2000). Two species of prairie dogs occur in Montana. The black-tailed prairie dog is widespread east of the Continental Divide while the white-tailed prairie dog (*C. leucurus*) has a more localized distribution in south-central Montana (Flath 1979). Black-tailed prairie dogs have experienced precipitous declines in the last century, mostly due to poisoning and sylvatic plague (Knowles 1999). These declines are evident in Montana where the area of active prairie-dog colonies declined from an estimated 48,000 to 52,000 ha in the mid-1980s to 26,400 ha in 1998 (Knowles 1999). Prairie dogs have declined in a similar manner in southern Phillips County to a present level of approximately 6,400 ha in 2000 (J. Grensten, pers. comm.). The dependency on prairie dogs in Montana is probably tied to two factors: habitat and food. Mountain Plovers prefer to nest on flat, arid landscapes, especially in areas that are intensively grazed (Knopf 1996b). In Montana, the only open, grazed habitat is found on active prairie-dog colonies. Prairie-dog colonies also harbor more food items than the surrounding habitats (Knopf 1996b), although it is unclear exactly how plovers utilize these resources (Olson 1985).

I studied the breeding biology and demography of Mountain Plovers in southern Phillips County, Montana from 1995 through 2000. I present the results of a study of their nesting biology where I modeled nest survival as a function of the sex of the incubating adult, daily nest age, and weather (Chapter 1; style after *Ecology*). I also report the results of a capture-recapture study in which I estimated age-specific annual survival, temporary emigration, and population size (Chapter 2; style after *Ecological Applications*). Finally, I present the results of a study of their population trends in southern Phillips County and comment on their current status and future prognosis there (Chapter 3; style after *Journal of Wildlife Management*).

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CHAPTER 1. NEST SURVIVAL MODELS FOR MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA.

ABSTRACT

The traditional method of estimating avian nest success has involved simple measures of apparent nest success or Mayfield constant nest survival models. Models that incorporate greater detail such as temporal variation in nest survival and covariates representative of individual nests have been largely ignored, but represent substantial improvement over traditional methods. I modeled daily nest survival of Mountain Plovers (*Charadrius montanus*) in southern Phillips County, Montana as a function of the sex of the incubating adult, nest age, year, linear and quadratic time trends, and two weather covariates (maximum daily temperature and daily precipitation) during a 6-year study (1995-2000). The 432 nests were skewed slightly in favor of male-tended nests (55%). Observed (31 May for females and 2 June for males) and expected (27 May for females and 26 May for males) mean nest initiation dates did not differ between nests tended by female and male plovers. I found that daily nest survival was a function of the sex of the incubating adult, daily nest age, a quadratic time trend, and daily precipitation. There was no evidence for yearly differences or an effect of maximum daily temperature on the nest survival of Mountain Plovers. Nests tended by female and male plovers differed in their probability of success ($\hat{S}_f$ = 0.35; $\hat{S}_m$ = 0.49); the slope coefficient for the additive male effect on nest survival was 0.37 (95% CI was 0.03, 0.71) on a logit scale. Daily survival rates of nests increased with nest age; the slope coefficient for daily nest age in the best model was 0.06 (95% CI was 0.04, 0.09) on a logit scale. Precipitation decreased nest survival to the next day; the slope coefficient for the additive effect of daily precipitation on nest survival was –1.08 (95% CI was –2.12, –0.13) on a logit scale. Seasonally, the daily nest survival of Mountain Plover nests was high early in the nesting season, dipped to a low in mid-season, and then gradually rose to a peak at the end of the nesting season. The nest success of Mountain Plovers appears to be higher than normal for a ground nesting bird. The use of this method for estimating nest success resulted in a less biased estimate of total nest success and allowed factors of interest such as maximum daily temperature, daily precipitation, and temporal variation to be easily included in the models.

Key words: *Charadrius montanus*, mating system, Mountain Plover, Montana, nest survival, program MARK.

INTRODUCTION

The study of nest success has received considerable attention from ornithologists and is a critical component of the study of the breeding biology of birds. Apparent nest success, defined here as the proportion of successful nests (those where ≥ 1 egg hatches) in a sample, is often positively biased because nest losses early in incubation are underrepresented (Mayfield 1961). To generate an unbiased estimate of apparent nest success it is necessary to follow a sample of nests that were found on the day they were initiated (Klett and Johnson 1982). Due to this inherent bias, Mayfield (1975) developed a method for estimating the daily survival of a sample of nests using exposure days (the cumulative number of days the nests in the sample were monitored) and the number of known losses. Mayfield estimated daily nest survival as 1 – [(number of nest losses)/(total exposure days)]. Nest success is then calculated as (daily nest survival)^n where n is the length of the nesting period (incubation or incubation + nestling period, depending on whether the species was precocial or altricial).

Implicit in Mayfield's estimator was the assumption that daily nest survival was constant in time and that the date of a hatch or loss was known exactly. However, field studies often do not collect nest information on a daily basis; rather, nests are checked at regular intervals of one to several days and the timing of a hatch or loss may not be known exactly. Because the timing of losses between nest checks is often unknown, the standard procedure has been to use the midpoint of the interval when calculating exposure days (Mayfield 1961). Considerable debate has focused on the use of the midpoint versus some other fraction of the interval between nest checks (Miller and Johnson 1978, Klett and Johnson 1982). Despite the problem of deciding which method should be used to calculate exposure days with the Mayfield estimator, Johnson (1979) showed that the estimates generally performed well when compared to maximum likelihood estimates and that they were robust to heterogeneity among nests.

Johnson (1979) and Bart and Robson (1982) expanded Mayfield's model and developed the theory to estimate time-specific nest survival rates, although their models were essentially identical to the one developed by Mayfield. Klett and Johnson (1982) later developed a way to estimate constant daily survival rates for different periods of the nesting cycle, although the choice of these periods was often arbitrary and not biologically meaningful.

There have been several recent advances that allow for more flexibility in modeling nest survival. Bart and Robson (1982) developed a generalized likelihood for estimating daily nest survival rates under assumptions of constant and time-specific survival. Other developments have included models that estimate daily nest survival across nest stages (for example, the transition between incubation and nestling stages) where the exact transition date between the stages is unknown (Stanley 2000) and methods for including the effects of observers on nest checks (Rotella et al. 2000). However, other intuitive factors such as nest age are often overlooked when estimating nest survival. Nest age should be an important factor to consider with older nests probably having higher survival in most bird species. Similarly, nest survival would be expected to vary during the nesting season with the exact pattern depending on the species being studied.

Due to a lack of available software to easily compute time-specific estimates of nest survival, most studies continue to use estimates of constant nest survival calculated using the Mayfield method. These studies have overlooked the opportunity to allow nest survival to vary in time, to fit models with time trends to nest survival, to use time-specific covariates such as weather, and to use individual covariates specific to each nest being monitored. Incorporating these variables into estimates of nest survival will generate unbiased and more biologically meaningful estimates of nest success.

Mountain Plovers (*Charadrius montanus*) are a declining shorebird of the western Great Plains (Knopf 1996). Their nesting biology has been well studied, especially in northeastern Colorado (Graul 1975, Miller and Knopf 1993, Knopf and Rupert 1996). Apparent nest success ranged from 26% to 65%, but none of these studies estimated nest survival. Young Mountain Plovers are precocial and leave the nest within a few hours of hatching (Knopf 1996), so nest success in this species refers to the incubation period only. Nest losses in published studies were attributed to a variety of predators including mammals, birds, and snakes.

Mountain Plovers have a rapid multi-clutch mating system in which a female may lay a clutch for a male and then lay a second clutch for herself (Graul 1973). Clutch size is typically 3 eggs (Knopf 1996) and does not differ between male- and female-tended nests. Graul (1973) estimated that about 20% of females lay clutches for a male and, in at least one instance, for more than one male. After egg laying a single adult plover (male or female) incubates each nest and there is not sharing of incubation duties.

This unusual mating system raises several questions about possible differences in the nest survival of male- versus female-tended nests.

I modeled the daily survival of 432 Mountain Plover nests monitored over six breeding seasons (1995-2000) in southern Phillips County, Montana. I used program MARK (White and Burnham 1999) to test for sex-, year-, and time-specific differences in nest survival and investigated the importance of two weather covariates (maximum daily temperature and daily precipitation) and nest age on daily nest survival rates. I computed mean nest initiation dates for nests tended by each sex, and then corrected those dates using a Horvitz-Thompson estimator to compute the expected number of nests initiated on a given date. I estimated the overall success of male- and female-tended Mountain Plover nests using the logistic regression equation from my best model with no precipitation effect.

METHODS

STUDY AREA

I studied Mountain Plovers on a 3000-km^2 area in southern Phillips County in north-central Montana (4740-4755N,10735-10830W; Figure 1.1). 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 is 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 (*Cynomys ludovicianus*) 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 (*Stipa 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, pers. comm.). Mean elevation was approximately 930 m.

I studied Mountain Plovers exclusively on or adjacent to active black-tailed prairie dog colonies because previous work had shown that Mountain Plovers preferentially used such sites in Montana (Knowles et al. 1982, Knowles and Knowles 1984). Prairie dog numbers fluctuate considerably in southern Phillips County. These fluctuations were largely due to sylvatic plague, an epizootic (Barnes 1993), although recreational shooting may have a negative impact on some of the smaller prairie-dog colonies (Vosburgh and Irby 1998). The last known major plague outbreak occurred in 1992-96. Colony areas were reduced by about 80% during this outbreak, but recovery since then was quite rapid at an increase of approximately 30% annually. The actual area occupied by prairie dogs within the study area increased from 1371 ha in 1995 to 5071 ha in 2000 (J. Grensten, pers. comm.). Inactive colonies, mostly the result of plague outbreaks, were not included in this total because habitat on such colonies rapidly became unsuitable for plovers, often within a matter of a few weeks.

LOCATING NESTS

I studied Mountain Plovers during six nesting seasons (1995-2000). Each year, fieldwork began on 19 or 20 May and continued until the last nest had hatched, usually in late July or early August. Active prairie-dog colonies within the study area were systematically searched for Mountain Plover nests ≥3 times each year. I 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. Hereafter, a nest is defined as a nest structure containing ≥1 egg. Once I found a nest, I marked it with small rockpiles or dried cattle droppings; these "natural" markers were used to minimize the possibility that a predator would cue in on the nest. On larger prairie-dog colonies with multiple plover nests I sometimes placed a small orange flag 25 m from the nest.

I trapped adult plovers immediately with a walk-in wire mesh trap placed over the nest. Juveniles, many of which returned to nest in subsequent years, were captured as chicks, usually ≥10 days of age. Both juvenile and adult plovers were weighed to the nearest gram and banded with a unique combination of four colored leg bands and an aluminum size 3A U. S. Fish and Wildlife Service numbered leg band.

Beginning in 1996, I collected a feather sample from every plover for gender determination; I collected only a limited number of feather samples in 1995.

Gender of Mountain Plovers cannot be reliably determined either in the hand or in the field, unless courtship is seen. Thus, the sex of each plover could only be determined using molecular techniques (Kahn et al. 1998, Griffiths et al. 1998, Fridolfsson and Ellegren 1999). Frozen feather samples taken from adult and juvenile plovers were analyzed by the Quinn lab at Denver University in Denver, Colorado (*n* = 350) and by AvianBiotech International in Jacksonville, Florida (*n* = 352). Initially, 224 samples were tested by Denver University in July 2000. An additional 263 samples were successfully sexed from 352 samples sent to AvianBiotech in April 2001. Sex determination followed the procedures outlined in Kahn et al. (1998). DNA was extracted following the protocol of the Wizard Genomic DNA Purification System by Promega. This technique examined a highly conserved gene (CHD) that is linked to the sex chromosome in birds. When electrophoresed, the PCR amplifications showed 2 bands for females (1 each for the W and Z chromosomes) and a single band for males (for the Z chromosome). Overall success in sexing plovers was 85% (487 of 576 samples were sexed). Included in this total were juvenile plovers (*n* = 177; many returned to nest in subsequent years).

Once found, nests were checked every 3-7 days until the eggs hatched or failed. A nest was considered successful if $\geq$1 egg hatched, regardless of the size of the clutch. Nest age was determined by floating the eggs (Table 1.1). Nest age could be accurately determined to within 1-2 days for most nests, especially for nests early or late in incubation and for nests with $\geq$3 nest checks. A small number of nests failed between the date they were found and the first nest check; for these nests I assigned them the mean age of their incubation stage when they were found (see Table 1.1). Most incubation stages covered an interval of only a few days and introduced little bias into survival estimates. However, one of the intermediate incubation stages covered 13 days and the use of the midpoint might have introduced a slight bias into the estimates of nest survival. I used eggshell evidence to infer hatching (Mabee 1997), although most (>90%) of the broods were seen post-hatch because they always remained on the same prairie-dog colony and were relatively easy to relocate. Hatch dates were determined using egg floatation (Table 1.1), the presence of eggshell fragments in the nest lining, or finding young in or near the nest. I could not accurately determine the hatch date for five nests that I was certain had hatched. For these nests, I used the last nest check as the hatch date to avoid positively biasing the number of exposure days.

The Colorado State University Animal Care and Use Committee approved the field methods used in this study (Protocol 98-134A-01).

NEST SURVIVAL MODEL

I modeled the daily survival rates (S_i) of Mountain Plover nests using the nest survival model in program MARK (White and Burnham 1999). The survival of a nest refers to the probability that a nest, as defined earlier, survives a specified time interval, although it was possible for the contents of the nest to occasionally change due to partial depredation of the eggs. This model is an extension of the model described by Bart and Robson (1982) and allows increased flexibility in modeling daily nest survival, including the use of individual and time-specific covariates. The assumptions of the model are:

1. The investigator has located a representative sample of nests.
2. Nests can be correctly aged when they are first found.
3. Nest fates are correctly determined.
4. Nest discovery and subsequent nest checks do not influence survival.
5. Nest fates are independent.

Minimally, the nest survival model required five pieces of information for each nest j out of a total of n nests:

1. The day the nest was found (k).
2. The last day the nest was checked alive (l).
3. The last day the nest was checked (m).
4. The fate of the nest (0 = successful, 1 = depredated) (f).
5. The number of nests with this encounter history.

In MARK, these pieces of information are used to generate an encounter history for each nest in LDLD format. There are eight possible ways to code the triplet involving k, l, and m (where $k \leq l \leq m$) and the fate (f) in the input file as shown in the following examples:

1. $k = 1, l = 3, m = 5$, and $f = 1$ returns a probability of $S_1S_2[1-S_3S_4]$

2. $k = 1, l = 3, m = 5$, and $f = 0$ is invalid and should be coded as $k = 1, l = 5, m = 5$

3. $k = 1, l = 3, m = 3$, and $f = 1$ is invalid and should be coded as $k = 1, l = 1, m = 3$

4. $k = 1, l = 3, m = 3$, and $f = 0$ returns a probability of S_1S_2

5. $k = 1, l = 1, m = 3$, and $f = 1$ returns a probability of $1-S_1S_2$

6. $k = 1, l = 1, m = 3$, and $f = 0$ is invalid

7. $k = 1, l = 1, m = 1$, and $f = 1$ is invalid

8. $k = 1, l = 1, m = 1$, and $f = 0$ is invalid

In example 3, the nest cannot be observed both alive and destroyed on the same day. In example 6, the nest was observed alive only on a single day; thus there is no information to estimate daily survival. In examples 7 and 8, there is also no information to estimate daily survival since the nest was only under observation for a single day. As an example, a nest with $k = 1, l = 3$, and $m = 5$ has an encounter history of 10 10 10 00 01 with cell probability $S_1S_2[1-S_3S_4]$.

