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Incubation behavior and dispersal patterns in the Mountain Plover (*Charadrius montanus*)

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**Incubation behavior and dispersal patterns in the
Mountain Plover (*Charadrius montanus*)**

by

Paul Daniel Blom Skrade

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Animal Ecology

Program of Study Committee:

Stephen J. Dinsmore, Major Professor

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Ames, Iowa

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TABLE OF CONTENTS

LIST OF TABLES	iii
LIST OF FIGURES	v
ACKNOWLEDGEMENTS	vii
CHAPTER I - INTRODUCTION	1
CHAPTER II - SEX-RELATED DISPERSAL IN THE MOUNTAIN PLOVER (<i>CHARADRIUS MONTANUS</i>)	5
CHAPTER III - INCUBATION BEHAVIOR OF THE MOUNTAIN PLOVER (<i>CHARADRIUS MONTANUS</i>)	32

LIST OF TABLES

<p>Table 2.1. Summary statistics of breeding dispersal distances (km) of Mountain Plovers (<i>Charadrius montanus</i>) in southern Phillips County, Montana, U.S.A., 1995-2007.</p>	26
<p>Table 2.2. Model selection results for a mixed model analysis of ln-transformed distances moved between successive nesting attempts by Mountain Plovers (<i>Charadrius montanus</i>) in Phillips County, Montana, U.S.A., 1995-2007. Model factors include sex (male or female plovers), fate (hatch or fail), and plague (nest colonies that experienced a sylvatic plague event between nesting attempts) along with two-way interactions of each of these, and year. Models are ranked by differences in Akaike’s Information Criterion (ΔAIC_C) adjusted for sample size, w_i is the Akaike weight and K represents the number of parameters.</p>	27
<p>Table 2.3. Model selection results for subsequent nest fate using a logistic regression of ln-transformed distances moved between successive nesting attempts by Mountain Plovers (<i>Charadrius montanus</i>) in Phillips County, Montana, U.S.A., 1995-2007. Model factors include sex (male or female plovers), initial nest fate (hatch or fail), and plague (nest colonies that experienced a sylvatic plague event between nesting attempts) along with two-way interactions of each of these. Models are ranked by differences in Akaike’s Information Criterion (ΔAIC_C) adjusted for sample size and K represents the number of parameters.</p>	28
<p>Table 3.1. Model selection results for a mixed model analysis of duration of nocturnal departure of incubating Mountain Plovers (<i>Charadrius montanus</i>) in Phillips County, Montana, U.S.A., 2006-2008. Model factors include sex (Sex; male or female), a linear</p>	

effect of day of incubation (Age; 1-31 days), a linear effect of day of sampling season (Season; 1-73), the quadratic effect of time of departure from middle of night (Time^2 ; half the length of time from sunset to the following sunrise), year (Year; 2006-2008), method of data collection (Method; video and temperature data loggers), and all the two-way interactions with important main effects. Models are ranked by differences in Akaike's Information Criterion (ΔAIC_C) adjusted for sample size, w_i is the Akaike weight, and K represents the number of parameters. 54

LIST OF FIGURES

- Figure 2.1. Linear dispersal distances (km) between successive nesting attempts of Mountain Plovers (*Charadrius montanus*) at the black-tailed prairie dog (*Cynomys ludovicianus*) complex level, Phillips Co. southern Phillips County, Montana, U.S.A., 1995-2007. “XX/Y/Z/0.00km” represents the year, sex of the tending adult (male/female), fate of the initial nest (successful/unsuccessful), and the distance moved.29
- Figure 2.2. Number of Mountain Plovers (*Charadrius montanus*) and the number of pairs of nesting attempts contributed to examine effects of previous nest fate, sex of the tending adult, and the presence of sylvatic plague on inter-year movements in southern Phillips County, Montana, U.S.A., 1995–2007.30
- Figure 2.3. Test for interaction between male and female Mountain Plover (*Charadrius montanus*) dispersal distances (km) in relation to fates of successive nesting attempts and presence or absence of sylvatic plague on their nest colony in southern Phillips County, Montana, U.S.A., 1995–2007. Points are constructed from means of ln-transformed distances between successive nesting attempts.....31
- Figure 3.1. Characteristic nest temperature trace (°C) of Mountain Plover (*Charadrius montanus*) nocturnal incubation behavior, Phillips County, Montana, U.S.A., 22–23 July 2007. Temperatures were recorded every minute using a data logger placed in the nest, while departure and return times were determined from remote video observation.55
- Figure 3.2. Characteristic nest temperature trace (°C) of Mountain Plover (*Charadrius montanus*) diurnal incubation behavior, Phillips County, Montana, U.S.A., 11 July 2007.

Temperatures were recorded every minute using a data logger placed in the nest, while departure and return times were determined from remote video observation.56

Figure 3.3. Number of departures from the nest video-hour⁻¹ by six male and 24 female Mountain Plovers (*Charadrius montanus*) observed in Phillips County, Montana, U.S.A., 2007. Time of day references the hour on a 24-hour clock, e.g., 00 refers to the hour from midnight to 1 a.m.57

Figure 3.4. Mean length of departure from the nest by six male and 24 female Mountain Plovers (*Charadrius montanus*) observed in Phillips County, Montana, U.S.A., 2007. Time of day references the hour on a 24-hour clock, e.g., 00 refers to the hour from midnight to 1 a.m.58

Figure 3.5. Model estimated lengths of nocturnal departures from incubation (hrs) in relation to the mid-time between sunset and sunrise for Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A. “Best” and “Second” refer to the top models that both incorporate a quadratic time effect along with a cubic time term and a linear time trend respectively.59

Figure 3.6. The effects of day of season on duration of nest departures (hrs) in relation to the mid-time between sunset and sunrise for Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A. Day 1 corresponds to 18 May and Day 75 corresponds to 31 July.60

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CHAPTER I

INTRODUCTION

The Mountain Plover (*Charadrius montanus*) is an uncommon and declining bird endemic to the Great Plains and Great Basin (Knopf and Wunder 2006). They breed in several western states, but the largest numbers occur in Montana, Wyoming, and Colorado (Knopf and Wunder 2006). The Montana breeding population nests primarily on active black-tailed prairie dog (*Cynomys ludovicianus*) colonies (Knowles et al. 1982, Knowles and Knowles 1984), which provide the mix of short-grass habitat and bare ground that this species prefers. Historically this type of habitat was found in areas of disturbance such as burned or heavily-grazed sites (Knopf and Wunder 2006). The disappearance of the American bison (*Bison bison*), increased fire suppression, and the removal of prairie dogs from much of the landscape are some of the factors that caused a decrease in suitable nesting habitat. Throughout their range, the characteristics of individual prairie-dog colonies are variable and subject to change as a result of sylvatic plague outbreaks (Collinge et al. 2005, Augustine et al. 2008).

Mountain Plovers are fairly large (90-110 g) and drably colored members of the Family Charadriidae. While they have low annual survival their first year of life (0.06; Dinsmore 2008), once they reach adulthood they are fairly long-lived. Recent estimates of annual survival rates of adults range from 0.74 to 0.96 (Dinsmore 2008) and there are several records of individuals older than five years and at least three records of individuals living >10 years (S. J. Dinsmore pers. comm.).

Mountain Plovers exhibit some degree of sociality, nesting in loose semi-colonies (Graul 1975), and they have an uncommon mating system known as a rapid multi-clutch (Graul 1973) where each member of a pair tends its own nest. While both male and female plovers tend individual nests unaided, and therefore have similar incubation and chick-

rearing responsibilities, it is thought that the males arrive first to the breeding grounds in early to mid-April, establish loose territories, and compete for females (Graul 1973). This is a “resource defense” system where the male digs scrapes and displays within his territory to court females and, once the pair-bond has been formed, she lays a 3-egg clutch in his territory. The male then incubates those eggs and tends to the resulting precocial chicks, brooding them at cooler temperatures and defending them from predators. Females have been observed mating with more than one male, suggesting that sequential polyandry may also occur (Graul 1973). Ultimately the female lays a separate 3-egg clutch that she tends to entirely by herself.

Their unique mating system has allowed for studies comparing the effectiveness of the two sexes at separately raising young. So far there has been evidence for differences in nest survival (Dinsmore et al. 2002) and brood survival (Dinsmore and Knopf 2005) with males having higher nest success and females having higher fledging success. Prior studies of Mountain Plovers have noted that banded individuals sometimes returned to the general area they had nested in previously (Graul 1973, Ellison-Manning and White 2001a, 2001b), even to the extent of using the same nest cup (Knopf and Wunder 2006), although there have been no comprehensive studies of their site fidelity.

The eggs are darkly colored and exceptionally thick for the Charadriinae (Graul 1975) which makes them susceptible to overheating during periods of high ambient temperature and solar radiation. During these times the incubating adult stands over the eggs to shade them, panting and gular fluttering to cool itself and unable to leave the nest to for self-maintenance (Knopf and Wunder 2006). Later in the season, when the temperatures are at their highest, birds would be confined to their nests during the day and so might have increased lengths of their nocturnal off-bouts. An early study of this species that looked at incubation found that adults were at their nest more frequently the closer the eggs were to hatching and incubating adults were away from the nest both during the day and at night

(Graul 1975). However, these results were based on a small number of nests and presence/absence of the incubating adult was noted at nest checks.

I examined the dispersal and incubation behavior of Mountain Plovers in Montana to expand on current knowledge of these important aspects of their life history. My objectives (Chapter II) were to 1) examine the influence of sex on natal dispersal of juvenile Mountain Plovers, 2) examine the influence of sex on intra-year breeding dispersal of adult Mountain Plovers, 3) model inter-year breeding dispersal of adult Mountain plovers and examine the effects of i) prior experience, ii) sex of the nest-tending adult, and iii) presence of sylvatic plague, and 4) see if the distance moved between successive nesting attempts could be used to predict subsequent nest fate. I also quantified incubation activity (Chapter III) of nesting Mountain Plovers using a combination of video monitoring and temperature data loggers to examine sex-specific differences in behavior. The purposes of this aspect of my study were to 1) describe the activity patterns of Mountain Plovers during the incubation stage, and 2) gain a better understanding of activity patterns in relation to sex of the tending adult, the nest age, and the time of the breeding season. By addressing these topics of Mountain Plover breeding biology I not only improve our knowledge of behavior in an uncommon mating system, but also provide insight into behaviors that might enable land managers to better address conservation issues facing this species.

Literature Cited

Augustine, D. J., S. J. Dinsmore, M. B. Wunder, V. J. Dreitz, and F. L. Knopf. 2008.

Response of mountain plovers to plague-driven dynamics of black-tailed prairie dog colonies. *Landscape Ecology* 23:689–697.

Collinge, S. K., W. C. Johnson, C. R. Ray, R. Matchett, J. Grensten, J. F. Cully Jr., K. L.

Gage, M. Y. Kosoy, J. E. Loye, and A. P. Martin. 2005. Landscape structure and plague occurrence in black-tailed prairie dogs on grasslands of the western U.S.A. *Landscape Ecology* 20:941–955.

- Dinsmore, S. J. 2008. Influence of drought on the annual survival of the Mountain Plover in Montana. *Condor* 110:45–54.
- Dinsmore, S. J., and F. L. Knopf. 2005. Differential parental care by adult Mountain Plovers, *Charadrius montanus*. *Canadian Field-Naturalist* 119:532–536.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Ellison Manning, A. E., and C. M. White. 2001a. Breeding biology of Mountain Plovers (*Charadrius montanus*) in the Uinta Basin. *Western North American Naturalist* 61: 223-228.
- Ellison Manning, A. E., and C. M. White. 2001b. Nest site selection by Mountain Plovers (*Charadrius montanus*) in a shrub-steppe habitat. *Western North American Naturalist* 61: 229-235.
- Graul, W. D. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12: 69-94.
- Graul, W. D. 1975. Breeding Biology of the Mountain Plover. *Wilson Bulletin* 87: 6-31.
- Knopf, F. L., and M. B. Wunder. 2006. Mountain Plover (*Charadrius montanus*). In *The Birds of North America*, no. 211 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Knowles, C. J., and P. R. Knowles. 1984. Additional records of Mountain Plovers using prairie dog towns in Montana. *Prairie Naturalist* 16:183–186.
- Knowles, C. J., C. J. Stoner, and S. P. Gieb. 1982. Selective use of Black-tailed Prairie Dog towns by Mountain Plovers. *Condor* 84:71–74.

CHAPTER II

SEX-RELATED DISPERSAL IN THE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*)

Abstract

The rapid multi-clutch mating system of the Mountain Plover (*Charadrius montanus*) provides an interesting opportunity to examine sex differences in natal and breeding dispersal. I used nest locations from a breeding population of plovers in north-central Montana over a 13-year period (1995-2007) to examine patterns of sex bias in their dispersal. Additionally, I looked at the influence of prior experience and sylvatic plague on breeding dispersal in successive years. I also modeled successive nest fate using breeding dispersal distance with sex, previous nest fate, and presence of sylvatic plague as covariates in the model. I found no sex-bias in natal dispersal or within-year breeding dispersal. The mean dispersal distance of male plovers in consecutive years was 2.75 km (95% CI 1.51 to 4.00) and for females was 4.64 km (95% CI 2.76 to 5.52). Birds that were successful moved 3.02 km (95% CI 1.87 to 4.17) on average between nesting attempts, while those whose nests had failed moved 5.06 km (95% CI 2.53 to 7.58). The best model of between-year breeding dispersal contained the full set of parameters, with sex of the tending adult and prior nest fate having the strongest effects. The estimate of dispersal distance for females was positive ($\hat{\beta}_{\text{Female}} = 0.86$, 95% CI 0.67 to 1.05) as well as the estimate of dispersal distance for birds whose nests had failed the previous year ($\hat{\beta}_{\text{Fail}} = 0.82$, 95% CI 0.52 to 1.13). There was a year effect but no effect of sylvatic plague on dispersal. This study not only provides a better understanding of dispersal in an uncommon mating system but also is important in understanding the movements of a species of conservation concern.

Introduction

While there has been much work done in the nearly three decades following Greenwood's (1980) review of mating systems, philopatry, and dispersal in birds, many of the driving forces behind dispersal are still poorly understood. Several factors are thought to influence a bird's movements, such as inbreeding avoidance, previous nest fate, sex of the individual, and habitat quality (Greenwood 1980, Greenwood and Harvey 1982) but the relative impacts of these factors differ among species and among studies. Both breeding dispersal (the distance a bird moves between successive nesting attempts) and natal dispersal (the movement from natal location to first breeding site), as defined by Greenwood and Harvey (1982), play roles in population ecology and evolution (Clobert et al. 2001) and so improving our understanding of the mechanisms influencing these movements should be prioritized.

