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DISSERTATION

POPULATION BIOLOGY OF MOUNTAIN PLOVERS IN SOUTHERN PHILLIPS COUNTY, MONTANA

Submitted by

Stephen J. Dinsmore

Department of Fishery and Wildlife Biology

PREVIEW

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.

Committee on Graduate Work

Gary C. White, Advisor

Department Head

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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.

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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

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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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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

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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

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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.

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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.

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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

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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.

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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.

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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.

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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

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