Nests were assigned to groups (males and females in each of 6 years) using the following lines in the input file in MARK:

Nest survival group=1;	k	l	m	f	number
/*GGOO, 1995-076*/	53	59	63	1	1;
/*OGDD, 1995-047*/	18	36	36	0	1;
/*WGDD, 1995-003*/	6	20	20	0	1;
/*OGDY, 1995-032*/	14	24	24	0	1;

etc.,

where individual nests within the group followed each group label; the comment at the beginning of each encounter history included the color band combination and the nest identification number and was followed by k, l, m, fate, and the number of nests with this history.

The likelihood (L) for the daily survival (S_i) from day i to day i+1 for a sample of n nests was:

$$L\left(S_i \mid k_j, l_j, m_j, f_j\right) \propto \prod_{j=1}^{n}\left[\left(\prod_{\text{for } i>l-1, i=k}^{l-1} S_i\right)\left(1-\prod_{l}^{m-1} S_i\right)^{f}\left(\prod_{l}^{m-1} S_i\right)^{1-f}\right]$$

assuming the fates of individual nests were independent.

To illustrate the model, suppose that a nest is found on day 3, is next checked alive on day 6, and is found to be depredated at the next check on day 10. The fate of this nest is coded as 1 (a failure).

			Day				
3	4	5	6	7	8	9	10
↑			↑				↑
Found			First check				Last check

This nest is known to have survived until day 6. The probability of surviving the first interval (from day 3 to day 6) is then

$$\prod_{\text{for } i>l-1, i=k}^{l-1} S_i = S_3 S_4 S_5$$

The nest was lost sometime between day 6 and day 10. The four possible outcomes explaining this loss are: the nest was lost between days 6 and 7 [$(1-S_6)$], the nest survived until day 7 and was lost between days 7 and 8 [$S_6(1-S_7)$], the nest survived until day 8 and was lost between days 8 and 9 [$S_6S_7(1-S_8)$], or the nest survived until day 9 and was lost between days 9 and 10 [$S_6S_7S_8(1-S_9)$]. The probability of not surviving this interval is then the sum of these probabilities, which can be written as

$$\left(1-\prod_{l}^{m-1} S_i\right)^{f} = 1 - S_6 S_7 S_8 S_9$$

where $f = 1$ in this example. The third term in the likelihood has a value of one. Thus, the overall probability of observing this encounter history is $S_3S_4S_5[1-S_6S_7S_8S_9]$.

In MARK, individual covariates can be incorporated into the nest survival model with the use of the logit or another link function. For example, a model with an intercept (β_1), an additive linear trend on survival (β_2), and an additive effect of nest age at time i (β_3) can be expressed in the form

$$\operatorname{logit}\left(\hat{S}_i\right) = \hat{\beta}_0 + \hat{\beta}_1(\text{trend}) + \hat{\beta}_2(\text{nestage}_i)$$

and the estimate of survival (S_i) is obtained by back transformation, where

$$\hat{S}_i = \frac{1}{1 + e^{-\left(\hat{\beta}_1 + \hat{\beta}_2(\text{trend}) + \hat{\beta}_3(\text{nestage}_i)\right)}}$$

As with other models in program MARK, a wide range of modeling options are available including model selection using AIC (Burnham and Anderson 1998), a full variance-covariance matrix of the β and S_i estimates, and model averaging (Burnham and Anderson 1998).

MODELING THE NEST SURVIVAL OF MOUNTAIN PLOVERS

I was interested in comparing traditional estimates of nest success (apparent nest success) with estimates of nest success calculated using daily nest survival rates. For each of the six years of the study, I first estimated apparent nest success as the proportion of nests that were successful in hatching ≥ 1 egg among a sample of nests whose fates were known. Nests of unknown fate were not included in this total. I also calculated a pooled apparent nest success for all nests independent of years.

I then modeled the survival of Mountain Plover nests in order to obtain a second estimate of total nest success. Here, I used the product of daily nest survival rates across the 29-day incubation period as a less-biased estimate of nest success. For my data, I standardized 19 May as day 1 and numbered all nest check dates sequentially thereafter. For each nest, I summarized the five pieces of information necessary to use the nest survival model in program MARK. Year and sex were then combined and modeled as groups, resulting in 12 groups for my analyses (2 sex groups in each of 6 years). For each nest I included

78 individual covariates. Measures of maximum daily temperature and daily precipitation were obtained from a weather station at the center of the study area (D. Veseth, pers. comm.). The remaining 76 individual covariates accounted for the daily age of the nest on each of the 76 days preceding an estimate of S_i. Beginning on the day the nest was found, I entered the nest age (in days) sequentially until it hatched at 29 days; all other values were zero. Thus, the nest age covariates took on values from 0 to 29. I always included covariates up to age 29 even if a nest was lost before reaching that age; once a nest was lost it contributed no additional information on survival and thus the age had no effect. I labeled these covariates Age1, Age2, ..., Age76. I modeled daily nest age as a single parameter in MARK. In MARK, I did not standardize individual covariates for nest age because the standardization changed the distribution of nest ages such that the difference between any two consecutive ages was not always equal. This problem arose because the distribution of nest ages was uneven across the 77-day nesting season.

I limited my analyses to a small set of models that examined the effects of year, the sex of the incubating adult, daily nest age, and two weather covariates on the daily nest survival of Mountain Plovers. I monitored nests across six nesting seasons, so I looked for nest survival differences among those years. Mountain Plovers of both sexes incubated separate nests, so I looked for differences between nests tended by male and female plovers. I also hypothesized that the nest age would influence daily nest survival with older nests having higher survival. For each of these three main effects (year, sex, and nest age), I fit two additional additive models, one with a linear and one with a quadratic trend on seasonal survival. I hypothesized that nest survival would gradually drop during the nesting season, but that the distribution of daily survival might be bimodal because of renesting efforts in the middle of the nesting season. Finally, I added two weather covariates (maximum daily temperature and daily precipitation) to the best model from the set of nine models listed above. I reasoned that the weather covariates would have the same general effect on any given model, so I chose to add them only to the best model to see if weather was an important predictor of nest survival. Mountain Plover eggshells are unusually thick and susceptible to heat (Knopf 1996) and I surmised that extreme temperatures would be negatively influence nest survival (e.g., maximum daily temperature). I also hypothesized that daily nest survival might be negatively affected by precipitation (daily precipitation) because one of the primary nest predators, the bull snake (*Pituophis melanoleucus*), would show decreased activity during such cool periods (Gibbons and Semlitsch 1987). I also ran the simplest model where only a single nest survival rate was estimated. Finally, I added one additional model with full year by day variation in order to assess the proportion of variation explained by the best model; this model was not in the set of models I considered for inference. Specifically, I considered the following 12 models in my analyses:

Model	Notation
1. Effect of sex only	S_{sex}
2. Effect of sex plus a linear trend	S_{sex+T}
3. Effect of sex plus a quadratic trend	S_{sex+TT}
4. Effect of year only	S_{year}
5. Effect of year plus a linear trend	S_{year+T}
6. Effect of year plus a quadratic trend	$S_{year+TT}$
7. Effect of sex plus nest age	$S_{sex+age}$
8. Effect of sex plus a linear trend and nest age	$S_{sex+T+age}$
9. Effect of sex plus a quadratic trend and nest age	$S_{sex+TT+age}$
10. Best model plus maximum daily temperature effect	S_{temp}
11. Best model plus daily precipitation effect	S_{precip}
12. Single estimate of daily survival	$S_{(.)}$

I 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). I calculated this quantity as

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

using log likelihoods from the best model, the global model, and the simplest (.) model. Here, the simplest model had a single estimate of daily survival (1 parameter) and the global model had full year by day variation in survival (912 parameters).

I ranked the set of R candidate models using AICc (Burnham and Anderson 1998), which was defined as

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

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 above equation was a correction for small sample size. Here, the sample size was the total number of days all nests were monitored, where each day corresponded to an independent Bernoulli trial. I did not correct for overdispersion in these data; there is currently no method for estimating extra binomial variation in the nest survival model.

Once AICc values were computed for each model, I ranked the R models relative to the model with the minimum AICc value. Comparisons between models were made using ΔAICc values, where for each model i

$$\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\min}$$

The ΔAICc values compared the relative distances between the best approximating model ($\text{AICc}_{\min}$) and each competing model (AICc_i). Generally, models with ΔAICc values ≤2 have strong support while those with ΔAICc values >10 have little support (Burnham and Anderson 1998). Normalized Akaike weights (w_i) were also computed for each of the R models as

$$w_i = \frac{e^{-\left\{\frac{\Delta\text{AICc}_i}{2}\right\}}}{\sum_{r=1}^{R} e^{-\left\{\frac{\Delta\text{AICc}_r}{2}\right\}}}$$

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). When building models, I used two link functions in MARK. Models incorporating an individual covariate used a logit link function; all other models used a sin link function. Formulae for the two link functions were

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

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

where X represents some variable of interest such as the daily age of the nest. I used back transformation to generate real parameter estimates.

ESTIMATING THE SUCCESS OF FEMALE- AND MALE-TENDED NESTS

I estimated total nest success as the probability that female- and male-tended Mountain Plover nests would survive the 29-day incubation period (S_f and S_m). The typical length of the incubation period is 29 days (Knopf 1996), although I occasionally noted that incubation was 1-2 days longer. For purposes of the estimating total nest success for each sex, I assumed the incubation period was always 29 days.

To properly estimate sex-specific nest success, I needed to account for the effect of differential nest survival on the nests I found. I first computed the weighted mean nest initiation date for birds of each sex based on observed nest data. Because I suspected nest initiation dates may have been biased, I corrected the mean nest initiation dates for each sex using a Horvitz-Thompson estimator (Horvitz and Thompson 1952). The use of this method provided an unbiased estimate of the number of nests that were initiated by each sex. To adjust for the number of nests that were initiated, I used the logistic regression equation from the best nest survival model to compute the probability that each nest had survived up to the date I actually found the nest. I then divided the observed frequency for each nest (always 1) by the probability that it survived until I found it and called the result the expected number of nests initiated. I then summed the frequencies of the expected number of nests by sex and calculated an expected mean nest initiation date for each sex.

Then, using the expected mean nest initiation date for each sex and the logistic regression equation from the best model, I computed the probability that a nest tended by a male or female plover would survive the 29-day incubation period. I computed this probability as the product of 29 consecutive daily survival estimates, beginning on the expected mean nest initiation date and ignoring the effects of daily precipitation. I tried computing the variance of S_f and S_m using the delta method (Seber 1982), but because these two parameters were highly correlated and the underlying model was non-linear, the delta method provided a poor estimate of precision.

RESULTS

I monitored 641 Mountain Plover nests during this study. Of this total, 57 contained insufficient data for nest survival analyses and 152 were tended by birds whose sex was not determined, resulting in a sample of 432 nests to estimate nest survival (Table 1.2). I monitored these nests for a total of 5,542 exposure days across a 77-day interval (19 May-3 August) during the 6-year study. After removing 15 renesting efforts, the sex ratio of plovers on nests was 230 males (55%) to 187 females (45%). Males ($n = 10$) renested more often than females ($n = 5$), although the sample size was small.

Observed mean initiation dates for nests tended by female and male Mountain Plovers did not differ (Females: mean = 31 May, SE = 2.01 days; Males: mean = 2 June, SE = 3.18 days) (Figure 1.2). When I corrected these estimates for the time interval before they were found, the expected mean nest initiation dates still did not differ between sexes (Females: mean = 27 May, SE = 6.18 days; Males: mean = 26 May, SE = 8.42 days).

APPARENT NEST SUCCESS

Annual nest success was 45-72% during the study; the low of 45% was in 1999 while the high of 72% was in 2000 (Table 1.2). Average annual nest success was 58% (95% CI was 40 to 76%) for 600 nests pooled across years.

NEST SURVIVAL

The daily survival of Mountain Plover nests was a function of both the sex of the incubating adult and nest age (Table 1.3). The proportion of deviance explained by the best model was 14% of variation. Nests tended by male Mountain Plovers had higher survival than those tended by females (Figure 1.3). The slope coefficient in the best model for the additive effect on survival of nests tended by males compared to females was $\hat{\beta}_{male} = 0.37$ (SE = 0.17, 95% CI was 0.03, 0.71) on a logit scale and this coefficient was always positive in models with sex effects. Models incorporating the daily age of the nest received substantial support; in the best model, $\hat{\beta}_{age} = 0.06$ (SE = 0.01, 95% CI was 0.04, 0.09) on a logit scale and this effect was always positive in models with age effects. Models with quadratic trends on nest survival received strong support; linear trends received less support. The confidence intervals for the slope coefficients of both the linear and quadratic trends included zero. There was no evidence of direct year effects on nest survival.

When daily precipitation was added to the best model, it improved that model substantially (an increase of 1.76 Δ-AICc units). Adding maximum daily temperature to the best model did not result in an improvement (2.00 Δ-AICc units below the best model with the addition of a single parameter). The slope parameter for daily precipitation was negative ($\hat{\beta}_{precip} = -1.08$, SE = 0.48, 95% CI was –2.02, –0.13) on a logit scale, but the confidence interval for the effect of maximum daily temperature on a logit scale included zero ($\hat{\beta}_{temp} = 0.01$, SE = 0.01, 95% CI was –0.02, 0.03).

The logistic regression equation (standard errors for each $\hat{\beta}_i$ are shown below in parentheses) for the best model was

$$\operatorname{logit}(\hat{S}_i) = \underset{(0.61)}{3.23} + \underset{(0.17)}{0.37}{*}\text{sex} + \underset{(0.01)}{0.06}{*}\text{nest age} - \underset{(0.04)}{0.06}{*}T + \underset{(0.0007)}{0.001}{*}TT - \underset{(0.48)}{1.08}{*}\text{precip}$$

In order to evaluate the effects of sex, precipitation, and daily nest age on the nest survival of Mountain Plovers, I plotted curves showing these effects for fixed values of each variable in the above equation. For nests early (nestage = 1) and late (nestage = 29) in incubation, I plotted the daily nest survival of female- (sex = 0) and male- (sex = 1) tended nests at levels of low (precip = 0 cm) and high (precip = 2.54 cm) precipitation. Daily nest survival rates of Mountain Plover nests gradually declined until mid-season, and then gradually rose to a peak at the end of the nesting season (Figure 1.3). When nest age was held constant at 1, nests tended by males had higher nest survival than nests tended by females, and nest survival was higher for both sexes when there was no precipitation (Figure 1.3).

Younger nests (age = 1) had low daily survival rates in mid-June. The daily survival of older nests (age = 29) showed a similar seasonal pattern, although the drop in mid-June was less pronounced.

Daily survival rates of nests of both sexes varied temporally. To illustrate seasonal patterns in daily nest survival rates and their precision, I plotted the predicted daily survival of three nests (1 early season, 1 mid-season, 1 late season) spread across the nesting season (Figure 1.4). Estimates of daily nest survival were generated by substituting the appropriate values (sex of the incubating adult, daily nest age, linear and quadratic time trend coefficients, and daily precipitation) into the logistic regression equation for the best model, ignoring whether or not the nest actually survived. The pattern for each nest is similar to the patterns in Figure 1.3 with daily survival increasing as the nest aged. The mid-season nest had the lowest overall survival while the late nest had the highest survival. Daily precipitation events resulted in sharp drops in nest survival on some dates.

SUCCESS OF FEMALE- AND MALE-TENDED NESTS

Using mean nest initiation dates for each sex and the logistic regression equation from the best model, the probability of a Mountain Plover nest surviving the 29-day incubation period was 0.35 for females and 0.49 for males. These estimates differ significantly because the logistic regression equation used to predict them contained the same six regression coefficients for each sex with only the sex effect ($\hat{\beta}_{male}$) differing significantly between the sexes.

DISCUSSION

NEST SURVIVAL

Studies of avian nesting ecology often report a measure of nest success. In altricial species, this measure refers to success during the incubation and nestling stages, often partitioning survival amongst these two stages. In precocial species such as the Mountain Plover, nest success is measured from the onset of incubation to hatching and does not measure survival of chicks during the post-hatch period.