One factor that influences both avian natal and breeding dispersal is the sex of the individual. There is often a sex bias in breeding site fidelity among migratory bird species. Males tend to be more philopatric than females (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997), although in sex-role reversed species, males tend to be the dispersing sex (Reed and Oring 1993, Clarke et al. 1997). This difference in dispersal is usually attributed to differing parental roles and is thought to be associated with resource or mate defense (Greenwood 1980). For example, in a situation where one sex must acquire and defend a territory, the advantage of site familiarity is thought to cause that sex to disperse shorter distances.

Other work has shown that previous nesting success can also affect avian breeding dispersal. Several studies of passerines have demonstrated how prior experience influences dispersal distances as well as the probability of dispersing (Haas 1998, Hoover 2003, Porneluzi 2003, Sedgwick 2004). Birds that have been previously successful tend to move shorter distances, have higher return rates and remain more site faithful than birds whose nests failed. This is based on the idea that at the end of a breeding season, individuals make a decision about whether or not to return to that site based on their success in that year. This

is often referred to as the “Decision Rule” in the Prior Experience Hypothesis (Haas 1998, Hoover 2003). However, the effects of previous fate can be confounded by variation between sex and age classes with females and younger birds more likely to disperse farther (Payne and Payne 1993).

Many studies of dispersal have focused on monogamous birds where parental roles are easily defined, although there have been exceptions with studies of communal and cooperative breeders (Bowen et al. 1989, Mulder 1995). The Charadriidae include diverse mating systems (Ligon 1999) that offer opportunities to study the roles of sex, prior experience, and habitat change in novel systems. The Mountain Plover (*Charadrius montanus*) is a fairly large (90-110 g) and drably-colored member of this family with a rapid multi-clutch mating system (Graul 1973) where each member of a pair tends its own nest. This mating system is uncommon within bird breeding biology literature (Lack 1968, Oring 1982, 1986). While both male and female Mountain Plovers tend individual nests unaided, and therefore have similar incubation and chick-rearing responsibilities, it is thought that the males arrive first to the breeding grounds in early to mid-April, establish loose territories, and compete for females (Graul 1973). This is a “resource defense” (rather than “mate defense”) system where the male digs scrapes and displays within his territory to court females, and females are predicted to be the dispersing sex.

The Mountain Plover is an uncommon and declining bird endemic to the Great Plains and Great Basin (Knopf and Wunder 2006). They breed in several western states, but the largest numbers occur in Montana, Wyoming, and Colorado (Knopf and Wunder 2006). The Montana plovers nest primarily on active black-tailed prairie dog (*Cynomys ludovicianus*) colonies (Knowles et al. 1982), which provide the mix of short-grass habitat and bare ground that this species prefers. Historically this type of habitat was characteristically found in areas of disturbance such as burned or heavily-grazed areas (Knopf and Wunder 2006). The disappearance of the American Bison (*Bison bison*), increase in fire suppression, and the

removal of prairie dogs from much of the landscape are some of the factors that caused a decrease in suitable nesting habitat. The characteristics of individual prairie dog colonies are variable and subject to sylvatic plague outbreaks. This epizootic can completely wipe out a prairie dog colony within the course of a single breeding season (Collinge et al. 2005, Pauli et al. 2006) making it unsuitable for nesting in the following year. Long-term studies of the plover in north-central Montana have allowed for studies comparing the effectiveness of the two sexes at separately raising young. So far there has been evidence for differences in nest (Dinsmore et al. 2002) and brood (Dinsmore and Knopf 2005) survival with male-tended nests and female-tended broods having greater success.

Previous studies of Mountain Plovers have noted that individual birds return to the general area they had nested in previously (Graul 1973, Manning and White 2001a, 2001b), even to the extent of using the same nest cup (Knopf and Wunder 2006), yet dispersal in this species has not been quantified. Such an understanding is necessary to better evaluate their use of this declining habitat. My objectives were to 1) examine the influence of sex on natal dispersal of juvenile Mountain Plovers, 2) examine the influence of sex on intra-year breeding dispersal of adult Mountain Plovers, 3) examine inter-year breeding dispersal of adult Mountain plovers and the effects of i) prior experience, ii) sex of the nest-tending adult, and iii) the presence of sylvatic plague, and 4) determine whether the distance moved between successive nesting attempts could be used to predict subsequent nest fate.

Methods

Study Area

I studied the dispersal of Mountain Plovers over 13 breeding seasons in an approximately 3000 km² area located in southern Phillips County in north-central Montana (47°40'– 47°55' N, 107°35'– 108°30' W). The study area is bordered by Highway 191 to the west, Beaver Creek to the north, the Sun Prairie and Content roads to the east, and the Missouri River to the south (Dinsmore et al. 2002). Roughly 2,250 km² 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). Vegetation in the study area is typical of shrub-steppe habitat with predominantly short sparse vegetation (Smith et al. 1984) consisting mostly of big sagebrush (*Artemisia tridentata*), silver sagebrush (*Artemisia cana*), greasewood (*Sarcobatus vermiculatus*), yellow sweetclover (*Melilotus officinalis*), green needlegrass (*Stipa viridula*), and western wheatgrass (*Agropyron smithii*) (Dinsmore et al. 2003). The disturbance regime includes grazing by domestic cattle (*Bos taurus*) and black-tailed prairie dogs.

In my study area plovers are closely tied to prairie dog dynamics (Knowles et al. 1982, Knowles and Knowles 1984, Dinsmore and Knopf 2005). Active black-tailed prairie dog colonies contain scattered areas of bare ground interspersed with sparse vegetation that include fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polyantha*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*), with older colonies having less grass than newer colonies. I use the term “prairie dog complex” for colonies that have movement of prairie dogs between them, but are distinct when mapped (Bever et al. 1997).

Nest searching and monitoring

I collected nesting data on Mountain Plovers during the 2006 and 2007 breeding seasons and combined these with data from the period 1995–2005 to examine dispersal in Mountain Plovers. Field work began in mid-May and continued until the end of the birds’ breeding season, usually late July or early August. Nest searching techniques were similar across years. All active black-tailed prairie dog colonies within the study area (~200) were systematically searched ≥ 3 times during the breeding season. This was done by driving slowly across the colony and periodically stopping to scan for plovers, with the vehicle functioning as a blind.

When an adult Mountain Plover was located I watched it from a distance until it returned to its nest. When the location was determined I then placed two small rock cairns approximately 2 m to either side of the nest to mark it for further relocation. This manner of marking, while additionally recording the coordinates using a hand-held global positioning system (GPS), made it possible to relocate nests and reduce the chance of attracting predators. Once found, nests were checked every 3–7 days until they had hatched or failed, and egg age was estimated by examining the specific gravity of eggs in a column of water (Westerskov 1950).

Capture and marking of Mountain Plovers generally followed the procedures described in Dinsmore et al. (2002). Hatch-year plovers were captured by hand prior to fledging. Plover chicks remained on their hatch colony until they fledged and were usually located either in the immediate proximity of the nest cup shortly after hatching or by waiting until the tending adult moved the chicks as a group with distraction displays. Adult Mountain Plovers remain with their chicks until fledging, brooding the chicks during cooler parts of the day and protecting them from predators. Nest-tending adult plovers were captured using a walk-in trap constructed of chicken wire placed over the nest. When birds were in hand, feather and blood samples were taken for future analysis and genetic sexing. Tarsus length, exposed culmen, and mass were all measured and recorded and also wing-chord for adults. Finally, plovers were leg-banded with an aluminum USGS size 3A band and a unique combination of four colored bands. This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol number 5-06-6129-Q.

Spatial data collection and preparation

At the end of the nesting season coordinates of all nests were recorded using a Trimble Geo XT[®] handheld GPS unit running TerraSync software (Trimble Navigation Limited Sunnyvale, CA). The GPS unit was placed in the empty nest cup and the location was averaged across 180 measurements taken every second. I mapped active black-tailed prairie

dog colonies by delineating the colony perimeter based on straight-line distances between active burrows. Active burrows were those burrows that had fresh (≤ 1 week old) droppings, fresh (≤ 1 week old) diggings, or harbored ≥ 1 prairie dog during my visit. Colonies in the study area were mapped every year except 1997, 2003, and 2006. All points and polygons were differentially corrected using Pathfinder Office Software (Trimble Navigation Limited Sunnyvale, CA) in Montana State Plane (NAD83) units. Colony centroids were determined by using ArcGIS (Version 9.2; ESRI, Redlands, CA) and I calculated the mean centroid for each colony over the entire study period, as not every colony was mapped in every year.

To examine natal dispersal in Mountain Plovers I used data from birds that were banded as chicks and were then either found on a nest or tending a brood in the study area the following year. If the location of their first nesting attempt was known I calculated the linear distance between the centroid of the colony where the bird had hatched and the coordinates of its first nesting attempt. To increase the sample size I also used data from one-year-old birds that returned to the study area and were found tending a brood on a colony. To produce natal dispersal distances for these individuals I measured from the centroid of the colony where they hatched to the centroid of the colony where they were brood-rearing.

To evaluate breeding dispersal I calculated the linear distance between consecutive nesting attempts. This was done at two levels: 1) Mountain Plovers that re-nested in the study area within a single breeding season because of initial nest failure and 2) plovers that had successive nesting attempts in the study area in consecutive years (Figure 2.1). All distances were ln-transformed to improve normality.

Establishing Effects

I determined the sex of all Mountain Plovers used in these analyses to ask questions about the role of sex in both natal and breeding dispersal patterns. Because these plovers are sexually monomorphic and cannot be reliably sexed at a distance or in hand, sex was determined from feather or blood samples by Avian Biotech International (Tallahassee, FL) using molecular

techniques outlined in Dinsmore et al. (2002). To compare differences in the distances moved between successive nesting attempts in relation to nest fate, the fates of nests had to be determined. This was done by using several pieces of information, usually a combination of nest age through egg-flotation, visual signs of disturbance, the presence of eggshell evidence in collected nest contents (Mabee 1997), and sightings of chicks in or near the nest cup or later on the prairie dog colony. A nest was considered successful if ≥ 1 egg hatched. I determined colony specific plague events to examine its effect on dispersal distances. Most plague occurs visibly during the summer months. By the end of the breeding season >95% of the prairie dogs have succumbed to the disease (Collinge et al. 2005, Pauli et al. 2006) and the colony is often hardly recognizable as such (pers. obs.). At each visit to a colony I visually noted prairie dog activity and signs of possible plague and later assigned plague prevalence (plague noted or absent) to each pair of successive nesting attempts. A colony experiencing a plague event showed reduced prairie dog activity, vegetative growth on burrows, and occasionally had sick or dying prairie dogs present. Although predation is the largest cause of nest failure in my study area (pers. obs.) other factors such as weather (high levels of precipitation or extreme temperatures; Dinsmore et al. 2002), human disturbance, and abandonment can also cause nest failure. Without including actual measurements for environmental variables for each breeding season, I used “year” as a surrogate to see if other effects influenced dispersal.

I developed a set of a priori predictions based on previous studies to explain Mountain Plover dispersal patterns. I outline these below in relation to natal dispersal and within- and between-year dispersal of adults.

Natal dispersal: In the majority of avian mating systems where males compete for females by defending suitable nesting habitat, females tend to be the dispersing sex (Greenwood and Harvey 1982). It is thought that male Mountain Plovers in Phillips County,

Montana defend nest territories that females then choose among, so I predicted that juvenile females would have greater natal dispersal distances than juvenile males.

Within-year breeding dispersal: The mechanisms are similar to natal dispersal because this is believed to be a resource-defense mating system (Greenwood 1980). Therefore I predicted greater within-year breeding dispersal distances for females than males.

Between Year Breeding Dispersal:

- 1) Based on the Decision Rule Theory of the Prior Experience Hypothesis (Greenwood 1980), Mountain Plovers that were successful the previous year would disperse shorter distances than those that were unsuccessful.
- 2) Similarly to natal and within-year dispersal, I expected males to be more site-faithful than females and would disperse shorter distances.
- 3) A plague event would make a colony uninhabitable for a nesting plover, so I predicted that birds that nested on colonies experiencing plague the previous year would disperse greater distances than those nesting on unaffected colonies.

Statistical Analyses

I examined dispersal for plovers that 1) made a second nesting attempt after a nest failure within a year, or 2) made successive nesting attempts in consecutive years. Any nests that were abandoned or where the fate might have been influenced by human activity were excluded. Over the 13-year period a number of plovers contributed more than one pair of nesting attempts to these analyses (Figure 2.2).

To examine differences in natal dispersal by sex I used the Wilcoxon-rank sum test in the JMP statistical package (Version 6; SAS Institute, Cary, NC). The effects of plague and year could not be rigorously tested due to small sample sizes. Differences between males and females were considered significant at $\alpha < 0.05$. I used the MIXED procedure in SAS (Version 9.1; SAS Institute, Cary, NC) to compare breeding dispersal distances while accounting for multiple contributions from individuals. I modeled ln-transformed distances

in relation to nest fate, sex of the tending adult, and whether the colony on which the first nest was located experienced plague between successive nesting attempts, although plague was not included in analyses of within-year breeding dispersal due to inadequate sample size. Each of these factors was binary and all possible combinations of main effects plus additive and two-way interactions were tested. I included two-way interactions because a plot of the means of the ln-transformed distances indicated that some might occur (Figure 2.3). I used Akaike's Information Criterion corrected for small sample size (AIC_C ; Akaike 1974) to determine the best model from this initial set. Then, I included the additive effect of year to any models of between-year dispersal with $\Delta AIC_C \leq 2$, as within-year dispersal again lacked sufficient samples. I reported model-averaged estimates of betas ($\hat{\beta}$ and 95% CI) with the unconditional 95% confidence intervals and used them for inference (Burnham and Anderson 2002).

To examine if dispersal distances could predict subsequent nest fate I used the Logistic procedure in SAS (Version 9.1; SAS Institute, Cary, NC). Again, I included the additive effects of sex, fate, and plague in the model, along with the two-way interactions of each of these. However, I did not include the effects of year because of limited sample sizes. I used AIC_C to determine which model was best supported and any models that were ≤ 2 ΔAIC_C from the best model were considered competitive and used for inference.

Results

Over the 13-year period, a total of 35 Mountain Plovers (14 males and 21 females out of >750 total) banded as chicks returned to nest the following year. The median natal dispersal distance for males was 13.24 km (mean = 14.38 km; 95% CI 7.23 to 21.54) and for females was 9.04 km (mean = 10.58 km; 95% CI 6.68 to 14.49) and they did not differ (Wilcoxon-rank sum, $z_{33} = 0.72$, $P = 0.46$). Only one male and one female returned to their natal colonies to breed, but roughly 30% of males and 40% of females nested on colonies within the prairie dog complex that included their natal colony.

There were 43 cases where Mountain Plovers re-nested during the same breeding season. Of these, 19 were males with a median breeding dispersal distance of 0.34 km (mean = 3.22 km, 95% CI 0.38 to 6.07) and 24 were females, whose median breeding dispersal was 0.67 km (mean = 3.51 km, 95% CI 1.56 to 5.46) and they did not differ (mixed model, $F_1 = 0.98$, $P = 0.40$). Nearly 70% of males and 60% of females remained on the same prairie dog colony of their initial nest attempt, and 75% and 70% respectively remained in the same prairie dog complex.

A total of 148 Mountain Plovers contributed 183 pairs of nesting attempts for analyses of breeding dispersal between years (Table 2.1). The results of the mixed model (Table 2.2) showed that in the first stage of the analysis, the two competitive models included all three of the main effects, plus the interactions of sex and plague and fate and plague. The second best model lacked the two-way interaction of sex and fate. In the second stage, the additive effect of year greatly improved both models. When the betas were model averaged there was strong evidence of both sex ($\hat{\beta}_{\text{Female}} = 0.86$, 95% CI 0.67 to 1.05) and fate ($\hat{\beta}_{\text{Fail}} = 0.82$, 95% CI 0.52 to 1.13) effects but no evidence of a plague effect ($\hat{\beta}_{\text{Plague}} = 0.40$, SE = 0.13, 95% CI -0.32 to 1.11). There was evidence that eight years differed when compared to the reference year (2002) and there was no effect of the two-way interactions (confidence intervals overlapping zero).

By sex, 66% of males and 50% of females returned to the previous year's colony to nest, and roughly 80% and 70% of each returned to the same prairie dog complex. Roughly 66% of birds whose nests were successful the previous year returned to the colony they had nested on previously, but only 40% of birds from nests that failed returned. At the prairie dog complex-level almost 80% of successful and 70% of unsuccessful birds nested in nearby colonies (<3 km) in the next nesting season. If the colony had experienced plague during the previous nesting attempt roughly 50% nested in a different colony the following year, and if there had been no plague, roughly 40% moved to a different colony. Almost 70% of birds on

plague-affected colonies and 77% on unaffected colonies nested in the same complex the next year.

The results of the model predicting nest fate from dispersal distance (Table 2.3) showed that the main effect of sex alone was in the best model, and sex was also included in two of the other three competitive models in the top four. While there was not strong evidence for any of the main effects in the competitive models, in the best two models there was weak evidence of a sex effect ($\hat{\beta}_{\text{sex}} = 0.27$, 95% CI -0.05 to 0.59).

Discussion

Natal dispersal distances were similar for male and female Mountain Plovers in southern Phillips County, Montana and these results are consistent with patterns in related species. In two recent studies of natal dispersal of Snowy Plovers (*C. alexandrinus*), one found evidence for female-biased dispersal (Stenzel et al. 2007), while the other found no sex bias (Colwell et al. 2007). Other studies of natal dispersal in plovers had similar results (Clarke et al 1997, Flynn et al. 1999), but studies of other Charadriiformes (sandpipers, gulls, curlews, and godwits) found both a female-biased natal dispersal (Clarke et al. 1997) as well as no sex bias (Gratto 1988). In the male nest-tending Red-necked Phalarope (*Phalaropus lobatus*, Schamel and Tracy 1991) and Spotted Sandpiper (*Actitis macularia*, Reed and Oring 1993) there was evidence for male-biased natal dispersal.

Out of >750 juvenile plovers banded in the study area over the 13-year period, only 35 returned and nested in their first year. One possible explanation might be that juveniles banded as young chicks (<1 week old) may not have survived. Estimates of juvenile annual survival are low (0.06; Dinsmore 2008) and survival is lowest right after hatch and increases as the chicks age (Lukacs et al. 2004, Dinsmore and Knopf 2005). Thus, many young chicks banded in their first week would not have survived to fledge, let alone return in a later year. Several birds returned to the study and were resighted but not found on nests during their first year and while other juveniles may have dispersed to nest in other areas such as Fort Belknap

Indian Reservation and southern Valley County, both <50 km from my study site. Moderate numbers of plovers nest at each site and juveniles color banded in Phillips County have been found breeding at each site in small numbers (S. J. Dinsmore, pers. comm.). The combination of these two phenomena could explain why such a small proportion (<5%) returned to the natal area to nest in their first year.

There have been few studies of within-year breeding dispersal distances and they appear to be more constrained than between-year movements, possibly limited by territory availability (Greenwood and Harvey 1982). Mountain Plovers in Phillips County, Montana may be experiencing habitat saturation because prairie dog colonies represent <1% of the landscape. Mountain Plovers enjoy some degree of sociality, and tend to form loose semi-colonies (Graul 1975). At the height of the breeding season preferred nesting locations might already be occupied causing birds that experience nest failure to disperse farther. While there are certainly other factors influencing within-year breeding dispersal, sex is still likely to be one of the most important, but it was probably undetectable in my study due to small sample sizes and large variability. Colwell et al. (2007) found Snowy Plovers breeding within a year often bred at a single site, rather than moving among sites and males tended to be slightly more sedentary than females. However, this species is able to produce multiple successful clutches within a breeding season which is likely to influence their dispersal.

The sex effect in the mixed model is the result of female Mountain Plovers having greater breeding dispersal between years than males. This fits with the hypothesis that in this male resource-defense system, male plovers would have shorter dispersal distances and remain more site faithful than females. This finding is consistent with several previous studies of Charadriidae that have shown female-biased between-year breeding dispersal (Johnson et al. 1993, Jackson 1994, Clarke et al. 1997, Flynn et al. 1999) although other studies of plovers have shown no sex bias (Thompson et al. 1994, Wallander and Andersson 2003). In species with solely male-tended nests there have been cases of no sex bias in site

fidelity (Schamel and Tracy 1991) as well as cases of male-biased dispersal (Oring and Lank 1982, Oring and Lank 1984).

Mountain Plovers whose nests were successful the previous year dispersed shorter distances than those that had failed, causing the strong fate effect in the mixed model. This increase in dispersal distance due to nest failure provides support for the “Decision Rule” theory of the Prior Experience Hypothesis, as birds that were successful tended to be more site-faithful. This has also been found with other Charadriiformes (Oring and Lank 1982, Gratto et al. 1985, Flynn et al. 1999) although some studies of different species of plovers found no effect of previous nest fate on site fidelity or dispersal (Wiens and Cuthbert 1988, Haig and Oring 1998a, 1998b, Colwell et al. 2007). While there are certainly other factors influencing dispersal in Mountain Plovers, it is clear that previous nest fate is important in their dispersal decisions.

Habitat quality is another factor that has been shown to influence breeding dispersal (Bollinger and Gavin 1989). In this system the removal of prairie dogs by sylvatic plague effectively reduces the suitability of a colony for nesting (Augustine et al. 2008). However, the effects of plague on breeding dispersal of Mountain Plovers are not as straightforward as initially hypothesized. The additive effect of plague and the two-way interactions of it with sex and fate are in both of the top models and suggest that plague is important in the dispersal decisions of Mountain Plovers. The lack of significance of the plague effect itself in these models would suggest that while knowledge of plague history may provide information on modeling their dispersal, it is not as important as knowing the sex of the tending adult or the ultimate fate of the nest. One possible explanation for the lack of a plague effect is that half of all the birds that nested on a colony that experienced a plague event attempted to nest on that colony the following year. If a bird initiates its nest early enough in the breeding season they could potentially be successful on that colony before the habitat becomes unsuitable by mid-summer. Older, more experienced birds arrive earlier in the breeding season than

younger birds (Oring and Lank 1982, Thompson and Hale 1991) and although the ages of plovers included in this study are unknown, this might be a result of that age effect.

In addition to influencing when birds arrive on the breeding grounds, age may also influence site fidelity and breeding dispersal in some species (Greenwood and Harvey 1982). Having more experience in an area allows older individuals to incorporate multiple years of nesting success with increasing site familiarity. The most recent estimates of annual survival of Mountain Plovers range from 0.74 to 0.96 for adults (Dinsmore 2008). This suggests that the plover is long-lived and indeed there are several records of individuals older than five years and at least three records of individuals living >10 years (S. J. Dinsmore pers. comm.). I was unable to incorporate age effects into my analyses as it is not possible to determine the age of an adult Mountain Plover in the field, and unless a bird had been banded as a chick its age is unknown. There were only 17 individuals banded as chicks that later had nesting attempts in successive years, six as 1-2 year-olds, six as 2-3 year-olds, and five that were older, and only one known-age bird re-nested within a breeding season. In other Charadriiformes it has been shown that the presence of a previous mate can override the urge to disperse following a failure (Naves et al. 2006). However, in Mountain Plovers it is difficult to determine who is paired with whom and further studies of this would have to be done using molecular techniques. In the rapid multi-clutch mating system of the Mountain Plover it is therefore difficult to address the influence of age or mate status on dispersal patterns.

The use of distance to estimate dispersal has been discouraged in favor of analyses of movements across a given number of territories (Greenwood and Harvey 1982). However, the territories of Mountain Plovers are not as structured as those of other bird species, and often overlap with those of neighbors. They also appear to change within a year and between years, making it extremely difficult, if not impossible, to analyze dispersal in this manner.

My examination of dispersal in Mountain Plovers provides a better understanding of this uncommon mating system. Male-biased site fidelity is at odds with previous studies of dispersal among male-incubators (Schamel and Tracy 1991, Reed and Oring 1993), although it is consistent with the male resource-defense system of the Mountain Plover. I confirmed that the role of prior experience is important in the dispersal behavior of this species, but in the future it would be beneficial to further explore the added effects of age and mate fidelity. In addition, my study demonstrates the movement of Mountain Plovers over a large area which is of importance to species where suitable breeding habitat is fragmented across a landscape. The decline in Mountain Plovers over the past 40 years has been partially attributed to habitat loss and so any information gained about breeding locations and site fidelity is of conservation importance.

Literature Cited

- Augustine, D. J., S. J. Dinsmore, M. B. Wunder, V. J. Dreitz, and F. L. Knopf. 2008. Response of mountain plovers to plague-driven dynamics of black-tailed prairie dog colonies. *Landscape Ecology* 23:689–697.
- Akaike, H. 1974. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *In* (B. N. Petran and F. Csaki, Eds.) International symposium on information theory. Second edition. Akademiai Kiado, Budapest, Hungary.
- Bevers, M., J. Hof, D. W. Uresk, and G. L. Schenbeck. 1997. Spatial optimization of prairie dog colonies for black-footed ferret recovery. *Operations Research* 45:495–507.
- Bollinger, E. K., and T. A. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk* 106:584–594.
- Bowen, B. S., R. R. Koford, and S. L. Vehrenkamp. 1989. Dispersal in the communally breeding Groove-Billed Ani (*Crotophaga sulcirostris*). *Condor* 91:52–64.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.

- Clarke, A. L., B.-E. Sæther, and E. Røskaft. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- Clobert, J., J. O. Wolff, J. D. Nichols, E. Danchin, and A. A. Dhondt. 2001. Pages xvii–xxi *In* (Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, Eds.) *Dispersal*. Oxford University Press, New York.
- Collinge, S. K., W. C. Johnson, C. R. Ray, R. Matchett, J. Grensten, J. F. Cully Jr., K. L. Gage, M. Y. Kosoy, J. E. Loye, and A. P. Martin. 2005. Landscape structure and plague occurrence in black-tailed prairie dogs on grasslands of the western U.S.A. *Landscape Ecology* 20:941–955.
- Colwell, M. A., S. E. McAllister, C. B. Millett, A. N. Transou, S. M. Mullin, Z. J. Nelson, C. A. Wilson, and R. R. LeValley. 2007. Philopatry and natal dispersal of the Western Snowy Plover. *Wilson Journal of Ornithology* 119:378–385.
- Dinsmore, S. J. 2008. Influence of drought on the annual survival of the Mountain Plover in Montana. *Condor* 110:45–54.
- Dinsmore, S. J., and F. L. Knopf. 2005. Differential parental care by adult Mountain Plovers, *Charadrius montanus*. *Canadian Field-Naturalist* 119:532–536.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2003. Annual survival and population estimates of Mountain Plovers in Southern Phillips County, Montana. *Ecological Applications* 13:1013–1026.
- Flynn, L., E. Nol, and Y. Zharikov. 1999. Philopatry, nest-site tenacity, and mate-fidelity of Semipalmated Plovers. *Journal of Avian Biology* 30:47–55.
- Gratto, C. L. 1988. Natal philopatry, site tenacity, and age of first breeding of the Semipalmated Sandpiper. *Wilson Bulletin* 100:660–663.

- Gratto, C. L., R. I. G. Morrison, and F. Cooke. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. *Auk* 102:16–24.
- Graul, W. D. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12:69–94.
- Graul, W. D. 1975. Breeding biology of the Mountain Plover. *Wilson Bulletin* 87:6–31.
- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* 115:929–936.
- Haig, S. M., and L. W. Oring. 1988a. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105:268–277.
- Haig, S. M., and L. W. Oring. 1988b. Distribution and dispersal in the Piping Plover. *Auk* 105:630–638.
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* 84:416–430.
- Jackson, D. B. 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, U.K. *Ibis* 136:463–473.
- Johnson, O. W., P. G. Connors, P. L. Bruner, and J. L. Maron. 1993. Breeding ground fidelity and mate retention in the Pacific Golden-Plover. *Wilson Bulletin* 105:60–67.
- Knopf, F. L., and M. B. Wunder. 2006. Mountain Plover (*Charadrius montanus*). In *The Birds of North America*, no. 211 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Knowles, C. J., and P. R. Knowles. 1984. Additional records of Mountain Plovers using prairie dog towns in Montana. *Prairie Naturalist* 16:183–186.