I modeled the daily survival of Mountain Plover nests as a function of six variables. I found no evidence for yearly differences in nest survival in the models I considered. However, there were large yearly differences in apparent nest success. This emphasizes the importance of understanding the differences between the two estimates. Measures of apparent nest success are biased high, and modeling nest survival and calculating nest success as the product of daily nest survival rates reduced this bias.

In this study, I present estimates of apparent nest success and estimates of nest success calculated from daily nest survival rates. Most ornithological studies report apparent nest success rather than provide valid estimates of nest survival. For shorebirds, Melvin et al. (1992) estimated the nest survival of protected and unprotected Piping Plover (*Charadrius melodus*) nests and Estelle et al. (1996) did the same for Pectoral Sandpiper (*Calidris melanotos*) nests. Their Mayfield estimates of daily survival for protected nests were high (0.994 for Piping Plovers and 0.982 for Pectoral Sandpipers) and contrasted with sharply lower estimates for unprotected nests. Their daily nest survival rates for protected nests were comparable to those I found for Mountain Plovers of both sexes, perhaps an indication that predation during the incubation stage was less of a problem for Mountain Plovers.

Mountain Plovers present a rare opportunity to assess the reproductive success of each sex, as measured by nest success. In this study, males were shown to have higher nest survival, and thus higher nest success, than females. There are several possible explanations for this difference. Because both sexes simultaneously incubated independent nests, they were subjected to similar risks while incubating. The differences in nest survival may be due to the reproductive costs of egg laying incurred by females prior to the onset of incubation. Egg laying is energetically expensive (Saether et al. 1986) compared to the courtship activities of the male. Female Mountain Plovers leave the first clutch to be tended by the male, so they have laid a minimum of 6 eggs (2 clutches) by the time they start incubation. This cost may be great and females may be in relatively poor condition when they begin incubation. Exactly how this translates into lowered nest success is not clear, but it could influence the frequency and length of departures from the nest to search for food, nest attentiveness in general, and other factors that might negatively affect nest survival. The differences may also be due to temporal patterns. Early nests, which are more likely to be tended by males, may have increased survival because of reduced predation, more favorable nesting conditions, or perhaps reduced intra-specific competition for limited resources on prairie-dog colonies.

I found that nest age was an important factor in the nest survival of Mountain Plovers. In many birds, nest survival increases during the incubation period, presumably because the most vulnerable nests are lost early in incubation. Others (see Johnson 1979) have also considered nest age to be important, but it was almost never incorporated into measures of nest success. Klett and Johnson (1982) found that the mortality of Mallard (*Anas platyrhynchos*) and Blue-winged Teal (*Anas discors*) nests declined with nest age, with most of the decline in the first 10 days. They investigated age effects by stratifying their sample of nests into 5-day age intervals and then running separate Mayfield estimates of constant survival for each interval. They later recommended this approach to test for age effects, although this is no longer necessary in program MARK. The best way to incorporate the effect of nest age is to use an individual covariate for each day.

There are several explanations for the pattern of nest survival found in Mountain Plovers. High nest survival early in the season may have resulted because most early nesters were older, experienced birds that had higher nest survival while the later nesting attempts by inexperienced younger birds contributed to the drop in survival in mid-season (see Ainley and Schlatter 1972). Perhaps changes in vegetation influenced nest survival. Mountain Plovers are adapted to landscapes with sparse vegetation and good visibility (Knopf 1996). Seasonal weather patterns cause vegetation height to generally increase in early summer (through June, at least), after which growth is slowed by the lack of moisture and increased grazing pressure by cattle. By late July, vegetation is typically shorter and has been thinned considerably. Greater vegetative cover early in the nesting season may inhibit the ability of an incubating bird to detect and successfully distract potential predators. Another explanation may have to do with the body condition of the incubating adult. It has been shown that body mass declines throughout the incubation period in most birds (Drent 1975). The condition of the incubating adult might affect both time spent incubating and the ability of the adult to ward off predators. This, in turn, could explain the initial drop in nest survival as the condition of early nesting adults declines. The subsequent increase in nest survival is perplexing and may be due to first nesting attempts by less experienced birds at a time when predation is reduced.

THE ROLE OF WEATHER

Daily precipitation had a strong negative effect on the nest survival of Mountain Plovers. The addition of this covariate (daily precipitation) to the best model (sex + nest age + *TT*) resulted in a substantial improvement in model weight. Precipitation per se may not have a direct impact because the incubating adult is unlikely to leave the nest, even in extreme weather. The only direct losses to precipitation were from occasional hailstorms that resulted in the loss of at least 7 out of 641 nests in the 6-year study (pers. obs.). Instead, it is likely that precipitation is correlated with other causal factors of nest loss such as the behavior patterns of possible nest predators.

I also hypothesized that maximum daily temperature would influence nest survival, although this effect was unimportant in the models I considered. I still believe overheating has some effect, especially on late nests when maximum temperatures often exceed 38C. Overheating will kill the developing embryos in a short time, perhaps in as little as fifteen minutes (pers. obs.), and is most likely to occur if the eggs are exposed to direct midday sunlight. Since only one adult tended each nest, I hypothesized that any disturbance during such warm periods might negatively influence nest survival, although this effect would only occur during warmer midday periods. The lack of an effect was probably because the adult, regardless of temperature, spent considerable time on the nest and was able to adequately shield the eggs from intense solar radiation.

PREDATION

The nest success of Mountain Plovers appears to be higher than normal for a ground nesting bird, most of which typically have apparent nest success rates of 20-50%. Baker et al. (1999) reported that depredation of artificial bird nests on prairie-dog colonies was higher than at off-colony sites. Using time-specific daily nest survival probabilities, they estimated the probability of surviving a 14-day incubation period at 0.34 to 0.52. They speculated that birds that had evolved with prairie dogs, such as the Mountain Plover, might have fitness advantages that allowed them to compensate for the high nest predation rates on prairie-dog colonies. It is also possible that prairie-dog colonies may provide additional protection from certain sources of predation because of the wariness of prairie dogs and their ability to evict bull snakes, a potential nest predator, from burrows (see Hoogland 1995).

Nest survival of Mountain Plovers varied temporally across the nesting season. Potential factors causing this pattern are many, and most are speculative. Possible nest predators in this region include bull snakes, coyotes (*Canis latrans*), badgers (*Taxidea taxus*), Ring-billed (*Larus delawarensis*) and California (*L. californicus*) gulls, and Black-billed Magpies (*Pica hudsonia*), although no studies have confirmed these speculations. The observed seasonal pattern in nest survival could be explained by daily and seasonal activity patterns exhibited by potential nest predators such as snakes (Pough et al. 1998) and mammals. The evidence for a daily precipitation effect on nest survival, and the suggestion that precipitation may be related to predator activities, could indicate that nest predators are using olfactory cues to locate plover nests. Scent is stronger during periods of increased moisture (Stoddart 1980), making it easier for predators using olfactory cues to find nests immediately after periods of rain. This, in turn, suggests that birds are not a major predator of Mountain Plover nests because they hunt primarily using visual, and not olfactory, cues.

INTERPRETATION OF RESULTS AND CONFOUNDED EFFECTS

I found that the observed and expected mean nest initiation dates of male- and female-tended Mountain Plover nests did not differ. This result was unexpected because female Mountain Plovers lay the first clutch for a male and then a second clutch for themselves (Graul 1973) and would be expected to have a later mean nest initiation date than males. However, I also have demonstrated that nests tended by males have much higher survival. Therefore, because a higher proportion of female-tended nests failed, many more females than males may be available for renesting attempts. Under this scenario, females may renest with males but may not always lay a second clutch for themselves. This could counterbalance the ordering of nesting by sex and might produce a similar or later mean nest initiation date for males. To further investigate nest initiation dates, I computed the expected number of nests initiated by date for each sex. This method corrected for the differences in nest survival between sexes, although there was still no difference in mean initiation dates of nests tended by male and female plovers.

The sex of the incubating adult, time trends, and nest age were important explanatory variables for the nest survival of Mountain Plovers. Data best fit a quadratic time trend with positive effects for sex of the incubating adult (male plovers had higher nest survival) and nest age. Thus, the daily survival of a nest increased over the 29-day incubation period and was higher for male-tended nests. However, each of these variables (sex, time, and nest age) may be confounded with individual heterogeneity (Burnham and Rexstad 1993, Natarajan and McCulloch 1999). Time variation in nest survival could be explained by the sex or experience of the incubating adult or perhaps some other factor that cannot be measured. Similarly, nest age differences could be explained by the fact that the most vulnerable nests are lost early in incubation; nests that are actually found tend to be those that have survived longer. This pattern of nest survival, where risk affects survival, may have contributed to the strong nest-age effect I found. By modeling nest age I was able to determine that nest survival increased at later incubation stages, but I cannot make any statements as to whether this was due to nest age alone, or to a combination of nest age and individual heterogeneity.

The results of this study demonstrate the bias that is caused by using measures of apparent nest success. Only in 1999 was apparent nest success similar to the total nest success estimated from daily nest survival rates. In all other years, apparent nest success was clearly and positively biased, and overestimated total nest success. Accurate measures of nest success preclude overestimates of reproductive rates and predictions about population growth.

As with any model, a careful consideration of the assumptions is necessary before making inferences. Of the five assumptions listed in the Methods section, two (numbers 1 and 3) were not a problem in this study. The assumption that all nests could be aged when found (assumption 2) was a slight problem. A small number of nests in the third incubation stage could not be aged and were assigned the mean age of that stage (13 days). This probably strengthened the age effect I found because the majority of these nests were probably <13 days old. The assumption of no observer impact on nest survival (assumption 4) was carefully considered and I attempted to minimize disturbances during nest checks, marked the nests in an inconspicuous manner, and avoided harassing the incubating adult. Assumption 5 (independent fates of nests) was met because there was no evidence of extra binomial variation that would indicate a lack of independence in the data. In summary, this study met the assumptions of the nest survival model with only a slight bias from the inability to accurately age nests at incubation stage 3.

IMPLICATIONS TO FUTURE STUDIES OF NEST SURVIVAL

The techniques outlined here will have broad application to nesting studies of birds. The results of field studies using the nest survival model in program MARK will reflect more biological reality because there is no assumption that survival is constant across time, nest age can be incorporated into survival estimates, and covariates unique to each nest can be modeled with nest survival. This model should also stimulate biologists to incorporate meaningful covariates into future analyses of nest survival. Some factors to consider include measures of the body condition of the incubating adult (mass, percent body fat, etc.), habitat characteristics of the nest-site, measures of individual heterogeneity such as nest attentiveness, an individual bird's prior experience, and possibly others. The flexibility to model nest survival in the presence of these factors will promote a better understanding of nest success.

Recommendations for future studies of nest survival include: 1) obtaining sufficiently large samples of nests to generate estimates of daily nest survival with reasonable precision, 2) conducting nest checks at regular intervals that are spaced to obtain adequate encounter histories while at the same time avoiding undue disturbance, 3) incorporating group effects such as age and sex of the incubating adult into estimates of nest survival, and 4) using meaningful individual covariates such as nest age, body condition of the incubating adult, and habitat features of the nest site.

ACKNOWLEDGMENTS

I am grateful to Fort Carson Military Reservation (U. S. Department of Defense), the U. S. Fish and Wildlife Service (Colorado Fish and Wildlife Management Assistance Office), the Biological Resources Division of the U. S. Geological Survey, the U. S. Bureau of Land Management (Malta Field Office, Montana), the Denver Zoological Foundation, and the Fort Belknap Tribal Community for financial support. The staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. J. J. Grensten and B. D. Rosenlund assisted with multiple aspects of the study. A. Brees, D. C. Ely, T. Hanks, J. G. Jorgensen, C. McQueary, and T. Vosburgh provided field assistance and S. Oyler-McCance and J. St. John assisted with the sexing work. I thank B. Matovitch, D. Robinson, and J. Robinson for allowing me access to their lands.

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Table 1.1. Nest ages of Mountain Plover nests in southern Phillips County, Montana as determined by egg floatation. Ranges for each incubation stage were determined from 31 nests that were followed from nest initiation to hatch.

Nest Age (days)	Mean age (days)	Description
1-3	2	Egg laying flat on bottom
2-6	4	Large end of egg beginning to float
6-18	12	Egg standing upright on bottom
16-18	17	Egg about to float to surface
16-20	18	Egg floating, top barely breaking water surface
20-26	23	Egg floating high, >25% above water surface
26-28	27	Egg floating with noticeable tilt; young often pipping
29-32	29	Eggs hatching (young leave nest within a few hours)

Table 1.2. Number of nests by sex and annual nesting success for Mountain Plovers in southern Phillips County, Montana, 1995-2000.

Year	Female	Male	Unknown	Nesting success (%)
1995	10	13	46	57
1996	23	29	21	53
1997	26	40	21	57
1998	35	55	22	64
1999	50	50	13	45
2000	48	53	29	72
Total	192	240	152	58 (SE = 9.2)

Table 1.3. Summary of model selection results for the nest survival of Mountain Plovers in southern Phillips County, Montana, 1995-2000. Models are ranked by ascending Δ-AICc; w_i is the model weight and K is the number of parameters. 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 $[L_s(\hat{\theta})]$.

Model	Deviance	K	AICc	Δ-AICc	w_i
$S_{\text{sex+age+}TT\text{+precip}}$	858.29	6	870.39	0.00	0.56
$S_{\text{sex+age+}TT}$	862.09	5	872.15	1.76	0.23
$S_{\text{sex+age}}$	868.12	3	874.14	3.75	0.09
$S_{\text{sex+age+}TT\text{+temp}}$	862.06	6	874.16	3.76	0.09
$S_{\text{sex+age+}T}$	868.05	4	876.10	5.71	0.03
$S_{\text{sex+}TT}$	888.92	4	896.97	26.58	0.00
$S_{\text{year+}TT}$	885.07	8	901.25	30.85	0.00
$S_{\text{sex+}T}$	895.61	3	901.64	31.25	0.00
S_{sex}	897.76	2	901.77	31.38	0.00
$S_{(.)}$	902.29	1	904.29	33.90	0.00
S_{year}	893.30	6	905.40	35.01	0.00
$S_{\text{year+}T}$	891.54	7	905.68	35.29	0.00

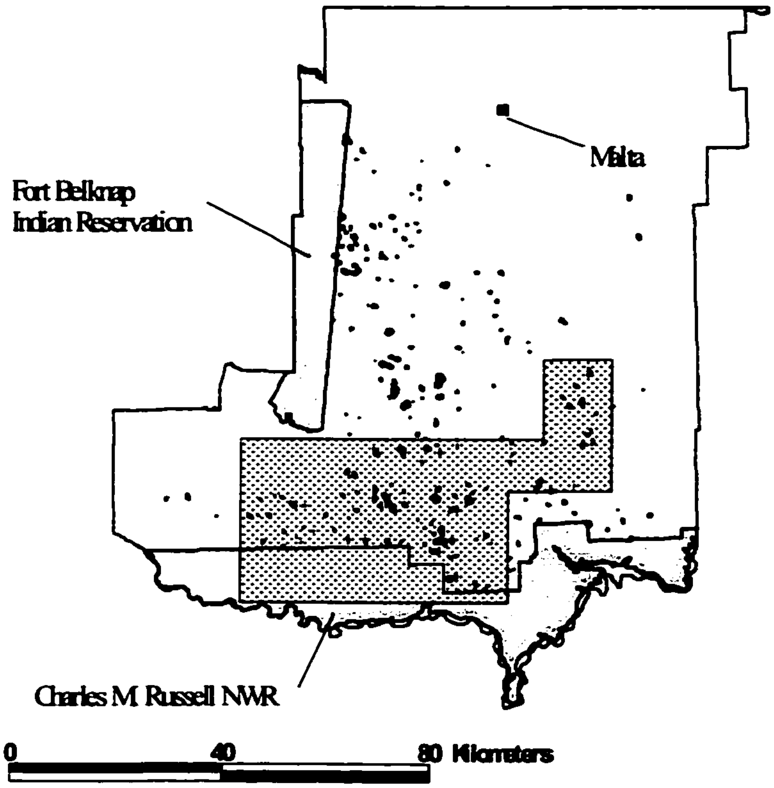

Figure 1.1. Map of southern Phillips County, Montana showing the 2000 distribution of black-tailed prairie dog colonies (in black). The stippled region represents the study area.

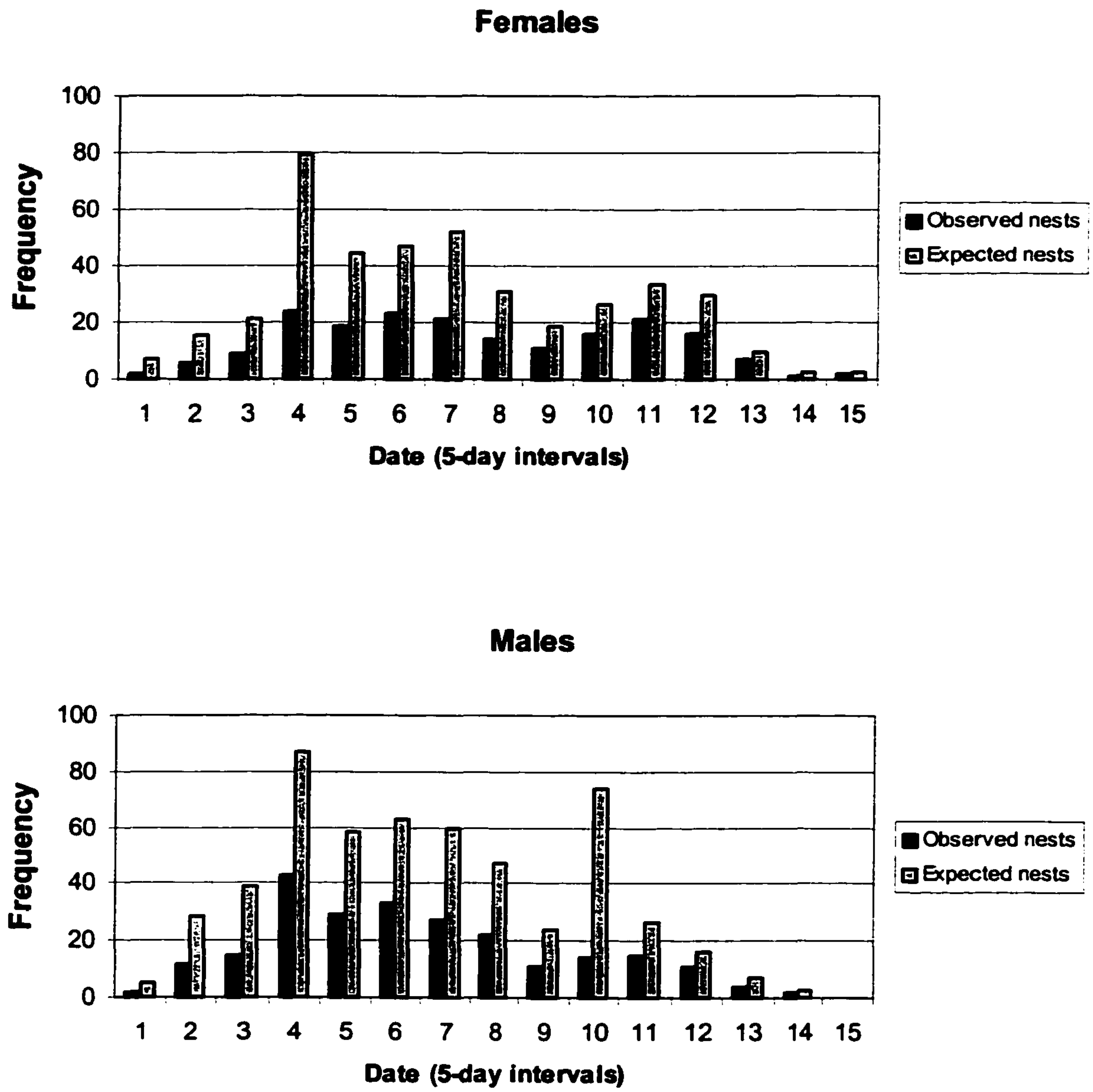

Figure 1.2. Observed and expected mean initiation dates for female- and male-tended Mountain Plover nests in southern Phillips County, Montana, 1995-2000. Date is arranged in 15 5-day intervals beginning on 26 April and ending on 6 July (72 days; the last interval is only 2 days). Mean nest initiation dates did not differ by sex (observed: 31 May for females and 2 June for males; expected: 27 May for females and 26 May for males).

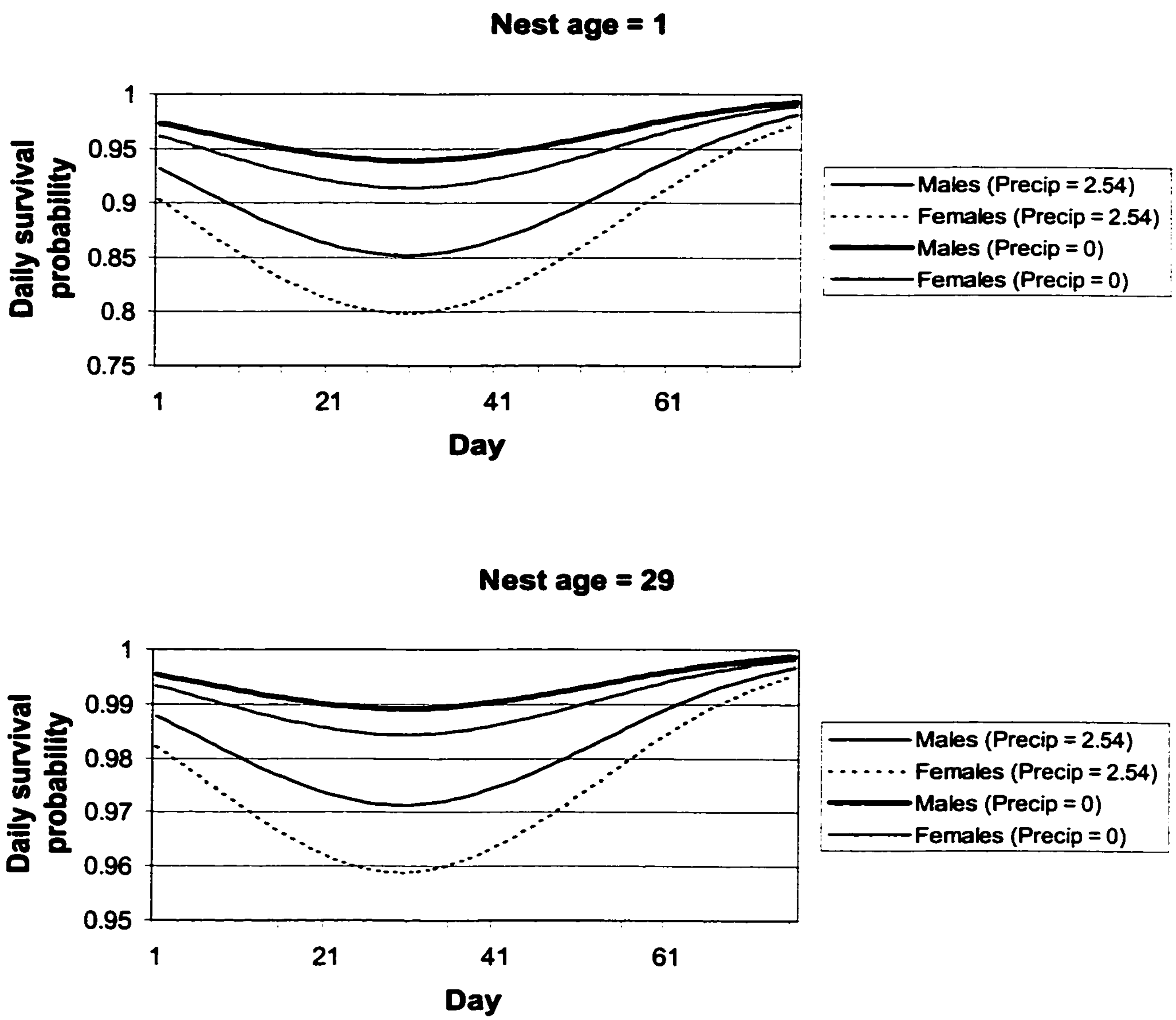

Figure 1.3. The effects of nest age (1- and 29-day old nests), sex, and daily precipitation (0 or 2.54 cm) on the daily survival rates of Mountain Plover nests in southern Phillips County, Montana. Day 1 corresponds to 19 May and day 77 corresponds to 3 August.

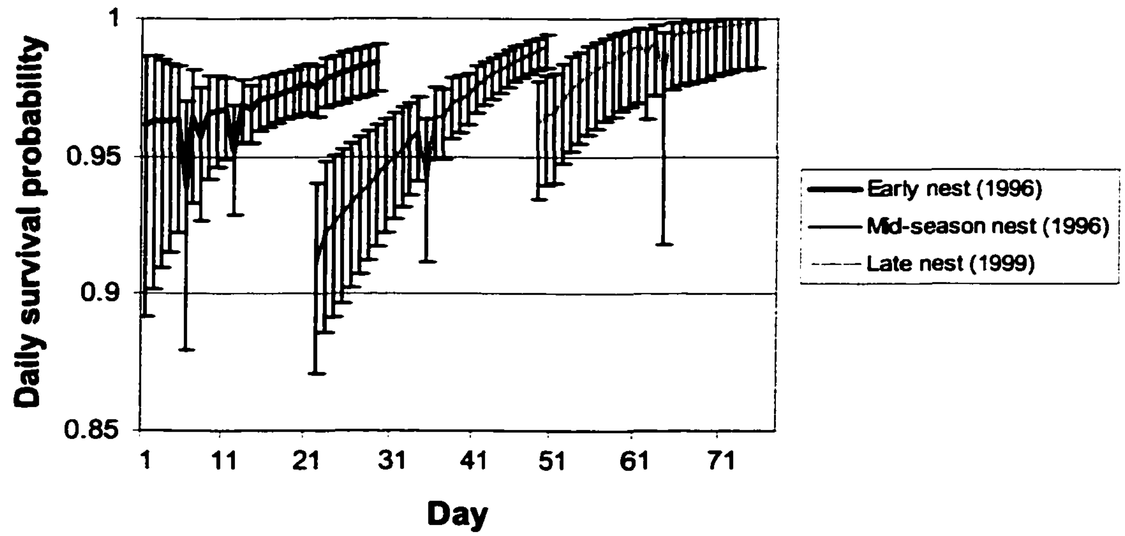

Figure 1.4. Predicted daily survival rates and 95% confidence intervals for 3 Mountain Plover nests in southern Phillips County, Montana. Estimates and confidence intervals were generated using the logistic regression equation from the best model. These three nests span the entire nesting season with an early nest (19 May-16 June 1996; days 1-29), a mid-season nest (9 June-7 July 1996; days 22-50), and a late nest (6 July-1 August 1999; days 49-75). Day 1 corresponds to 19 May and day 77 corresponds to 3 August. The sharp downward spikes in each graph represent the effects of precipitation.

CHAPTER 2. ANNUAL SURVIVAL AND POPULATION ESTIMATES OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA.

ABSTRACT

Information about the demography of declining species is especially relevant to their conservation and future recovery. Knowledge of survival rates and population numbers can be used to assess long-term viability and population trends, both of which are of interest to conservation biologists. I used capture-recapture techniques to study the demography of Mountain Plovers (*Charadrius montanus*) in southern Phillips County, Montana in 1995-2000. I 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. I modeled annual survival rates as a function of two age classes (adults and juveniles), body mass at capture (juveniles only), a transmitter effect in 1999, and annual area occupied by prairie dogs within the study area. I modeled year-specific capture probabilities to include a resighting effect (r) for plovers that had been marked in a prior year. The results supported age-specific differences in annual survival that were a function of juvenile body mass and were 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 was 0.25, 1.28) on a logit scale. 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 was –0.00003, –0.0001) on a logit scale. Estimated annual apparent survival rates were 0.46 to 0.49 for juvenile and 0.68 for adult plovers. Using these estimates, the mean life span of a Mountain Plover was 1.92 (SE = 0.17) years 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 was –0.86, –0.11) on a logit scale. The size of this adult Mountain Plover population was estimated at between 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. This study provided the first age-specific estimates of annual survival for Mountain Plovers, and the first estimates of the size of this breeding population. Adult survival was low compared to many other shorebirds, although other members of the *Charadriidae* have similar low annual adult survival. Given the low annual survival rates and low mean life expectancy of Mountain Plovers, I conclude that sustainable, local populations are currently maintained by annual rates of productivity greater than those for other ground-nesting birds.

Key words: *Charadrius montanus*, 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). But 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 are extremely important, and combined with information about productivity, are critical to assess long-term viability. Detailed studies of demography are thus vital to fully 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. The 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; it is either assumed to be permanent, or it is ignored entirely. Biologically, these assumptions are unrealistic and emigration and immigration may be important factors to population growth. 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 where all individuals do not return to the breeding grounds every year or individuals that inhabit a boundary region of the study area and 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 with core breeding areas in eastern Montana, the eastern two thirds of Wyoming, and eastern Colorado. The species is an endemic bird of the Great Plains (Mengel 1970), which as a group may have shown the greatest recent declines of any group of birds (Knopf 1996a). Continental numbers may have 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 8,000-10,000 birds (Knopf 1996b). Concerns over declines led to a 1997 proposal to federally list the Mountain Plover (Miller and Knopf 1993) and it was proposed as a Threatened species in early 1999 (U. S. Department of the Interior 1999).

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 away from Colorado, mostly local studies of their distribution and breeding biology. Other localized studies have looked at their 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 their 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 I 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. I 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). I also estimated annually the number of breeding adult plovers at this isolated breeding area.

METHODS

Study area

I studied Mountain Plovers on a 3000-km^2 area in southern Phillips County in north-central Montana (4740-4755N,10735-10830W; Figure 2.1). 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 is 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 (*Cynomys ludovicianus*) 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 (*Stipa 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, pers. comm.). Mean elevation was approximately 930 m.

I studied Mountain Plovers exclusively on, or adjacent to, active black-tailed prairie dog colonies. Prior work had shown that plovers were uncommon but widespread on active prairie dog colonies in southern Phillips County and that Mountain Plovers were mostly restricted to such sites in this area (Knowles et al. 1982, Knowles and Knowles 1984). 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 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 (Figure 2.2). On the annual census by BLM staff, they used a portable global positioning unit to delineate the boundaries of active prairie-dog colonies. In 4 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) 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, there were 8675 ha of prairie dogs in southern Phillips County, but this total dropped markedly by the time this study began in the mid-1990s. 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. Inactive colonies were not included in this total because they were essentially unsuitable for plovers. Annual fluctuations in area occupied by prairie dogs were largely caused by sylvatic plague, an epizootic (Barnes 1993), although recreational shooting may have 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 I 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

I studied Mountain Plovers during six breeding seasons (1995-2000). Each year, fieldwork began on 20 May and extended through 20 July. I systematically searched all known active prairie-dog colonies within the study area $\geq$3 times each year for plovers. On these searches I slowly drove a vehicle across each colony and periodically stopped to scan for plovers. Individual adult plovers were watched from a distance until they returned to a nest. Once a nest was located, the adult was trapped immediately with a walk-in wire mesh trap placed over the nest and then banded with a unique combination of four colored leg bands and an aluminum size 3A USFWS numbered leg band. Color band combinations were derived from six possible colors (red, orange, yellow, dark blue, green, and white), which were chosen to minimize possible reading errors. I used UV stable Darvac leg bands (A. C. Hughes, London) to reduce color fading. All birds were weighed to the nearest gram with a spring scale prior to release. Beginning in 1996, I collected a feather sample from every plover for determining sex by DNA analyses; I collected only a limited number of feather samples in 1995 (see Chapter 1). In 1999, 40 plovers (28 adults and 12 fledglings) were fitted with transmitters (Advanced Telemetry Systems, Isanti, MN) to estimate chick and fledgling survival. Transmitters were 3.0 grams (adults) and 1.4 grams (fledglings) and were glued to the back of the bird using an epoxy (Titan Corporation, Lynnwood, WA). Most transmitters were carried by the bird for <30 days and all transmitters were lost when the birds molted prior to their fall migration. All plovers were released within 15 min of capture. Capture techniques did not result in any immediate mortalities. Juvenile plovers were typically banded as flightless chicks ($\geq$10 days old). In July of most years, small numbers of plovers of both ages were captured and banded at night. The birds were located at roosts with a spotlight, approached on foot, and netted.