- Knowles, C. J., C. J. Stoner, and S. P. Gieb. 1982. Selective use of Black-tailed Prairie Dog towns by Mountain Plovers. *Condor* 84:71–74.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co., London.
- Ligon, J. D. 1999. The evolution of avian breeding systems. Oxford University Press, New York.
- Lukacs, P. M., V. J. Dreitz, F. L. Knopf, and K. P. Burnham. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. *Condor* 106:926–931.
- Mabee, T. J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bulletin* 109:307–313.
- Manning, A. E., and C. M. White. 2001a. Breeding biology of Mountain Plovers (*Charadrius montanus*) in the Uinta Basin. *Western North American Naturalist* 61:223–228.
- Manning, A. E., and C. M. White. 2001b. Nest site selection by Mountain Plovers (*Charadrius montanus*) in a shrub-steppe habitat. *Western North American Naturalist* 61:229–235.
- Mulder, R. A. 1995. Natal and breeding dispersal in a co-operative, extra-group-mating bird. *Journal of Avian Biology* 26:234–240.
- Naves, L. C., J. Y. Monnat, and E. Cam. 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current? *Oikos* 115:263–276.
- Oring, L. W. 1982. Avian mating systems. Pages 1–92 in *Avian Biology*, Vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- Oring, L. W. 1986. Avian polyandry. Pages 309–351 in *Current Ornithology*, Vol. 3 (R. F. Johnston, Ed.). Plenum Press, New York.
- Oring, L. W., and D. B. Lank. 1982. Sexual selection, arrival time, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behavioral Ecology and Sociobiology* 10:185–191.

- Oring, L. W., and D. B. Lank. 1984. Population studies of the polyandrous Spotted Sandpiper. *Auk* 100:272–285.
- Pauli, J. N., S. W. Buskirk, E. S. Williams, and W. H. Edwards. 2006. A plague epizootic in the black-tailed prairie dog (*Cynomys ludovicianus*). *Journal of Wildlife Diseases* 42:74–80.
- Payne, R. B., and L. L. Payne. 1993. Breeding dispersal in Indigo Buntings: circumstance and consequences for breeding success and population structure. *Condor* 95:1–24.
- Porneluzi, P. A. 2003. Prior breeding success affects return rates of territorial male ovenbirds. *Condor* 105:73–79.
- Reed, J. M., and L. W. Oring. 1993. Philopatry, site fidelity, dispersal, and survival of Spotted Sandpipers. *Auk* 110:541–551.
- Schamel, D., and D. M. Tracy. 1991. Breeding site fidelity and natal philopatry in the sex role-reversed Red and Red-Necked Phalaropes. *Journal of Field Ornithology* 62:390–398.
- Sedgwick, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *Auk* 121:1103–1121.
- Smith, G. W., N. C. Nydegger, and D. L. Yensen. 1984. Passerine bird densities in shrubsteppe vegetation. *Journal of Field Ornithology* 55:261–264.
- Stenzel, L. E., G. W. Page, J. C. Warriner, J. S. Warriner, D. E. George, C. R. Eyster, B. A. Ramer, and K. K. Neuman. 2007. Survival and natal dispersal of juvenile Snowy Plovers (*Charadrius alexandrinus*) in central coastal California. *Auk* 124:1023–1036.
- Thompson, P. S., and W. G. Hale. 1991. Age-related reproductive variation in the Redshank (*Tringa totanus*). *Ornis Scandinavica* 22:353–359.
- Thompson, P. S., D. Baines, J. C. Coulson, and G. Longrigg. 1994. Age at first breeding, philopatry, and breeding site-fidelity in the Lapwing *Vanellus vanellus*. *Ibis* 136:474–484.

- Wallander, J., and M. Andersson. 2003. Reproductive tactics of the Ringed Plover (*Charadrius hiaticula*). *Journal of Avian Biology* 34:259–266.
- Westerskov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56–67.
- Wiens, T. P., and F. J. Cuthbert. 1988. Nest-site tenacity and mate retention of the Piping Plover. *Wilson Bulletin* 100:545–553.

Table 2.1. Summary statistics of breeding dispersal distances (km) of Mountain Plovers (*Charadrius montanus*) in southern Phillips County, Montana, U.S.A., 1995-2007.

Time	Test	N	Median dist. (km)	Mean dist. (km)	95% CI
Between years	Hatch	135	0.31	3.02	1.87–4.17
	Fail	48	1.56	5.06	2.53–7.58
	Male	105	0.31	2.75	1.51–4.00
	Female	78	0.65	4.64	2.76–6.52
	No Plague	164	0.42	3.51	2.39–4.63
	Plague	19	0.65	3.96	0.11–7.80

Table 2.2. Model selection results for a mixed model analysis of ln-transformed distances moved between successive nesting attempts by Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A., 1995-2007. Model factors include sex (male or female plovers), fate (hatch or fail), and plague (nest colonies that experienced a sylvatic plague event between nesting attempts) along with two-way interactions of each of these, and year. Models are ranked by differences in Akaike's Information Criterion (ΔAIC_C) adjusted for sample size, w_i is the Akaike weight and K represents the number of parameters.

Model	ΔAIC_C ¹	w_i	K
<u>Step 1</u>			
Sex + Fate + Plague + Sex*Plague + Fate*Plague + Sex*Fate	15.70	0.00	7
Sex + Fate + Plague + Sex*Plague + Fate*Plague	16.50	0.00	6
Sex + Fate + Plague + Sex*Plague + Sex*Fate	17.90	0.00	6
Sex + Fate + Plague + Sex*Fate + Fate*Plague	19.20	0.00	6
Sex + Fate + Plague + Sex*Fate	21.00	0.00	5
Sex + Fate + Plague	21.90	0.00	4
Sex + Fate + Sex*Fate	22.20	0.00	4
Sex + Fate	23.00	0.00	3
Fate + Plague + Fate*Plague	27.60	0.00	4
Sex + Plague + Sex*Plague	29.10	0.00	4
Fate + Plague	29.50	0.00	3
Fate	30.10	0.00	2
Sex + Plague	31.90	0.00	3
Sex	33.60	0.00	2
Plague	39.80	0.00	2
<u>Step 2</u>			
Sex + Fate + Plague + Year + Sex*Plague + Fate*Plague + Sex*Fate	0.00	0.60	17
Sex + Fate + Plague + Year + Sex*Plague + Fate*Plague	0.80	0.40	16

¹ The AIC_C value for the best model was 702.60

Table 2.3. Model selection results for subsequent nest fate using a logistic regression of ln-transformed distances moved between successive nesting attempts by Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A., 1995-2007. Model factors include sex (male or female plovers), initial nest fate (hatch or fail), and plague (nest colonies that experienced a sylvatic plague event between nesting attempts) along with two-way interactions of each of these. Models are ranked by differences in Akaike's Information Criterion (ΔAIC_C) adjusted for sample size and K represents the number of parameters.

Model	ΔAIC_C ¹	K
Sex	0.00	2
Sex + Fate	0.51	3
Fate	1.32	2
Sex + Plague	1.78	3
Sex + Fate + Sex*Fate	2.01	4
Sex + Fate + Plague	2.19	4
Plague	2.21	2
Fate + Plague	2.67	3
Sex + Plague + Sex*Plague	3.54	4
Fate + Plague + Fate*Plague	3.69	4

¹ The AIC_C value for the best model was 237.04

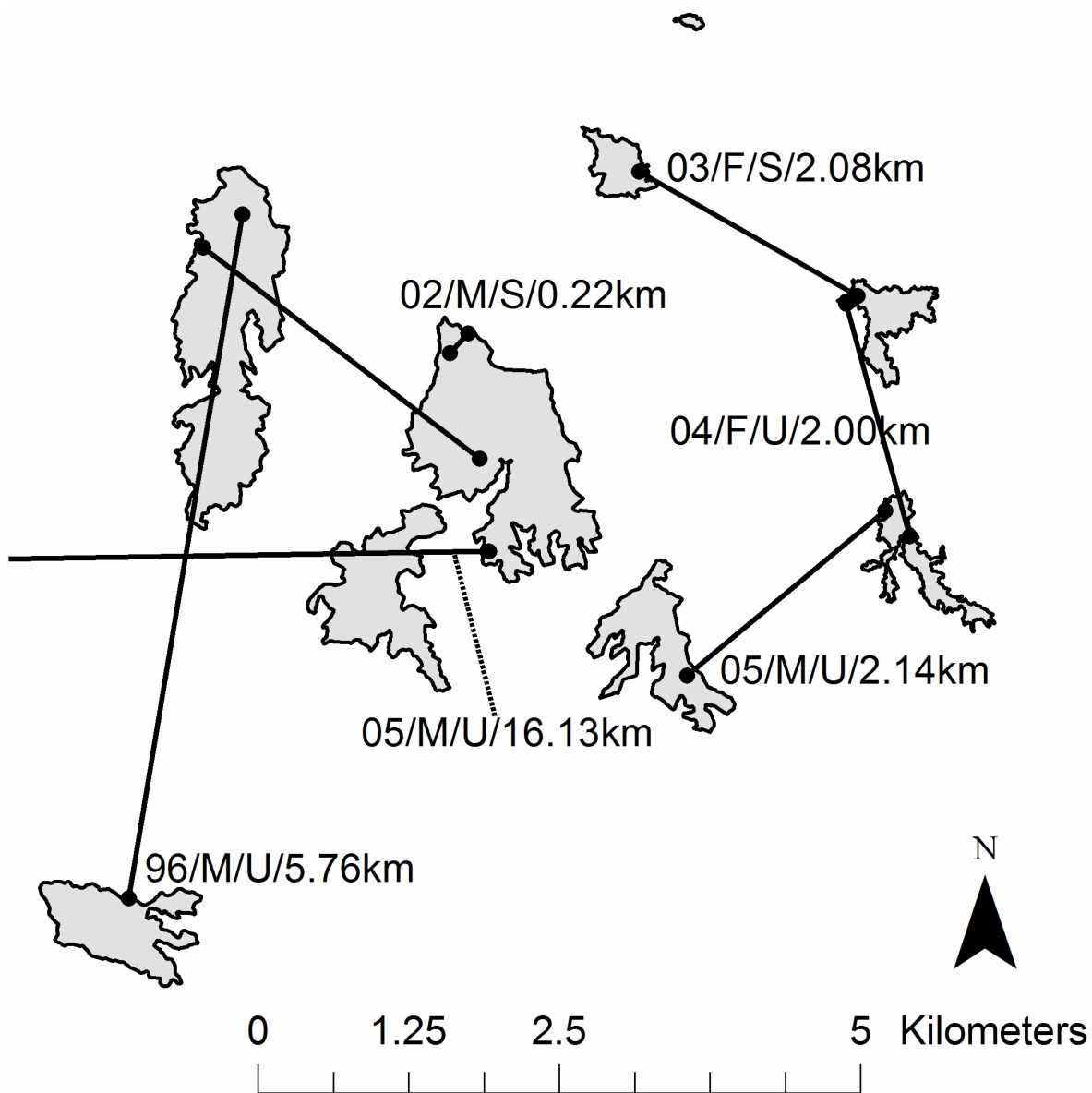


Figure 2.1. Linear dispersal distances (km) between successive nesting attempts of Mountain Plovers (*Charadrius montanus*) at the black-tailed prairie dog (*Cynomys ludovicianus*) complex level, Phillips Co. southern Phillips County, Montana, U.S.A., 1995-2007. “XX/Y/Z/0.00km” represents the year, sex of the tending adult (male/female), fate of the initial nest (successful/unsuccessful), and the distance moved.

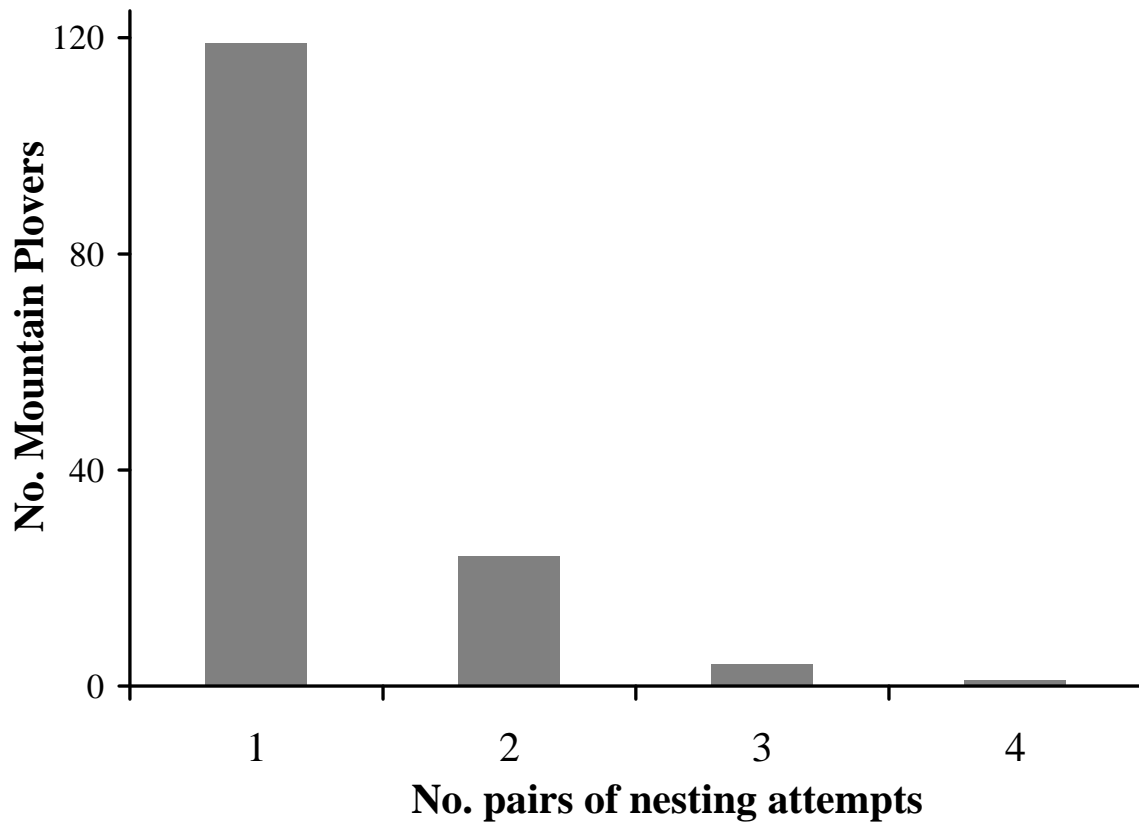


Figure 2.2. Number of Mountain Plovers (*Charadrius montanus*) and the number of pairs of nesting attempts contributed to examine effects of previous nest fate, sex of the tending adult, and the presence of sylvatic plague on inter-year movements in southern Phillips County, Montana, U.S.A., 1995–2007.