The Colorado State University Animal Care and Use Committee approved the field methods used in this study (Protocol 98-134A-01).

Surveys for marked plovers

Active prairie-dog colonies were searched $\geq$3 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 I encountered on surveys I recorded the age (adult or juvenile) and exact sequence of color bands, if the bird was marked. Because Mountain Plovers were generally not wary, they were easy to approach and virtually all band combinations were read successfully.

The robust design model

To model demographic parameters such as apparent survival, I used the robust design model (Pollock 1982, Kendall et al. 1995, Kendall et al. 1997, Schwarz and Stobo 1997). The robust design incorporates features of both the open and closed capture-recapture models. 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 sampling periods is used to estimate conditional capture (p_{ij}) and recapture (c_{ij}) probabilities and population size (N_i). A pooled capture probability ($p_i^{\bullet}$) is then calculated for each primary sampling period as

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

and 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.
6. Marked individuals are representative of the population being sampled.

Population modeling

I 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. In order to use individual covariates on capture and recapture probabilities and remove the estimates of population size from the likelihood, I used Huggins' estimator (Huggins 1989, 1991). Using this approach, I estimated annual apparent survival rates for 5 years (1995-1999) and the adult population size for 6 years (1995-2000).

I defined three secondary sampling periods (20 May-10 June, 11-30 June, and 1-20 July) within each year. I 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 (2 age classes in each of 6 years) and two individual covariates (body mass at capture and a 1999 transmitter effect) for each bird.

My general approach to modeling demographic parameters followed Pollock et al. (1990), Lebreton et al. (1992), and Burnham and Anderson (1998). I first came up with a list of *a priori* factors that I believed would influence one or more of these parameters. Using these factors, I defined a set of 18 candidate models. The model set included a fully parameterized global model and 18 additional models supported by biological hypotheses. My justification for the factors affecting these parameters is outlined below.

Annual survival (ϕ_i)

I used only 2-age class models to estimate annual survival. Mountain Plovers breed at age 1 (pers. obs.), so models with any additional age classes seemed unnecessary. I considered models that allowed juvenile survival to vary annually, but I modeled adult survival primarily as constant across years. I 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, I 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. I 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.

I modeled juvenile survival as a function of body mass at capture. I hypothesized that there would be a positive linear relationship between body mass and juvenile survival because mass was positively correlated with age. Because I did not know the hatch date of all chicks, I was unable to model an age effect on juvenile survival. I allowed juvenile mass effects to be both constant across years and to have separate year effects. I also considered the possible effects of a transmitter on the survival of a sample of plovers of both ages in 1999. I 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, I considered the effect of annual area occupied by prairie dogs on the survival of Mountain Plovers.

Other studies found a strong relationship between plovers and prairie dogs in Montana. If, as it has been suggested (Knopf 1996b), 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 relate to survival. I hypothesized that 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 of habitat. I 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 tied to active black-tailed prairie-dog colonies in southern Phillips County, and I hypothesized that they might move between colonies both within and between years. Although I made an attempt to survey all active prairie-dog colonies in the study area, I undoubtedly missed a few small (<5 ha) colonies each year. There were also large complexes of prairie-dog colonies in the surrounding counties and it was possible small numbers of plovers might emigrate there temporarily before returning to the study area. Therefore, temporary emigration in Mountain Plovers seemed plausible in southern Phillips County. Due to identifiability problems, all the gammas are estimable only if certain constraints are included (see Kendall et al. 1995, Kendall et al. 1997). Because these emigration parameters are often difficult to estimate, I considered only six simple models for γ_i'' and γ_i'. I modeled the effects of age (adults and juveniles) on each parameter, and then simplified each model to one with no age effects. I also considered a model where I set γ_i'' and γ_i' equal to evaluate an hypothesis of random emigration, and then I further constrained both gammas to be equal to zero.

Conditional capture (p_{ij}), resighting (r_{ij}), and recapture probabilities (c_{ij})

In order 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). I 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 recapture (c_{ij}) are estimated for each primary sampling period. This approach was not applicable to my 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, I split the probability of first capture into the probability of physical capture (p_{ij}) and the probability of first capture by resighting (r_{ij}).

I 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, I considered models that forced the relationship $p = r + C$ where C was some negative constant. I call this relationship a resighting effect. I also hypothesized that the probability of recapture in a given year (c) was equal to the probability of first captures by resighting (r), or that $r = c$. All recaptures were by resightings, and I saw no reason why they should differ from the initial resighting of a previously marked plover. I 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 the above models, I 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. I 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 my ability to capture and resight plovers. When I began modeling, I immediately encountered identifiability problems with the 1995 data. Initial capture probabilities in 1995 were extremely low and I was forced to use models in which all the p's were constant for this year.

Goodness-of-fit

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. I followed this procedure to assess goodness-of-fit.

I 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). I calculated this quantity as

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

using log likelihoods from the best model, the global model, and the simplest (.) model. Here, the (.) model had 3 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. I ranked the set of R candidate models using AICc (Burnham and Anderson 1998), which was defined as

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

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 above equation was a correction for small sample size. Here, the sample size was the total number of releases (new releases plus resightings). I 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 AICc values were computed for each model, I ranked the R models relative to the model with the lowest AICc value. Comparisons between models were made using ΔAICc values, where for each model i

$$\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\min}$$

The ΔAICc values compared the relative distances between the best approximating model ($\text{AICc}_{\min}$) and each competing model (AICc_i). Generally, models with Δ-AICc values ≤ 2 have strong support while those with ΔAICc values >10 have little support (Burnham and Anderson 1998). Normalized Akaike weights (w_i) were also computed for each of the R models as

$$w_i = \frac{e^{-\left\{\frac{\Delta AICc_i}{2}\right\}}}{\sum_{r=1}^{R} e^{-\left\{\frac{\Delta AICc_r}{2}\right\}}}$$

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, I 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), I computed the survival using the mean estimate of the covariate(s). When building models, I 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

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

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

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

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

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

with sampling variance

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

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

$$95\%\text{CI}_\text{L}=\hat{\bar{\varphi}}_i-1.96\left[\hat{\text{SE}}\left(\hat{\bar{\varphi}}_i\right)\right]$$

$$95\%\text{CI}_\text{U}=\hat{\bar{\varphi}}_i+1.96\left[\hat{\text{SE}}\left(\hat{\bar{\varphi}}_i\right)\right]$$

where

$$\hat{\text{SE}}\left(\hat{\bar{\varphi}}_i\right)=\sqrt{\hat{\text{var}}\left(\hat{\bar{\varphi}}_i\right)}$$

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

Estimating mean life span

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

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

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

$$\hat{\text{Var}}(\text{MLS})=\left\{\frac{\partial(\text{MLS})}{\partial(\varphi_J)}\right\}^2\text{Var}(\varphi_J)+\left\{\frac{\partial(\text{MLS})}{\partial(\varphi_A)}\right\}^2\text{Var}(\varphi_A)+2\left\{\frac{\partial(\text{MLS})}{\partial(\varphi_J)}*\frac{\partial(\text{MLS})}{\partial(\varphi_A)}\right\}\text{Cov}(\varphi_J,\varphi_A)$$

where

$$\frac{\partial(\mathrm{MLS})}{\partial(\varphi_J)}=\left\{\frac{1}{\varphi_J*\ln(\varphi_J)^2}-\frac{1}{\ln(\varphi_A)}+\frac{1}{\ln(\varphi_J)}-\frac{1}{\ln(\varphi_J)^2}\right\}$$

and

$$\frac{\partial(\mathrm{MLS})}{\partial(\varphi_A)}=\frac{\varphi_J}{\varphi_A*\ln(\varphi_A)^2}$$

Estimating population size

I estimated the annual size of the breeding population (number of adult plovers) using the Huggins robust design in program MARK. I modeled adults as a single group with seven individual covariates per bird. Each bird had one covariate for a resighting effect in each year (6 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 zero. With this model structure, I used MARK to generate estimates of annual population size and the appropriate standard errors.

RESULTS

During the 6-year study, I individually color banded 620 Mountain Plovers (374 adults and 246 juveniles; Table 2.1). The total number of releases (newly-marked plovers plus resightings of previously-marked plovers) was 1,735. The low number of juveniles banded in 1996, 1997, and 1999 was due to poor reproduction in those years. Samples of adult plovers were similar between years. Juvenile body mass varied greatly (mean = 61.50 grams, SD = 17.38; range 20-110 grams) and generally increased with the age of the chick. Band loss during the study was minimal. Only 9 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 re-banded and released. The others were not identifiable.

Model selection results

The pooled results from Tests 2 and 3 in program RELEASE showed there was a good fit to the reduced Cormack-Jolly-Seber model (χ^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 2.2). At least six additional models could be considered competing models (Δ-AICc 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.

Body mass was an important predictor of juvenile survival (in the best model, $\hat{\beta}_{mass}$ = 0.77; 95% CI was 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 non-significant additive effect on a logit scale of area occupied by prairie dogs on survival ($\hat{\beta}_{prairie-dog}$ = –0.00004; 95% CI was –0.00003, 0.0001). A common additive transmitter effect on all birds (Δ-AICc = 1.79) had better support than a model where the transmitter effect varied by age (Δ-AICc = 3.83); the transmitter effects were non-significant in both models. There was little support for time variation in survival. The fourth and fifth best models had non-significant 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 (Δ-AICc = 2.60) and adults (Δ-AICc = 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. I found weak support for models where γ'' and γ' were equal (Δ-AICc = 2.28) and no support of a model where they were both set to zero (no emigration; Δ-AICc = 76.72).

I found strong evidence for a resighting effect. The resighting effect was always negative (in best model, $\hat{\beta}_{resighting}$ = –0.49; 95% CI was –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 (Δ-AICc = 5.35) and had little weight.

Parameter estimates

The model-averaged estimates of the annual survival of Mountain Plovers were 0.46 to 0.49 for juveniles and 0.68 for adults (Figure 2.3). 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 (SE = 0.06; 95% CI was 0.14, 0.37) for juveniles and 0.22 (SE = 0.04; 95% CI was 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 (SE = 0.18; 95% CI was 0.18, 0.78) for juveniles and 0.47 (SE = 0.17; 95% CI was 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 to 0.74). Resighting and recapture probabilities were also quite high (range 0.49 to 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 (SE = 0.19; 95% CI 1.55, 2.29). This estimate was calculated using ϕ_J = 0.4759 (SE = 0.0745) and ϕ_A = 0.6775 (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 (Figure 2.4). Estimates from 1995 were imprecise and of little use. Beginning in 1996, the estimates showed a general increase in plover numbers through 1998, when the population stabilized at approximately 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. Site fidelity of adult plovers appeared high with many 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, I 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 likely close to true survival.

For juvenile Mountain Plovers, the interpretation of survival estimates was not as straightforward. At least some juvenile plovers permanently emigrated from the study area. Surveys of Fort Belknap Indian Reservation, 40 km to the northwest, turned up at least two plovers (out of a total of 284 examined for bands) that had been banded as juveniles in the study area. Similar surveys of prairie-dog colonies along the Milk River southwest of Malta turned up three more plovers (out of a total of 84 examined for bands), also all banded as juveniles in the study area. Undoubtedly, small numbers of juvenile Mountain Plovers banded in southern Phillips 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 $\geq$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 post-hatch (pers. obs.), so many young plovers died before they could be banded. In this study, juvenile survival measured the probability of surviving from about 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 either positive.

Adult Mountain Plovers had an estimated annual survival rate of 0.68. The low adult annual survival was surprising and contrasted with a higher annual survival for several shorebird species (Table 2.3).

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. 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 favored plovers with 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 reproductive output for each pair relative to most other shorebirds (6 versus 3 or 4 eggs), although this output may be even greater if suspected sequential polyandry is occurring. Their uniparental care strategy is probably more costly than most other breeding strategies in 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 (Saether 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 most 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 (no losses between mid-May and late July; Miller and Knopf 1993) and in winter in central California (survival rate of 0.95 for the period 1 November to 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 were recently shown to have similar low annual survival (Table 2.3) and high over-winter survival (no losses between mid-August and late April; Drake et al. 2001).

A comparison between the juvenile survival of Mountain Plovers versus 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 at 0.39, which is similar to the estimate for Mountain Plovers. I found no other estimates of juvenile survival among the *Charadriidae*.

I estimated the mean life span of Mountain Plovers as 1.92 years. The low estimated life span of Mountain Plovers is not surprising given that the longevity record is 8 years (pers. obs.), 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 2.3); none have used the robust design to estimate survival in the presence of temporary emigration. Whereas 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 sub-adult age classes may effectively represent 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.

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

I 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 I did not know the age of every juvenile plover I banded, I was unable to use this as a covariate in my models. Instead, I used body mass, which I suspected was highly correlated with age. Because of this confounding of age and body mass, the significance of my finding is less clear. Body mass appears to be a good predictor of juvenile Mountain Plover survival, although the causal factor may be age and not body mass.

Population estimates

The annual estimate of the number of breeding adult Mountain Plovers in the study area varied from 95 (1996) to 180 (1999) birds. Estimates of population size in 1995 were imprecise compared to estimates in all other years. This lack of precision 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. But, more important, 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 likely the result of observer inexperience and my lack of familiarity with the study area during the pilot year of 1995.

The relatively low estimate of the number of breeding Mountain Plovers was unexpected because previous ad hoc estimates placed the number at about 400-500 individuals. My estimates of population size appear to be accurate as 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 large colonies that were most likely to be occupied by plovers (Olson-Edge and Edge 1987). The combination of good coverage and high capture probabilities support the accuracy of the population estimates, given the assumption that few plovers nest off prairie-dog colonies. Few plovers and only seven nests have been seen 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. What is more likely is that the increase in available plover habitat (e. g., the area occupied by prairie dogs) attracted plovers from outside the study area, with immigration accounting for most of the population increase. The source of these immigrants is unknown, but the most likely locales are Blaine and Valley counties. The increase from 1997 to 1998 (134 to 170 birds) can be explained in a similar manner. Since 1998, the size of the population has leveled off, despite the continued increase in area occupied by prairie dogs. This hints that there may be some carrying capacity that has been reached, or that issues such as behavioral regulation of density, habitat quality, or mortality during other portions of the annual cycle are having a greater influence on population growth.

Population estimates of Mountain Plovers in southern Phillips County appeared to track changes in area occupied by prairie dogs closely. Black-tailed prairie dogs were in the last stages of a major outbreak of sylvatic plague in 1995. In 1988, prior to the plague outbreak, area occupied by prairie dogs in the study area had reached 8675 ha, but this total was reduced to 1371 ha in 1995 (Figure 2.2). The area occupied by prairie dogs was lowest in 1995-1996 and have since steadily risen in a nearly linear fashion at an average of 30% per year (J. Grensten, pers. comm.). 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 (Δ-AICc = 0.90, $w_i = 0.12$). However, the coefficient for this effect was non-significant. 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 whether or not plovers will occupy the colony.