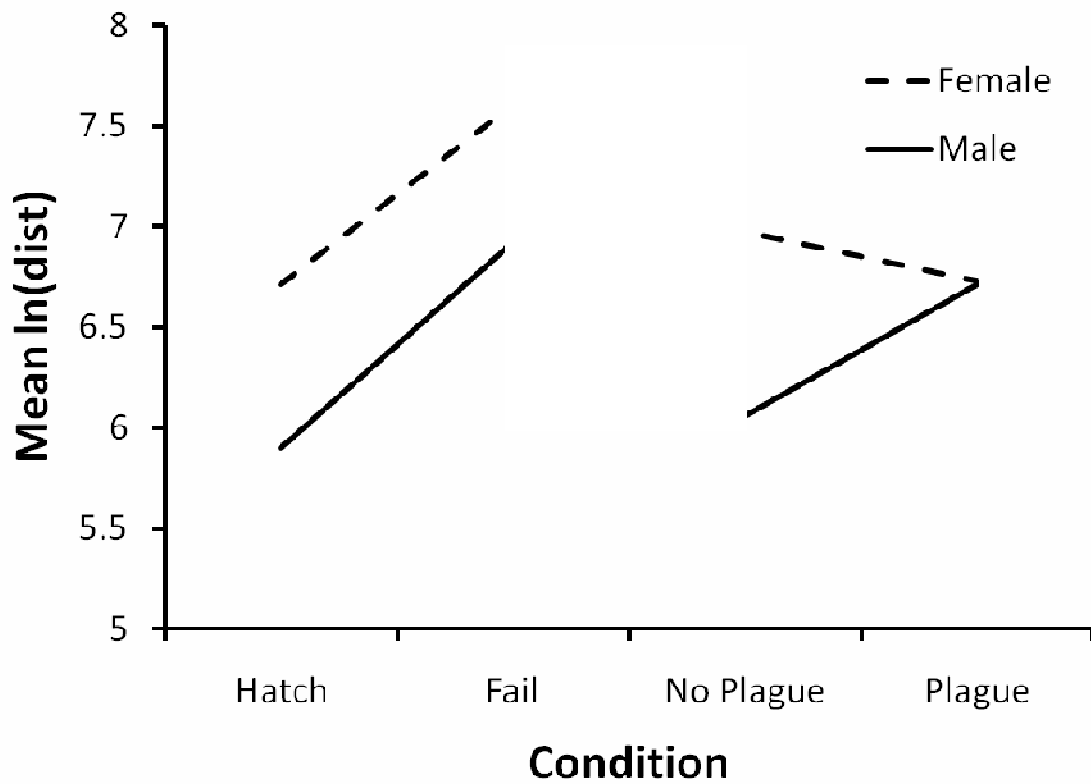


Figure 2.3. Test for interaction between male and female Mountain Plover (*Charadrius montanus*) dispersal distances (km) in relation to fates of successive nesting attempts and presence or absence of sylvatic plague on their nest colony in southern Phillips County, Montana, U.S.A., 1995–2007. Points are constructed from means of ln-transformed distances between successive nesting attempts.

CHAPTER III

INCUBATION BEHAVIOR OF THE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*)

Abstract

I monitored incubation activity of Mountain Plovers (*Charadrius montanus*) in Montana using a combination of video monitoring and temperature data-logging. The rapid multi-clutch mating system of the Mountain Plover provides an interesting opportunity to examine sex-specific differences in uniparental care. To explore possible sex differences in breeding behavior I modeled the duration of departures of incubating adults to see if activity patterns differed between sexes. In addition, the effects of time of day, nest age, day of season, and year were also included. I recorded 857 hours of video of 24 incubating Mountain Plovers at 25 nests during the 2007 field season and >10,000 hours of temperature data from 117 individuals at 142 nests during the 2006-2008 nesting seasons. Video data revealed that males on average made 1.48 departures hour⁻¹ over the course of a 24-hour period (n = 6 deployments, SE = 0.35) and females made 1.41 departures hour⁻¹ (n = 26 deployments, SE = 0.11). From the combined video and temperature data males contributed 1,925 nocturnal departures with a mean duration of 0.38 hr (SE = 0.01) while females contributed 2,716 nocturnal departures with a mean duration of 0.36 hr (SE = 0.01). The quadratic effect of the time of departure was the most important factor in the length of nocturnal off-bouts. Other effects that were included in competitive models were the cubic and linear effects of time of departure and the highest ambient temperature the previous day. The day of incubation and the day of the season were also important in explaining duration of off-bouts. Sex was not an important predictor of duration of departure. This study not only provides further information about incubation patterns in an uncommon mating system, but also is important to gaining a better understanding of behavior in this species of conservation concern.

Introduction

While caring for their young, animals must constantly weigh the costs and benefits of their current reproductive effort with that of future efforts (Clutton-Brock 1991). For an incubating bird, one of the decisions it must make is at what time and for how long it can leave its nest without inhibiting embryonic development while tending to its own needs. Periodic cooling of an egg during off-bouts for personal maintenance can severely hinder development, and impact embryonic metabolic processes (Olson et al. 2006). Additionally, increased activity at the nest can increase the risk of predation (Martin et al. 2000). Thus, the incubating adult must not make too many departures from the nest or allow the eggs to cool. However, if the nest is left exposed in a hot environment, the results can be more drastic as the eggs can become overheated and inviable (Bennett and Dawson 1979, Grant 1982).

The reasons for leaving a nest during incubation are varied. A bird must sustain its own energy requirements by periodically getting off to feed while still attempting to keep its eggs at a fairly constant temperature (Carey 1980). In some species, the need to defend its territory from competitors will draw a bird away from its nest (Graul 1973), or at other times an incubating bird must leave its nest to avoid detection by a predator in the area, or by performing distraction displays to draw the predator away. Additionally, there is often a need to maintain a pair-bond between paired individuals through continued courtship or paired feeding (Cézilly et al. 2000). Another reason to leave the nest might be to seek an additional mating opportunity as in many polygynous and polyandrous species (Oring and Maxson 1977, Oring 1986). Whatever the reason for a departure from the nest, there is an energetic cost of having to re-warm eggs that have cooled during the off-bout (Vleck 1981a).

Among shorebirds (Charadriiformes) there is a wide variety of parental care systems ranging from biparental, where both parents share in the tasks of incubation and brood-rearing, to uniparental care by either males or females (Oring 1986, Reynolds and Székely

1997). In a few species, as in Sanderlings (*Calidris alba*), Temminck's Stints (*Calidris temminckii*), and Mountain Plovers (*Charadrius montanus*), males and females tend to separate nests. This rapid multi-clutch system provides an interesting opportunity to examine sex-specific differences in behavior.

The Mountain Plover is a species of conservation concern that breeds in open, flat, disturbed areas of the Great Plains and Great Basin (Knopf and Wunder 2006). The female lays her first clutch of three eggs in a shallow scrape on exposed ground which is tended entirely by the male. She then lays a second 3-egg clutch at a different location that she tends alone. The eggs are darkly colored and exceptionally thick for the Charadriinae (Graul 1975). As the eggs of Mountain Plovers are susceptible to over-heating (Knopf and Wunder 2006), during periods of high ambient temperature and solar radiation the tending adult is often found egg-shading and cooling itself by gular fluttering, similar to other shorebirds (Amat and Mosero 2004) although it has been suggested that egg-shading does more to cool the adult than the actual eggs because a standing adult loses heat more effectively than a sitting one does (Downs and Ward 1997). In species with biparental care the non-incubating adult is able to relieve the other when it is particularly hot so that it can feed or cool itself (Ward 1990, Amat and Mosero 2004). At times when the Mountain Plover is confined to its nest during the day it is suspected that the bird must feed at night to meet its own energy demands.

There are several clues that suggest that Mountain Plovers are active for long periods at night. Similar to other shorebirds (Wallander 2003), nesting Mountain Plovers have been observed away from their nests throughout the night (Graul 1975, pers. obs.), although these observational data are insufficient to firmly establish nocturnal activity patterns. Physically, Mountain Plovers have large eyes in relation to the size of their head, which allows them and their close relatives: Killdeer (*C. vociferus*), Piping Plovers (*C. melodus*), and Semipalmated Plovers (*C. semipalmatus*), to be either cathemeral (active at all times of the day) or

crepuscular (active at dawn and dusk; Hall and Ross 2007). Insects in the Orders Orthoptera and Coleoptera make up a large part of the diet of Mountain Plovers (Knopf and Wunder 2006). Crickets (Burpee et al. 1993), ground beetles (Ottesen 1985, Lövei and Sunderland 1996), and darkling beetles (Parmenter et al. 1989) are all active at night. However, studies of nocturnal foraging behavior in breeding Piping Plovers showed that foraging rates were considerably lower than during the day (Staine and Burger 1994). A low nocturnal foraging rate means that plovers would have to spend more time away from the nest to obtain the same amount of food as they would during the day.

Previous studies of Mountain Plovers have suggested a sex effect on nest survival where males have slightly higher nesting success than females (0.49 for males, 0.33 for females; Dinsmore et al. 2002). This difference could be a result of differing incubation behavior. Skutch (1949) hypothesized that increased activity at the nest due to the feeding of altricial young during brood-rearing attracted attention to the nest leading to a higher depredation rate than in the incubation stage. Condition has been shown to influence incubation activity in uniparental systems (Wiebe and Martin 2000) so if female Mountain Plovers must re-establish their own body condition after laying multiple clutches of eggs, then perhaps they will require more departures from the nest to forage than males. A study of incubating Killdeer, a close relative of the Mountain Plover with biparental care, showed that females had higher energy expenditure during the laying stage than males, that males spent significantly more time incubating, and females either lost or abandoned their nests when their mate was removed but males were able to successfully hatch chicks (Brunton 1988).

A previous study of the breeding biology of the Mountain Plover showed a tendency for daily nest survival to increase as a function of nest age (Dinsmore et al. 2002). Once again this might be a result of a change in the incubation pattern, such as less activity at the nest later in incubation. A small study of diurnal incubation in this species suggests that this

is the case, as incubating adults spent more time at the nest the closer the eggs were to hatch (Graul 1975).

Nest attentiveness can be monitored through a wide range of observational and remote-monitoring approaches. Recent studies have validated the use of temperature data loggers to measure survival of songbird nests (Weidinger 2006) and indicate the onset of incubation and timing of nest failure in shorebirds (Hartman and Oring 2006). However, few studies have examined incubation activity in an open-cup ground-nesting plover by using these data loggers (Tulp and Schekkerman 2006, Schneider and McWilliams 2007). I quantified incubation activity of nesting Mountain Plovers using a combination of video monitoring and temperature data loggers to examine sex-specific differences in behavior. The purposes of my study were to 1) describe the activity patterns of Mountain Plovers during the incubation stage, and 2) gain a better understanding of activity patterns in relation to sex of the tending adult, the nest age, and the time of the breeding season.

Methods

Study Area

I observed Mountain Plover incubation activity using remote data loggers over three consecutive breeding seasons (2006-2008) and continuously video-monitored a small sample of nests during the 2007 season. All observations were made in an approximately 3000 km² area located in southern Phillips County in north-central Montana (47°40'– 47°55' N, 107°35'– 108°30' W). The study area is roughly bordered by roads to the west and east (Highway 191, the Sun Prairie and Content roads) and by Beaver Creek and the Missouri River to the north and south respectively (Dinsmore et al. 2002). Approximately 75% of the land 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 experiences high ambient temperature fluctuations in the summer months, often ranging from below 10°C to above 40°C (National Oceanographic and

Atmospheric Administration 2006, 2007). Vegetation in the study area is typical of shrub-steppe habitat with predominantly short sparse vegetation (Smith et al. 1984) consisting mostly of big sagebrush (*Artemisia tridentata*), silver sagebrush (*Artemisia cana*), greasewood (*Sarcobatus vermiculatus*), yellow sweetclover (*Melilotus officinalis*), green needlegrass (*Stipa viridula*), and western wheatgrass (*Agropyron smithii*) (Dinsmore et al. 2003). The disturbance regime includes grazing by domestic cattle (*Bos taurus*) and black-tailed prairie dogs (*Cynomys ludovicianus*).

In my study area plovers are closely tied to prairie dog dynamics (Knowles et al. 1982, Knowles and Knowles 1984, Dinsmore and Knopf 2005). Active black-tailed prairie dog colonies contain scattered areas of bare ground interspersed with sparse vegetation that include fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polyantha*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*), with older colonies having less grass than newer colonies.

Nest searching and monitoring

Field work each year began in mid-May and continued until the end of the birds' nesting season, usually late July or early August. Nest searching techniques were similar across years. All active black-tailed prairie dog colonies within the study area (~200) were systematically searched ≥ 3 times during the breeding season. This was done by driving slowly across the colony and periodically stopping to scan for plovers, with the vehicle functioning as a blind. After locating a plover, I observed it from a distance until it returned to its nest. Once the bird sat down on the nest and its location was determined, I then placed two small rock cairns approximately 2 m to either side of the nest to mark it for future relocation. This manner of marking, while additionally recording the coordinates using a hand-held global positioning system (GPS), made it possible to relocate nests and reduce the chance of attracting predators. Once found, nests were checked every 3–7 days until they

had hatched or failed, and all egg ages were estimated by examining their specific gravity in a column of water (Westerskov 1950).

Capture and marking of Mountain Plovers generally followed the procedures described in Dinsmore et al. (2002). Nest-tending adult plovers were captured using a walk-in trap constructed of chicken wire and placed over the nest. When birds were in hand, feather and blood samples were taken for future analysis and genetic sexing and each plover was leg-banded with an aluminum USGS size 3A band and a unique combination of four colored bands. Because these plovers are sexually monomorphic and cannot be reliably sexed at a distance or in hand, sex was determined from feather or blood samples by Avian Biotech International (Tallahassee, FL) using molecular techniques outlined in Dinsmore et al. (2002). This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol number 5-06-6129-Q.

Video camera deployment and monitoring

I recorded incubation behavior at 25 nests of 24 incubating Mountain Plovers during the 2007 field season. I used a high resolution closed circuit video camera (Fieldcam type DHD4PTLV160/MIDICAM field television system assembled by Fuhrman Diversified Inc., Seabrook, TX) with a side-mounted 36 LED array infrared lamp to record 24-hour activity at the nest. The camera was mounted on a 1.2 m piece of rebar that was partially buried so that the lens of the camera housing was 0.7 m above ground and 1.9 m to the south of the nest. Consistently placing it to the south ensured fairly consistent light exposure and allowed me to note which direction the incubating adult travelled when leaving from and returning to the nest.

I recorded video imaging at 15 frames second⁻¹ and at the best possible quality onto an IDE hard-drive in a digital video recorder. The recorder was housed in a weatherproof case (0.45 x 0.35 x 0.15 m) connected to the camera by a 50 m cable, although the case and the two 12 V/100 Ah deep cycle batteries used to power the system were placed in the

nearest depression or behind a large prairie dog mound. The cable was sprayed once a week with Ropel[®] liquid animal repellent to prevent it from being gnawed by prairie dogs and the Ropel was reapplied after heavy rain. The digital video recorder case and batteries were camouflaged by covering them with burlap.

To minimize the possibility of nest abandonment and avoid possible behavioral changes due to recent handling, I only used the camera at nests of previously marked individuals. I used a laptop computer connected to the digital recorder to center the focus of the camera on the nest and the entire deployment process took about 20 min. I removed the video monitoring system after 24 hours unless I was unable to reach the nest due to inclement weather. I attempted to select nests for video monitoring at random, but sometimes deviated from this approach because of logistical constraints or a desire to better balance the sample with respect to sex of the nest-tending adult or nest age.

Data logger deployment and recording

I used 11 HOBO H8 external temperature data loggers (Model H08-002-02, Onset Computer Corporation, Bourne, MA) to monitor 124 Mountain Plover nests from 117 individuals over the three years of the study (2006: $n = 31$, 2007: $n = 64$, 2008: $n = 29$). Three loggers were used in 2006 and eight more were purchased prior to the 2007 field season. Each logger consisted of an internal sensor housed in a 6.1 cm x 4.8 cm x 2.03 cm case with an additional 30.5 cm external sensor cable. Data logger cases were coated in paraffin wax and placed in a small re-sealable plastic bag along with a small amount of Drierite[®] (Anhydrous Calcium Sulfate, CaSO₄) desiccant to prevent the logger from becoming wet. Despite these precautions, five loggers were lost in 2007 and 2008 when they became submerged for an extended period of time during heavy, continuous rain.

I carefully placed the logger at each nest-site while the eggs were removed from the nest to determine nest age. Starting in the nest contents I dug a shallow trench (approximately 5 cm x 35 cm) away from the nest and arranged the data logger so that the tip

of the external probe was in the center of the nest. I then buried the logger and the cable from the probe, covering the portion of the probe in the nest with a thin layer of nesting material before replacing the eggs. This entire process took 3-5 minutes depending on soil compaction.

In 2006 I recorded nest temperature every 30 seconds, continually recording and overwriting the oldest data from deployment until collection, and yielding 1 day and 9 hours of data with at least one full night of observations. The loggers were set to continuously overwrite so that any effects of human disturbance from capture and marking, data logger deployment, or visits to check nest status would not be included in the observation. However, because of the continuous over-writing, occasionally all incubation behavior was lost if a nest hatched or was depredated >33 hours before collection.

After reviewing video recordings of behavior early in 2007, I decided that a time-delay of two hours would allow the bird sufficient recovery time from human disturbance. I also increased the recording time to once every minute because departures could easily be determined from a small number of in-field examination of concurrent temperature and video recordings of this length. This also increased the sampling time for each nest to 2 days 18 hours before the memory was exhausted, and I disabled the over-writing function to limit problems noted earlier. This recording method was repeated in 2008.

I attempted to select nests for data logger monitoring at random, but this was difficult because of logistical constraints and because I often did not know the sex of the tending adult until after nesting was completed. Thus, I opportunistically monitored some nests and attempted to maintain a balanced sample of known-sex and known-age nests throughout each nesting season. This approach also resulted in multiple samples of the same bird within a nesting season, although never on consecutive days.

Data analysis

I used a two-step process to validate the video data and then incorporate the data logger information into my analyses. I began by carefully reviewing the video data and noting times when the bird first appeared in the camera view and from what general cardinal direction. A bird was considered “on the nest” when it settled over the eggs, as noted by the adult walking over the space with its legs apart. I also noted other activities such as egg-shading, distraction displays, and on one occasion, courtship display. If other recognizable organisms entered the visible area I noted the time of their appearance along with the behavioral response of the tending adult. The time of departure from the nest, the method of leaving (flew, ran, stepped off while picking at the ground), and the general cardinal departure direction were also noted.

I used two computer programs, both obtained from the Cornell Laboratory of Ornithology (Ithaca, NY), to define nest departures and their duration for incubating Mountain Plovers from the data loggers. Program RHYTHM (Cooper and Mills 2005) was used to convert temperature data files from data loggers into bioacoustic files, which are usually used to examine bird songs and calls. This program detects departures and returns using the minimum length of off-bout time, the minimum temperature decrease to be considered a departure, and the rate of change (heating or cooling) of $\text{degree} \cdot \text{minute}^{-1}$ to be considered a departure or return.

These parameters were estimated from a sample of 15 data logger deployments that had simultaneous video camera data (Figure 3.1). RHYTHM files were then opened in program RAVEN Pro (Version 1.3 for Windows) to check for accuracy. From the comparison of the Program RHYTHM output to the results of the simultaneous camera and data logger deployments it became apparent that the temperature data loggers were unable to accurately document off-bouts that occurred in periods with similar ambient and nest temperatures, such as in late morning and early evening. Additionally, they were unable to accurately provide information on departures in the middle of the day due to greater

fluctuations in ambient temperature (Figure 3.2). Because of these difficulties, I limited the data analysis to nocturnal departures between sunset and the following sunrise. Daily sunrise and sunset schedules for my study site for the three years of the study were obtained from the Astronomical Applications Department of the United States Naval Observatory.

I used the MIXED procedure in SAS (Version 9.1; SAS Institute, Cary, NC) to determine when the duration of nocturnal off-bouts was similar for all 15 nights where both data loggers and video were used. The two methods did not differ in either duration or time of the departures of durations >5 min ($P > 0.60$). Differences that occurred for off bout durations of <5 min could have been due to any number of influences, such as the data logger missing shorter off-bouts because of the one-minute time-span between temperature readings, or false-positive short departures caused by the bird's activity during incubation (turning eggs or adjusting itself over the eggs). On the basis of this finding I chose to include in the analysis only departures >5 minutes in length.

Statistical Analyses

I used the MIXED procedure in SAS (Version 9.1; SAS Institute, Cary, NC) to model duration of nocturnal departures from the nests of incubating Mountain Plovers. In addition to sex of the tending adult, other effects included in the model set were the linear effect of nest age (day of incubation determined from a combination of egg flotation and known hatch dates; Westerskov 1950) and the linear effect of day of the sampling season. I also included a linear, quadratic, and cubic effect of time of departure from the middle of the night. Lastly, I included tests for differences in departure durations by year and for the effect of method of collection (video or data logger). To examine the effect of ambient temperature I included the highest recorded temperature during the previous day, as temperatures higher than 43°C probably cause irreversible injury to the developing chick (Grant 1982) although Mountain Plovers exhibit cooling behavior at temperatures lower than this (30°C). These temperatures were obtained from a NOAA weather station within the study area. I used Akaike's

Information Criterion corrected for small sample size (AIC_C ; Akaike 1974) and a hierarchical modeling approach to determine which model was the best. Any models with $\Delta AIC_C \leq 2$ were considered competitive and used for inference. Parameter estimates were then model-averaged and estimates of the betas ($\hat{\beta}$) were reported with the unconditional standard error and unconditional 95% confidence intervals (Burnham and Anderson 2002). I began by considering only main effects models and determined their initial importance on the basis of model selection results and an examination of the effect itself (e.g., those where the 95% CI for the effect did not overlap zero). I then combined all important main effects in additive and two-way interactions to further explore patterns of nest departures. As a final step I included the effect of ambient temperature and any models with $\Delta AIC_C \leq 2$ were considered competitive and used for inference.

Results

I recorded 857 video-hours and from these data I determined that males on average made 1.48 departures video-hour⁻¹ ($n = 6$ deployments, $SE = 0.35$) spending on average 9% ($SE = 4.60\%$) of the observed time off the nest. Females made 1.41 departures hour⁻¹ ($n = 24$ deployments, $SE = 0.11$) and spent 10% ($SE = 1.67\%$) of the observed time away from the nest. Departures occurred at all hours of the day (Figure 3.3). However, during the day the birds would make frequent, short departures to prevent the eggs from over-heating in the sun while longer departures generally occurred in the mornings and early evenings (Figure 3.4). I logged >10,000 hours of temperature data during the 2006-2008 nesting seasons. After limiting the data to departures that occurred between the hours of sunset and sunrise I found that males contributed 1,925 departures with a mean duration of 0.38 hr ($SE = 0.01$) while females contributed 2,716 departures with a mean duration of 0.36 hr ($SE = 0.01$).

The results of the first step of the mixed model (Table 3.1) found that models that included combinations of the quadratic, cubic, and linear effects of the time of nocturnal departure along with the linear effect of season were competitive (Figure 3.5, $\hat{\beta}_{\text{Time}^2} = -$

0.01102, 95% CI -0.01341 to -0.00863, $\hat{\beta}_{\text{Time}^3} = -0.00123$, 95% CI -0.0167 to -0.00078, $\hat{\beta}_{\text{Time}} = -0.01221$, 95% CI -0.01713 to -0.00730). In the second step the additive effect of highest ambient temperature from the previous day greatly improved the models, but there was no longer evidence of a season effect (confidence intervals overlapping zero). I found that as the highest ambient temperature the previous day increased, the length of time that an incubating plover spent away from the nest decreased ($\hat{\beta}_{\text{Temperature}} = -0.00258$, 95% CI -0.00408 to -0.00107). There was no evidence for a sex, nest age, year, or method effect (confidence intervals of all effects overlapped zero) and the models containing two-way interactions of main effects were not considered competitive.

Discussion

The time at which a Mountain Plover departs from its nest clearly plays an important role in the duration of its off-bout. This activity pattern is influenced by the previous day's ambient temperature, which is consistent with previous findings (Conway and Martin 2000). A previous study of uniparental incubation activity in arctic shorebirds found that the incubating adult made very few and shorter departures at the coldest times of the day (Tulp and Schekkerman 2006). The inability to make foraging excursions because of high temperatures during the previous day should lead to an increase in the amount of time spent away from the nest that night but this was not found to be the case. As ambient temperature increased, plovers spent less time away from their nest at night which suggests that some other factor is influencing their behavior.

In addition to the time of departure, the day of the season was initially an important predictor of duration of nocturnal departures. While not as important in determining the duration of off-bouts, it is understandable that the later it gets in the breeding season, the lower the chances are of being able to re-nest in the case of a nest failure (Knopf and Wunder 2006). This might cause incubating birds to make shorter or fewer departures, similar to the effect that day of incubation has been found to have (Graul 1975, this study). Another

possible explanation might be that as the season progresses, neighboring nests are either successful or fail, causing those birds to leave the area. This might reduce competition for resources and therefore reduce foraging times (Dobbs et al. 2007), or perhaps the birds no longer leave the nest because of territorial disputes. Additionally, longer nocturnal departures earlier in the season might indicate an attempt to maintain a pair-bond or initiate a new pairing. Johnson et al. (2002) found that some species of shorebirds even have nocturnal copulations.

It was predicted that Mountain Plovers would spend less time away from the nest as the predicted hatch date approached. Graul (1975) found a similar effect on diurnal incubation with a small sample of nesting Mountain Plovers at a site in Colorado. This increase in nest attentiveness is possibly a result of the increasing investment the adult has made. This is reinforced by other behavioral changes Mountain Plovers exhibit as the nest age increases: during the egg-laying stage the tending adult is rarely on the nest except when the egg is threatened by environmental conditions (Graul 1975). Also, during the majority of incubation the adult sneaks away from the nest at a sign of a possible threat; however in the days leading up to hatching the adult will perform elaborate distraction displays (McCaffery et al. 1984). These behavioral shifts could produce the estimated increase in daily survival that follows nest age.

The lack of a strong sex effect in any of the models implies that male and female Mountain Plovers have similar nocturnal departure patterns. Although there was a significant difference in the reproductive effort of male and female Killdeer (Brunton 1988), both sexes of Mountain Plover have the same physical demands during incubation. However, if female Mountain Plovers are in poor physical health compared to males because of the demands of egg-laying, they might be able to delay their own nest initiation (Knopf and Wunder 2006) to improve their condition. Another possible reason for a lack of behavioral differences between the sexes of this species might be because of their reduced clutch size. In the

majority of Charadriidae the typical clutch size is four eggs (Maclean 1972) as compared to three in Mountain Plovers (Knopf and Wunder 2006). It has been shown that increases in clutch size produce increases in the energy cost of incubation (Thomson et al. 1998) and so perhaps the low physical demands of incubating a smaller clutch than closely related shorebirds of similar size means that sex differences are difficult to distinguish.

I found no strong effect of year on the length of nocturnal departures of Mountain Plovers, although many factors can contribute to inter-annual variation in the incubation behavior of nest-tending plovers. Abnormally wet, or cold, or sunny breeding seasons might produce different behavioral responses. Graul (1975) attributed differences between two years of diurnal nest-attentiveness in this species to warmer temperatures in one of the years. One factor that might influence Mountain Plover incubation behavior is tied to their relationship with prairie dogs. Sylvatic plague is an epizootic that can completely eliminate a prairie dog colony over the course of a breeding season, making it unsuitable for a nesting plover (Augustine et al. 2008). During outbreaks of sylvatic plague plovers tend to concentrate on the remaining suitable colonies, often at higher densities than in non-plague years. The closer proximity to other nesting plovers might cause territorial adults to leave their nests more frequently in years following a plague event.

Although there have been many studies of nest attendance in birds, few can be practically applied to open-cup ground-nesting shorebirds. Direct observation and video-monitoring require a large time commitment, many methods have a high monetary cost (e.g., video-monitoring), destroying an egg to implant a thermocouple is not feasible when working with a species of conservation concern, and pressure-sensitive balances placed under the eggs require removal of the nest contents. One method that was successfully used to monitor incubation activity in Snowy Plovers (*C. alexandrinus*) was a transponder system that identified which adult was incubating along with the time and date (Kosztolányi and Székely 2002). However, this method also required the complete removal of the nest

contents to bury an antenna, recorder and cables. While the data loggers used in this study were unable to accurately measure nest-attentiveness at all hours of the day, the method was fairly unobtrusive and inexpensive and provided valuable information about the nocturnal activities of this species.