The parallel relationship between Mountain Plover and black-tailed prairie dog numbers in southern Phillips County was expected. Earlier studies noted this pattern (Knowles et al. 1982, Olson and Edge 1985), and observations from this study further strengthened the apparent tie between these species. The high pooled capture probabilities support the claim that most plovers are essentially restricted to prairie-dog colonies in this region. This dependency was especially apparent during the post-breeding period when individual plovers moved daily between prairie-dog colonies, some as far as 50 km distant. This logic would be flawed if a subset of the population avoided prairie-dog colonies.

Conservation of Mountain Plovers in Phillips County, Montana

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

Mountain Plovers showed an affinity for prairie-dog colonies in southern Phillips County and their numbers seemed to closely track changes in black-tailed prairie dog distribution. Plover numbers were reduced in years following outbreaks of sylvatic plague, but rapidly recovered soon thereafter. If sylvatic plague again reduces prairie dog numbers in southern Phillips County, biologists may have an opportunity to study its effect on plovers. Although large areas of suitable plover habitat may be available at nearby sites (e. g., Fort Belknap Indian Reservation), Mountain Plovers appear faithful to breeding sites and may be reluctant to move even short distances. Adult plovers didn't disperse from the study area, even though plovers occupied surrounding areas and the distances involved (<50 km) would not seem to provide a barrier for a plover.

The affinity Mountain Plovers show for black-tailed prairie-dog colonies in Montana differs from habitat preferences throughout the remainder of the breeding range (Knopf 1996b). The reasons for this include increased visibility (important for detecting predators), an abundance of preferred food items (Olson 1985), and possibly vegetative differences that may be important for nesting (Olson and Edge 1985). As suggested by Olson (1985), and confirmed by this study, prairie-dog colonies represent a preferred habitat for Mountain Plovers in Montana. Habitat limitations, more than any other factor, seem to drive the number of plovers in this region. 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).

ACKNOWLEDGMENTS

I am grateful to Fort Carson Military Reservation (U. S. Department of Defense), the U. S. Fish and Wildlife Service (Colorado Fish and Wildlife Management Assistance Office), the Biological Resources

Division of the U. S. Geological Survey, the U. S. Bureau of Land Management (Malta Field Office, Montana), the Denver Zoological Foundation, and the Fort Belknap Tribal Community for financial support. The staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. J. J. Grensten and B. D. Rosenlund assisted with multiple aspects of the study. A. Brees, D. C. Ely, T. Hanks, J. G. Jorgensen, C. McQueary, and T. Vosburgh provided field assistance. I thank B. Matovitch, D. Robinson, and J. Robinson for allowing me access to their lands.

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Table 2.1. Reduced m-array for Mountain Plovers of both age classes banded in southern Phillips County, Montana, 1995-1999. R_i is the total number of releases (new birds plus live recaptures) in year i, $m_{i,j}$ is the number of recaptures in year j of birds released in year i, r_i is the sum of all recaptures in year i, m_j is the number of animals captured in year j, and z_j is the number of animals recaptured in a year other than year j.

1995

Juveniles

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
1	69	11	2	1	0	0	14
2	11		7	1	0	0	8
3	9			6	0	0	6
4	8				3	0	3
5	3					0	0
m_j		11	9	8	3	0	
z_j		3	2	0	0	0	

Adults

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
1	66	34	6	0	1	0	41
2	34		21	2	1	0	24
3	27			12	0	1	13
4	14				9	0	9
5	11					3	3
m_j		34	27	14	11	4	
z_j		7	4	3	1	0	

1996

Juveniles

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
2	14		4	0	0	0	4
3	4			3	0	0	3
4	3				2	0	2
5	2					0	0
m_j		0	4	3	2	0	
z_j		0	0	0	0	0	

Adults

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
2	45		20	4	0	0	24
3	20			14	0	2	16
4	18				7	1	8
5	7					4	4
m_j		0	20	18	7	7	
z_j		0	4	2	3	0	

1997

Juveniles

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
3	22			5	0	1	6
4	5				2	0	2
5	2					0	0
m_j		0	0	5	2	1	
z_j		0	0	1	1	0	

Adults

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
3	66			30	2	0	32
4	30				14	2	16
5	16					7	7
m_j		0	0	30	16	9	
z_j		0	0	2	2	0	

1998

Juveniles

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
4	46				17	3	20
5	18					12	12
m_j		0	0	0	17	15	
z_j		0	0	0	3	0	

Adults

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
4	75				43	3	46
5	43					24	24
m_j		0	0	0	43	27	
z_j		0	0	0	3	0	

1999

Juveniles

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
5	40					6	6
m_j		0	0	0	0	6	
z_j		0	0	0	0	0	

Adults

i	R_i	$m_{i,j}$ j=2	3	4	5	6	r_i
5	66					34	34
m_j		0	0	0	0	34	
z_j		0	0	0	0	0	

Table 2.2. Summary of model selection results for Mountain Plovers in southern Phillips County, Montana, 1995-2000. Models are ranked by ascending Δ-AICc; w_i is the model weight and K is the number of parameters. Apparent survival (ϕ), temporary emigration (γ'' and γ'), and capture (p, r) and recapture (c) probabilities included the effects of two age classes (age: adults and juveniles), a transmitter in 1999 (transmitter), additive mass effect on juvenile survival (juv+mass), annual area occupied by prairie dogs (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 $[L_s(\hat{\theta})]$.

Model	Deviance	K	AICc	Δ-AICc	w_i
$\phi_{\text{age, juv+Mass}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4090.40	24	4139.10	0.00	0.19
$\phi_{\text{age, juv+Mass, all+prairie dog area}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4089.25	25	4140.01	0.90	0.12
$\phi_{\text{age, juv+Mass}}\ \gamma''_{\text{age}}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4089.27	25	4140.03	0.92	0.12
$\phi_{\text{age, juv+Mass, adult+}T}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4089.69	25	4140.45	1.35	0.10
$\phi_{\text{age, juv+}T\text{+Mass}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4089.96	25	4140.72	1.62	0.09
$\phi_{\text{age, juv+Mass, transmitter}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4090.14	25	4140.90	1.79	0.08
$\phi_{\text{age, juv+Mass}}\ \gamma''_{(.)}\ \gamma'_{\text{age}}\ p_t = r_{t+C} = c_t$	4090.29	25	4141.05	1.94	0.07
$\phi_{\text{age, juv+Mass}}\ \gamma''_{(.)} = \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4094.74	23	4141.38	2.28	0.06
$\phi_{\text{age, juv*year+common Mass}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4084.76	28	4141.71	2.60	0.05
$\phi_{\text{age, juv+Mass}}\ \gamma''_{\text{age}}\ \gamma'_{\text{age}}\ p_t = r_{t+C} = c_t$	4089.24	26	4142.06	2.95	0.04
$\phi_{\text{age, juv+Mass, transmitter *age}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4090.11	26	4142.93	3.83	0.03
$\phi_{\text{age, juv*year}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4088.20	27	4143.09	3.98	0.03
$\phi_{\text{age, juv+Mass}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_t = c_t$	4097.81	23	4144.45	5.35	0.01
$\phi_{\text{age, juv+Mass, adult*year}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4088.91	28	4145.86	6.75	0.01
$\phi_{\text{age}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4099.85	23	4146.50	7.40	0.00
$\phi_{\text{age, juv+Mass separate}}\ \gamma''_{(.)}\ \gamma'_{(.)}\ p_t = r_{t+C} = c_t$	4084.12	33	4149.36	10.25	0.00

$\phi_{\text{age, juv+Mass}}\ \gamma''_{(.)}=\gamma'_{(.)}=0\ p_t = r_{t+C} = c_t$	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

Table 2.3. Estimates of annual survival rates for shorebirds derived from capture-recapture studies.

Species	Adult survival	Juvenile survival	Reference
Burhinidae			
Stone-curlew	0.83	0.61	Green et al. (1997)
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
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 (1996)
Semipalmated Sandpiper	0.53-0.73 (males)		Sandercock and Gratto-Trevor (1996)
Semipalmated Sandpiper	0.43-0.71 (females)		Sandercock and Gratto-Trevor (1996)
Temminck's Stint	0.81		Hilden (1978)

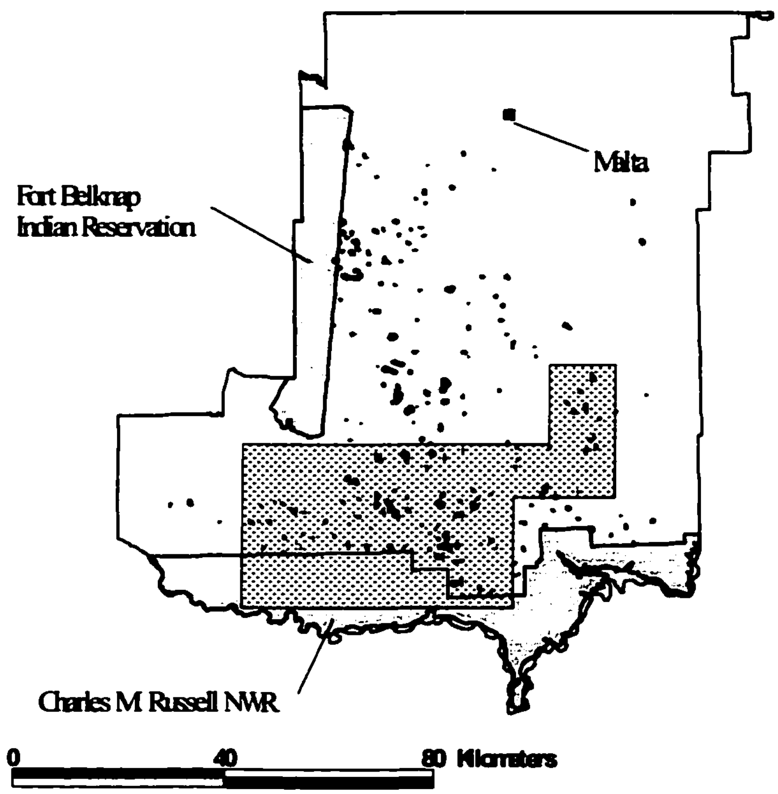

Figure 2.1. Map of southern Phillips County, Montana showing the distribution in 2000 of black-tailed prairie-dog colonies. The stippled region represents the study area.

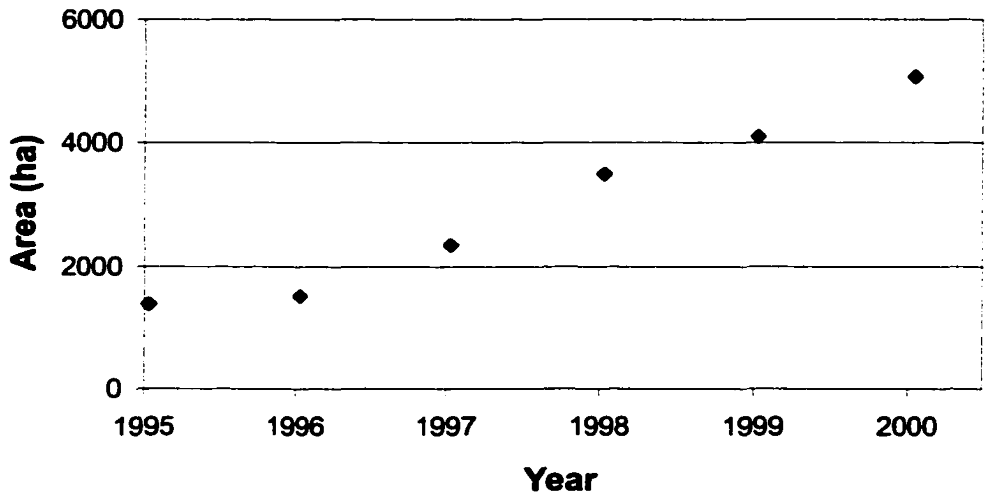

Figure 2.2. Area occupied by black-tailed prairie dogs calculated from annual Bureau of Land Management surveys in southern Phillips County, Montana, 1995-2000.

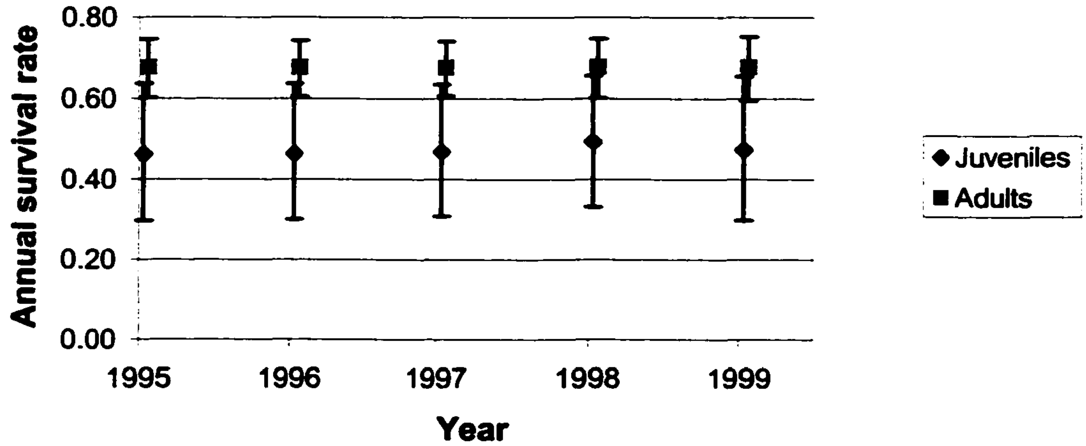

Figure 2.3. Annual age-specific apparent survival rates and 95% confidence intervals of Mountain Plovers in southern Phillips County, Montana, 1995-1999.

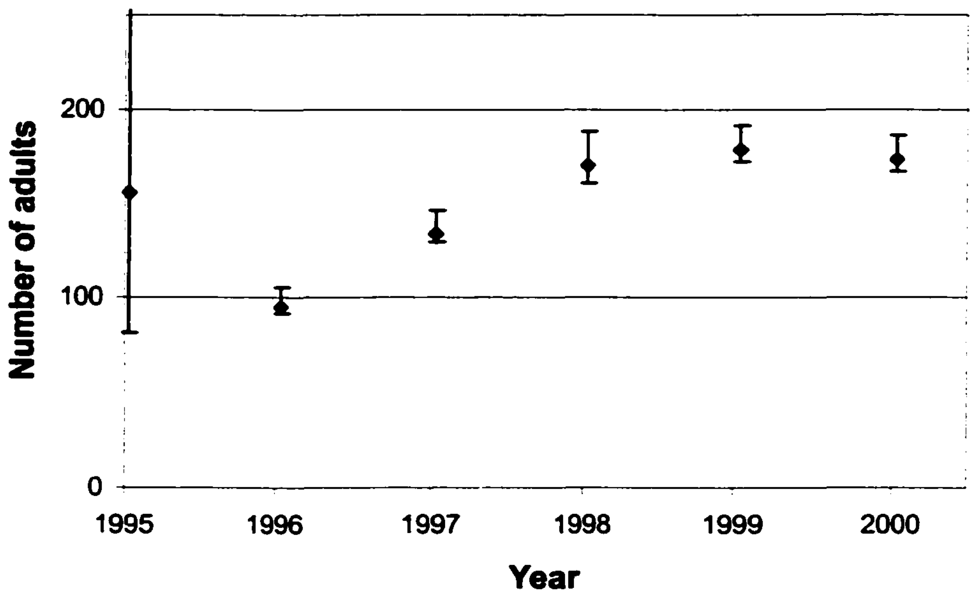

Figure 2.4. Number and 95% confidence intervals of breeding adult Mountain Plovers in southern Phillips County, Montana, 1995-2000. The upper confidence limit for 1995 was 579 birds and was omitted so that the scale of the graph was readable.

CHAPTER 3. THE STATUS OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA.

ABSTRACT: I estimated the annual recruitment rate (f) and the annual rate of population change (λ) for a local population of mountain plovers (*Charadrius montanus*) in southern Phillips County, Montana in 1995-2000 using the Pradel models. I modeled λ as a constant across years, as a linear time trend, as year-specific, and with an additive effect of area occupied by prairie dogs. Recruitment rate was modeled as a function of area occupied by prairie dogs with the remaining model structure identical to the best model to estimate λ. The results indicated a strong negative effect of area occupied by prairie dogs on both λ (slope coefficient on a log scale was –0.11; 95% CI was –0.17, –0.05) and f (slope coefficient on a logit scale was –0.23; 95% CI was –0.36, –0.10). There was also good evidence for a negative time trend on λ; this model had substantial weight (w_i = 0.31) and the slope coefficient on the linear trend on a log scale was –0.10 (95% CI was –0.15, –0.05). Yearly estimates of λ were >1 in all years except 1999, indicating that the population initially increased and then stabilized in the last year of the study. There was weak evidence for year-specific estimates of λ; the best model with year-specific estimates had a low weight (w_i = 0.02), although the pattern of yearly estimates of λ closely matched those estimated with a linear time trend. In southern Phillips County, the population trend of mountain plovers closely matched the trend in the area occupied by black-tailed prairie dogs. Black-tailed prairie dogs declined sharply in the mid-1990s in response to an outbreak of sylvatic plague, but their numbers have steadily increased since 1996 in concert with increases in plovers. This hints that the conservation of mountain plovers in this region is closely linked to the available area occupied by prairie dogs. Threats to prairie dogs such as sylvatic plague and recreational shooting may pose indirect threats to mountain plovers.

JOURNAL OF WILDLIFE MANAGEMENT 00(0):000-000

Key words: *Charadrius montanus*, Montana, mountain plover, population trend, prairie dog, status.

The finite rate of population change, lambda (λ), is often of fundamental importance to ecologists interested in assessing the status of a population. Estimates of lambda can show that a population is increasing ($\lambda > 1$), stable ($\lambda = 1$), or declining ($\lambda < 1$) and provide a more formal means of interpreting estimates of population size. Understanding these rates becomes even more important for rare or declining species that require immediate intervention to rescue them from further declines or even extinction.

The traditional method of estimating λ has been with the use of Leslie projection matrices (Leslie 1945, Caswell 2001). Under this method, measures of average age-specific survival and fecundity are used to "project" population growth over a specified period. However, this method does have problems. The most important flaw is that the rates that are often used represent averages over a specified time period, so predicted values of λ are also averages and may not be reasonable predictors of future trends. Additionally, estimates of λ from projection matrices may be biased downward if there is substantial emigration, particularly among juvenile age classes (Franklin et al. 1996).

Pradel (1996) introduced a reparameterization of the Jolly-Seber model to estimate the finite rate of population change (λ) in addition to apparent survival (ϕ) and conditional capture probability (p). Unlike the Leslie projection matrix, this method directly accounts for both internal (reproduction and mortality) and external (immigration and emigration) influences on the population of interest and is an improvement because λ is estimated directly from the data.

Mountain plovers are a local and declining shorebird of the western Great Plains (Knopf 1994). Perceived declines led to a proposal to list them as a Threatened species in 1999 (U. S. Department of the Interior 1999). Rigorous assessment of plover status and trends at key breeding areas is needed and will provide a better understanding of local population dynamics and help future conservation efforts for this species.

Herein I provide estimates of annual rates of population change (λ) from 1995-1999 for a population of mountain plovers in southern Phillips County, Montana. Southern Phillips County is thought to contain the largest breeding population of plovers in Montana and one of the largest in North America (Knopf and Miller 1994). Population trends at this site are discussed in light of the total size of this population (Chapter 2) and changes in the area occupied by black-tailed prairie dogs. I then comment on the status and future outlook for mountain plovers at this key breeding site and identify several aspects of their biology needing further study.

STUDY AREA

I studied mountain plovers on a 3000-km^2 area in southern Phillips County in north-central Montana (4740-4755N,10735-10830W; Figure 3.1). 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 is 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 (*Cynomys ludovicianus*) 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 (*Stipa 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, pers. comm.). Mean elevation was approximately 930 m.

I studied mountain plovers exclusively on or adjacent to active black-tailed prairie-dog colonies because previous work had shown that mountain plovers preferentially used such sites in Montana (Knowles et al. 1982, Knowles and Knowles 1984). Prairie dog numbers fluctuate considerably in southern Phillips County, mainly as a result of outbreaks of sylvatic plague, an epizootic (Barnes 1993), although recreational shooting may have a negative impact on some of the smaller prairie-dog colonies (Vosburgh and Irby 1998). Prairie dogs have rapidly recovered from the last major plague outbreak in 1992-96. Colony areas were reduced by about 80% during this outbreak, but have since increased from

1371 ha in 1995 to 5071 ha in 2000 (J. Grensten, pers. comm.; Figure 3.2). Inactive colonies, mostly the result of plague outbreaks, were not included in this total because habitat on such colonies rapidly became unsuitable for plovers, often within a matter of a few weeks.

METHODS

Capture and marking

I studied mountain plovers from 20 May-20 July during six breeding seasons (1995-2000). Active prairie-dog colonies within the study area were systematically searched $\geq$3 times each year. On these searches I slowly drove a vehicle across each colony and periodically stopped to scan for plovers. Individual adult birds 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 banded with a unique combination of four colored leg bands and an aluminum size 3A USFWS 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. I used UV stable Darvac leg bands (A. C. Hughes, London) to reduce color fading. All plovers were released within fifteen minutes of capture. Juvenile plovers were typically banded as flightless chicks (>10 days old). In July of most years, small numbers of plovers of both ages were trapped and banded at night. The birds were located at roosts with a spotlight, approached on foot, and captured in a large dip-net. Capture techniques did not result in any immediate mortalities. The Colorado State University Animal Care and Use Committee approved the field methods used in this study (Protocol 98-134A-01).

Surveys for marked plovers

All known active prairie-dog colonies within the study area were searched $\geq$3 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 I encountered on surveys I recorded the age (adult or juvenile) and exact sequence of color bands, if the bird was marked.

Estimating population trends (λ)

I estimated the finite rate of population change (λ) and recruitment (f) using the Pradel lambda models (Pradel 1996) in program MARK (White and Burnham 1999). I estimated annual apparent survival and population size earlier using the robust design (Chapter 2); the focus here is only on estimates of λ and f. Models to estimate λ directly from a robust design study have not been developed, so I was forced to slightly modify my approach to estimating λ and f with this model.

Releases and live resightings of banded plovers were summarized in encounter history format with six encounter occasions, one for each year of the study. I only used information from adult plovers, which included all birds first banded as adults and all juveniles that were subsequently resighted as adults. Using this approach, I was able to estimate the annual rate of the breeding adult population change (λ) for 5 years (1995-1999) and recruitment (f) for 5 years (1996-2000).

My general approach to modeling λ and f followed Lebreton et al. (1992) and Burnham and Anderson (1998). I first developed a list of *a priori* factors influencing each parameter (ϕ, p, f, λ), and then used this information to define a set of candidate models.

The Pradel models allow the simultaneous estimation of apparent survival (ϕ) with capture probability (p) and the finite rate of population change (λ) or recruitment (f). Because there was only a single encounter occasion per year, the recapture probability (c) could not be estimated. Under this model, population change is estimated as

$$\hat{\lambda}_t = \frac{N_{t+1}}{N_t}$$

where N_t represents the population size at some time t. Between times t and t+1 the population changes as a function of births, deaths, emigration, and immigration. Thus, changes in λ are a function of apparent survival, recruitment, and movement.

In order to estimate λ using the Pradel model, annual apparent survival and initial capture probability had to be modeled correctly. For mountain plovers, I modeled apparent survival (ϕ) as year-specific in this analysis. Because I believed λ was changing annually, it made sense to also allow survival to vary annually, even though I suspected yearly differences in adult survival were small (see Chapter 2). For comparison, I also included a single model where apparent survival was constant across years.

The initial capture of mountain plovers occurred by either physical capture (p) or resighting (r), and I knew from earlier work that the probability of physical capture was much lower than resighting probability (Chapter 2). In an earlier analysis, I showed that models where $p = r + C$, where C was some constant, received the best support (Chapter 2). Limitations in the structure of the Pradel model prohibited modeling p and r separately, so I was forced to model all initial captures with probability p. I considered two constraints on capture probability: I let it be constant across years [$p_{(.)}$] and allowed it to vary by year [$p_{(t)}$]. Because differences in yearly capture probabilities using the robust design were small (Chapter 2), I hypothesized that models with constant capture probability would receive better support than those with time-specific capture probability, but this was somewhat speculative. The use of both of these constraints on capture probability was therefore considered partly exploratory.

For lambda (λ), I considered four constraints in my models. I considered two models with full time variation where λ varied by year [$\lambda_{(t)}$]; ϕ was also year-specific in both models while p was constant in one model and year-specific in the other. I also considered a model where λ had a linear time trend [$\lambda_{(T)}$]; ϕ was year-specific and p was constant. Finally, I considered a model where λ was constant [$\lambda_{(.)}$], but only when ϕ and p were also constant; a model with constant λ and time variation on ϕ and p was nonsensical. Finally, I considered a model where λ was a function of the hectares of active prairie-dog colonies [$\lambda_{\text{prairie dog}}$]. This latter model was an attempt to solidify the relationship between these two species that I found earlier (Chapter 2). Thus, temporal variation in λ was accounted for by recruitment and immigration in the first case and by recruitment, immigration, and apparent survival in the second case. Lambda models were modeled on a log scale, where

$$\log(\lambda) = \hat{\beta}_0 + \hat{\beta}_1(X)$$

and X represents some variable of interest such as the area occupied by prairie dogs or a linear time trend.

In an attempt to better understand possible causes of annual population trends, I also considered a single model where recruitment (f) was estimated instead of population trend (λ). In this model, recruitment was a function of the hectares of active prairie-dog colonies and used the same constraints on ϕ and p that were in the best survival and λ model. Here, f is defined is the number of new animals in the population at time i, per animal that was in the population at time i–1 (Franklin 2000). The relationship between lambda, apparent survival, and recruitment is simply $\lambda = \phi + f$. Therefore, f estimates the portion of apparent survival that is due to recruitment. Recruitment models were modeled on the logit scale, where

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

where X represents some variable of interest such as the area occupied by prairie dogs.

With these guidelines, I considered the following six models to estimate λ and f:

1. $\phi_{(.)}\ p_{(.)}\ \lambda_{(.)}$
2. $\phi_{(t)}\ p_{(.)}\ \lambda_{(T)}$
3. $\phi_{(t)}\ p_{(.)}\ \lambda_{(t)}$
4. $\phi_{(t)}\ p_{(t)}\ \lambda_{(t)}$
5. $\phi_{(t)}\ p_{(.)}\ \lambda_{\text{prairie dog}}$
6. $f_{\text{prairie dog}}$ with ϕ and p structure from best λ model

Goodness-of-fit

I used the total chi-square value from Tests 2 and 3 in program RELEASE (Burnham et al. 1987) as a test of goodness-of-fit of my mountain plover data to the Pradel lambda model. I checked for overdispersion in these data using an estimate of c from RELEASE, obtained by dividing the total chi-square by its degrees of freedom.

I 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). I calculated this quantity as

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

using log likelihoods from the best model, the global $\{\phi_{(t)}\ p_{(t)}\ \lambda_{(t)}\}$ model, and the simplest $\{\phi_{(.)}\ p_{(.)}\ \lambda_{(.)}\}$ model. Here, the simplest model had 3 parameters (ϕ, p, and λ) and the global model had full year effects on ϕ, p, and λ (15 parameters).

Model selection

An appropriate model was selected using the methodology of Burnham and Anderson (1998). First, I ranked the set of R candidate models using Akaike's Information Criterion (AIC; Akaike 1973). AIC provides a means of objectively ranking a set of models and then selecting a "best approximating" model or models for inference (Burnham and Anderson 1998). To correct for possible small sample bias, I used AICc to rank models. AICc was defined as

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

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. Here, the sample size was the total number of releases (new releases plus resightings). The second term in the above equation was a correction for small sample size.

Once AICc values were computed for each model, I ranked the R models relative to the model with the minimum AICc value. Comparisons between models were made using ΔAICc values, where for each model i

$$\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\min}$$

The ΔAICc values compared the relative distances between the best approximating model ($\text{AICc}_{\min}$) and each competing model (AICc_i). Generally, models with ΔAICc values ≤ 2 have strong support while those with ΔAICc values >10 have little support (Burnham and Anderson 1998). Normalized Akaike weights (w_i) were also computed for each of the R models as

$$w_i = \frac{e^{-\left\{\frac{\Delta \mathrm{AICc}_i}{2}\right\}}}{\sum_{r=1}^{R} e^{-\left\{\frac{\Delta \mathrm{AICc}_r}{2}\right\}}}$$

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). Parameter estimates in MARK are maximum likelihood estimates with 95% confidence intervals based on a logit or log transformation. Instead of using parameter estimates from a single "best" model, I model averaged (Burnham and Anderson 1998) parameter estimates across all five candidate 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.

Using the Akaike weight and estimate of lambda (λ) from each of the R models, I computed a model averaged estimate of λ as

$$\bar{\hat{\lambda}}_i = \sum_{r=1}^{R} w_i \hat{\lambda}_i$$

with sampling variance

$$\hat{\mathrm{var}}\left(\bar{\hat{\lambda}}_i\right) = \left[\sum_{r=1}^{R} w_i \sqrt{\hat{\mathrm{var}}\left(\hat{\lambda}_i \middle| M_i\right) + \left(\hat{\lambda}_i - \bar{\hat{\lambda}}_i\right)^2}\,\right]^2$$

where M_i was the ith model in the candidate set (Buckland et al. 1997). The 95% confidence interval for model-averaged estimates of λ was

$$95\%\mathrm{CI}_{\mathrm{L}} = \bar{\bar{\lambda}}_i - 1.96\left[\hat{\mathrm{SE}}\left(\bar{\bar{\lambda}}_i\right)\right]$$

$$95\%\mathrm{CI}_{\mathrm{U}} = \bar{\bar{\lambda}}_i + 1.96\left[\hat{\mathrm{SE}}\left(\bar{\bar{\lambda}}_i\right)\right]$$

where

$$\hat{\mathrm{SE}}\left(\bar{\bar{\lambda}}_i\right) = \sqrt{\hat{\mathrm{var}}\left(\bar{\bar{\lambda}}_i\right)}$$

RESULTS

The pooled results from Tests 2 and 3 in program RELEASE showed there was a good fit to the Pradel lambda model (χ^2_{10} = 10.33, $P = 0.41$). There was no evidence of extra binomial variation in these data ($\hat{c}$ = 1.03). The proportion of deviance explained by the best model was 49% of variation. Model-averaged estimates of λ showed that the population of mountain plovers in southern Phillips County, Montana increased rapidly from 1995-1998 and then appeared to stabilize in 1999 (Figure 3.3). During the period of increase from 1995-98, the estimates of λ were >1, but λ could not reliably be judged different from 1 in 1999.

I found good evidence supporting an effect of the hectares of active prairie-dog colonies on λ, but the effect on the log scale was negative { $\hat{\beta}_{prairie\text{-}dog}$ = –0.11; 95% CI was –0.17, –0.05}. I also found good evidence for a negative linear time trend in λ on the log scale in the third best model { $\hat{\beta}_T$ = –0.09; 95% CI was –0.14, –0.04}. This model had stronger support ($w_i = 0.31$) than models where λ was time-specific or constant across time (Table 3.1).

Using the best lambda and survival model, I estimated recruitment instead of lambda (Table 3.1). This model received only slightly less support than the best λ model (Δ-AICc = 0.07, $w_i = 0.32$). The effect of area occupied by prairie dogs was still strongly negative on the logit scale { $\hat{\beta}_{prairie\text{-}dog}$ = –0.23;

95% CI was –0.36, –0.10} in this model. Estimates of f gradually declined from 0.72 in 1996 to 0.38 in 2000 (Table 3.2).