Recordings of nest or egg temperature of cavity- or cup-nesting birds often clearly show adult incubation activity (Vleck 1981b, Voss et al. 2008), but the resolution at which on- and off-bouts can be determined in open-cup ground-nesting shorebirds is much harder to ascertain. One study of ground-nesting shorebirds in Siberia (Tulp and Schekkerman 2006) was successful in measuring activity using temperature data loggers because the ambient temperature was always lower than the nest temperature. However, in a similar study in Massachusetts investigators were unable to accurately estimate nest attendance of a Piping Plover (Schneider and McWilliams 2007). While use of this type of data logger was minimally invasive, it was unable to accurately examine activity during a large portion of the day. Many factors can influence the accuracy of these data loggers but the most important appear to be occasions when ambient and nest temperatures are similar and the logger simply does not recognize departures, and when ambient temperatures are greater than nest temperatures and the temperature data are no longer interpretable. Some other factors that might influence the results of the data logger might be occasional direct contact with the brood patch or the ability of the eggs to retain heat.

Additional research should examine condition of Mountain Plovers throughout incubation to provide further information about the factors that might influence incubation activity. A study of Eurasian Dotterels (*C. morinellus*), a close relative of the Mountain Plover, showed that body mass of incubating males decreased during the time period when they were the sole incubator, but in cases where the incubation duties were shared with females the mass of those males was 6.8% greater than that of the uniparental males (Holt et al. 2002). Dotterels are forced to expend greater energy warming their eggs in a cooler

climate than Mountain Plovers but they are still constrained to their nest, similar to Mountain Plovers at times when air temperatures are $>30^{\circ}\text{C}$. Instead of expending energy warming their eggs, Mountain Plovers must pant and gular-flutter while shading their eggs. These activities are also physically demanding, and when combined with the inability to leave their nests to forage because of possible egg overheating it was expected that incubating adults would have longer nocturnal departures following hot days. However, instead of increasing the time spent away from the nest at night, this study showed that incubating adults had shorter off-bouts on days of higher ambient temperatures. One possible explanation for this might be that the physical demands of incubation during these hotter days are less than on cooler days, regardless of the costs of self-cooling.

My study of nocturnal incubation behavior in this unusual mating system not only adds to the literature on incubation but it also provides information on the natural history of this species of conservation concern. While I was unable to find a difference in the time that male and female plovers spent away from their nests at night, there may be differences in incubation behavior that were not detected. In addition to condition, another possible effect that might have influenced the length of a nocturnal off-bout is the length of the departure immediately prior to that departure, or perhaps activity is influenced by light availability based on the phases of the moon (Jetz et al. 2003). One other avenue for possible research might be to quantify the directions from which the incubating adult left from and returned to the nest. As scent predators (e.g., snakes and coyotes) are thought to be the main nest predators, perhaps male Mountain Plovers approach and leave the nest from fewer directions, providing fewer scent trails for predators to follow. Knowing more information about the incubating behavior of this species of conservation concern might allow a manager to selectively protect nests that are more at risk of failure early in incubation and early in the breeding season.

Literature Cited

- Akaike, H. 1974. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *In* (B. N. Petran and F. Csaki, Eds.) International symposium on information theory. Second edition. Akademiai Kiado, Budapest, Hungary.
- Amat, J. A. and J. A. Masero. 2004. How Kentish Plovers, *Charadrius alexandrinus*, cope with heat stress during incubation. *Behavioral Ecology and Sociobiology* 56:26–33.
- Augustine, D. J., S. J. Dinsmore, M. B. Wunder, V. J. Dreitz, and F. L. Knopf. 2008. Response of mountain plovers to plague-driven dynamics of black-tailed prairie dog colonies. *Landscape Ecology* 23:689–697.
- Bennett, A. F., and W. R. Dawson. 1979. Physiological responses of embryonic Heermann's Gulls to temperature. *Physiological Zoology* 52:413–421.
- Brunton, D. H. 1988. Energy expenditure in reproductive effort of male and female Killdeer (*Charadrius vociferus*). *Auk* 105:553–564.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.
- Burpee, D. M. and S. K. Sakaluk. 1993. The effect of pair formation on diel calling patterns in two cricket species, *Gryllus veletis* and *Gryllodes sigillatus* (Orthoptera: Gryllidae). *Journal of Insect Behavior* 6:431–440.
- Carey, C. 1980. The ecology of avian incubation. *BioScience* 30:819–824.
- Cézilly, F., M. Prénault, F. Dubois, B. Faivre, and B. Patris. 2000. Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. *Behavioural Processes* 51:83–92.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton.
- Conway, C. J. and T. E. Martin. 2000. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* 11:178–188.

- Cooper, C.B. and H. Mills. 2005. New software for quantifying incubation behavior from time-series recordings. *Journal of Field Ornithology* 76:352–356.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Dinsmore, S. J., and F. L. Knopf. 2005. Differential parental care by adult Mountain Plovers, *Charadrius montanus*. *Canadian Field-Naturalist* 119:532–536.
- Dobbs, R. C., T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes. 2007. Population density affects foraging behavior of male Black-throated Blue Warblers during the breeding season. *Journal of Field Ornithology* 78:133–139.
- Downs, C. T., and D. Ward. 1997. Does shading behavior of incubating shorebirds in hot environments cool the eggs or the adults? *Auk* 114:717–724.
- Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithological Monographs* 30:1–75.
- Graul, W. D. 1973. Breeding adaptations of the Mountain Plover (*Charadrius montanus*). Ph. D. dissertation, University of Minnesota, St. Paul.
- Graul, W. D. 1975. Breeding biology of the Mountain Plover. *Wilson Bulletin* 87:6–31.
- Hall, M. I. and C. F. Ross. 2007. Eye shape and activity pattern in birds. *Journal of Zoology* 271:437–444.
- Hartmann, C. A., and L. W. Oring. 2006. An inexpensive method for remotely monitoring nest activity. *Journal of Field Ornithology* 77:418–424.
- Holt, S., D. P. Whitfield, K. Duncan, S. Rae, and R. D. Smith. 2002. Mass loss in incubating Eurasian Dotterel: adaptation or constraint? *Journal of Avian Biology* 33:219–224.
- Jetz, W., J. Steffen, and K. E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* 103:627–639.
- Johnson, M., J. P. Beckmann, and L. W. Oring. 2002. Temperate breeding shorebirds copulate at night. *Wader Study Group Bulletin* 97:45–46.

- Knopf, F. L. and M. B. Wunder. 2006. Mountain Plover (*Charadrius montanus*). In *The Birds of North America*, no. 211 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Knowles, C. J., and P. R. Knowles. 1984. Additional records of Mountain Plovers using prairie dog towns in Montana. *Prairie Naturalist* 16:183–186.
- Knowles, C. J., C. J. Stoner, and S. P. Gieb. 1982. Selective use of Black-tailed Prairie Dog towns by Mountain Plovers. *Condor* 84:71–74.
- Kosztolányi, A., and T. Székely. 2002. Using a transponder system to monitor incubation routines of Snowy Plovers. *Journal of Field Ornithology* 73:199–205.
- Lövei, G. L. and K. D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Reviews of Entomology* 41:231–256.
- Maclean, G. L. 1972. Clutch size and evolution in the Charadrii. *Auk* 89:299–324.
- McCaffery, B. J., T. A. Sordahl, and P. Zahler. 1984. Behavioral ecology of the Mountain Plover in northeastern Colorado. *Wader Study Group Bulletin* 40:18–21.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B* 267:2287–2293.
- National Oceanic and Atmospheric Administration. 2006. Climatological data annual summary, Montana 109 (13). National Climatic Data Center, Ashville, North Carolina.
- National Oceanic and Atmospheric Administration. 2007. Climatological data annual summary, Montana 110 (13). National Climatic Data Center, Ashville, North Carolina.
- Olson, C. R., C. M. Vleck, D. Vleck. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and biochemical zoology* 79:927–936.

- Oring, L. W. 1986. Avian polyandry. Pages 309–351 in *Current Ornithology*, Vol. 3 (R. F. Johnston, Ed.). Plenum Press, New York.
- Oring, L. W. and S. J. Maxson. 1977. Instances of simultaneous polyandry by a Spotted Sandpiper (*Actitis macularia*). *Ibis* 120 3:349–353.
- Ottesen, P. S. 1985. Diel activity patterns of south Scandinavian high mountain ground beetles (Coleoptera, Carabidae). *Holarctic Ecology* 8:191–203.
- Parmenter, R. R., C. A. Parmenter, and C. D. Cheney. 1989. Factors influencing microhabitat partitioning among coexisting species of arid-land darkling beetles (Tenebrionidae): behavioral responses to vegetation architecture. *Southwestern Naturalist* 34:319–329.
- Reynolds, J. D. and T. Székely. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behavioral Ecology* 8:126–134.
- Schneider, E. G. and S. R. McWilliams. 2007. Using nest temperature to estimate nest attendance of Piping Plovers. *Journal of Wildlife Management* 71:1998–2006.
- Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455.
- Staine, K. J. and J. Burger. 1994. Nocturnal foraging behavior of breeding Piping Plovers (*Charadrius melodus*) in New Jersey. *Auk* 111:579–587.
- Thomson, D. L., P. Monaghan, and R. W. Furness. 1998. The demands of incubation and avian clutch size. *Biological Reviews* 73:293–304.
- Tulp, I. and H. Schekkerman. 2006. Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *Journal of Avian Biology* 37:207–218.
- Vleck, C. M. 1981a. Energetic cost of incubation in the Zebra Finch. *Condor* 83:229–237.
- Vleck, C. M. 1981b. Hummingbird incubation: Female attentiveness and egg temperature. *Oecologia* 51:199–205.

- Voss, M. A., M. A. Rutter, N. G. Zimmerman, and K. M. Moll. 2008. Adaptive value of thermally inefficient male incubation in Barn Swallows. *Auk* 125:637–642.
- Wallander, J. 2003. Sex roles during incubation in the Common Ringed Plover. *Condor* 105:378–381.
- Ward, D. 1990. Incubation temperatures and behavior of Crowned, Black-winged, and Lesser Black-winged Plovers. *Auk* 107:10–17.
- Weidinger, K. 2006. Validating the use of temperature data loggers to measure survival of songbird nests. *Journal of Field Ornithology* 77:357–354.
- Westerskov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56–67.
- Wiebe, K. L. and K. Martin. 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. *Behavioral Ecology and Sociobiology* 48:463–470.

Table 3.1. Model selection results for a mixed model analysis of duration of nocturnal departure of incubating Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A., 2006-2008. Model factors include sex (Sex; male or female), a linear effect of day of incubation (Age; 1-31 days), a linear effect of day of sampling season (Season; 1-73), a linear effect of time of departure from middle of night (Time; half the length of time from sunset to the following sunrise), the quadratic effect of time of departure from middle of night (Time²; half the length of time from sunset to the following sunrise), the cubic effect of time of departure from middle of night (Time³; half the length of time from sunset to the following sunrise), year (Year; 2006-2008), method of data collection (Method; video and temperature data loggers), ambient temperature (Temp; high temperature for the previous day), and all two-way interactions with important main effects. Models are ranked by differences in Akaike's Information Criterion (ΔAIC_C) adjusted for sample size, w_i is the Akaike weight, and K represents the number of parameters.

Model	ΔAIC_C^1	w_i	K
<u>Step 1</u>			
Time ² + Time ³	35.40	0.00	3
Time ² + Time	36.30	0.00	3
Time ² + Time ³ + Season	37.20	0.00	4
Time ² + Time + Season	38.00	0.00	4
Time ² + Time ³ + Age	38.80	0.00	4
Time ² + Time + Age	39.80	0.00	4
Time ² + Time ³ + Time	43.60	0.00	4
Time ²	49.90	0.00	2
Time ² + Season	50.60	0.00	3
Time ² + Age	51.80	0.00	3
Time ² + Season + Age	58.30	0.00	4
Time ² + Season + Time ² *Season	63.30	0.00	4
Time ² + Age + Time ² *Age	66.60	0.00	4
Temp	76.80	0.00	2
Time ² + Season + Age + Time ² *Season + Time ² *Age + Season*Age	84.20	0.00	7
Time ³	105.00	0.00	2
Time ³ + Time	113.70	0.00	3
Intercept only	113.90	0.00	1
Season	114.10	0.00	2
Age	115.00	0.00	2
Method	115.60	0.00	2
Sex	117.40	0.00	2
Season + Age + Season*Age	120.80	0.00	4
Year	121.00	0.00	3
Season + Age	121.30	0.00	3
<u>Step 2</u>			
Time ² + Time ³ + Temp	0.00	0.53	4
Time ² + Time + Temp	0.30	0.46	4
Time ² + Time ³ + Season + Temp	8.60	0.01	5

¹ The lowest AIC_C value for the best model was 5024.30

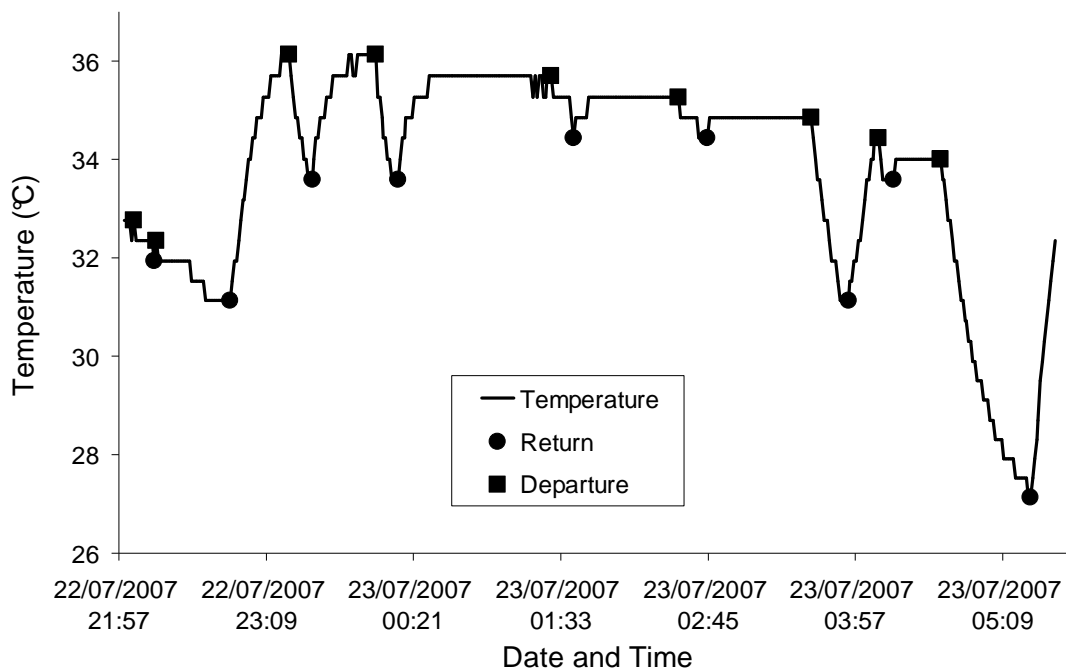


Figure 3.1. Characteristic nest temperature trace ($^{\circ}\text{C}$) of Mountain Plover (*Charadrius montanus*) nocturnal incubation behavior, Phillips County, Montana. 22–23 July 2007. Temperatures were recorded every minute using a data logger placed in the nest, while departure and return times were determined from remote video observation.