DISCUSSION

Mountain plovers in southern Phillips County appear to have rebounded from low population levels in the mid-1990s. This pattern paralleled a simultaneous decline and recovery in the area occupied by black-tailed prairie dogs due to an outbreak of sylvatic plague. Since 1998, there is evidence that the population has stabilized at around 175 individuals (see also Chapter 2). These results suggest that the population increased rapidly from 1995 to 1998, possibly from in situ reproduction, but more likely from a combination of reproduction and immigration from surrounding areas such as Fort Belknap Indian Reservation (Chapter 2).

Interpretation of λ

The model selection results generally agreed with earlier findings on apparent survival and capture probabilities, lending support to estimates of λ from the Pradel model. Earlier, I found that adult survival showed little annual variation, and that capture probabilities were high with only slight annual variation (Chapter 2). Pradel models with the same constraints on apparent survival and capture probability received the best support of the models I considered. Due to limitations in the Pradel model that forced capture probabilities to be estimated as a single parameter, these estimates of λ should still be interpreted with some caution. Improper modeling of capture probabilities may have resulted in slightly biased estimates of annual population trends. Ultimately, a robust design Pradel model is needed to properly model capture probabilities and generate less biased estimates of λ for this population.

Estimates of λ are susceptible to bias if the size of the study area changed during the study (Franklin et al. 1999). In this study, population trends represent real trends and are not a reflection of changes in the size of area studied. The boundaries of the study area were fixed for the duration of the 6-year study. Within the study area, an attempt was made to survey all known prairie-dog colonies for plovers. Some small colonies were occasionally missed, but plovers seldom occupied these colonies (Olson-Edge and

Edge 1987). Thus, study area coverage was nearly complete each year and population trends reflected real changes in the numbers of mountain plovers within this area.

Prognosis

At present, the mountain plover population in southern Phillips County appears to be stable at about 175 individuals (Chapter 2). The viability of such a small population is unknown, although they successfully rebounded from estimated population levels below 100 individuals in the mid-1990s. In 2000-2001, there were signs of another sylvatic plague outbreak in prairie dog populations in southern Phillips County. Because mountain plovers in this region are closely tied to black-tailed prairie dog numbers, any future reductions in area occupied by prairie dogs will likely negatively impact plovers. Monitoring should be used to follow plovers through a sylvatic plague outbreak to note the timing and magnitude of declines and recovery and to continue to correlate these changes to the area occupied by prairie dogs.

I cannot address whether the estimate of 175 breeding adults is sufficient to sustain this population for an extended period of time. Despite their small numbers, mountain plovers in southern Phillips County were able to increase rapidly and nearly doubled their population size between 1996 and 1999. My results indicate that recruitment was rather high in 1995, but gradually declined with an increase in the area occupied by prairie dogs, a pattern similar to that exhibited by estimates of annual survival (Table 3.2). The high estimates of recruitment relative to estimates of survival suggest that recruitment was an important component of population growth in this population. This in turn suggests that immigration may have played an important role in this rapid recovery.

The strong negative relationship I found between the area occupied by prairie dogs and both λ and f was unexpected. The area occupied by prairie dogs is a preferred habitat for mountain plovers in this region (Olson 1984) and a predictor of population size (Chapter 2), so I initially expected to find a positive relationship between this measure and both population growth and recruitment. Perhaps the area occupied by prairie dogs is not the best measure of plover habitat; colony-specific features, the spatial arrangement of colonies, or the site fidelity of plovers are all perhaps more important and not related to the total area occupied by prairie dogs.

This information should provide a more solid foundation on which to build conservation measures for mountain plovers. Mountain plovers were recently identified as "highly imperiled" in a review of North American shorebirds, one of five shorebird species receiving this designation (Brown et al. 2001). A petition to federally list the species as Threatened is still under review. With this heightened interest in their conservation, mountain plovers will undoubtedly be the subject of various measures designed to reverse their recent declines.

Research needs

Many research questions remain about mountain plover biology and ecology. Our understanding of their mating system is improving; mountain plovers may regularly practice sequential polyandry rather than strict monogamy (pers. obs.). The skewed sex ratio I found on nests is certainly indicative that something other than monogamy is taking place, at least in Montana. If the mating system is not monogamous, then there is reason to suspect that annual apparent survival may be sex-specific. The habitat requirements of mountain plovers in Montana and elsewhere need further investigation, particularly their preference for active prairie-dog colonies. Why are certain colonies preferred over others? Why does colony usage by plovers change annually for some colonies, but remains consistently high or low for others?

MANAGEMENT IMPLICATIONS

The patchy distribution, low breeding densities, and widespread declines of mountain plovers make them a clear candidate for conservation measures. Plovers are a highly specialized, endemic bird of the western Great Plains and have adapted to an herbivore-driven, arid ecosystem. Threats to their continued existence are many and include habitat loss on the breeding and wintering grounds, regional changes in grazing practices, declines of a primary herbivore (black-tailed prairie dogs), and perhaps threats from agriculture (Knopf and Rupert 1996).

One of the greatest threats to mountain plovers in Montana, and possibly elsewhere within their breeding range, is the continued loss of prairie-dog colonies. Early studies in Montana identified the importance of prairie dogs to mountain plovers (Knowles et al. 1982, Olson and Edge 1985), and I have shown that their numbers closely track changes in area occupied by prairie dogs (Chapter 2). Montana has recently begun work on a statewide prairie dog management plan (Knowles 1999) and it is hoped that this plan will be used to increase prairie dog numbers in the state. The results of this study illustrate that mountain plovers are at least partly dependent on black-tailed prairie dogs, and that the conservation of prairie dogs is thus imperative for plovers.

Threats to prairie dogs in Montana are many and include sylvatic plague, conversion of native lands for agriculture, recreational shooting, and poisoning (Knowles 1999). Of these threats, the latter two are the easiest to address when managing for mountain plovers. Poisoning is having less of an impact on prairie dog numbers in Montana because of the high cost and the reduced need to control prairie dogs due to the impact of plague. Maintenance of poisoning laws, including its ban on federal lands, should minimize impacts to plovers. Recreational shooting is a more contentious issue. A study in southern Phillips County found that the population size of colonies where shooting of prairie dogs was occurring declined during the summer period, although early summer (pre-shooting) densities were not different between "shot" and "non-shot" colonies (Vosburgh and Irby 1998). Recreational shooting of prairie dogs undoubtedly impacts their local numbers, especially on smaller colonies, although impacts on a larger, regional scale are unknown. As suggested by Vosburgh and Irby (1998), shooting pressure may invoke a compensatory response with higher reproduction on "shot" colonies. This, in turn, suggests that light shooting pressure may be sustainable and does not pose either a direct or indirect threat to mountain plovers by reducing colony areas. Currently, the BLM in Phillips County discourages prairie dog shooting and several key colonies for plovers are closed to shooting.

ACKNOWLEDGMENTS

I am grateful to Fort Carson Military Reservation (U. S. Department of Defense), the U. S. Fish and Wildlife Service (Colorado Fish and Wildlife Management Assistance Office), the Biological Resources Division of the U. S. Geological Survey, the U. S. Bureau of Land Management (Malta Field Office, Montana), the Denver Zoological Foundation, and the Fort Belknap Tribal Community for financial support. The staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. J. J. Grensten and B. D. Rosenlund assisted with multiple aspects of the study. A. Brees, D. C. Ely, T.

Hanks, J. G. Jorgensen, C. McQueary, and T. Vosburgh provided field assistance. I thank B. Matovitch, D. Robinson, and J. Robinson for allowing me access to their lands.

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Table 3.1. Summary of model selection results for the population trends of breeding adult mountain plovers in southern Phillips County, Montana, 1995-2000. Models are ranked by ascending Δ-AICc; w_i is the model weight and K is the number of parameters. Apparent survival (ϕ), capture probability (p), recruitment rate (f), and the finite rate of population change (λ) were modeled to include no time effects (.), a linear time trend (T), full time effects (t), or an effect of area occupied by prairie dogs (prairie dog). 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 $[L_s(\hat{\theta})]$.

Model	Deviance	K	AICc	Δ-AICc	w_i
$\phi_{(t)}\ p_{(.)}\ \lambda_{\text{prairie dog}}$	2565.05	8	2581.24	0.00	0.33
$\phi_{(t)}\ p_{(.)}\ f_{\text{prairie dog}}$	2565.12	8	2581.31	0.07	0.32
$\phi_{(t)}\ p_{(.)}\ \lambda_{(T)}$	2565.21	8	2581.40	0.17	0.31
$\phi_{(t)}\ p_{(.)}\ \lambda_{(t)}$	2564.71	11	2587.06	5.83	0.02
$\phi_{(t)}\ p_{(.)}\ \lambda_{(.)}$	2581.34	3	2587.37	6.13	0.02
$\phi_{(t)}\ p_{(t)}\ \lambda_{(t)}$	2564.07	15	2594.71	13.47	0.00

Table 3.2 Model averaged (except for f) estimates ($\pm$SE) of apparent survival (ϕ), recruitment (f), and finite rate of population change (λ) from the Pradel model for adult mountain plovers in southern Phillips County, Montana, 1995-2000.

Year	ϕ	f	λ
1995	0.68 (0.06)	NA	1.42 (0.10)
1996	0.69 (0.05)	0.72 (0.08)	1.34 (0.07)
1997	0.63 (0.04)	0.69 (0.07)	1.22 (0.04)
1998	0.62 (0.04)	0.57 (0.04)	1.08 (0.04)
1999	0.63 (0.05)	0.44 (0.04)	0.99 (0.06)
2000	NA	0.38 (0.04)	NA

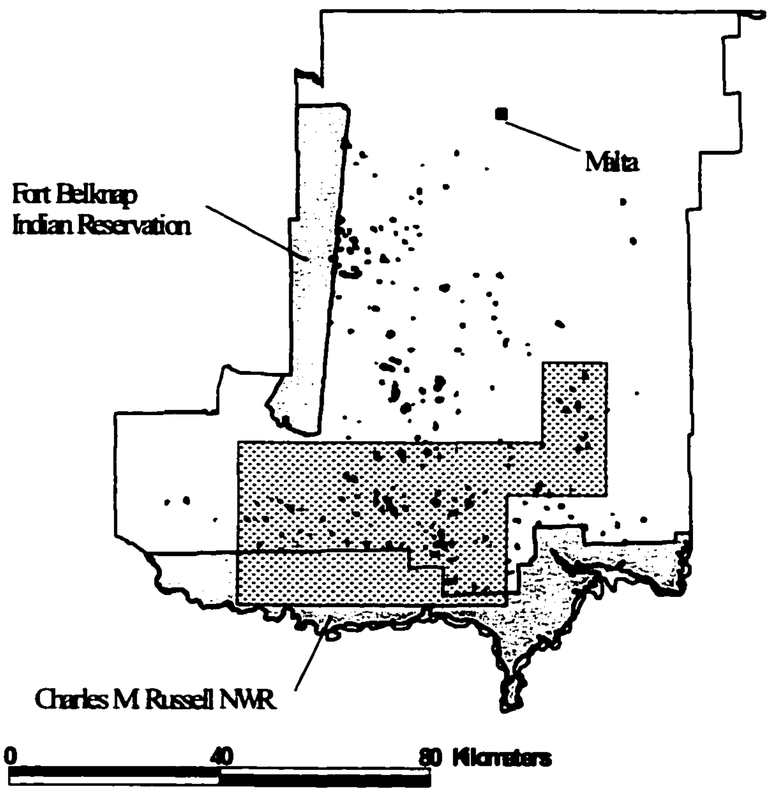

Figure 3.1. Map of southern Phillips County, Montana showing the distribution in 2000 of black-tailed prairie-dog colonies. The stippled region represents the study area.

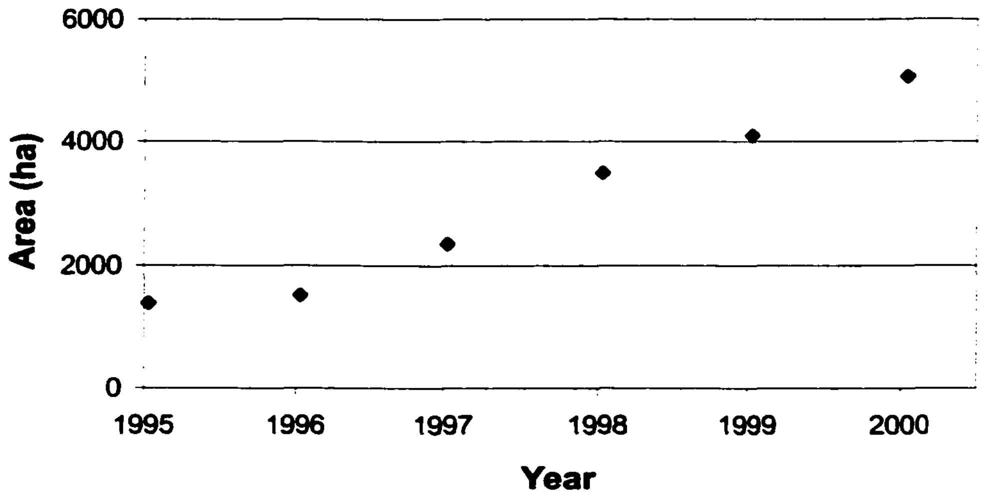

Figure 3.2. Area occupied by black-tailed prairie dogs in southern Phillips County, Montana, 1995-2000. Areas were calculated from annual Bureau of Land Management surveys; areas from 1998 and 2000 are from complete censuses while all other estimates are predicted areas based on annual samples of one third of all known colonies.

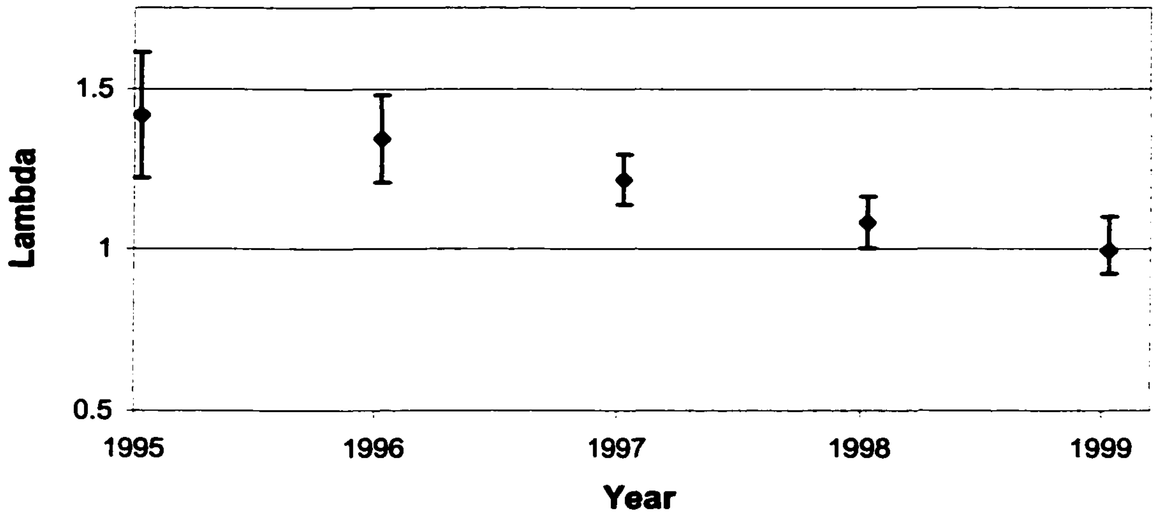

Figure 3.3. Model-averaged estimates and 95% confidence intervals of annual population trends (λ) for adult mountain plovers in southern Phillips County, Montana, 1995-1999.