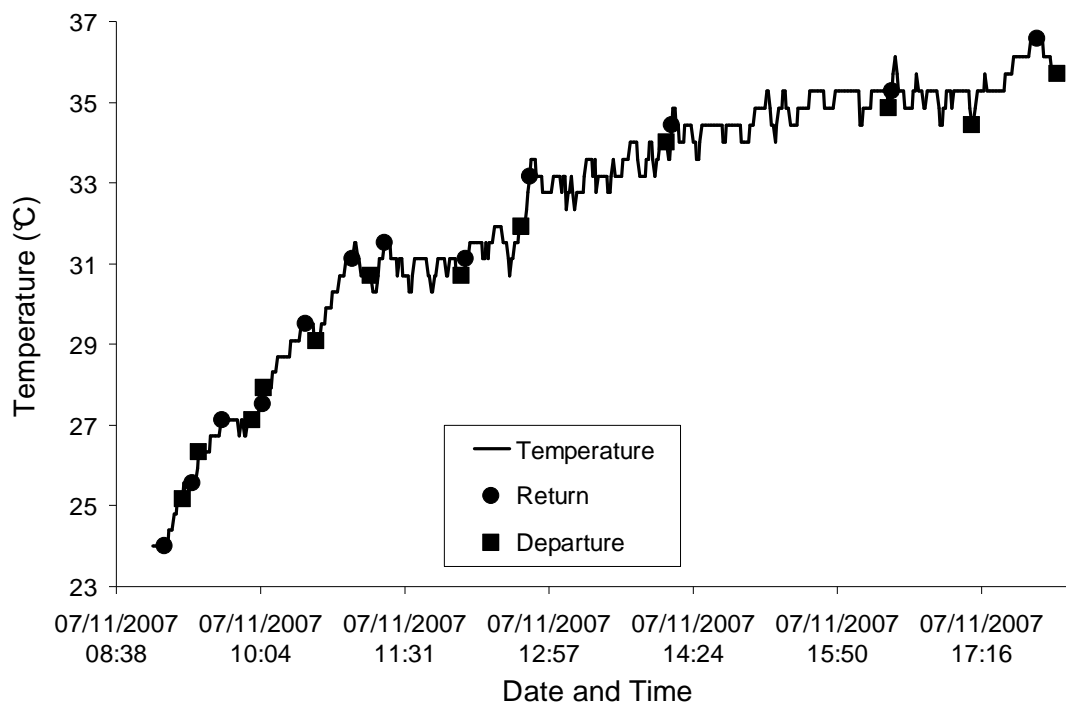


Figure 3.2. Characteristic nest temperature trace ($^{\circ}\text{C}$) of Mountain Plover (*Charadrius montanus*) diurnal incubation behavior, Phillips County, Montana, U.S.A., 11 July 2007. Temperatures were recorded every minute using a data logger placed in the nest, while departure and return times were determined from remote video observation.

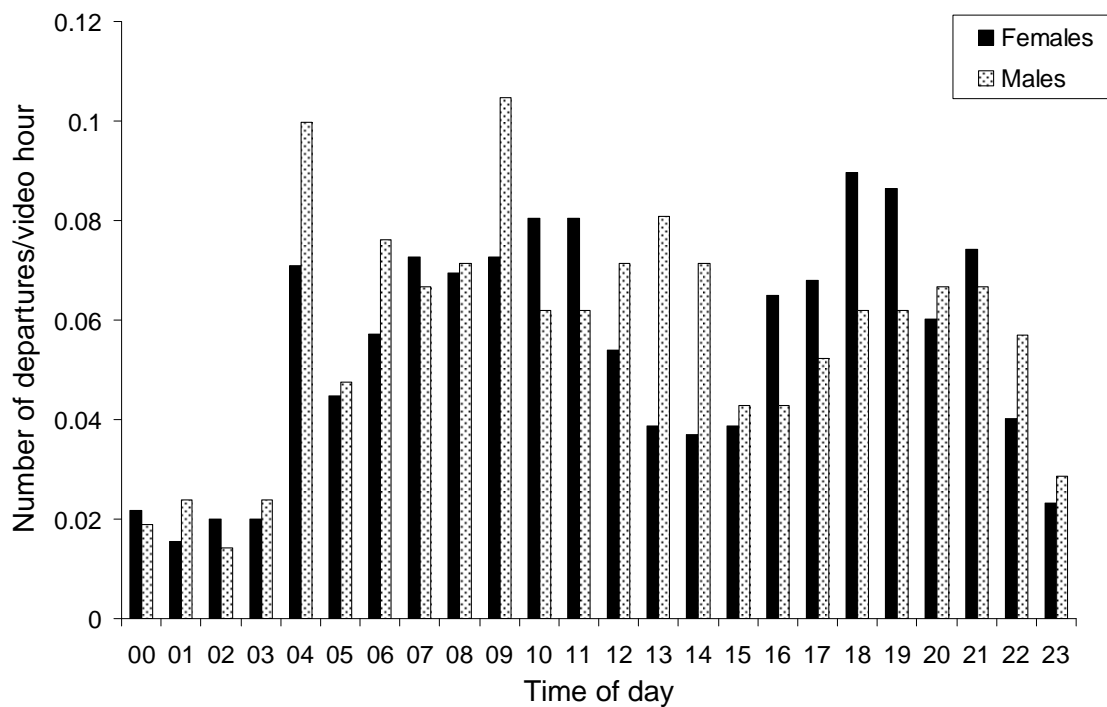


Figure 3.3. Number of departures from the nest video-hour⁻¹ by six male and 24 female Mountain Plovers (*Charadrius montanus*) observed in Phillips County, Montana, U.S.A., 2007. Time of day references the hour on a 24-hour clock, e.g., 00 refers to the hour from midnight to 1 a.m.

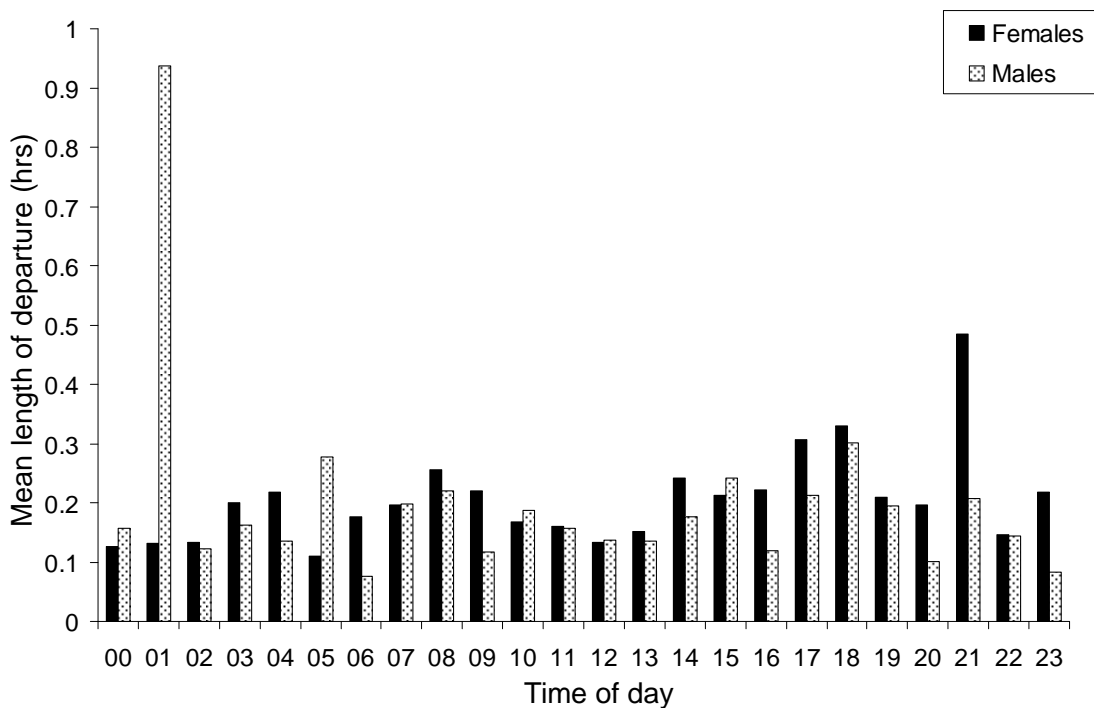


Figure 3.4. Mean length of departure from the nest by six male and 24 female Mountain Plovers (*Charadrius montanus*) observed in Phillips County, Montana, U.S.A., 2007. Time of day references the hour on a 24-hour clock, e.g., 00 refers to the hour from midnight to 1 a.m.

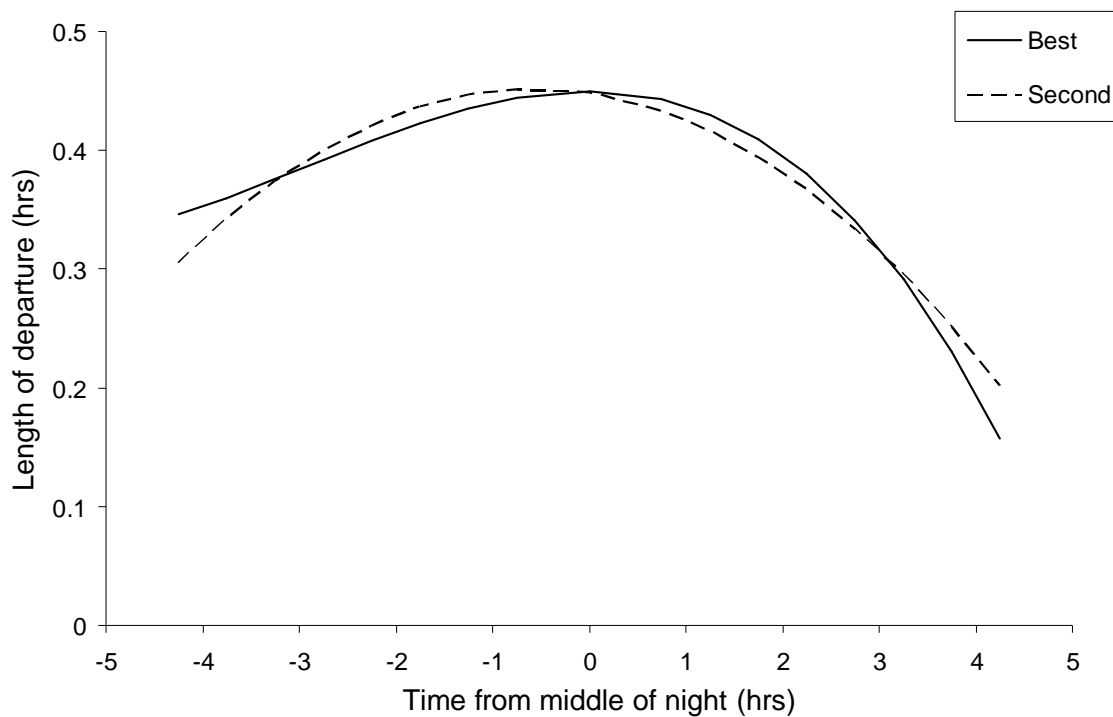


Figure 3.5. Model estimated lengths of nocturnal departures from incubation (hrs) in relation to the mid-time between sunset and sunrise for Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A. “Best” and “Second” refer to the top models that both incorporate a quadratic time effect along with a cubic time term and a linear time trend respectively.

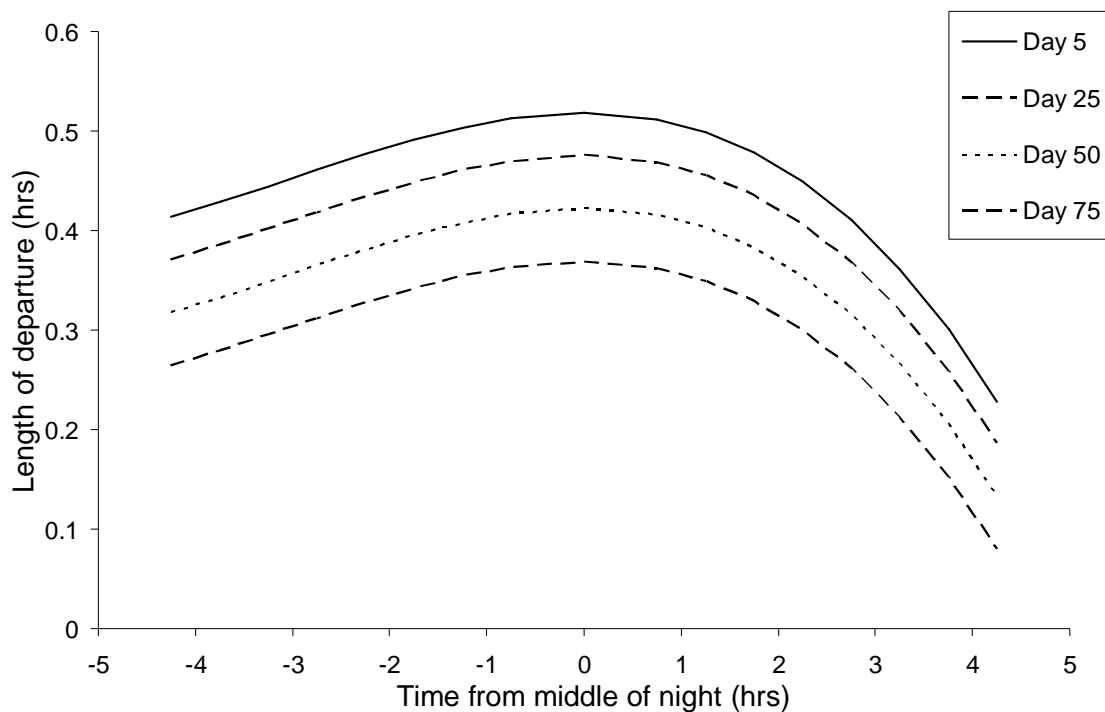


Figure 3.6. The effects of day of season on duration of nest departures (hrs) in relation to the mid-time between sunset and sunrise for Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, U.S.A. Day 1 corresponds to 18 May and Day 75 corresponds to 31 July.